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Variable and spatially explicit response of fish larvae to the playback of local, continuous reef soundscapes

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ABSTRACT: Understanding the cues that drive larval fish settlement is critical for managing reef systems under stress. Reef sound is increasingly reported to influence fish recruitment, yet the physical and acoustic environment in which larval fish settle varies in space and time. Accordingly, testing potential settlement cues under different conditions is vital for understanding their ecological importance. We conducted 2 sets of field playback experiments in St. John, US Virgin Islands, one nearshore (10 m depth) and the second 'offshore' (25 m depth), to assess the effects of reef soundscape playback on settlement rates of multiple reef fish families. In each experiment, nightly currents were quantified and we replicated the diel soundscape cycle using high, low, and control (silent) amplitude recordings from nearby reefs. The first experiment revealed significant current-based, down-stream reduction in larval fish catches in subsurface light traps and a significant effect of increasing amplitude of reef playbacks on larval lizardfish (Synodontidae) catches. In the second, offshore experiment which had no current effect, increasing reef playback amplitude led to a significantly greater catch of parrotfish (Scaridae) larvae and decreased larval pelagic fish catch. Total reef fish larvae only showed attraction to reef playbacks at the most nearshore site. This work demonstrates that while sound can play a role in the settlement of certain reef fishes, responses are influenced by multiple factors, including larger-scale physical processes, underscoring the need to consider the scale of soundscape cues for reef fish settlement within an oceanographic context.

KEY WORDS: Fish larvae · Settlement · Cue · St. John · USVI

1. INTRODUCTION

Most species of reef fish exhibit a biphasic life cycle with a defined larval stage, often in the pelagia, followed by settlement on or near reefs and subsequent metamorphosis into demersal juveniles (Johannes 1978). These larvae are typically transported offshore, far from appropriate adult habitats such as coral reefs. At the end of the pelagic phase, finding favorable settlement habitat is critical to their survival, and evidence indicates that larval individuals can use a variety of navigational cues to increase successful recruitment to the juvenile population (Montgomery et al. 2001, Leis et al. 2002).

The majority of fish larvae settle at night (Dufour & Galzin 1993, Kingsford 2001), indicating a need for non-visual cues to be used in orientation and habitat selection. While damselfish and cardinalfish

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use cues such as geomagnetic fields (O'Connor & Muheim 2017) and celestial patterns (Mouritsen et al. 2013, Faillettaz et al. 2015), many studies of larval fish settlement responses focus on olfactory and auditory cues (Leis et al. 2011). Olfactory cues may extend many kilometers from coral reefs via currents and outgoing tides (Atema et al. 2002, Paris et al. 2013). Reef fish develop olfactory systems early on in their larval stage, allowing them to utilize this cue (Wright et al. 2005, Lara 2008). However, olfaction is current-dependent and a diffusive gradient of olfactory cues at scales relevant to reef fish larvae may not exist (Atema et al. 2002, Burgess et al. 2007). Thus reef fish larvae must integrate other sensory systems for navigation and habitat selection (Atema et al. 2015).

Sound can provide a directional cue for settling larvae to follow that is reflective of habitat properties, and likely complementary to olfactory cues (Tolimieri et al. 2000, Leis et al. 2003, Simpson et al. 2004, Huijbers et al. 2012). Coral reef soundscapes are composed of biological sounds, such as fish calls and pulses from snapping shrimp, and abiotic sounds, including crashing of shoaling waves on reef structure (Myrberg & Riggio 1985, Mann & Lobel 1997, Kaplan et al. 2015). These sounds are often higher amplitude than the background noise of the open ocean, which may allow acoustic cues from the reef to be used as a navigational and habitat selection cue by fish larvae (Tolimieri et al. 2004, Montgomery et al. 2006, Mann et al. 2007, Simpson et al. 2008b, Staaterman et al. 2013). While biotic sounds span a broad range of frequencies — largely between 100 and 1000 Hz in the case of reef fish calls, to greater than 100 kHz in the case of snapping shrimp — it is suggested that most fish larvae are not capable of hearing frequencies above a few kHz, making low frequency sounds the most relevant portion of the soundscape for larval fish navigation (Myrberg & Riggio 1985, Schmitz 2002, Egner & Mann 2005, Wright et al. 2005, Fay & Popper 2012, Tricas & Boyle 2014). It is also worth noting that all fish are considered to hear particle motion which serves a vector providing direction, as opposed to sound pressure which represents a scalar and also requires a compressible air cavity such as swim bladder (Zeddies et al. 2012, Popper & Hawkins 2018). Despite this assumption, at present little is known about larval orientation to different components of sound other than tendencies to be more attracted to certain frequencies (Simpson et al. 2008b) and that some larvae with gas-filled swim bladders are able to respond to sound pressure (Salas et al. 2019).

Numerous field studies in the Indo-Pacific have suggested that the larvae of multiple reef fish taxa are attracted to the playback of reef soundscapes and may use them as navigational cues to locate suitable settlement habitat (Tolimieri et al. 2000, 2004, Leis et al. 2003, Simpson et al. 2004). Often the results are very pronounced, with reef fish taxa such as Apogonidae, Pomacentridae, and Lethrinidae settling at 2–10 times the rate in traps with reef sounds when compared to quiet light traps without acoustic treatments (Tolimieri et al. 2000, Simpson et al. 2004). Such studies have laid the foundation for understanding how reef-settling larvae may use sound cues.

However, settlement cues often act on a range of scales and in the context of other variables such as local hydrography; accordingly, assessing the importance of acoustic cues in their broader oceanographic context is vital. Leis et al. (2003) indicated that positive responses of larvae to reef soundscape playbacks may be location-dependent. Limited knowledge of the operational scales of reef sound propagation has made it difficult to interpret the role sound plays in larval settlement (Leis et al. 2003, Mann et al. 2007, Kaplan & Mooney 2016). Modeling and measurements of cue range have been contradictory, ranging from tens of kilometers to a few hundred meters (Mann et al. 2007, Radford et al. 2011b, Kaplan & Mooney 2016). While past experiments have set the foundation for reef fish playback experiments and indicate that reef fish will respond to playback of reef soundscapes, there have been difficulties in accurate replication of reef soundscapes and control of other cues and currents in field experiments. Further, previous studies that tested the effect of reef soundscapes on larval settlement often applied repeated short recordings (30 s to 15 min) of crepuscular fish choruses for playback treatments (Tolimieri et al. 2000, 2004, Simpson et al. 2004, 2008b, Gordon et al. 2018). However, reef soundscapes can vary substantially throughout diel and lunar cycles (Staaterman et al. 2013, Kaplan et al. 2015), and it is poorly understood how settling larval fish may respond to a more naturally varying soundscape, including crepuscular periods with amplified fish chorusing and midnight periods with 2–10 times lower acoustic power (Kaplan et al. 2015, 2018). Further, in any sensory study it is critical to monitor the output levels of the presented stimuli, as these will vary (particularly in natural environments, where environmental conditions can easily influence output levels; Atema 2012); a lack of stimulus measurement throughout previous reef playback experiments has thus limited the ability to quantify the soundscape treatments received by fish larvae. Finally, settlement is more than a simple sensory response; animal movement and opportunity to settle may also be influenced by current, tides, and other physical conditions (Green & Edmunds 2011); thus, to properly evaluate settlement it is critical to address conditions and local oceanographic factors, including swimming capabilities of the larvae under these conditions.

The goal of our study was to determine whether the playback of reef soundscapes mimicking natural acoustic conditions influences the settlement of reef fish larvae on a nightly time scale. The study was carried out on the south (leeward) coast of the island of St. John, US Virgin Islands (USVI), within the boundaries of the USVI National Park, over 2 settlement seasons (third-quarter to new moons in summer) and 2 locations (nearshore and offshore of Reef Bay). The first experiment was conducted nearshore using continuous recordings of nearby reefs taken during a prior visit to the sampling region. These recordings were synchronized to the natural diel acoustic cycle of the reefs. The second experiment was conducted offshore using continuous recordings of nearby reefs taken within days of the experiment to capture relative lunar patterns and natural diel acoustic cycles, providing the ecologically relevant soundscape cue. Additionally, the experiments differed in location, and current patterns for both experiments were evaluated with an offshore oceanographic buoy or acoustic Doppler current profiler (ADCP). We hypothesized that, in both experiments, increasing sound levels of reef playback would result in an increase in reef fish settlement, yet not an increase in the abundance of non-reef fish larvae collected. This work expands the range of playback experiments on fish larvae into the Caribbean, leverages oceanographic measurements to better interpret the physical influences on settling larvae, and provides the opportunity to elucidate the effects of playback of ambient reef soundscapes on the settlement of fish taxa which have not been previously assessed.

2. MATERIALS AND METHODS

2.1. Expt 1

2.1.1. Site description

Experiments in the summer of 2016 were conducted approximately 200 m off the south shore of the island of St. John, USVI (18.307° N, 64.753° W) during the third quarter and new moon of June and July 2016, representing the lunar window of peak settlement for Caribbean reef fishes (D'Alessandro et al. 2007) (Fig. 1). Visual surveys that included extensive swimming and towing a snorkeler behind a small boat were used to ensure no reef structures were present within at least 250 m of the experimental location to minimize confounding acoustic settlement cues from nearby reefs, with the region being primarily sand and patchy seagrass. These surveys found Joel's Shoal to be the nearest reef, ~300 m southwest of our experimental setup (Fig. 1; Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m653p131_supp.pdf). Six pairs of moorings were placed approximately parallel to the shore, under the assumption that larvae would be arriving from offshore (exact distance to shore varied; Table S1). Depth was 10 m at each mooring to minimize variability in sound propagation among systems.

2.1.2. Experimental moorings

Two moorings per site were deployed, one equipped with larval fish light traps, and the second with an underwater loudspeaker, together allowing us to assess the effects of the playback of reef soundscapes on the settlement of reef fish larvae. The mooring with the loudspeaker consisted of a concrete block on the seafloor, connected with a line to the surface attached to a round float and a urethane ring float (Fig. 2a). Electronic equipment, including a 12 V lead-acid battery, 220 W amplifier, audio player, and transformer, was housed in a waterproof case mounted on the ring float. An underwater loudspeaker (Lubell LL916C, Lubell Labs) was attached to the concrete block and connected to the electronic equipment in the waterproof case floating at the surface. Prior to experimental trials, recordings were taken at 25 m intervals from a playback system playing reef sound with a root mean square sound pressure level (SPL_{rms}) of 150 dB re 1 µPa at 1 m above the speaker to assess the minimum distance between playback systems needed to prevent acoustic overlap of playbacks. No discernable differences from ambient soundscapes were present at a distance of 200 m from the speaker, as SPL_{rms} values equaled that of the ambient soundscape at this distance (visual inspection of spectrograms further confirmed this). Moorings were thus spaced at 200 m intervals. This spacing may have resulted in some overlap of acoustic treatments but bathymetry and presence of nearby reefs precluded greater spacing of experimental moorings.

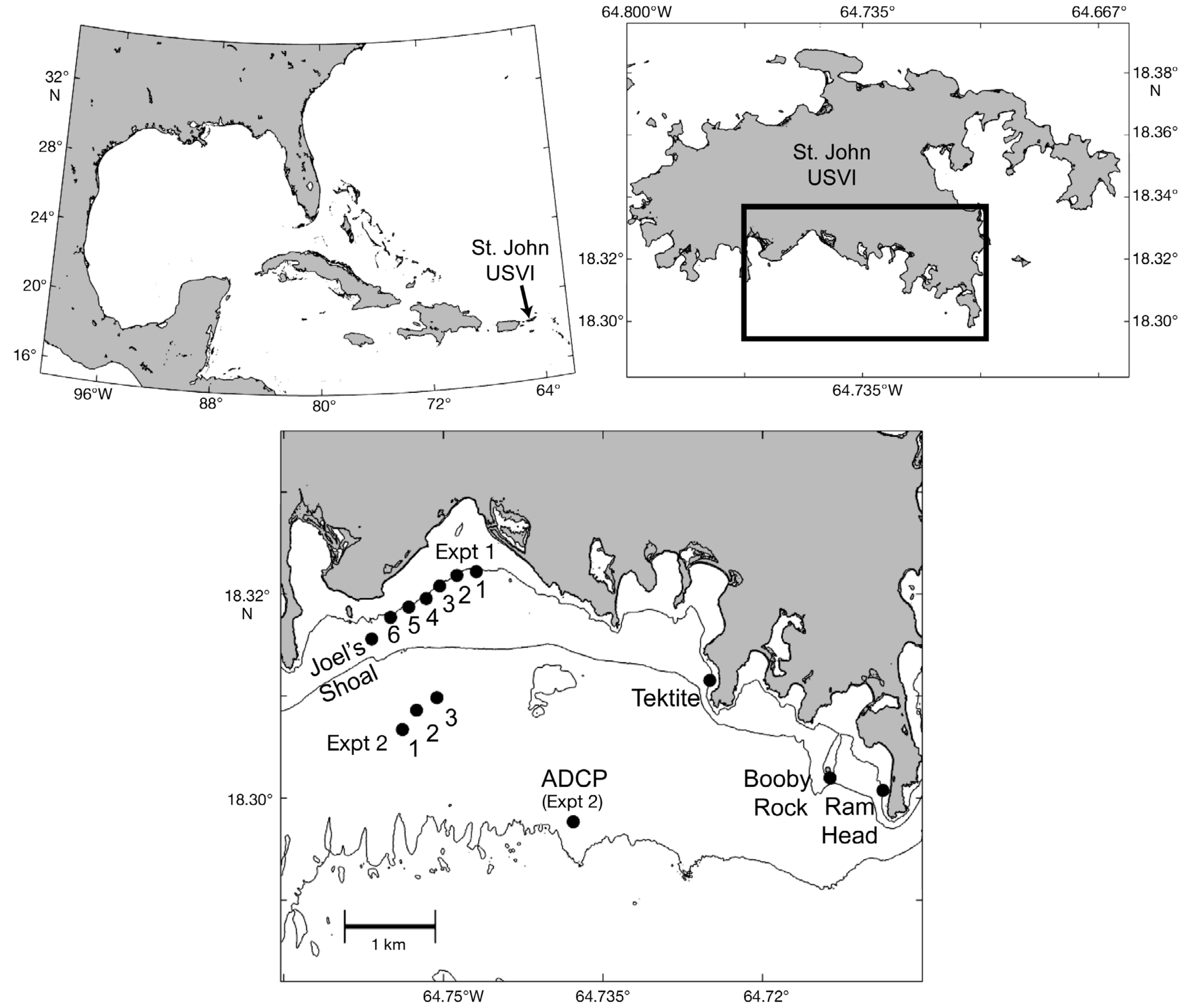

Fig. 1. Experiment locations on the south shore of St. John, including location of St. John within the greater Caribbean. Recordings from the reefs Tektite, Booby Rock, and Ram Head were used in playback experiments; Joel's Shoal represents the nearest reef to our experimental site. Thin lines: 10, 20, and 30 m isobaths

A light trap, designed as a tapered cylinder with 505 µm mesh (Sponaugle & Cowen 1996), was suspended from the round float at the top of each light trap mooring (spanning a depth of 1–2 m), 10 m offshore of the speaker using 12 m of mooring line (significant wave height did not exceed 2 m during the experiment and tidal range is minimal, ~0.2 m). This added length was necessary to keep the mooring on the ground, yet may add some inter-nightly variability to the distance from the moored speaker to the light trap, likely resulting in 15 m distance from speaker to light trap based on local currents (though this could vary from 10–18 m among nights). Winds were moderate for all but one night of experiments, and thus there was not a large degree of variability in abiotic noise (Table S2). Traps were deployed prior to sunset and retrieved just after sunrise. Light traps were used to quantify settlement, as many reef fish larvae are attracted to light and settle at night (Victor 1991, Sponaugle & Cowen 1996, Tolimieri et al. 2000). The light may extend a maximum of 50 m, but likely less given

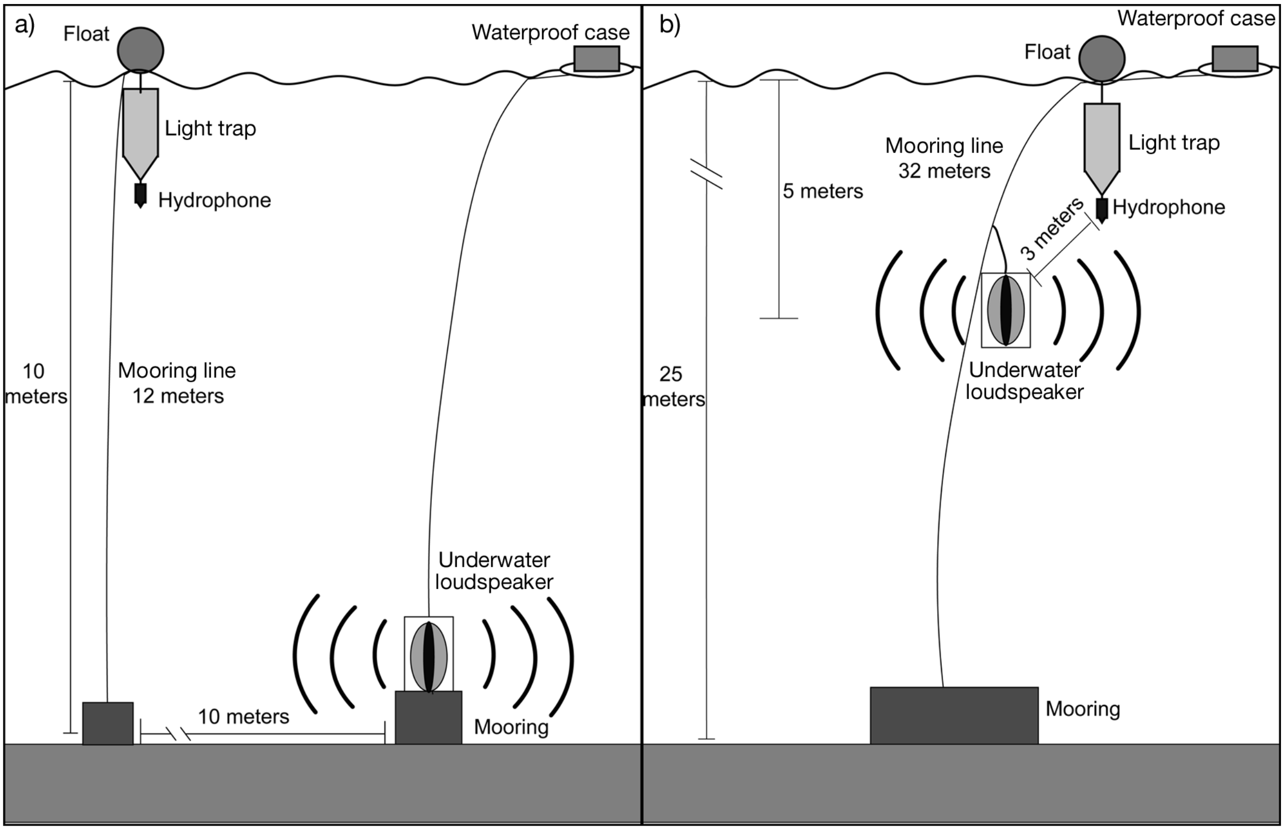

Fig. 2. Schematic of the playback mooring design for (a) Expt 1 (in 2016) and (b) Expt 2 (in 2017). Light traps with hydrophones attached were suspended from a surface float. An underwater speaker played pre-recorded reef sounds at 5 m depth. Electronic equipment powering the underwater speaker was housed in the waterproof case at the surface

local visibility and extended a substantially shorter distance than the soundscape playbacks (>100 m difference; Simpson et al. 2004). A broadband acoustic recorder (DMON; Woods Hole Oceanographic Institution; Kaplan et al. 2015; flat frequency response from 100 Hz to 50 kHz and total design sensitivity of −167 dB re V/µPa) was attached to the bottom of each light trap and recorded at a sampling rate of 120 kHz continuously throughout the deployment. Hydrophones were placed on the light traps to confirm that the speakers were broadcasting reef soundscapes throughout the night, allowing the removal of any trials that contained equipment failures and to ensure that the SPL_{rms} of the playbacks were comparable to the original recordings of nearby reefs. The playback experiment was conducted for 8 nights with 3 nights occurring in early June and 5 in late June and early July (Table S3). Hydrophones were deployed for 2 additional nights (3 June and 6 July) when experiments did not occur to test for variability in the ambient soundscape among mooring locations.

2.1.3. Acoustic treatments

Natural reef soundscape treatments were randomly selected 24 h periods from a 4 d continuous recording of 2 nearby reefs, Tektite (18.310° N, 64.722° W) and Ram Head (18.301° N, 64.704° W) (Fig. 1). Initial recordings were made in August 2013 using a 120 kHz sampling rate and 50 kHz low-pass filter (Kaplan et al. 2015), and were down-sampled to 48 kHz for this experiment. The reef soundscape recordings were amplified using Adobe Audition (Adobe Systems) to ensure broadband SPL_{rms} were similar to the original reef recordings. At the initiation of a given trial, the playback recordings were started at the time of day matching the start time of the experiment. This allowed the playback recordings to match the diel cycle, including the crepuscular fish chorus, of the local coral reefs. High and low sound level treatments were manipulated through the volume settings on the audio players such that the full-band SPL_{rms} (0.1–20 kHz) of the high and low treatments were approximately 120 and 115 dB re

1 µPa, respectively. Because decibels are logarithmic, this 5 dB difference is equivalent to one treatment being about twice the amplitude of the other in terms of sound pressure. A silent file was played on loop as the silent control treatment to account for potential effects of the electromagnetic field generated by the playback equipment. Locations of treatments (high, low, and silent) were randomly selected each night to minimize confounding spatial effects on settlement (Table S4).

2.1.4. Data processing

Acoustic recordings of the playback treatments and original recordings of reef soundscapes were processed using Matlab 9.2 (MathWorks). Prior to calculating $\mathrm{SPL}_{\mathrm{rms}}$, data were down-sampled to 48 kHz and filtered to a 100–3000 Hz band (low-band) using a 4th order Butterworth filter for analyses relating playback to fish catches, though power spectral density (PSD) was also computed for the 100–20 000 Hz band (see Figs. 3 & S2). This frequency range omits low frequency (<100 Hz) electronic noise from the recording system, encompasses acoustic frequencies that reef fish are known to detect (Fay & Popper 2012, Tricas & Boyle 2014), and is near the approximate cutoff frequency (~128 Hz) for this experiment based on water temperature, depth, and substrate (Larsen & Radford 2018). The $\mathrm{SPL}_{\mathrm{rms}}$ values were calculated from 1 min samples, each spaced 5 min apart, to generate a median $\mathrm{SPL}_{\mathrm{rms}}$ for each treatment level of each trial; median values were used because soundscape data are often not normally distributed (Kaplan et al. 2015). This also minimized the effects of noise from passing vessels, which generate high amplitude, but short duration, low frequency sounds that inflate mean $\mathrm{SPL}_{\mathrm{rms}}$ values (Kaplan & Mooney 2015). However, files containing boat noise from the vessel used to deploy and recover the experimental equipment were excluded from use in the analysis. For each treatment in each trial and the original recordings of reef soundscapes used for playbacks, PSDs (in dB re 1 $\mu\mathrm{Pa}^2$/Hz, with 1 Hz and 1 s bins, with 50% overlap of time bins) of each recording were calculated using Welch's method to assess the power of the soundscape at various frequencies (Welch 1967). Spectrograms were constructed by piecing together 1 min integrations of PSD. The number of files containing boat noise in our playbacks was identified via visual analysis of spectrograms from each 1 min recording (Kaplan et al. 2015).

Light traps were retrieved each morning beginning at sunrise and larvae were immediately preserved in 95% ethanol. Reef fish larvae were then identified by first separating them into categories of demersal reef fish and pelagic fish. Demersal reef fish larvae were then identified morphologically to family and enumerated. Although snappers are demersal reef fish as adults, they were analyzed separately and not included in total demersal reef fish counts, as snappers often settle in mangrove and seagrass habitats and migrate to reefs later in life (Laegdsgaard & Johnson 2001, Nagelkerken et al. 2002, Watson et al. 2002). While parrotfish also often settle in seagrass, there has been observed variability in settlement patterns within this family and we have thus classified them within total demersal reef fish (Bellwood 1988, Ishihara & Tachihara 2011).

2.1.5. Current data

Current data for the nights of the 2016 experiment were estimated from Caribbean Integrated Coastal Ocean Observing System (CariCOOS; https://caricoos.org) buoy 41052 located south of St. John at 18.249° N, 64.763° W, 6.5 km away from the experiment location. Current direction and magnitude were vertically averaged for the upper 25 m of the water column to result in a mean current direction and magnitude for each night. Data were provided hourly and thus hours between 19:00 and 05:00 h local time were selected to encompass the dark period when the experimental light traps were fishing effectively. While the currents measured at this buoy may have differed from those alongshore at our light traps, those currents likely generate, and are thus representative of, the zonal direction of the alongshore current nearby our experiment (Green & Edmunds 2011).

2.1.6. Statistical analysis

The effect of the playback of reef soundscapes in the 2016 experiment was tested through generalized linear mixed-effects models following a negative binomial distribution using the 'lme4' package in R statistical software (version 3.2.4; Bates et al. 2015). The negative binomial model was appropriate for the over-dispersed and patchy count data. Models were specified to test for relationships between number of reef fish collected (response variable) and low-band

(100–3000 Hz) median SPL_{rms} (dB re 1 µPa). These models were created for the total number of demersal reef fish larvae collected and the frequently caught demersal reef fish taxa. Pelagic fish larvae were not consistently retained or enumerated during this experiment, precluding our ability to test the effect of reef soundscape playback on their capture. The 'larval pool' of settling larvae typically exhibits substantial variation among nights, thus trial number was included as a random effect (Victor 1986, Richards & Lindeman 1987, D'Alessandro et al. 2007). Site and audio track ID (recording number) were also included as random effects to account for location-specific differences in catchability and for the potential for different reef recordings to elicit distinct responses by fish larvae (Gordon et al. 2018). Lunar effects remain possible, but our limited number of recordings and nights sampled precluded a thorough analysis of these effects. Wald Type II tests were performed to assess the effect of median SPL_{rms} on reef fish settlement, and variance attributed to each random effect was recorded. Negative binomial linear mixed-effect models treating sound playback as an ordinal categorical predictor (high, low, silent) were also created for each category of fish larvae for comparison. Random effects were treated in an identical manner as models created using low-band SPL_{rms}. Models with sound level as an ordinal categorical predictor were fitted using orthogonal polynomial contrasts, and thus both a linear and quadratic term are incorporated (as there are 3 levels). These ordinal models were created for comparison with models treating low-band SPL_{rms} as a continuous predictor given that previous experiments used treatments instead of measurements of sound output as predictors (Gordon et al. 2018, 2019). We therefore present them as such while focusing on the negative binomial linear mixed effect models that treat low-band SPL_{rms} as a continuous predictor, as we believe this is more representative of differences in the sound field larvae encountered as they approached each light trap.

Throughout the course of our experiment, surface currents in the waters immediately south of St. John were predominately westward and therefore our experimental moorings were generally along current. Thus, the hypothesis of downstream reduction of larval reef fish catches was tested to determine the effect of local hydrography on larval fish catches in our light traps. Total reef fish catches (and catches of abundant taxa) by location and night were fit to a monotonic decreasing regression (i.e. decreasing trap probability with increasing distance downstream) via a point-adjacent-violators algorithm using the R package 'isotone' (Mair et al. 2009). The log-likelihood of the model fit with observational data was compared to a null model that assumed probability of catching fish at each trap was equal, which resulted in a likelihood ratio. Significance of model fit was determined through randomization tests; specifically, the p-value was estimated as the portion of likelihood ratios from models fit with randomized catch data that exceeded the likelihood ratio of the model fit with observed data.

2.2. Expt 2

2.2.1. Site description

In 2017, the experimental location was moved offshore — away from alongshore current — to reduce the likelihood of downstream decreases in measured larval settlement (as observed in Expt 1). The move offshore resulted in each of the 3 moorings being deployed at a depth of 25 m (Fig. 1).

2.2.2. Experimental moorings

Each mooring consisted of 2 concrete blocks on the seafloor with one line to the surface attached to a round float and a urethane ring float (Fig. 2b). The electronic equipment remained the same as Expt 1, except the underwater loudspeaker was attached to the mooring line at 5 m depth to minimize variability in distance between the speaker and light trap. Prior to experimental trials, recordings from a system playing reef sound with a SPL_{rms} of 130 dB re 1 µPa at 4 m above the speaker were taken at multiple 25 m intervals away from the system to assess the distance between playback systems needed to prevent acoustic overlap of playbacks. The change from 150 dB re 1 µPa came about due the speaker being suspended from the surface as opposed to the seafloor, and 4 m was chosen as the speaker was 5 m below the surface and the hydrophone was lowered from the boat 1 m below the water line (thus 4 m separation). Visual inspection of spectrograms and SPL_{rms} values of these recordings revealed no discernable differences from ambient soundscapes at 250 m from the playback speaker, a larger distance than 2016 owing to decreased sound attenuation at greater depths. Thus, moorings were spaced at 275 m intervals as a compromise to minimize overlap of sound fields from adjacent speakers yet keep the moorings within a distance that would allow each trap to be exposed to a similar pool of pre-settlement larvae and not create a substantial cross-shelf or depth gradient in the spacing of traps.

A light trap (same specifications as 2016) was suspended from the round float at the top of each mooring at 1–2 m depth directly above the speaker. A hydrophone (SoundTrap ST300, Ocean Instruments) was attached to the bottom of each light trap and recorded at a sampling rate of 48 kHz for 63 s every 5 min to acquire sufficient recordings of playbacks while maximizing the efficiency of data processing. The playback experiment was conducted for 13 nights, with 10 nights occurring in July and 3 in August.

2.2.3. Acoustic treatments

Soundscape playback treatments consisted of natural reef soundscapes, recorded continuously for 24 h from 1–4 nights prior to each trial. This allowed us to closely match season and lunar phase of fish settlement (unlike Expt 1), as reef soundscapes are known to vary (though weakly) at these temporal scales (Staaterman et al. 2013, Kaplan et al. 2015, 2018, Lillis & Mooney 2018). Recordings were made using a SoundTrap ST300 with a 48 kHz sampling rate, at 2 reefs, both with high coral cover and fish abundance relative to other reefs in the region (Booby Rock, 18.302° N, 64.710° W; Tektite, 18.310° N, 64.722° W; Fig. 1), maximizing the likelihood of elevated SPL_{rms} in frequencies below 3000 Hz (Kaplan et al. 2015). While it is unlikely that most fish hear the high frequencies of snapping shrimp (Myrberg & Riggio 1985, Egner & Mann 2005, Wright et al. 2005, Fay & Popper 2012, Tricas & Boyle 2014), it is worth noting that these reefs had similar SPL_{rms} in the snapping shrimp acoustic band (which generally have greatest acoustic energy above 2000 Hz). Five continuous recordings of reef sounds were collected and used for playbacks (Table S5). Three of these recordings were collected at Tektite reef and 2 at Booby Rock reef. Most recordings were used for less than 3 playbacks, except for 20–23 July when the same recording was used for 4 experiments due to time constraints precluding the collection and processing of an additional continuous recording. Overall, this randomization of multiple acoustic treatments sought to reduce pseudoreplication of sound stimuli and more closely replicate natural soundscapes from reefs with abundant fish sounds.

The continuous recordings of reef soundscapes were amplified and initiated, and treatments (high, low, silent) were assigned in the same manner as Expt 1.

2.2.4. Data processing

Acoustic recordings of the playback treatments and original recordings of reef soundscapes were processed using Matlab 9.2 (MathWorks). SPL_{rms} values for low-band (100–3000 Hz) frequencies for each treatment and PSDs were calculated in the same manner as Expt 1, including identical treatment of vessel noise.

Light traps were retrieved, samples preserved, and larval fish were identified in nearly the exact same manner as Expt 1. The only exception was that pelagic fish larvae were identified to family and demersal reef fish were identified to lowest possible taxonomic unit for abundant families in Expt 2.

2.2.5. Current data

An ADCP (Nortek Aquadopp 600 kHz) was deployed ~2 km to the southeast of the 2017 experiment location (18.298 °N, 64.736° W; Fig. 1). Current magnitude and direction data were collected every 30 min at 1 m depth intervals. Current magnitude and direction data for the upper 25 m were vertically averaged over the course of each night, from 19:00–05:00 h local time, to estimate mean current direction throughout the water column. The mean current direction for each night was then used to inform us of whether local currents were in-line with our experimental setup, permitting the exclusion of nights when currents may have altered the apparent effects of the sound treatments.

2.2.6. Statistical analyses

As in Expt 1, generalized linear mixed-effect models with a negative binomial distribution were used to test the effect of reef soundscape playback on reef fish settlement, using the 'lme4' package in R (version 3.2.4; Bates et al. 2015). Median low-band (100–3000 Hz) SPL_{rms} was used as a fixed effect with site, date, and track ID included as random effects. Models were formed for total demersal reef fish and abundant reef fish taxa. Pelagic fish larvae were collected and enumerated in Expt 2 and thus were also included in the taxa tested.

The effect of the playback of reef soundscapes in the 2017 experiment (Expt 2) was also tested through multinomial logistic regressions using the 'nnet' package in R (Venables & Ripley 2002). The multinomial approach permits inference about site-specific responses of fish larvae to sound levels, which was possible in 2017 both due to the lack of apparent current interference with this experiment and the onshore–offshore placement of the experimental moorings. Models were created to test for significant relationships between the trap where each fish was captured and the difference in median $\mathrm{SPL_{rms}}$ of each trap from a reference trap (Trap 1 in our case) within a night. These models test how the probability of a fish larva entering a trap is affected by the difference in amplitude of the playback at that trap to a reference trap, thus simulating a choice scenario determining if fish are more or less likely to enter a trap if it is louder or quieter than adjacent traps. A reference level is needed for multinomial models, and thus the number of larvae in Trap 1 was arbitrarily chosen to be the reference trap for these analyses. The model is represented by 2 equations, one relating catch in Trap 2 to catch in Trap 1 and a second relating catch in Trap 3 to Trap 1. The difference in median $\mathrm{SPL_{rms}}$ of each trap from Trap 1 were used as regressors. This resulted in the following set of equations representing the model used for testing the effects of reef soundscape playback on reef fish settlement:

$$\ln\left[\frac{\mathrm{pr}=\mathrm{Trap}\ 2}{\mathrm{pr}=\mathrm{Trap}\ 1}\right]= \alpha_1+\beta_1\left(\mathrm{SPL}_2-\mathrm{SPL}_1\right)+\beta_2\left(\mathrm{SPL}_3-\mathrm{SPL}_1\right) \quad (1)$$

$$\ln\left[\frac{\mathrm{pr}=\mathrm{Trap}\ 3}{\mathrm{pr}=\mathrm{Trap}\ 1}\right]= \alpha_2+\beta_3\left(\mathrm{SPL}_2-\mathrm{SPL}_1\right)+\beta_4\left(\mathrm{SPL}_3-\mathrm{SPL}_1\right) \quad (2)$$

where pr represents probability, SPL_i represents the median low-band $\mathrm{SPL_{rms}}$ at trap i, α_i represents an intercept of the model, and β_i represents the coefficient for regressor i. As with the generalized linear mixed-effect models, multinomial logistic regression models were created for the total demersal reef fish larvae, total pelagic fish larvae, and frequently caught demersal reef fish taxa. For each taxon, model coefficients were tested for significance using Wald tests. To visualize model output, one of the regressors was held constant while the second was varied over a range of median $\mathrm{SPL_{rms}}$ differences.

3. RESULTS

3.1. Acoustic description of playbacks

Monitoring the acoustic conditions of Expt 1 showed that the acoustic reef playbacks were typically at their intended $\mathrm{SPL_{rms}}$, with approximately 3–5 dB re 1 µPa differences among treatments though their PSD was variable in the low frequencies and more consistent at higher frequencies (Figs. 3a,b & S2, Table S3) and some variability among nights potentially due to the varying distance of the light trap from the speaker based on currents. However, silent treatments showed elevated SPLs on multiple nights, either as result of nearby fishes or occasional overlap with an adjacent playback treatment. The low treatment was also quieter on some nights as a result of amplifier or speaker malfunction. Further, each recording showed different levels of boat noise, with boat noise occurring in 9.6% of 1 min files for the Tektite recording and only 3.8% of files for the Ram Head recording (Table S6).

In Expt 2, silent treatment (ambient) soundscapes showed little variation among sites and dates, with median low-band $\mathrm{SPL_{rms}}$ of approximately 98 dB re 1 µPa for most recordings, demonstrating minimal spatial and temporal heterogeneity in the ambient soundscape of the experimental site (Table S5). Recordings of the playback treatments showed median received $\mathrm{SPL_{rms}}$ varied by night, with only some nights showing distinct high and low signals as designed (Table S5). One night (12 Aug) was excluded from analysis due to light trap equipment failures and a second due to recorder malfunction (22 Jul). Audio files were also unrecovered from 2 nights (15 and 16 Jul) and thus unable to be used. PSD of the playback of reef sounds was elevated compared to that of the original reef recordings (Figs. 3c & 4) in low frequencies (<3 kHz) though more notable differences occurred in the high frequencies (3–6 kHz; Fig. S3). Each original recording again showed different levels of boat noise, though all in low quantities (<5% of files; Table S6).

Differences among playback treatments for both experiments primarily occurred in the low frequencies (<3 kHz) as evident in the power spectra and spectrograms (Figs. 3c,d & 4). Power in the high frequency band (3–20 kHz) was generally consistent throughout the recordings of playbacks, with the occasional variability in low frequencies (100–3000 Hz) from strong low frequency fish calls (Fig. S4). These low frequency pulses were apparent in playback recordings but rare in recordings of the control site. Moderate elevations in $\mathrm{SPL_{rms}}$ were observed in

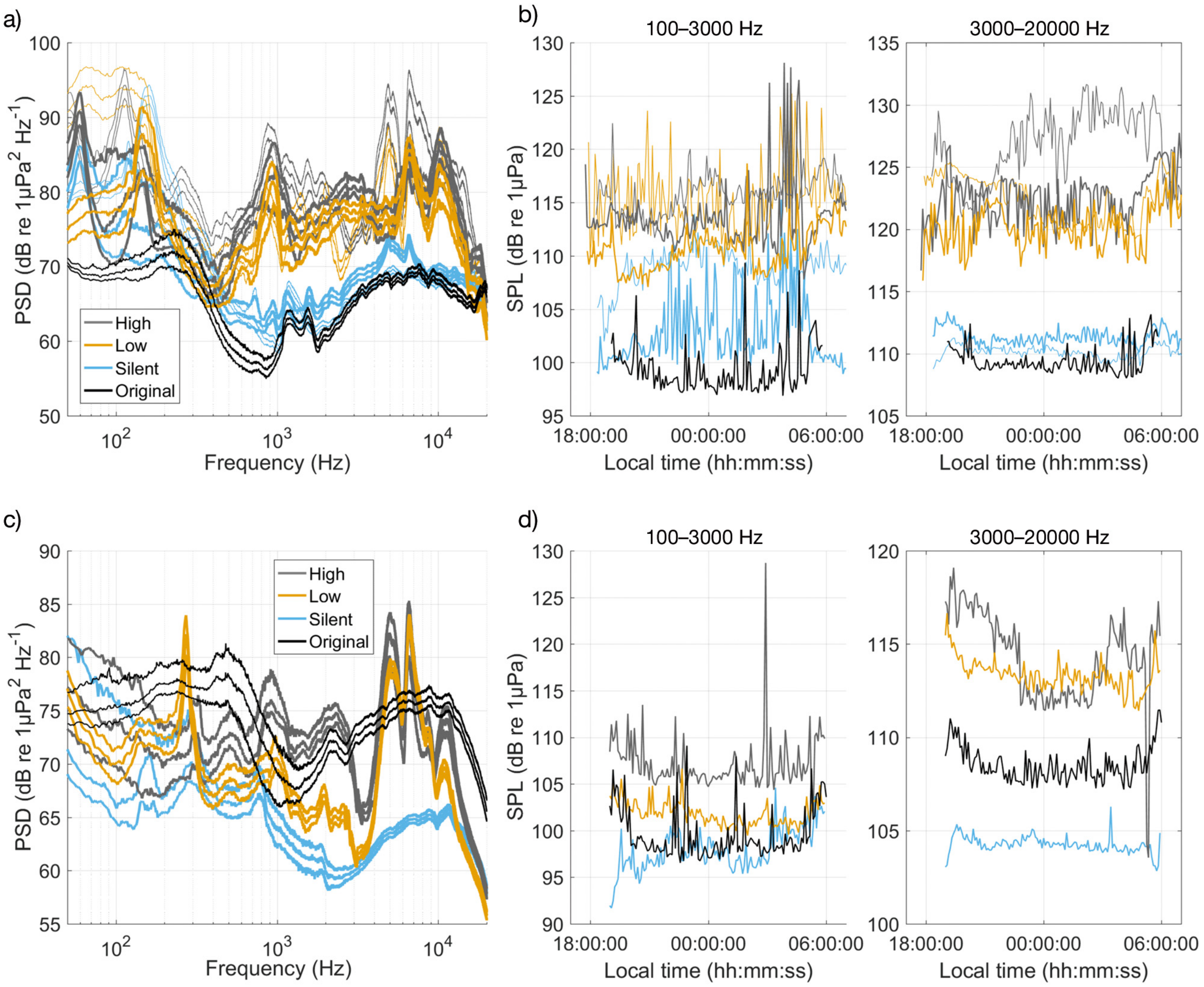

Fig. 3. (a) Power spectral densities (PSD) for the full frequency band (100–20 000 Hz) and (b) sound pressure levels (SPL) in low (100–3000 Hz) and high (3000–20 000 Hz) frequency bands for playback trial 4 (6–7 June) in 2016, and the original recording used for this playback, of Ram Head reef, recorded 2–3 August 2013. The levels shown for the original recording were amplified by a factor of 50 for playbacks. In corresponding colors for high, low, and silent treatments, thin and thick lines represent data from the 2 separate sites assigned to that treatment. (c) PSD and (d) SPL for playback trial 8 (20–21 July) in 2017, and the original recording used for this playback, of Tektite, recorded 17–18 July 2017. PSD and SPL were integrated over 1 min time bins, and PSD was calculated in 1 Hz bins. PSD curves for each site and the original reef recording include 3 lines: the median curve across the entire night (in the middle), and the 25th and 75th percentiles, below and above the median, respectively. In (d), The peak at 02:55:00 h for the high treatment (low frequency band) is a hydrophone artefact, and the trough at 05:15:00 h for the high treatment (high frequency band) is a 10 min period where the playback temporarily paused

higher frequencies relative to control sites, but we did not focus on these frequencies due to the assumption that most fish larvae cannot hear sound at these higher frequencies (see Section 2.1.4).

3.2. Current data

Current data from the CariCOOS buoy indicated that mean nightly currents during Expt 1 ranged from 3.6–20.6 cm s^{-1} and were primarily westward and in-line (within 20°) with Sites 2–6 (Fig. 5a; vectors indicate direction current is heading toward).

Currents recorded from the nearby ADCP in Expt 2 ranged from 2.6–19.1 cm s^{-1} and were more variable in direction in 2017 than 2016, with most nights showing mean current toward the northwest (Fig. 5d). These currents were not in-line with our experimental moorings and thus we assumed prevailing currents were not driving site-specific catches of larval fishes.

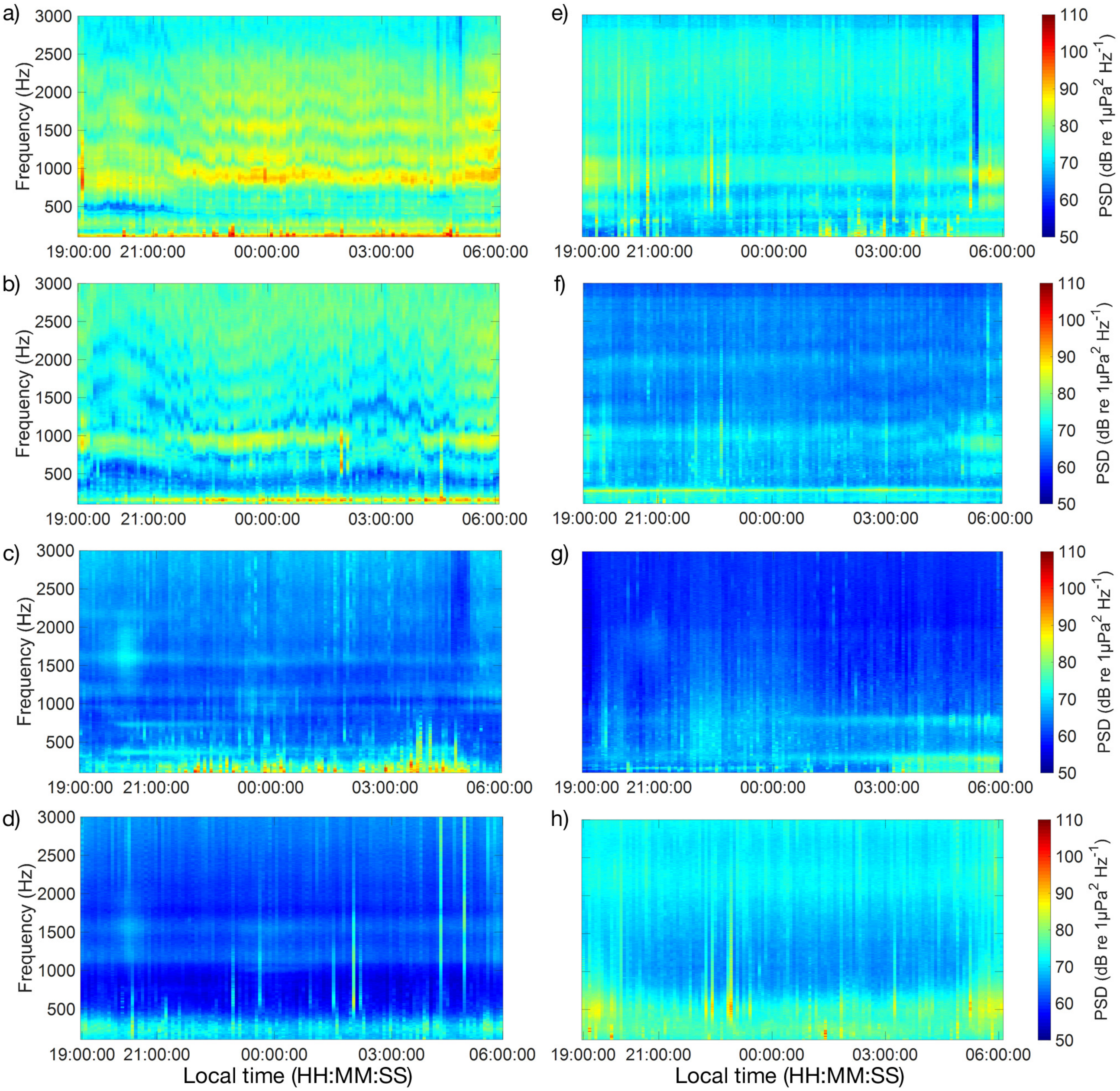

Fig. 4. Low-band (100–3000 Hz) power spectral densities (PSD) of recorded playbacks and original files used for playbacks for 2 representative nights; (a–d) 6–7 June 2016, for 3 playback treatments: (a) high, Site 4; (b) low, Site 2; (c) silent, Site 5, and (d) the original reef recording (not amplified) from Ram Head on 2–3 August 2013; (e–h) 20–21 July 2017, for 3 playback treatments: (e) high, Site 2; (f) low, Site 1; (g) silent, Site 3, and (h) the original reef recording (not amplified) from Tektite on 17–18 July 2017. PSD shown is integrated over 1 min time bins and in 1 Hz frequency bins. In (e), there was reduced PSD around 05:15:00 h for a 10 min period where the playback temporarily paused

3.3. Larval catches

In Expt 1, a total of 555 reef fish from 18 families were collected over 7 nights of the experiment. Nightly catches were variable, ranging from 27–244 fish in a night. The dominant families of reef fishes were labrisomids (Labrisomidae; n = 240), damselfish (Pomacentridae; n = 102), lizardfish (Synodontidae; n = 71), and snapper (Lutjanidae; n = 45; Table S7).

Generalized linear mixed-effect models indicated that median low-band (100–3000 Hz) $\mathrm{SPL_{rms}}$ had a significant, positive fixed effect for Synodontidae ($p < 0.05$), yet not for total reef fish, Labrisomidae, Poma-

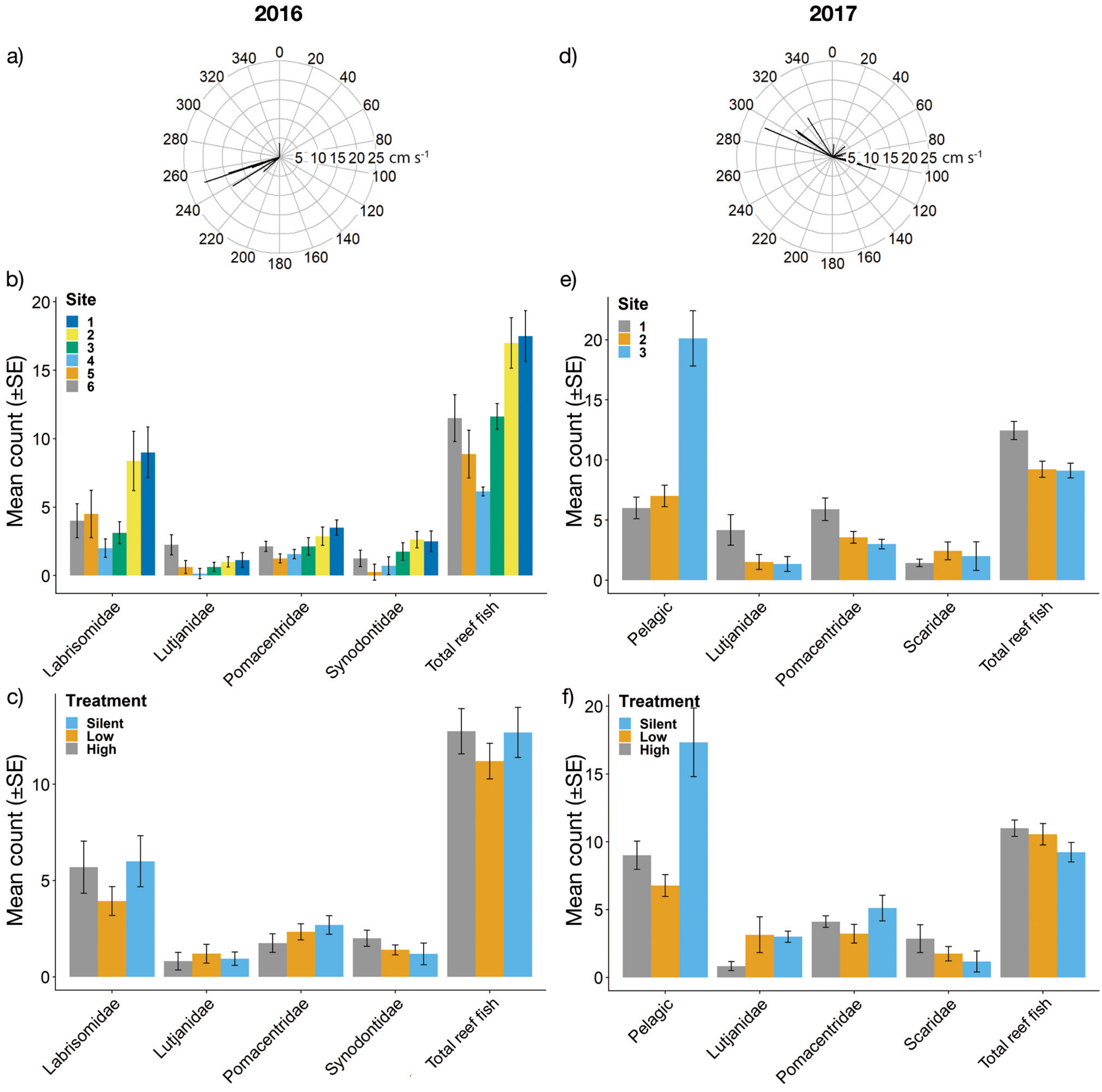

Fig. 5. Mean nightly current direction and magnitude for (a) 2016 and (d) 2017 with mean catch of common taxa by site in (b) 2016 and (e) 2017 and by intended acoustic treatment in (c) 2016 and (f) 2017

centridae, or Lutjanidae ($p > 0.05$; Table 1, Fig. 6a). Date and site contributed significantly to variance in the intercept as random effects, while track ID was insignificant (Table 1). No fixed effects for models treating sound treatment as an ordinal predictor were significant, though a positive linear effect of sound treatment on catch of Synodontidae and a negative linear effect of sound treatment on Pomacentridae were the closest to significance (Table S8).

Catch of reef fish taxa by site indicated downstream drop-off (Fig. 5b). Monotonic decreasing regression indicated significant downstream, current-based reduction in catches of total reef fish, Synodontidae, Labrisomidae, Pomacentridae, and Lutjanidae ($p < 0.001$). Downstream drop-off was most pronounced in Synodontidae and Labrisomidae, with Lutjanidae showing the least amount of down-stream drop-off as determined from fitted trap probabilities (Table 2).

In Expt 2, a total of 621 larvae were collected over 9 nights, of which 319 were considered to belong to families of demersal reef fish. Twenty-one families of

Table 1. Slope estimates of fixed and random effects for negative binomially distributed linear mixed effect models for Expt 1. SPL: sound pressure level (root mean square); RE: random effect

Taxon	Count	Predictor	Type	Effect size (variance if RE)	SE	p
Total reef fish	510	Lowband SPL (100–3000 Hz)	Fixed	0.015	0.032	0.645
		Date	Random	0.435	0.659	
		Site	Random	0.086	0.294	
		TrackID	Random	<0.001	<0.001	
Synodontidae	71	Lowband SPL (100–3000 Hz)	Fixed	0.158	0.055	0.004
		Date	Random	0.051	0.225	
		Site	Random	0.236	0.486	
		TrackID	Random	<0.001	<0.001	
Pomacentridae	102	Lowband SPL (100–3000 Hz)	Fixed	−0.006	0.053	0.906
		Date	Random	0.515	0.717	
		Site	Random	0.030	0.173	
		TrackID	Random	<0.001	<0.001	
Lutjanidae	45	Lowband SPL (100–3000 Hz)	Fixed	0.007	0.025	0.790
		Date	Random	2.613	1.617	
		Site	Random	0.510	0.714	
		TrackID	Random	<0.001	<0.001	
Labrisomidae	240	Lowband SPL (100–3000 Hz)	Fixed	0.026	0.037	0.489
		Date	Random	4.335	2.082	
		Site	Random	0.127	0.357	
		TrackID	Random	<0.001	<0.001	

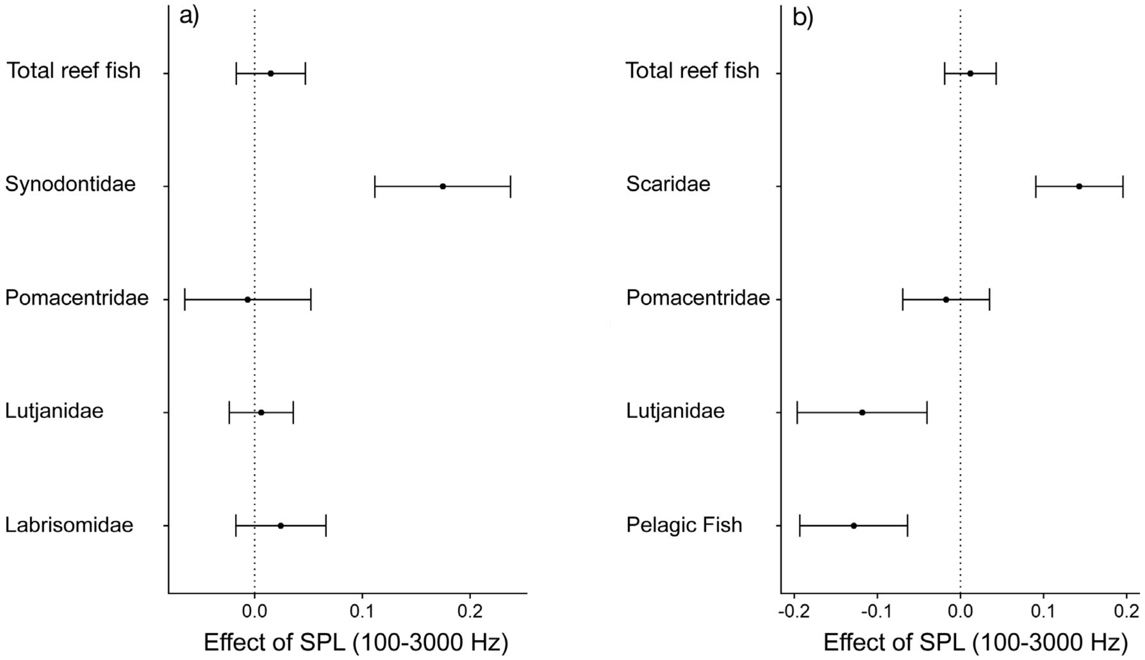

Fig. 6. Slope estimates (±SE) of the effect of median low-band sound pressure level (SPL) on the catch of commonly caught larval fish taxa in (a) 2016 and (b) 2017

demersal reef fish were captured, with damselfish (Pomacentridae; n = 112), snappers (Lutjanidae; n = 42; though not considered reef settling), parrotfish (Scaridae; n = 41), and labrisomids (Labrisomidae; n = 28) representing the most frequently caught families of reef fish. All other families occurred infrequently and in low abundances (Table S9). Larvae of pelagic fishes were also frequently caught in light traps, totaling 297 individuals, with jacks (Carangidae; n = 107), sardines (Clupeidae; n = 70), silversides (Atherinidae; n = 68), and driftfishes (Nomeidae; n = 14) representing the most frequently

Table 2. Expt 1: monotonic regression estimates of probability of entering each trap as fit via pool-adjacent-violator algorithms

Taxa	Trap 1 probability (Upstream)	Trap 2 probability	Trap 3 probability	Trap 4 probability	Trap 5 probability	Trap 6 probability (downstream)	p
Total reef fish	0.247	0.247	0.167	0.113	0.113	0.113	<0.001
Synodontidae	0.289	0.289	0.197	0.075	0.075	0.075	<0.001
Pomacentridae	0.275	0.216	0.157	0.118	0.118	0.118	<0.001
Lutjanidae	0.200	0.178	0.156	0.156	0.156	0.156	<0.001
Labrisomidae	0.289	0.277	0.108	0.108	0.108	0.108	<0.001

collected families. One barracuda *Sphyraena barracuda* larva was captured yet placed in neither the demersal reef fish nor pelagic fish category due to use of mangrove and seagrass habitat as juveniles and their variable habitat use as adults (de Sylva 1963, O'Toole et al. 2011). Our most offshore light trap collected the most reef fish larvae (Site 1, n = 112) with the inshore traps collecting fewer individuals (Site 2, n = 83; Site 3, n = 82; Fig. 5e).

Generalized linear mixed-effect models indicated that median low-band (100–3000 Hz) SPL_{rms} was a significant, positive fixed effect for Scaridae ($p < 0.01$), yet not for total reef fish, Pomacentridae, or Lutjanidae ($p > 0.05$; Table 3, Fig. 6b). Median low-band SPL_{rms} was a significant, negative fixed effect for larvae of pelagic fish ($p < 0.05$; Fig. 6b). Date and site often contributed significantly to variance in the intercept as random effects, while track ID was insignificant (Table 3). Sound level also showed a significant, positive linear effect on catches of Scaridae larvae in models using sound treatment as an ordinal predictor (Table S10). However, results from these models differed in determination of significance from using sound level as a continuous regressor for Lutjanidae (ordinal model showed significant, negative linear effect of sound) and for pelagic fish (ordinal model showed insignificant, negative linear effect of sound; Table S10).

Multinomial logistic regression indicated that differences in median low-band SPL_{rms} among traps were significant predictors of the probability of entering either Trap 2 or Trap 3 relative to Trap 1 for total reef fish, Pomacentridae, Lutjanidae, and pelagic fish ($p < 0.05$), but not Scaridae ($p > 0.05$; Table 4). However, median low-band SPL_{rms} difference did not have a significant and intuitive effect

Table 3. Slope estimates of fixed and random effects for negative binomially distributed linear mixed effect models for Expt 2. SPL: sound pressure level (root mean square); RE: random effect

Taxon	Count	Predictor	Type	Effect size (variance if RE)	SE	p
Total reef fish	277	Lowband SPL (100–3000 Hz)	Fixed	0.000	0.031	0.997
		Date	Random	0.171	0.414	
		Site	Random	<0.001	<0.001	
		TrackID	Random	<0.001	<0.001	
Scaridae	41	Lowband SPL (100–3000 Hz)	Fixed	0.143	0.053	0.006
		Date	Random	0.908	0.953	
		Site	Random	<0.001	<0.001	
		TrackID	Random	0.462	0.680	
Pomacentridae	112	Lowband SPL (100–3000 Hz)	Fixed	−0.017	0.052	0.743
		Date	Random	<0.001	<0.001	
		Site	Random	<0.001	<0.001	
		TrackID	Random	<0.001	<0.001	
Lutjanidae	42	Lowband SPL (100–3000 Hz)	Fixed	−0.118	0.078	0.129
		Date	Random	0.649	0.806	
		Site	Random	0.100	0.316	
		TrackID	Random	<0.001	<0.001	
Pelagic fish	297	Lowband SPL (100–3000 Hz)	Fixed	−0.128	0.065	0.048
		Date	Random	<0.001	<0.001	
		Site	Random	0.079	0.281	
		TrackID	Random	<0.001	<0.001	

(i.e. probability of entering Trap 2 responding to difference in SPL$_{\text{rms}}$ of Trap 2 from Trap 1, or probability of entering Trap 3 responding to difference in SPL$_{\text{rms}}$ of Trap 3 from Trap 1) for Pomacentridae. Generally, decreased probability of catches compared to Trap 1 at louder SPL$_{\text{rms}}$ were apparent across taxa at Trap 2 (middle site) while increased probability of catches at SPL$_{\text{rms}}$ occurred at Trap 3 for total reef fish and Scaridae (most nearshore site; Fig. 7).

4. DISCUSSION

Our work indicates that certain taxa of reef fish in the Caribbean are attracted to continuous playback of local reef soundscapes. Yet the response was not consistent among all reef fish taxa, with only lizardfish showing significant attraction to louder playback of low frequency reef soundscapes in Expt 1 (2016; though there were low catches of lizardfish in 2017) and parrotfish indicating significant attraction to louder playback of low frequency reef soundscapes in Expt 2 (2017; low catches of parrotfish in 2016). Decreased catches of larvae of pelagic fish taxa occurred with louder playback of low frequency reef soundscapes in Expt 2, suggesting that reef sounds may be a deterrent for these larvae. This response by non-reef settlers is potentially adaptive since avoiding a coral reef's abundant predators would enhance survival (Simpson et al. 2011).

Many previous studies have shown significant positive response of reef fishes to sound at multiple life stages, including increased catches of larval stages in light traps (Tolimieri et al. 2000, Simpson et al. 2004, 2008a,b, Leis & Lockett 2005, Radford et al. 2011a, Gordon et al. 2018). However, our results indicate that the response of reef fish to sound stimuli was not ubiquitous among reef taxa collected, which contrasts with many previous studies on the effect of soundscape playback on reef fish settlement in the Pacific. Our results suggest reef soundscape playback may not elicit as strong a response from reef fish, particularly in exposed areas such as the south coast of St. John with moderate currents (Green & Edmunds 2011). It is also possible that larvae in the Caribbean may not respond as notably to acoustic cues as fish taxa in the Pacific, possibly due to the differences in soundscapes, reef condition, or olfactory cues between the Atlantic and Pacific (Staaterman et al. 2013). Playbacks used in our experiments also had lower amplitudes than many previous studies testing the effect of soundscape playback on reef fish settlement, which may have further contributed to the weaker response of many taxa to our playbacks (Tolimieri et al. 2004, Simpson et al. 2008a,b, Gordon et al. 2018), although these differences in estimated

Table 4. Slope estimates for multinomial logistic regressions performed on catches from Expt 2 (2017). SPL: sound pressure level (root mean square)

Taxon	Count	Predictor	Trap	Effect size	SE	p (Wald's test)	Residual deviance
Total reef fish	277	Trap 2 lowband SPL–Trap 1 lowband SPL	2	−0.054	0.035	0.127	33.952
		Trap 2 lowband SPL–Trap 1 lowband SPL	3	−0.027	0.038	0.467	
		Trap 3 lowband SPL–Trap 1 lowband SPL	2	−0.008	0.025	0.766	
		Trap 3 lowband SPL–Trap 1 lowband SPL	3	0.059	0.025	0.019	
Scaridae	41	Trap 2 lowband SPL–Trap 1 lowband SPL	2	0.030	0.078	0.701	13.708
		Trap 2 lowband SPL–Trap 1 lowband SPL	3	0.297	0.310	0.338	
		Trap 3 lowband SPL–Trap 1 lowband SPL	2	0.007	0.072	0.918	
		Trap 3 lowband SPL–Trap 1 lowband SPL	3	0.198	0.128	0.121	
Pomacentridae	112	Trap 2 lowband SPL–Trap 1 lowband SPL	2	−0.023	0.051	0.651	44.288
		Trap 2 lowband SPL–Trap 1 lowband SPL	3	−0.068	0.052	0.193	
		Trap 3 lowband SPL–Trap 1 lowband SPL	2	−0.106	0.043	0.013	
		Trap 3 lowband SPL–Trap 1 lowband SPL	3	−0.050	0.045	0.265	
Lutjanidae	42	Trap 2 lowband SPL–Trap 1 lowband SPL	2	−0.388	0.138	0.005	4.376
		Trap 2 lowband SPL–Trap 1 lowband SPL	3	−0.324	0.140	0.021	
		Trap 3 lowband SPL–Trap 1 lowband SPL	2	−0.028	0.102	0.780	
		Trap 3 lowband SPL–Trap 1 lowband SPL	3	−0.053	0.104	0.611	
Pelagic fish	297	Trap 2 lowband SPL–Trap 1 lowband SPL	2	−0.157	0.042	<0.001	131.034
		Trap 2 lowband SPL–Trap 1 lowband SPL	3	0.035	0.039	0.227	
		Trap 3 lowband SPL–Trap 1 lowband SPL	2	0.050	0.041	0.378	
		Trap 3 lowband SPL–Trap 1 lowband SPL	3	0.015	0.033	0.642	

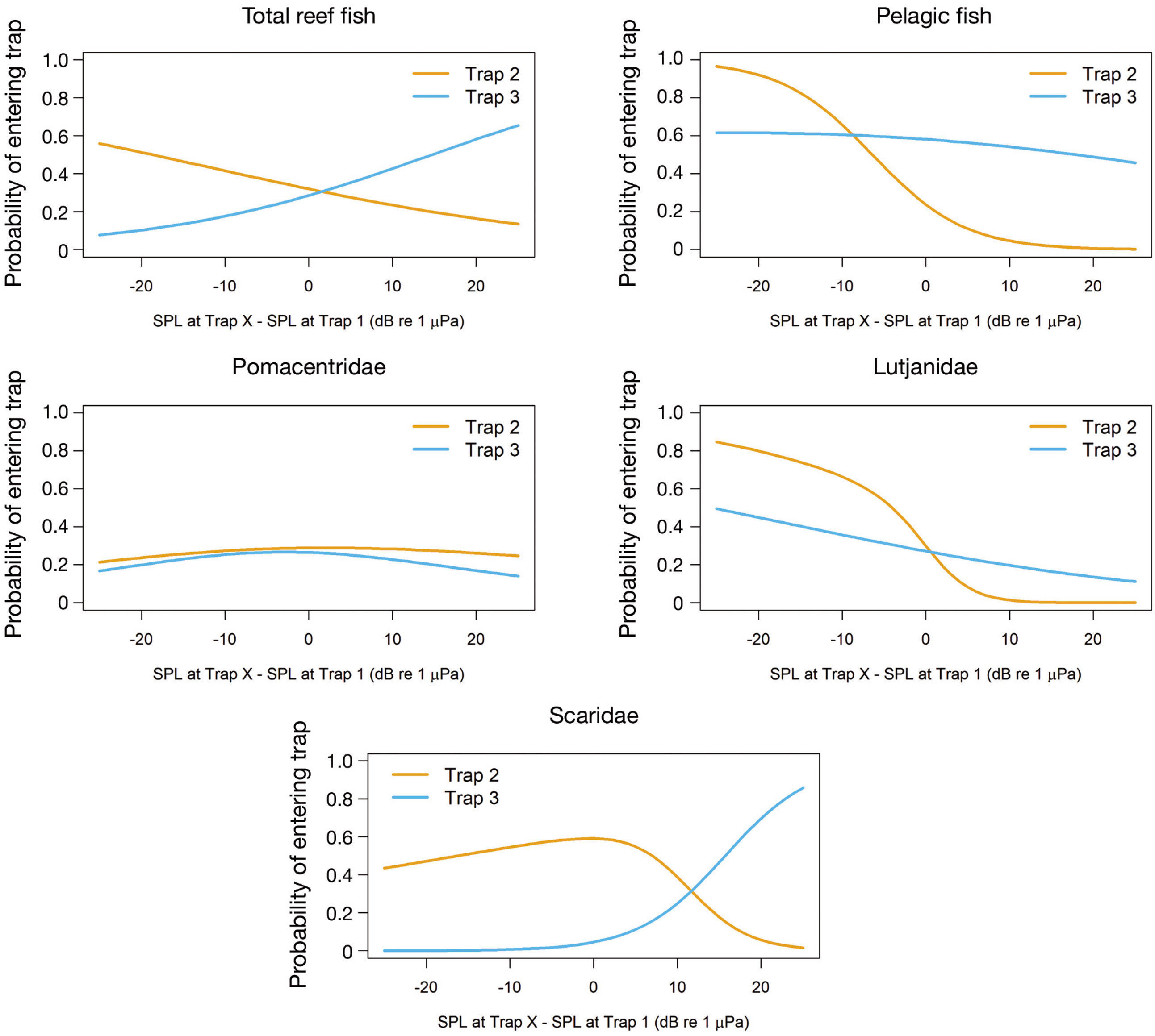

Fig. 7. Predicted probability curves indicating the change in probability of fish taxa entering a trap based on the difference in median low-band sound pressure level (SPL) between that trap and Trap 1. Gold lines: probability of entering Trap 2 based on a range of differences in median low-band SPL from Trap 1. Blue lines: probability of entering Trap 3 based on a range of differences in median low-band SPL from Trap 1

amplitudes could be due to propagation and measurement differences among studies or due to performing our experiment near an exposed coastline. The sound levels presented to fish larvae in this study were within the range of low frequency reef sounds measured in other locations (Staaterman et al. 2013, 2014, Piercy et al. 2014, Radford et al. 2014, Bertucci et al. 2016, Gordon et al. 2018) and were representative of the reef sound levels locally settling reef fish larvae likely experience (Kaplan et al. 2015). Indeed, while there was some inter-nightly variability among playback levels, our playbacks of reef soundscapes were within the amplitude ranges recorded on nearby reefs in the same time period. However, it is worth noting that there were often differences in the PSD of the playbacks and the original recordings below 500 Hz, and these differences, while common in other playback experiments (e.g. Lillis et al. 2013, Gordon et al. 2019), may have contributed to lower observed responses of reef fish larvae to the playbacks (Figs. 3 & 4).

Taxa of reef fish larvae collected in our experiments did not show a strong overlap with the most abundant taxa collected in previous studies in the Pacific (e.g. Lutjanidae, Larbisomidae, Scaridae, Synodontidae) and this lack of overlap provides opportunity to gain insight on the responses of these fishes to reef soundscapes (Figs. 5 & 6; Tolimieri et al. 2000, Simpson et al. 2004, 2008b, Leis & Lockett 2005, Radford et al. 2011a, Gordon et al. 2018). Parrotfish (Scaridae) are often considered to be a critical family of fishes for their role as herbivores on reefs, yet few studies have analyzed their response to settlement cues (Mumby et al. 2007, Bozec et al. 2016, Bruno et al. 2019). Radford et al. (2011a) observed movement of parrotfish juveniles toward playback of reef soundscapes, though they did not have a sufficient sample size to observe a significant response. Thus, our work supports this previous indication that parrotfish are attracted to reef soundscapes. Further, lizardfish are not commonly discussed in settlement and habitat selection cue studies despite our observation of their significant response to playback of reef soundscapes. Lizardfishes are important mesopredators on reefs, indicating ecosystem-level importance to understanding factors affecting their settlement (Sweatman 1984). Previous work indicates that lizardfish settlement is affected by temperature and wind-induced turbulence (Lemberget et al. 2009). Our study suggests that reef soundscapes and prevailing alongshore current can be added to these factors driving patterns in lizardfish settlement (Figs. 5b,c & 6a).

Damselfish (Pomacentridae) were the most notable family to overlap with previous experiments, with the remarkable result that damselfish were not caught at significantly higher abundances at light traps adjacent to louder reef soundscape playbacks in our experiments (Fig. 6). This contrasts with previous studies where damselfish showed some of the strongest positive responses to elevated soundscape playbacks (Simpson et al. 2004, 2008a, Leis & Lockett 2005, Gordon et al. 2018, 2019). However, most of the damselfish collected in our experiment belonged to the genus *Stegastes*, while previous studies have predominantly caught members of the genera *Chromis* and *Pomacentrus* (Leis & Lockett 2005, Simpson et al. 2008a, Gordon et al. 2018, 2019). There may be sensory differences between these genera, as species-level differences in hearing thresholds have been observed (Egner & Mann 2005, Wright et al. 2005). It is also possible that there are basin-level (Indo-Pacific vs. Atlantic) differences in the response of this family of fishes to reef soundscapes or that pomacentrids require higher amplitude sound stimuli than those used in our study.

When interpreting conclusions from our work, it is important to note that our experiments collected substantially fewer individuals than many of these previous studies. This is a product of performing our experiment in the Caribbean where light trap catches of settling reef fishes are relatively low compared to Pacific reefs (Sponaugle & Cowen 1996, Sponaugle et al. 2005, D'Alessandro et al. 2007). Owing to the low numbers, we also did not test species-level responses to playback of reef soundscapes. As a result, species-level attraction and avoidance of reef soundscapes would be obscured by performing statistical tests at the family level (Parmentier et al. 2015), though studies such as Gordon et al. (2018) observed rather consistent species-level responses to reef soundscape playback within Pomacentridae. Additionally, the lower number of individual fishes and nights limits the statistical power in our experiments, leading to a high chance of false negatives. Some groups (e.g. Labrisomidae in Expt 1 and Lutjanidae in Expt 2) may have had significant responses to soundscape playback if we were able to collect greater numbers. It is also important to note that many factors changed between Expt 1 and Expt 2, and thus while each experiment provides insight to different aspects of the response of larval fish to reef playback, we are unable to directly compare the 2 experiments.

However, notably, catches of reef fish larvae were site-dependent in each experiment, with observations of significant drop-off in downstream catches in Expt 1 (Fig. 5b), and our most offshore mooring collecting the highest abundance of total reef fish larvae, damselfish, and snappers in Expt 2 (Fig. 5c). In Expt 1, the greatest factor was likely local, alongshore currents that advected larvae along the coast, which was how our light traps were arranged in this experiment (though it is worth noting the large light trap to speaker distance may have dampened an observed response to sound). Similar current effects have been noted along this coastline for coral larvae (Green & Edmunds 2011). The observation of downstream drop-off of larvae in 2016 led to modification of the study for 2017, where traps were moved offshore to minimize the effect of the current. ADCP measurements confirmed that the mean nightly currents did not align with our light traps in 2017 (Fig. 5d). However, the difference in average current direction between experiments was also likely a result of performing Expt 2 (2017) closer to the wet season when mean flow near St. John shifts from predominantly westward throughout the water column to a mix of northwestward and northeastward flow (Chérubin et al. 2011, Chérubin & Garavelli 2016).

Our first experiment indicates that the importance of navigation and habitat selection cues such as sound must be put into the context of hydrographic drivers of reef fish settlement. There has been increased interest in including cues in dispersal modeling efforts. These models often couple individual-based models with oceanographic models to determine the effects of hydrographic processes and larval fish behaviors on larval fish distribution and settlement (Staaterman et al. 2012, Staaterman & Paris 2014). However, while debatable (see Clark et al. 2020), Leis (2018) raised concern that climate change — namely ocean acidification — would cause dispersal patterns to be reduced to the 'passive dispersal paradigm.' Our study indicates that playback of reef soundscapes at SPLs representative of local reefs in St. John may not induce a strong enough response by most fish taxa to overwhelm the effects of local hydrography (though differences in ambient and payback spectra may contribute to this). Settlement processes in our study region may thus be closer to the passive paradigm than expected — even prior to substantial levels of acidification.

Our second experiment identified location-specific responses to sound, specifically that total reef fish and parrotfish larvae only showed a positive response to louder playbacks at the most nearshore location and seemed to avoid louder playbacks at the middle, more offshore location (Fig. 7). This result indicates that reef fishes may only be attracted to sound either as a navigation or habitat selection cue when they are nearshore, limiting the offshore distance over which this cue may be used by reef fish larvae. Olfactory, magnetic, and celestial cues are broadly considered to be important at long distances (>1 km) from reefs while sound may be used at closer distances (Atema et al. 2002, Paris et al. 2013, Staaterman & Paris 2014, Kaplan & Mooney 2016). Our study supports the concept that larvae likely do not use sound as a long-distance navigation cue and, further, that reef fish larvae may not be very responsive to this cue until they are approaching settlement habitat. Other studies, namely that of Leis et al. (2003), also showed a pattern of higher catches of reef fish larvae at light traps adjacent to playbacks in the nearshore and middle depth areas yet lower catches at louder traps at the offshore sites. Their findings — in conjunction with our observations of a variable response of reef fish larvae to reef soundscape playback based on cross-shelf location — emphasizes the complexity in the response of reef fish larvae to reef soundscapes and that nuance in fish response to soundscapes should be considered in both modeling efforts and discussion of observed patterns in reef fish settlement.

Our results indicate that larvae of pelagic fishes avoided reef soundscape playbacks, suggesting that sound can be used as a navigational cue for habitat selection by these taxa (Figs. 6b & 7). The response of larvae of pelagic fishes to reef-borne cues is poorly studied (but see Tolimieri et al. 2000). Reefs represent an area of high predation, and thus larvae of pelagic fish taxa may avoid these areas to obviate entering the 'predation gauntlet' reefs tend to exert on small fishes (Almany & Webster 2006, Stier et al. 2017). Presence of predators, or merely indications of their presence, have been shown to alter behavior of both reef fishes and young pelagic fishes (Romare & Hansson 2003, Catano et al. 2016). Thus, it is possible that our observations of lower catches of larvae of pelagic fish species at traps adjacent to louder reef soundscape playbacks may be due to predation avoidance. Avoidance of reef soundscapes has been suggested for other non-reef taxa such as holoplankton, a group likely to become prey on reefs (Simpson et al. 2011). Reefs often harbor numerous zooplanktivorous fishes which may deplete local zooplankton abundances, making these locations non-ideal foraging location for planktivorous pelagic fish larvae (Hamner et al. 1988, Kingsford & MacDiarmid 1988). Reefs may therefore represent areas of high predation and poor feeding opportunity for larvae of pelagic fishes, particularly zooplanktivorous species such as 2 of the dominant taxa (Atherinidae, Clupeidae) collected in our experiments.

While this study presents developments in understanding the use of sound as a settlement cue for fish larvae, especially in combination with hydrography, it is uncertain how important sound is compared to other factors, including other settlement cues. Reef fish larvae can travel great distances during their pelagic stage so the 'limited' range of the acoustic cues (~250 m) used in our experiment stresses the need for caution in discussion of the role of sound in the long-distance attraction and settlement of fish larvae. Our ca. 250 m distance estimate may even be too large, as reef fish larvae detect particle motion of acoustic fields (as opposed to sound pressure, though some larvae may also sense pressure), which can be attenuated at even shorter distances from reefs (Mann et al. 2007, Kaplan & Mooney 2016). Further, propagation distances in shallower locations such as reef flats may be even smaller (e.g. few meters; Gordon et al. 2019). Thus, with sound only extending a maximum of a few hundred meters from a reef, reef fish must either be transported near the reef passively (currents) or have recognized a different navigational cue that resulted in directional swimming toward the reef. Reef fish larvae likely use other navigational cues such as olfactory cues that extend from reefs and may travel much further distances (Atema 2012, Paris et al. 2013).

Additionally, playbacks of soundscapes do not perfectly match original recordings, and thus the applicability of results from playback studies remains uncertain. While the median SPL_{rms} and PSD of our reef soundscape playbacks were similar to the original recordings, there were notable differences at higher frequencies. Fish larvae are assumed to not be capable of hearing high frequencies but it remains possible that differences between the playback and natural soundscapes affect the patterns of fish settlement that we observed. While playback experiments are some of our best insights into reef fish response to sound, differences in original vs. playback soundscapes caution extending the results from playback experiments into decisive inferences about natural processes. Further, the inconsistencies between original recordings and playbacks observed in this study and others indicate that additional research on playback methodology is needed, though in our case these inconsistencies may have been in part a result of the directional speaker orientation changing with respect to the acoustic recorder due to currents and wave action (Tolimieri et al. 2004, Lillis et al. 2013). The light trap method used in this study also limits the scale at which we can confidently assess the use of sound by reef fish larvae. Light from light traps may extend close to 50 m in very clear water, making it impossible to determine if reef fish larvae are using sound for navigation or habitat selection at scales less than 50 m (Simpson et al. 2004). Visibility was low in our study area (~15–20 m) compared to some other reef systems and thus it is likely that the range the light travelled was smaller in our study, yet we were still unable to assess usage of sound as a settlement cue and for habitat selection at short distances. Additionally, the light trap method is not a perfect or accurate representation of the settlement process for fishes, despite its ubiquitous use (e.g. Tolimieri et al. 2000, Simpson et al. 2004, Gordon et al. 2018). Using light traps may be measuring mid-water orientation more than true settlement, limiting the extent to which results from such studies can be extended to understanding natural settlement.

Our study improves our understanding of the use of sound as a settlement cue by fish larvae through assessing the attraction of various taxa of fish larvae to the playback of locally representative recordings of reef soundscapes and further places these responses in the context of local hydrography and cross-shelf location. The results reported here indicate a number of reef fish taxa may not be attracted to the playback of reef soundscapes and that larvae of non-reef fish may be actively avoiding these soundscapes. Further, our first experiment indicated that the capacity for fish larvae to select louder reef soundscapes may be overwhelmed by local currents. Many taxa of fish may also only respond to reef soundscapes when in nearshore waters where they are in proximity to reefs and preparing for settlement. Despite the indication of significant effects of reef sound playback on the settlement of reef fish larvae from this study and others, it is important to note the limited spatial extent that acoustic cues may be used for navigation by reef fish larvae. Reef fish larvae likely use a variety of navigational cues, with the relative importance of sound compared to other cues in the settlement process remaining an area for further investigation.

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