



SPECIAL FEATURE:
HONORING CHARLES H. PETERSON, ECOLOGIST

Passive acoustic monitoring complements traditional methods for assessing marine habitat enhancement outcomes

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Abstract. Habitat enhancement, often accomplished through the introduction of artificial structures, is a common strategy used by marine resource managers to provide habitat subsidies, protect sensitive habitat, and create new fishing opportunities. Traditional monitoring methods for assessing habitat enhancement outcomes face numerous limitations, including dependence on environmental conditions and trade-offs between sampling frequency and duration. Passive acoustic monitoring (PAM) is not subject to these same limitations and offers many advantages as a complement to traditional monitoring methods. Our team opportunistically monitored the soundscape and community development of a newly deployed artificial reef and compared it to that of a nearby established artificial reef using PAM and underwater time-lapse videos. Specifically, we compared the sound pressure level (SPL) timeseries, dusk peak in SPL, and dusk power spectrum between the two artificial reefs to evaluate whether and on what timescale the soundscapes converged. Additionally, we tracked temporal patterns in species-specific vocalizations to identify the trajectory of community development on the new reef. Lastly, we compared the qualitative conclusions drawn from PAM to previously published results from video monitoring of the same two artificial reefs. PAM identified minimal difference in mean low-frequency SPL between the two reefs at the onset of monitoring. Though the timeseries correlation, dusk SPL, and dusk power spectra all varied across sampling periods, there were periods of low-frequency soundscape alignment at four and eleven months following artificial reef deployment, associated with the presence of fish chorusing. The high-frequency timeseries on each reef were well correlated during all sampling periods, despite an initial SPL difference of 17 dB. Throughout monitoring, high-frequency sound levels became more similar between the reefs but did not converge. While video monitoring suggested that demersal species did not colonize the reef until five months post-deployment, patterns in species-specific vocalizations suggested that toadfish (*Opsanus* sp.) a cryptic, demersal species may have colonized the new reef within two weeks. Our findings demonstrate that passive acoustic monitoring is a useful complement to traditional methodologies and can provide a more holistic view of community development than visual monitoring alone.

Key words: community development; cryptic species; habitat enhancement; passive acoustic monitoring; Special Feature: Honoring Charles H. Peterson, Ecologist.

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INTRODUCTION

Marine ecosystems are increasingly threatened by habitat degradation and overharvesting of fish populations (Halpern et al. 2019). In many regions, resource managers have attempted to combat the negative consequences of these threats through habitat enhancement, or the introduction of artificial, human-made structures (Baine 2001). These structures can help achieve an array of goals, including increasing habitat availability (Bortone 2011), enhancing fishery yield (Leitão et al. 2009), replacing the function of previously lost or degraded natural habitat (Pickering et al. 1998), supplementing existing habitat, and protecting sensitive habitats from destructive anthropogenic activity, such as benthic trawling (Relini and Orsi Relini 1989). Furthermore, habitat enhancement can help support coastal cultures and economies by creating new fishing and ecotourism opportunities, as well as reducing fishing pressure on natural habitats (Al-Horani and Khalaf 2013). While habitat enhancement offers many potential benefits to coastal ecosystems, ensuring a positive effect requires careful planning and assessment of habitat enhancement outcomes (Becker et al. 2018).

To assess whether the goals of habitat enhancement are achieved, enhancement projects require explicit statement of objectives paired with a consistent monitoring strategy following introduction of artificial structures (Pratt 1994). Depending on the intended goal of the habitat enhancement, monitoring projects have focused on observing ecological or population dynamics (Rilov and Benayahu 2002), evaluating design effectiveness (Sherman et al. 2002), or assessing socioeconomic outcomes (Whitmarsh et al. 2008). A literature review on the trends in artificial reef research in the last 60 yr, published by Lima et al. (2019) found that among habitat enhancement monitoring projects, ecology, and specifically community structure, was the most common research focus. Previous studies on artificial reef community development have found

that colonization of introduced structures occurs rapidly (Cummings 1994), but often includes fluctuations in abundance and community structure over varied timescales (Scarcella et al. 2015). Understanding the patterns of community development, as well as the successional processes that underlie them, can illuminate whether habitat enhancement efforts achieve the intended outcome and on what timescale.

A variety of monitoring methods are available to evaluate the effectiveness of habitat enhancement in achieving prescribed goals. Diver-based visual censuses and videography methods are most frequently used to assess community development following introduction of offshore artificial reefs (Lima et al. 2019). In coastal and intertidal ecosystems, by comparison, habitat enhancement monitoring is often accomplished using nets and traps. These traditional sampling methods face multiple challenges, including that they can be a time-consuming and expensive process that is dependent on appropriate environmental conditions and are further complicated by difficult to access locations. As a result, these methods involve a trade-off between the temporal resolution of sampling and duration of the monitoring effort (Bortone 2006). The resulting decisions made about monitoring study design can affect the ability to interpret the ecological implications of the results.

An alternative to traditional monitoring is passive acoustic monitoring (PAM), which records the soundscape, including biological, geological, and anthropogenic sounds. Because the detection of sound is independent of light availability and currents, PAM offers many advantages for sampling difficult to access habitats, especially where traditional monitoring is complicated by adverse weather conditions, changing tides, turbidity, complex benthic structures, and nocturnal animal activity. Furthermore, PAM is a non-invasive method with reduced observer bias or artifacts compared with visual census (Van Parijs et al. 2009). Recently, there has been rapidly rising interest in developing PAM methodologies that can be used in management or conservation

contexts, such as biodiversity assessment (Mooney et al. 2020), evaluation of habitat restoration (Butler et al. 2016), and tracking population distribution shifts associated with climate change (Davis et al. 2020).

The use of artificial habitats for the management, restoration, and enhancement of marine ecosystems has expanded to a global practice with active artificial reef programs across temperate and tropical regions (Seaman 2007). In the presented case study, we evaluated the trajectory of soundscape development on a newly deployed artificial reef offshore of North Carolina (NC), USA. Specifically, we tested whether and on what timescale the soundscape of a new artificial reef converged with that of a nearby established artificial reef and evaluated the trajectory of soundscape development through temporal patterns in species-specific sound production. This passive acoustic monitoring was conducted simultaneously with underwater time-lapse videography, the results of which were previously published in Paxton et al. (2018). In addition to the soundscape analyses, we compared the qualitative conclusions drawn from each monitoring methodology.

METHODS

To enhance understanding of the trajectory of community development following artificial reef deployment, our team opportunistically monitored the fish community and soundscape using time-lapse underwater videography and passive acoustic methods at a newly deployed artificial reef and a nearby established artificial reef in Onslow Bay, NC, USA. The seafloor of Onslow Bay is heterogeneous, consisting of intermixed regions of rocky-reef ledges, exposed hardbottom pavements, sand flats, and numerous artificial reefs (Gregg and Murphey 1994, Riggs et al. 1996). This complexity, in combination with its position near a biogeographic boundary between temperate and tropical systems, makes it a useful system to explore community development dynamics. The two reefs sampled consisted of an existing 89-m long landing craft repair ship named USS *Indra*, scuttled in 1992 (34.5623°N, 76.8515°W; henceforth called “established reef”), and a newly deployed 33-m long US Army tugboat, renamed *James J. Francesconi*, (34.5634°N,

76.8552°W; henceforth called “new reef”), that was scuttled by the NC Division of Marine Fisheries’ (DMF) Artificial Reef program on 7 May 2016. The two reefs lie 438 m apart, at a depth of 20 m, within the state-designated artificial reef site AR-330 (Comer and Love-Adrick 2016; Fig. 1). Given their proximity, we assumed that the environmental conditions at each site were the same.

Within AR-330, there are numerous additional artificial reef structures that were not sampled (Fig. 1). Approximately 50 m west of the new reef, a second vessel (20-m tugboat) was sunk on the same day in 2016. All other artificial reefs were deployed between 1990 and 2012 and would be considered established communities. Most of these structures are of low-vertical relief, created out of miscellaneous materials including concrete pipes, reef balls, or fiberglass domes. There are also six high vertical relief reefs made of other vessel types including sailboats, barges, and an aircraft (Comer and Love-Adrick 2016). The reef types are distinguished by vertical relief because they often support different fish communities (Paxton et al. 2017). Adjacent to the sampled established reef lies two sailboats, ~33 and 50 m away, as well as multiple regions of concrete pipes ~200–300 m away. Nearest to the sampled new reef is a small group of fiberglass domes ~50 m away, and multiple regions of concrete pipes that range from ~100–400 m away.

We monitored both reefs during six sampling periods between two weeks and 11 months following deployment of the new reef. The sampling dates were as follows: 18–24 May 2016; 22–27 July 2016; 14–17 September 2016; 27–31 October 2016; 3–7 December 2016; and 21–26 April 2017. The soundscape was recorded concurrently and continuously on the new and established artificial reefs. Recordings were made using a calibrated omni-directional hydrophone at a 96 kHz sampling rate (SoundTrap 202 STD; Ocean Instruments, Auckland, New Zealand). The hydrophones were mounted to a 0.5-m tall weighted, metal frame and placed on top of the artificial reef structure at the stern of the ship. The positions were fixed across all sampling periods. All acoustic analyses were conducted in MATLAB (MATLAB 2018) using purpose-written code.

The continuous recordings were subsampled to two-minute samples every 15 min to match

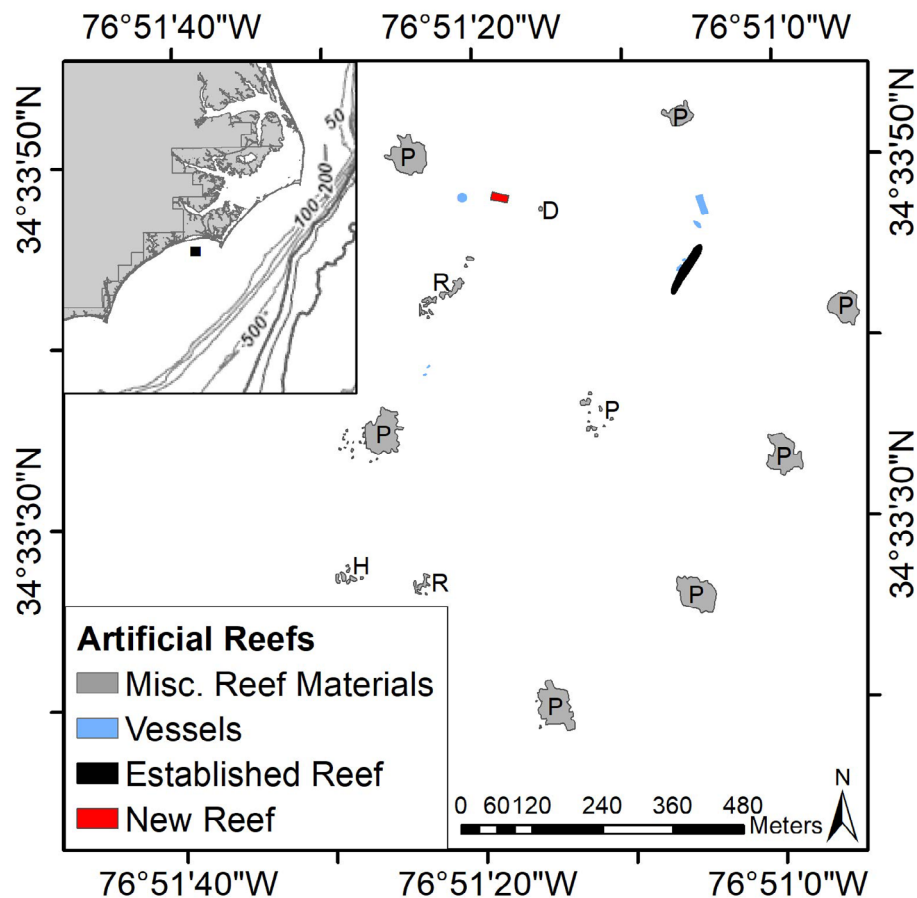


Fig. 1. Position of AR-330 within Onslow Bay, NC, USA (inset map), and of the sampled reefs in relation to each other and surrounding artificial reefs. The reefs sampled in this study are labeled as “Established reef” and “New reef” as referred to in the text. The “Miscellaneous Reef Materials” consist of artificial structures with low-vertical relief (P: concrete pipes, R: reef balls, H: “H” units, D: fiberglass domes) that were deployed between 1990 and 2005. The “Vessels” consist of high relief structures (e.g., sailboats and aircraft) deployed between 1994 and 2012, except for the vessel point adjacent to the new reef, which is a tugboat deployed on the same day as the new reef (7 May 2016). (Inset basemap: General Bathymetric Chart of the Oceans; NOAA NCEI).

the duty cycle commonly used in marine passive acoustic research. This subsampling reduced computational challenges associated with acoustic analysis while retaining the natural variability of the underwater soundscape (Bohnenstiehl et al. 2018). The data were response corrected to micropascals (μPa) using a hydrophone-specific calibration value. Initial analyses in the time and frequency domain revealed a substantial amount of anthropogenic noise intrusion and several anomalously high amplitude impulsive signals, likely produced when a swimming animal collided with the hydrophone or instrument frame

(i.e., “fish bumps,” Buskirk et al. 1981, Bowman & Wilcock 2014). Even a single fish bump within a two-minute audio file distorted the average power spectrum and sound pressure level (SPL), complicating the interpretation of biological acoustic activity. To reduce the impact of these anomalies, each two-minute file was subdivided into consecutive nonoverlapping 5-s windows, and the data were further subsampled by selecting the four quietest windows within the file (sensu Van Hoeck et al. 2020). All subsequent analyses were conducted using the average power spectrum and root-mean-square (RMS)

amplitude calculated from these subsamples. Comparisons of power spectral density (PSD) and the SPL timeseries between the full two-minute files and subsamples confirmed that the anomalies were removed, but the natural biological variability was preserved (see Fig. S1 in Van Hoesck et al. 2020).

The frequency content of each file was described by its average acoustic spectra calculated by Fourier transform (NFFT = 2^{15} points, 0% overlap, Hanning window). To analyze the sounds associated with fish and invertebrates separately, the data were divided into low- and high-frequency bands of 0.15–2 kHz, dominated by fish sounds, and 7–15 kHz, dominated by snapping shrimp (*Alpheus* sp.), respectively. The selected frequency bands intentionally exclude intermediate frequencies that contain overlaps between fish and invertebrate sounds (e.g., Ricci et al. 2016). The RMS sound pressure level (SPL) within each frequency band was calculated by summing the power within the limits of the frequency band.

To evaluate how the soundscape developed on the newly deployed reef in relation to the established reef, we investigated the SPL timeseries of the low- and high-frequency bands and calculated the correlation coefficient between the two sites within each sampling period. The timeseries were visualized using a three-point moving average to smooth out stochastic variability in SPL and improve interpretation of diel patterns. In addition to the correlation coefficient, we qualitatively compared the distribution of observed SPLs for each site within sampling period to evaluate whether the soundscapes had converged. Due to observed diel patterns in SPL with increased biological acoustic activity at dusk, we isolated the files between sunset and astronomical twilight (~1.25–1.75 h of duration) for further inspection. This method also excluded a series of harmonic sounds observed at midnight on both sites whose source could not be determined as biological or anthropogenic.

We conducted a two-way repeated-measures ANOVA to investigate whether there was an interactive effect between site and sampling period on the observed dusk SPLs in both frequency bands. We summarized each site by calculating the average SPL at dusk for each day within a sampling period; as such, each day was

considered a replicate. We confirmed the assumptions of the ANOVA were met by checking for outliers and inspecting QQ plots for normality. While there was one outlier in the low-frequency band and two in the high-frequency band, removing the outliers did not change the results of the ANOVA, so we proceeded with all data points. Because the interaction between site and sampling period was significant, we evaluated the effect of site during each sampling period using a one-way ANOVA. Lastly, to understand which comparisons were driving observed differences between the sites, we conducted pairwise *t*-tests between the sites at each sampling period. All statistical analyses were conducted in R version 4.0.2 using the “rstatix” package (R Core Team 2020, Alboukadel 2021).

Next, we evaluated the trajectory of community development in the soundscape by comparing the average low-frequency dusk power spectrum on each reef within sampling period using the 0.05–0.95 quantiles as a measure of variance. As animal vocalizations have distinct time and frequency characteristics, seasonal changes in power spectral density facilitated identification of species-specific colonization patterns for soniferous species. To evaluate whether the identities of fishes producing sounds were the same between the new and established reef, we visually screened the spectrogram of each two-minute file and aurally confirmed species identity when applicable. During multiple sampling periods, frequent vocalizations by a toadfish species (*Opsanus* sp.; first two harmonics 0.15–0.4 kHz) (e.g., Fine 1978; Ricci et al. 2017) and an unidentified species (0.4–0.8 kHz) were recorded. Due to the strength of these vocalizations in the acoustic spectra, we focused on the temporal patterns of these vocalizations to understand the dynamics of low-frequency soundscape development.

We acknowledge that identifying the source of recorded sounds and interpreting the ecological significance of our results are complicated by aspects of our study design as well as the presence of other structured habitats adjacent to both the new and established reefs (Fig. 1.) Because this was an opportunistic study, the new reef site was not monitored before the tugboat was scuttled. Additionally, single element hydrophones, such as the SoundTraps used in this study, are

not able to determine source locations. Consequently, the relative amplitudes of the signals recorded at both reefs must be used to make inferences about the source location. Assuming a simple cylindrical spreading model, the minimum transmission loss from the surrounding habitats to the new reef would be ~17 dB. If calls recorded on the established reef were sourced on-reef, but those recorded on the new reef originated from the surrounding habitats, we would expect calls recorded at the new reef to have systematically lower amplitudes. However, if the received call amplitudes are similar between the two reefs, it would imply that either sound production is local to both reefs or that both recordings are sampling the ambient soundscape sourced from more distant habitats. We evaluate these scenarios specifically for oyster toadfish boat whistles by haphazardly selecting calls at both reef sites and comparing the SPL within their lowest harmonic band.

Lastly, to evaluate whether results from passive acoustic monitoring and video monitoring were analogous, complementary, or conflicting, we compared the qualitative conclusions drawn from each method. The comparison consisted of community dynamics including the rate of colonization and whether convergence was observed, as well as colonization dynamics of specific taxonomic groups, including demersal fishes, piscivorous fishes, and invertebrates.

RESULTS

Diel patterns in the low-frequency soundscape (0.15–2 kHz) varied between the reefs and across sampling periods, often associated with changes in dominant vocalizers. During the first two sampling periods, mean SPLs on the two reefs were within 5.3 and 6.5 dB of one another, respectively. At two weeks post-deployment of the new reef, the correlation coefficient was 0.48, and at two months post-deployment, the correlation coefficient was 0.54. During the third sampling period, four months following artificial reef deployment, the SPL timeseries of the reefs were highly correlated ($cc = 0.93$), night SPLs on the new reef were occasionally higher than those of the established reef, and the distributions of observed SPLs on each site were closely aligned with a mean SPL difference of <1 dB (Fig. 2). The

third sampling period contained multiple sound sources that dominated the low-frequency soundscape on both reefs, including one feature below 0.5 kHz at dusk and a second at 0.5–1.5 kHz in the hours around midnight. The identity of these sounds could not be determined.

During all subsequent sampling periods, SPLs on the new reef tended to be lower than those of the established reef, but their timeseries remained similar. The correlation coefficient between the timeseries on each reef was 0.67 with a mean SPL difference of 9.9 dB at five months, and 0.64 with a mean SPL difference of 5.9 dB at seven months post-deployment of the new reef. During the final sampling period, eleven months following reef deployment, the timeseries were highly correlated ($cc = 0.84$) and low-frequency SPL again closely aligned between the sites with a mean SPL difference of 3.9 dB (Fig. 2).

Comparisons of dusk SPLs revealed that the low-frequency soundscape (0.15–2 kHz) varied by an interaction between site and sampling period (repeated-measures ANOVA, $F_{5,15} = 24.831$, $P < 0.001$). One-way ANOVAs of the effect of site within sampling period identified statistically significant differences in dusk SPL between the established reef and the new reef during May ($F_{1,6} = 521.0$, $P < 0.001$), July ($F_{1,5} = 336.0$, $P < 0.001$), September ($F_{1,3} = 11.2$, $P = 0.04$), October ($F_{1,4} = 137.0$, $P < 0.001$), and December ($F_{1,6} = 68.1$, $P = 0.001$). Pairwise comparisons between the sites within each sampling period revealed that SPLs were lower on the new reef during all deployments except September, when they were higher on the new reef, and April, when they did not differ between the reefs (Fig. 3A).

Diel patterns in the high-frequency soundscape (7–15 kHz), predominately snapping shrimp snaps, were consistent across both reefs and all sampling periods (Fig. 4). While SPLs on the new reef were always lower than those on the established reef, similar temporal patterns resulted in strong correlations between the timeseries in each sampling period, with correlation coefficients ranging between 0.81 and 0.94. The strength of this correlation varied across all sampling periods, with no apparent trend relating to time since artificial reef sinking. Inspection of the observed SPL distributions showed that they did

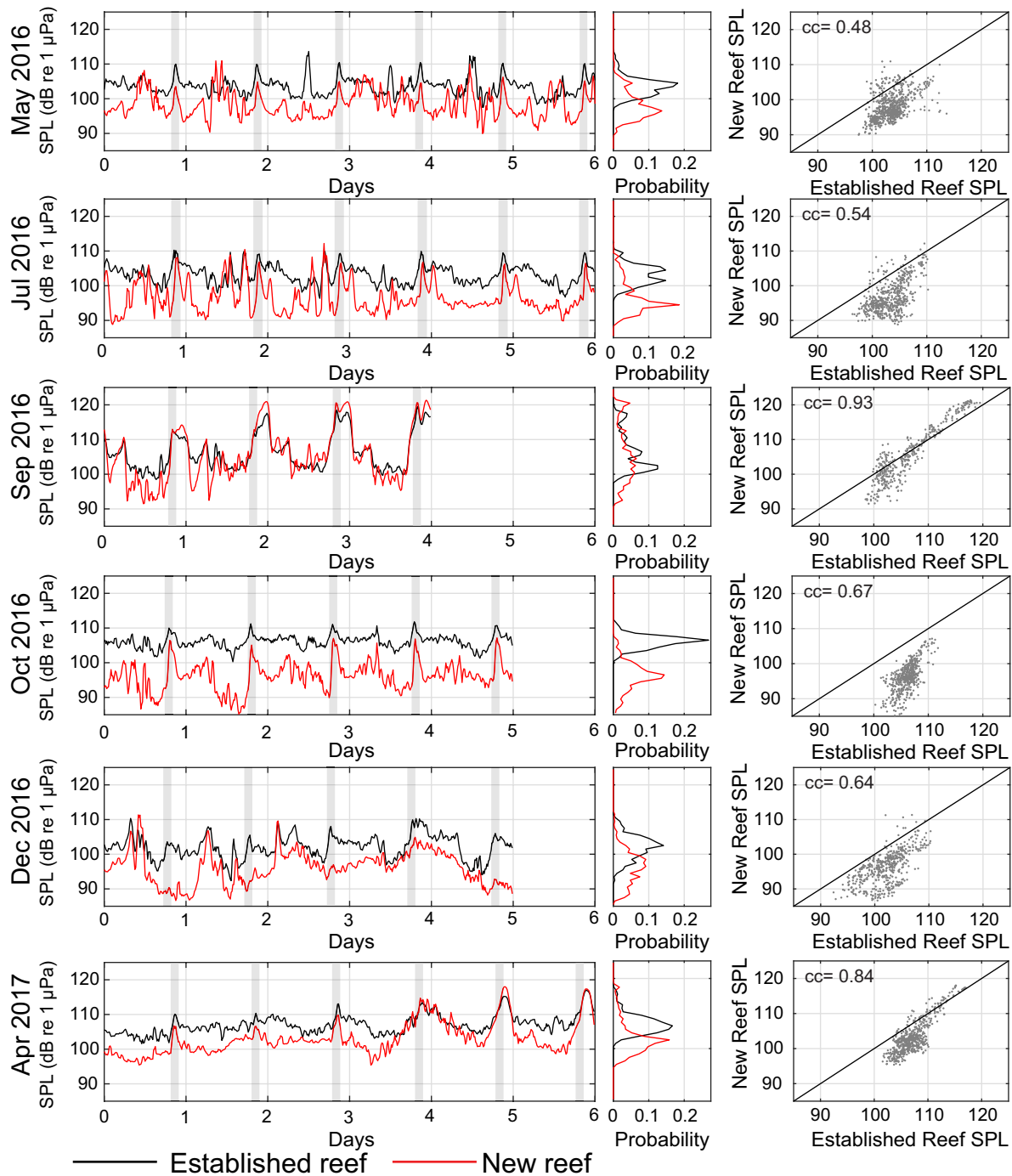


Fig. 2. Correlation between the low-frequency (0.15–2 kHz) SPL timeseries. SPL timeseries (left), SPL distribution (center), and timeseries correlation with 1:1 line and correlation coefficient (cc; right). Comparisons between the SPL timeseries show that the established reef (black) had a stable temporal pattern, with dusk (gray bands) peaks in acoustic activity, while the new reef (red) exhibited more diurnal variability.

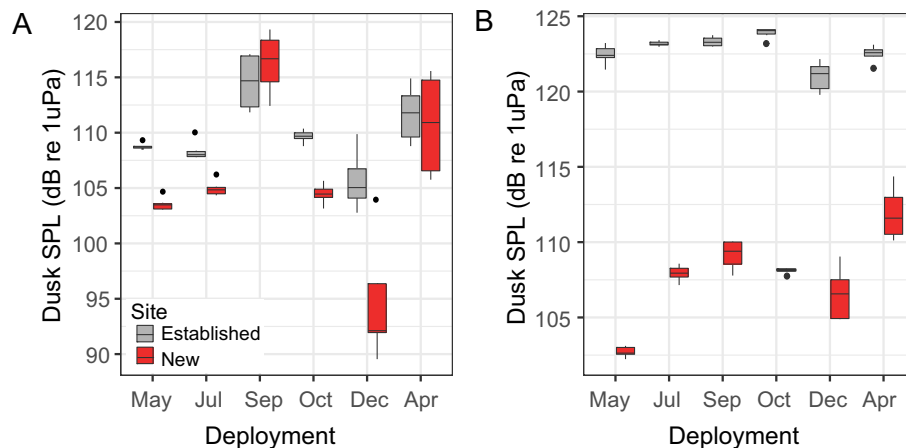


Fig. 3. Dusk SPL in the (A) low-frequency and (B) high-frequency bands. Note that the time scale of the *x*-axis is not linear. The black bar is the median while the lower and upper edges of the box are the first and third quartiles. The whiskers extend to either the most extreme value or 1.5 times the interquartile range, and any outliers are plotted individually.

not overlap during the first four sampling periods but did become more similar during the final two sampling periods, with the greatest overlap observed during the final sampling period. Moreover, the mean difference in SPL between the reefs decreased from 17.4 dB during the first sampling period, to 10.3 dB during the final sampling period.

Dusk SPLs in the high-frequency soundscape (7–20 kHz) varied by an interaction between site and sampling period (repeated-measures ANOVA, $F_{5,15} = 47.6$, $P < 0.001$). One-way ANOVAs on the effect of site within sampling period and pairwise comparisons between the sites revealed that SPLs were significantly lower on the new reef during all sampling periods (May: $F_{1,5} = 11891.0$, $P < 0.001$; July: $F_{1,5} = 4215.0$, $P < 0.001$; September: $F_{1,3} = 1254.0$, $P < 0.001$; October: $F_{1,4} = 10487.0$, $P < 0.001$; December: $F_{1,5} = 394.0$, $P < 0.001$; April: $F_{1,5} = 394.0$, $P < 0.001$). Inspection of the seasonal variation within each site revealed that average high-frequency SPLs on the established reef increased by 0.7 dB between the first two sampling periods but increased by 5.2 dB on the new reef (Fig. 3B).

Analysis of the average low-frequency sound power spectrum at dusk revealed that soundscape activity on both reefs varied seasonally. Comparisons between the reefs, and

specifically the 0.05–0.95 quantile range, suggest that dusk acoustic activity on the new reef exhibited greater variability. Across all sampling periods, acoustic activity in some frequency bands did overlap, such as 0.15–0.4 kHz in May, and 0.4–0.8 kHz in July and October; additionally, the power spectrum on both reefs closely aligned during September and April (Fig. 5). The PSD consistently increased from 1 to 2 kHz on the established reef due to snapping shrimp activity overlap in the low-frequency band.

Spectrogram inspection of audio files at dusk revealed that during the first and last sampling periods, in May 2016 and April 2017, the same vocalizations were observed. On the established reef, the May and April soundscape both consisted of choruses of an unidentified knock in the 0.4–0.8 kHz range (Figs. 5, 6). Similarly, on the established reef, the May soundscape included frequent toadfish vocalizations while the April soundscape contained toadfish choruses. Conversely, on the newly deployed reef, the May soundscape consisted of frequent toadfish vocalizations, but the unidentified knock chorus was absent. In April, eleven months following artificial reef deployment, toadfish and knock choruses were present on both reefs (Fig. 6). During the first sampling period, the average SPL of the first toadfish harmonic on

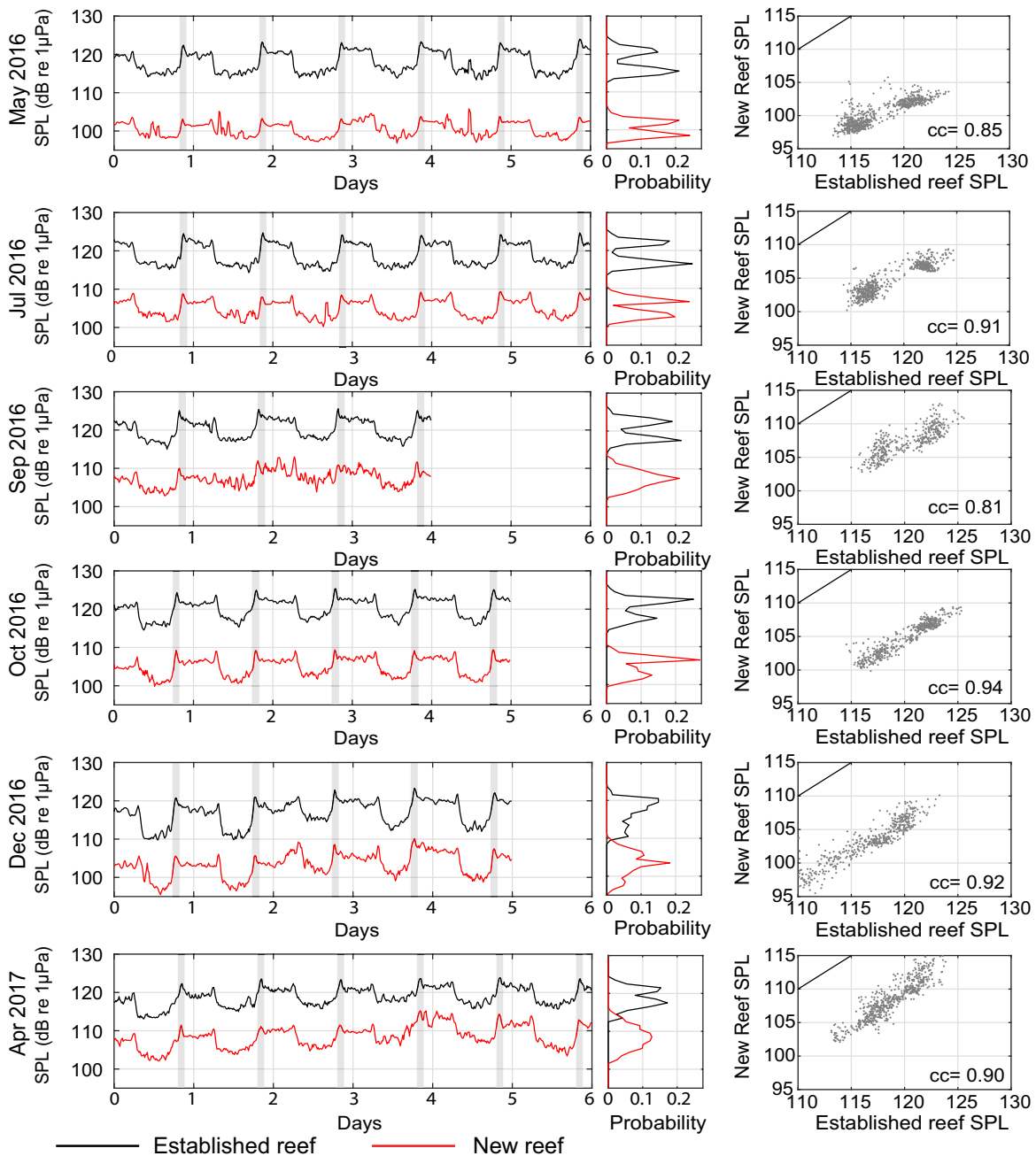


Fig. 4. Correlation between the high-frequency (7–15 kHz) SPL timeseries. SPL timeseries (left), SPL distribution (center), and timeseries correlation with 1:1 line and correlation coefficient (cc; right). Despite consistently lower SPLs on the new reef (red) than the established reef (black), their timeseries were highly correlated during all sampling periods.

the established reef was 99.8 dB, and the maximum observed was 110 dB. On the new reef, the average SPL was 97.4 dB, and the maximum was 104 dB.

Previously published results of the underwater video analyses revealed that fishes rapidly colonized the new reef structure and that the community composition on the two reefs converged

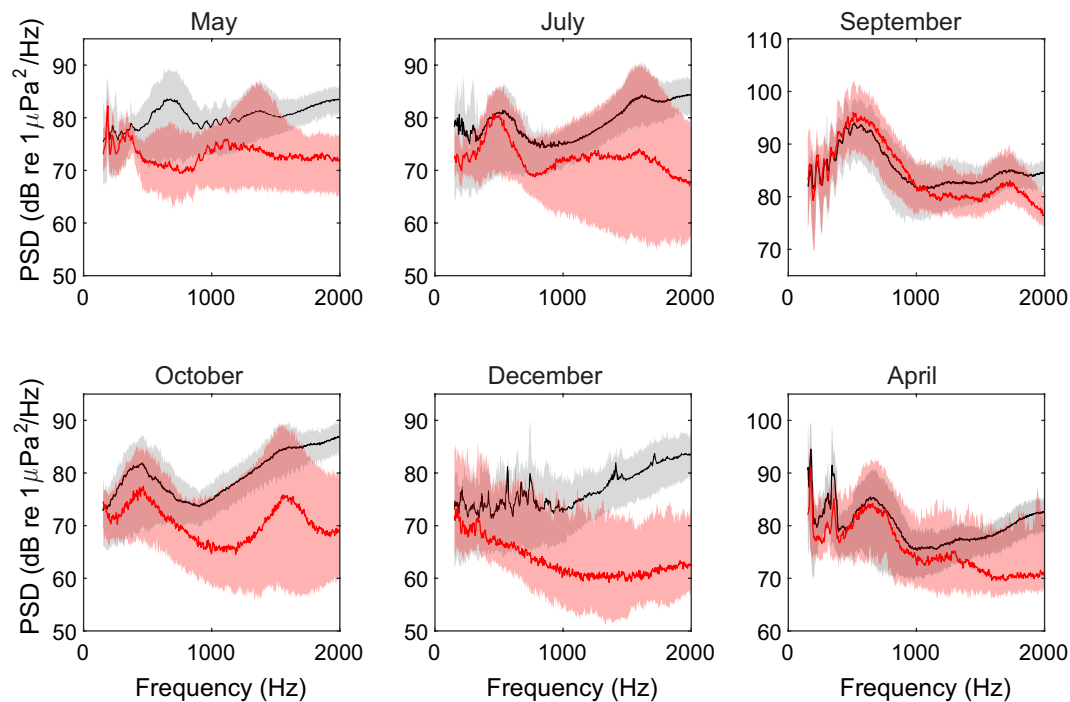


Fig. 5. Average low-frequency power spectrum at dusk. The shaded regions show the 0.05–0.95 inter-quantile range (IQR) for each reef. The 190 Hz peak on both reefs during May indicates the rapid colonization of toadfish, while the absence of the 500–1000 Hz peak on the new reef during May and its presence in April indicates the slower colonization by the unidentified knock species.

within five months (Paxton et al. 2018). While the results of video monitoring and PAM both suggest rapid fish colonization and soniferous fish community alignment, the video analysis suggested that the trajectory of community development consisted of conspicuous, water-column species appearing first (e.g., jacks [Carangidae] and scad [*Decapterus* sp.]) and demersal species (e.g., black sea bass [*Centropristis striata*]) exhibiting relatively slower colonization. In contrast, frequent toadfish vocalizations on the new reef during the first sampling period, observed at a similar sound level to those on the established reef, suggest that some cryptic, demersal species may have rapidly colonized the new reef (Table 1).

DISCUSSION

We investigated the trajectory of soundscape development on a newly deployed artificial reef

and a nearby established reef using passive acoustic monitoring and compared the results to that of traditional monitoring via underwater videos. Though video monitoring provided detailed analysis of colonization trajectory, PAM provided additional insights into community development not captured by visual monitoring. Specifically, the video data suggested that demersal species did not colonize the new reef until five months after its deployment whereas PAM revealed that at least one cryptic, demersal species (i.e., toadfish) may have been present at the new reef within two weeks. Moreover, the high-frequency soundscape revealed details of invertebrate colonization not available from video monitoring. Our findings demonstrate that passive acoustic monitoring is a promising complement to traditional visual surveys to assess the effectiveness of habitat enhancement, by elucidating a more holistic view of community development dynamics.

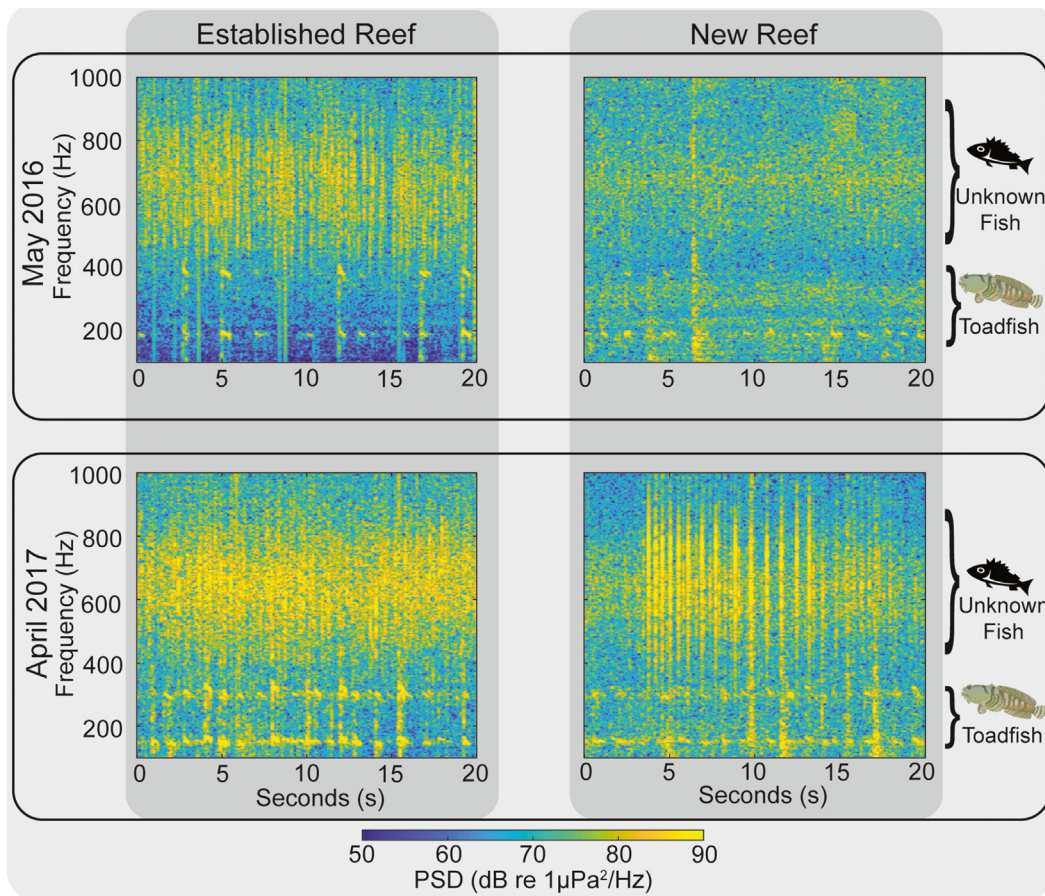


Fig. 6. Representative spectrograms of the dusk soundscape on both reefs during the May 2016 and April 2017 sampling periods. The spectrograms are 20-s samples from a representative file, recorded at the same time on both reefs. Comparisons among the four soundscapes suggest that toadfish rapidly colonized the new reef, shown by vocalizations present on both reefs during May 2016, while the unknown knock species exhibited a slower colonization, demonstrated by the presence of chorusing on established reef and lack of chorusing on the new reef during May.

Table 1. Comparison of qualitative conclusions drawn from video and passive acoustic monitoring (PAM).

Conclusions drawn	Video monitoring	PAM
Rapid fish colonization	Yes	Yes
Fish community convergence	Yes	Mixed (fish chorusing alignment)
Demersal species colonization	5 months	Toadfish within two weeks
Piscivorous species colonization	Within two weeks	Not available
Invertebrate colonization	Not available	Increasing, but not converged

Passive acoustic monitoring

The results of PAM identified seasonally variable low-frequency soundscapes with periods of temporary alignment between the reefs. Due to the opportunistic nature of this study, we were unable to monitor the soundscape at the new reef prior to artificial reef deployment. This lack of a soundscape baseline complicated interpretation of the variability as soundscape development or seasonal variability.

The alignment of the soundscapes (SPL time-series correlation, similarity in dusk SPL and dusk power spectra) during September and April

occurred when they were dominated by fish chorusing and other persistent low-frequency sounds. Because fish chorusing is a periodic phenomenon, and the timing of the toadfish and unidentified knock chorusing match previous soundscape descriptions of offshore reefs in our study region, we expect this alignment would persist annually (Rice et al. 2016, Van Hoeck et al. 2020). Despite the temporal variation in soundscape alignment, the SPL correlation between the sites was never lower than during the first two sampling periods, indicating that the diel soundscape patterns were becoming more similar over time.

Investigation of the power spectrum of each soundscape was the most informative measure of community development and alignment between the reefs. Because animal vocalizations are species-specific, with a unique time and frequency signature, we were able to track the presence and behavior of multiple soniferous species. By focusing on the first and last sampling period, when the established reef soundscape consisted of the same dominant vocalizers, comparisons between the power spectra of the reefs facilitated interpretation of colonization dynamics of chorusing species. Specifically, the power spectra revealed rapid colonization by toadfish and slower colonization by the species producing the unidentified knock.

Without visual confirmation, we are unable to say for certain whether toadfish were present on-reef within two weeks; however, comparison between the received call amplitudes provides evidence that toadfish were vocalizing proximal to the hydrophone on both reefs. For example, the sound level of the first toadfish harmonic observed on each reef during the first sampling period differed by only 2 dB, with amplitudes approaching the documented source levels for toadfish boatwhistles (Luczkovich et al. 2016). Additionally, during the first sampling period, choruses of the unidentified knock (0.4–1.2 kHz) were recorded on the established reef, but not the new reef, suggesting that not all low-frequency sounds were transmitted between the reefs.

Current limitations of PAM include the challenges of identifying vocalizations to species and interpreting soundscape dynamics. While our findings reveal exciting ecological implications for colonization of novel habitat by cryptic

species and soundscape development generally, we are unable to interpret the ecological implications of the slower colonization by the unidentified knock species compared with the toadfish species or of the unidentified sound sources observed in September. Additionally, without a control site at unstructured habitat within our study region, we are unable to interpret ecological significance of ambient soundscape variability during non-chorusing periods. Due to the battery-life constraints of the underwater video cameras, we sampled the reefs during multiple short sampling periods. If the hydrophones had been deployed separately from the cameras and recorded on a duty cycle for the duration of the study period, we may have captured additional colonization dynamics. With increased global coverage of marine soundscape studies and advancements in automated detection and classification, the number of documented vocalizations and acoustic catalogues are increasing. These technologies and open-access sharing will be crucial for expanding the practical application of PAM to monitoring and conservation contexts.

PAM and traditional method comparisons

Throughout the literature on passive acoustic monitoring of marine soundscapes and its application to management questions, a common theme has been the benefit of PAM for understanding the presence of cryptic fishes and invertebrates (Staaterman et al. 2017, Putland et al. 2018, Mooney et al. 2020). For example, despite decades of monthly diver-based visual census in a marine protected area in the Adriatic Sea, it was unknown that a cryptic cusk eel, *Ophidion rochei*, was present until it was identified by PAM (Picculin et al. 2019). Within the context of this study, PAM identified colonization of novel habitat by toadfish, a cryptic demersal fish species, approximately four months earlier than detected for conspicuous demersal fish species by video monitoring. Previous diver-based visual censuses of fish communities in Onslow Bay suggest that toadfish have a very low density of one individual per hectare (Whitfield et al. 2014) and are usually found on top of artificial reef structure as opposed to adjacent sand flats (Rosemond et al. 2018). As fish choruses are associated with spawning behaviors, it is likely that toadfish populations have higher densities, at least seasonally, and that these

visual surveys may have underestimated the density of cryptic fishes.

Although invertebrates were not the focus of the underwater video monitoring, our snapping shrimp results align with the findings of other studies on invertebrate colonization dynamics. The strong correlation between the high-frequency SPL timeseries, but ~17 dB difference in SPL suggests that the snaps recorded on the new reef during early sampling periods originated on adjacent habitats. The sustained lower SPLs on the new reef suggest that snapping shrimp density had not converged with that of the established reef by 11 months post-artificial reef deployment. Despite this, the substantial increase in dusk SPL on the new reef but not the established reef between the first two and the last two sampling periods suggests that snapping shrimp may have begun to colonize the new reef within two months after artificial reef deployment and that their density continued to increase. Similar to our findings, benthic assemblages on artificial reef offshore of Southeastern Florida, USA, were variable for the first four years following artificial reef deployment (Thanner et al. 2006), and on artificial reefs in the Red Sea, the benthic community still had not stabilized after 10 yr (Perkol-Finkel and Benayahu 2005).

Ecological context of colonization trajectory

Hypotheses explaining the trajectory of novel habitat colonization often center around priority effects and their resulting trophic interactions (Fukami 2015). For example, the rapid colonization by planktivorous fish species documented by video monitoring was hypothesized to be driven by high zooplankton abundance above the novel structure. Manipulative experiments in coral reef communities suggest that high abundances of these fishes in the water-column could facilitate colonization by piscivorous species, which, through predation pressure, could inhibit demersal species colonization (Almany 2003, Stier et al. 2017). It was also hypothesized that demersal species may have been slower to colonize because they often rely on benthic biota as a food source, which is slower to appear on novel structures (Paxton et al. 2018).

Interestingly, the rapid colonization by toadfish identified by PAM suggests that not all demersal species were excluded by early arrival of

piscivores, nor were they deterred by the lack of benthic biota present in the early stages. This finding may provide support for the hypothesis that the role of physical structure as refuge is an important driver of colonization dynamics and community structure (Hixon and Beets 1993, Caley and John 1996, Schroeter et al. 2015). For example, a species that relies primarily on the physical structure for refuge could be expected to quickly colonize novel habitat (Keller et al. 2017). Toadfish, which predominately hide in crevices in the habitat structure, may rely more heavily on the presence of structure than prey availability for colonization (Fine 1978). In oyster reef systems, Oyster toadfish (*Opsanus tau*) are known to facilitate oyster survival by eliciting predator avoidance behavior by mud crabs, thereby reducing mud crab predation on juvenile oysters (Grabowski 2004). If similar trophic dynamics occur on offshore reefs, then it could be hypothesized that the rapid colonization by toadfish may facilitate the colonization of the reef structure by benthic biota, as well as the subsequent colonization of conspicuous demersal species that rely on this biota as a food source.

In the context of evaluating habitat enhancement outcomes, the comparison with an adjacent established reef was essential to interpreting the time-lags of community development on the newly deployed reef. While PAM revealed additional insights compared with video monitoring within the first two weeks following artificial reef deployment, it is important to note that the PAM timeseries consisted of six sampling periods, up to 11 months following deployment of the new reef, whereas the video timeseries consisted of only the first three sampling periods, up to four months post-reef deployment. This extended soundscape sampling revealed nuanced information on colonization patterns, specifically the unidentified knock species and snapping shrimp, not available in the video data.

Though our research is a case study on offshore artificial reefs, the use of artificial structures as supplemental habitat or replacement for degraded natural habitat is common across marine systems (Becker et al. 2018). Our findings demonstrate that passive acoustics, especially when used in combination with traditional methods, offer a compelling approach to elucidate patterns and time-lags in community

development and improve assessment of habitat enhancement outcomes.

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LITERATURE CITED

- Alboukadel, K. 2021. rstatix: pipe-Friendly Framework for Basic Statistical Tests. R package version 0.7.0. <https://CRAN.R-project.org/package=rstatix>
- Al-Horani, F. A., and M. A. Khalaf. 2013. Developing artificial reefs for the mitigation of man-made coral reef damages in the Gulf of Aqaba, Red Sea: coral recruitment after 3.5 years of deployment. *Marine Biology Research* 9:749–757.
- Almany, G. R. 2003. Priority effects in coral reef fish communities. *Ecology* 84:1920–1935.
- Baine, M. 2001. Artificial reefs: a review of their design, application, management and performance. *Ocean & Coastal Management* 44:241–259.
- Becker, A., M. D. Taylor, H. Folpp, and M. B. Lowry. 2018. Managing the development of artificial reef systems: the need for quantitative goals. *Fish and Fisheries* 19:740–752.
- Bohnenstiehl, D. R. D., R. P. Lyon, O. N. Caretti, S. W. Ricci, and D. B. Eggleston. 2018. Investigating the utility of ecoacoustic metrics in marine soundscapes. *Journal of Ecoacoustics* 2:#R1156L.
- Bortone, S. A. 2006. A perspective of artificial reef research: the past, present, and future. *Bulletin of Marine Science* 78:1–8.
- Bortone, S. A. 2011. Introduction to the role of artificial reefs play in fisheries management. Pages 1–5 *in* S. A. Borton, F. P. Brandini, G. Fabi, and S. Otake, editors. *Artificial reefs in fisheries management*. CRC Press, Boca Raton, Florida, USA.
- Bowman, D. C., and W. S. D. Wilcock. 2014. Unusual signals recorded by ocean bottom seismometers in the flooded caldera of Deception Island volcano: volcanic gases or biological activity? *Antarctic Science* 26:267–275.
- Buskirk, R. E., C. Frohlich, G. V. Latham, A. T. Chen, and J. Lawton. 1981. Evidence that biological activity affects Ocean Bottom Seismograph recordings. *Marine Geophysical Researches* 5:189–205.
- Butler, J., J. A. Stanley, and M. J. I. Butler. 2016. Underwater soundscapes in near-shore tropical habitats and the effects of environmental degradation and habitat restoration. *Journal of Experimental Marine Biology and Ecology* 479:89–96.
- Caley, M. J., and J. S. John. 1996. Refuge availability structures assemblages of tropical reef fishes. *Journal of Animal Ecology* 65:414.
- Comer, A. M., and R. Love-Adrick. 2016. North Carolina division of marine fisheries artificial reef guide. NC Division of Marine Fisheries, Morehead City, North Carolina, USA.
- Cummings, S. L. 1994. Colonization of a nearshore artificial reef at Boca Raton (Palm Beach County), Florida. *Bulletin of Marine Science* 55:1193–1215.
- Davis, G. E., et al. 2020. Exploring movement patterns and changing distributions of baleen whales in the western North Atlantic using a decade of passive acoustic data. *Global Change Biology* 26:4812–4840.
- Fine, M. L. 1978. Seasonal and geographical variation of the mating call of the oyster toadfish *Opsanus tau* L. *Oecologia* 36:45–57.
- Fukami, T. 2015. Historical contingency in community assembly: integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics* 46:1–23.
- Grabowski, J. H. 2004. Habitat complexity disrupts predator-prey interactions but not the trophic cascade on oyster reefs. *Ecology* 85:995–1004.
- Gregg, K., and S. Murphey. 1994. The role of vessels as artificial reef material on the Atlantic and Gulf of Mexico coasts of the United States. Special Report Number 38 of the Atlantic States Marine Fisheries Commission, Morehead City, North Carolina, USA.
- Halpern, B. S., M. Frazier, J. Afflerbach, J. S. Lowndes, F. Micheli, C. O'Hara, C. Scarborough, and K. A.

- Selkoe. 2019. Recent pace of change in human impact on the world's ocean. *Scientific Reports* 9:11609.
- Hixon, M. A., and J. P. Beets. 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs* 63:77–101.
- Keller, D. A., R. K. Gittman, R. K. Bouchillon, and F. J. Fodrie. 2017. Life stage and species identity affect whether habitat subsidies enhance or simply redistribute consumer biomass. *Journal of Animal Ecology* 86:1394–1403.
- Leitão, F., M. N. Santos, K. Erzini, and C. C. Monteiro. 2009. *Diplodus* spp. assemblages on artificial reefs: importance for near shore fisheries. *Fisheries Management and Ecology* 16:88–99.
- Lima, J. S., I. R. Zalmon, and M. Love. 2019. Overview and trends of ecological and socioeconomic research on artificial reefs. *Marine Environmental Research* 145:81–96.
- Luczkovich, J. J., C. S. Krahforst, K. E. Kelly, and M. W. Sprague. 2016. The Lombard effect in fishes: How boat noise impacts oyster toadfish vocalization amplitudes in natural experiments. *Proceedings of Meetings on Acoustics* 27:10035. <https://doi.org/10.1121/2.0000340>
- MATLAB. 2018. 9.1.0.441655 (R2019a). The MathWorks Inc., Natick, Massachusetts, USA.
- Mooney, T. A., L. Di Iorio, M. Lammers, T. Lin, S. L. Nedelec, M. Parsons, C. Radford, E. Urban, and J. Stanley. 2020. Listening forward: approaching marine biodiversity assessments using acoustic methods. *Royal Society Open Science* 7:201287.
- Paxton, A. B., E. A. Pickering, A. M. Adler, J. C. Taylor, and C. H. Peterson. 2017. Flat and complex temperate reefs provide similar support for fish: evidence for a unimodal species-habitat relationship. *PLOS ONE* 12:e0183906.
- Paxton, A. B., L. W. Revels, R. C. Rosemond, R. V. Van Hoeck, H. R. Lemoine, J. C. Taylor, and C. H. Peterson. 2018. Convergence of fish community structure between a newly deployed and an established artificial reef along a five-month trajectory. *Ecological Engineering* 123:185–192.
- Perkol-Finkel, S., and Y. Benayahu. 2005. Recruitment of benthic organisms onto a planned artificial reef: shifts in community structure one decade post-deployment. *Marine Environmental Research* 59:77–99.
- Picciulin, M., L. Kéver, E. Parmentier, and M. Bolgan. 2019. Listening to the unseen: Passive acoustic monitoring reveals the presence of a cryptic fish species. *Aquatic Conservation: Marine and Freshwater Ecosystems* 29:202–210.
- Pickering, H., D. Whitmarsh, and A. Jensen. 1998. Artificial reefs as a tool to aid rehabilitation of coastal ecosystems: investigating the potential. *Marine Pollution Bulletin* 37:505–514.
- Pratt, J. R. 1994. Artificial habitats and ecosystem restoration: managing for the future. *Bulletin of Marine Science* 55:268–275.
- Putland, R. L., A. G. Mackiewicz, and A. F. Mensinger. 2018. Localizing individual soniferous fish using passive acoustic monitoring. *Ecological Informatics* 48:60–68.
- R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Relini, G., and L. Orsi Relini. 1989. Artificial reefs in the Ligurian Sea (Northwestern Mediterranean): aims and Results. *Bulletin of Marine Science* 44:743–751.
- Ricci, S. W., D. R. Bohnenstiehl, D. B. Eggleston, M. L. Kellogg, and R. P. Lyon. 2017. Oyster toadfish (*Opsanus tau*) boatwhistle call detection and patterns within a large-scale oyster restoration site. *PloS one* 12:e0182757.
- Ricci, S., D. Eggleston, D. Bohnenstiehl, and A. Lillis. 2016. Temporal soundscape patterns and processes in an estuarine reserve. *Marine Ecology Progress Series* 550:25–38.
- Rice, A. N., J. L. Morano, K. B. Hodge, and C. A. Muirhead. 2016. Spatial and temporal patterns of toadfish and black drum chorusing activity in the South Atlantic Bight. *Environmental Biology of Fishes* 99:705–716.
- Riggs, S. R., S. W. Snyder, A. C. Hine, and D. L. Mearns. 1996. Hardbottom morphology and relationship to the geological framework: mid-Atlantic continental shelf. *Journal of Sedimentary Research* 66:830–846.
- Rilov, G., and Y. Benayahu. 2002. Rehabilitation of coral reef-fish communities: the importance of artificial-reef relief to recruitment rates. *Bulletin of Marine Science* 70:185–197.
- Rosemond, R. C., A. B. Paxton, H. R. Lemoine, S. R. Fegley, and C. H. Peterson. 2018. Fish use of reef structures and adjacent sand flats: implications for selection minimum buffer zones between new artificial reefs and existing reefs. *Marine Ecology Progress Series* 587:187–199.
- Scarcella, G., F. Grati, L. Bolognini, F. Domenichetti, S. Malaspina, S. Manoukian, P. Polidori, A. Spagnolo, and G. Fabi. 2015. Time-series analyses of fish abundance from an artificial reef and a reference area in the central-Adriatic Sea. *Journal of Applied Ichthyology* 31:74–85.
- Schroeter, S. C., D. C. Reed, and P. T. Raimondi. 2015. Effects of reef physical structure on development of benthic reef community: a large-scale artificial reef experiment. *Marine Ecology Progress Series* 540:43–55.

- Seaman, W. 2007. Artificial habitats and the restoration of degraded marine ecosystems and fisheries. *Hydrobiologia* 580:143–155.
- Sherman, R. L., D. S. Gilliam, and R. E. Spieler. 2002. Artificial reef design: void space, complexity, and attractants. *ICES Journal of Marine Science* 59:196–200.
- Staaterman, E., M. B. Ogburn, A. H. Altieri, S. J. Brandl, R. Whippo, J. Seemann, M. Goodison, and J. E. Duffy. 2017. Bioacoustic measurements complement visual biodiversity surveys: preliminary evidence from four shallow marine habitats. *Marine Ecology Progress Series* 575:207–215.
- Stier, A. C., S. W. Geange, K. M. Hanson, and B. M. Bolker. 2017. Predator density and timing of arrival affect reef fish community assembly. *Ecology* 94:1057–1068.
- Thanner, S. E., T. L. McIntosh, and S. M. Blair. 2006. Development of benthic and fish assemblages on artificial reef materials compared to adjacent natural reef assemblages in Miami-Dade County, Florida. *Bulletin of Marine Science* 78:57–70.
- Van Hoeck, R. V., A. B. Paxton, D. W. R. Bohnenstiehl, J. C. Taylor, F. J. Fodrie, D. P. Nowacek, C. M. Voss, and C. H. Peterson. 2020. Soundscapes of natural and artificial temperate reefs: similar temporal patterns but distinct spectral content. *Marine Ecology Progress Series* 649:35–51.
- Van Parijs, S. M., C. W. Clark, R. S. Sousa-Lima, S. E. Parks, S. Rankin, D. Risch, and I. C. Van Opzeeland. 2009. Management and research applications of real-time and archival passive acoustic sensors over varying temporal and spatial scales. *Marine Ecology Progress Series* 395:21–36.
- Whitfield, P. E., R. C. Muñoz, C. A. Buckel, B. P. Degan, D. W. Freshwater, and J. A. Hare. 2014. Native fish community structure and Indo-Pacific lionfish *Pterois volitans* densities along a depth-temperature gradient in Onslow Bay, North Carolina, USA. *Marine Ecology Progress Series* 509:241–254.
- Whitmarsh, D., M. N. Santos, J. Ramos, and C. C. Monteiro. 2008. Marine habitat modification through artificial reefs off the Algarve (southern Portugal): an economic analysis of the fisheries and the prospects for management. *Ocean and Coastal Management* 51:463–468.

DATA AVAILABILITY

Data and code are available from Zenodo: <https://doi.org/10.5281/zenodo.5553006>

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3840/full>