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JOURNAL OF ECOACOUSTICS
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Drifting hydrophones as an ecologically meaningful approach to underwater soundscape measurement in coastal benthic habitats

Original paper

Article history:
Received: 10 October 2017
Accepted: 3 January 2018
Published: 6 February 2018

Check for updates

*Correspondence:
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Peer review:
Double blind

Keywords:
benthic ecology; acoustic cues; soundscape measurement; habitat-related sound; benthic communities; drifters

Citation:
Lillis A., Caruso F., Mooney T. A., Llopiz J., Bohnenstiehl D., and Eggleston D. B. (2018). Drifting hydrophones as an ecologically meaningful approach to underwater soundscape measurement in coastal benthic habitats. Journal of Ecoacoustics. 2: #STBDH1.
https://doi.org/10.22261/JEA.STBDH1

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Abstract

The ambient acoustic environment, or soundscape, is of broad interest in the study of marine ecosystems as both a source of rich sensory information to marine organisms and, more broadly, as a driver of the structure and function of marine communities. Increasing our understanding of how soundscapes affect and reflect ecological processes first requires appropriate characterization of the acoustic stimuli, and their patterns in space and time. Here, we present a novel method developed for measuring soundscape variation, using drifting acoustic recorders to quantify acoustic dynamics related to benthic habitat composition. Selected examples of drifter results from sub-tidal oyster-reef habitats in Pamlico Sound, North Carolina, USA, and from coral reef habitats in St. John, US Virgin Islands, highlight the efficacy and utility of this approach in quantifying soundscape variation in diverse habitats. The platform introduces minimal noise into the acoustic recordings, and allows sampling at spatial scales that might typically be overlooked using stationary hydrophone methods. We demonstrate that mobile hydrophone recording methods offer new insight into soundscape variation and provide a complementary approach to conventional passive acoustic monitoring techniques.

Introduction

The combination of biotic and abiotic sounds that form the acoustic environment of a particular location, known as the "soundscape," is increasingly recognized as a key structural component of ecological communities, with influence on a range of ecological processes including habitat selection, navigation, reproduction, and predator-prey interactions for a wide variety of taxa (Cotter, 2008; Pijanowski et al., 2011; Farina, 2014). In marine bioacoustics, passive acoustic assessments have long been centered on the specific communicative signals of mammals and fishes (Reviewed in: Myrberg Jr., 1997; Ramcharitar et al., 2006; Fay et al., 2008; Van Parijs et al., 2009; Zimmer, 2011; Au and Lammers, 2016). More recently, however, the totality of the acoustic environment comprising all biological, geophysical, and anthropogenic sources has been documented as an important source of sensory information for organisms of a broader range of taxa, and the composition of soundscapes is now implicated in numerous behavioral and ecological processes (Cotter, 2008; Fay, 2009). Moreover, the recognition that marine ecosystems are facing anthropogenic noise pressures, as well as habitat changes that may alter the structure and function of soundscapes, has driven research on the relationship between ecological processes and underwater soundscapes (*e.g.*, Lillis et al., 2014b; Ruppé et al., 2015; Kaplan et al., 2015; Bohnenstiehl et al., 2016; Butler et al., 2016; Bertucci et al., 2016; Staaterman et al., 2017).

Adequate characterization of the acoustic environment is an essential first step to develop and test hypotheses in the burgeoning discipline of soundscape ecology. New acoustic analysis approaches to quantify the spatiotemporal variation in ambient sound continue to be developed and applied in both terrestrial and marine systems (*e.g.*, Sueur et al., 2008; Pijanowski et al., 2011; Gasc et al., 2013; McWilliam and Hawkins, 2013; Lillis et al., 2014a; Staaterman et al., 2014; Pieretti et al., 2017). Studies in shallow water coastal and estuarine systems provide evidence that soundscapes reflect specific benthic habitat types (*e.g.*, rocky reefs, coral reefs, oyster reefs), as well as the structure of marine communities (Radford et al., 2010; Lillis et al., 2014a; Piercy et al., 2014; Kaplan et al., 2015). These distinct acoustic characteristics may, in turn, influence key ecological processes such as larval fish and invertebrate orientation and settlement (Radford et al., 2007; Simpson et al., 2008; Stanley et al., 2011; Lillis et al., 2013). Given that underwater soundscapes can exhibit high spatiotemporal variation, yet logistical constraints may limit data collection to few hydrophones and/or small deployment windows, interpreting ecological meaning from soundscape “snapshots” can be challenging (McWilliam and Hawkins, 2013; Lillis et al., 2016).

The benthos of estuarine and coastal areas typically comprise a mosaic of different habitat types. For instance, coastal and estuarine habitats may transition from reef to sandflat to seagrass to reef over relatively small spatial scales (Sheaves, 2009; Lillis et al., 2014a; Ricci et al., 2016). The acoustic characterization of such environments at appropriate spatiotemporal scales is particularly challenging. For example, while sound may propagate long distances in open-ocean free-field environments (Au and Hastings, 2008), propagation and attenuation patterns are often not well-known in nearshore-coastal habitats (but see [Radford et al., 2011; Lillis et al., 2014a; Kaplan and Mooney, 2016]) and distinct soundscapes may not actually propagate far in structurally complex shallow water habitats. Stationary acoustic recorders provide high temporal fidelity for passive acoustic monitoring in a given location, and measurements at multiple locations may help identify spatial differences, however, multiple passive acoustic recorders can still prove costly and selection of appropriate deployment sites challenging. These limits in technology and logistical constraints create trade-offs in sampling designs that require creative and carefully conceived approaches to meet the goals of the soundscape measurement.

With these considerations in mind, we developed a measurement approach using passive drifting hydrophone recorders to explore estuarine and coastal soundscape dynamics with fine spatiotemporal resolution, complementary to stationary recording platforms. Since drifters move with and at the speed of ocean currents, they mimic the acoustic experience of passive planktonic organisms and are well-suited for capturing acoustic variability at scales relevant to processes such as larval dispersal and habitat selection (Lillis et al., 2014b). Moreover, drifters offer a technique to efficiently survey the soundscape across a study area and inform the development of long-term stationary recording schemes (*i.e.*, measure scales of spatial variability, identify locations of particular acoustic interest). Gliders, autonomous vehicles, or other mobile hydrophone platforms also provide a method to acoustically sample over multiple scales and along programmed paths of interest, but typically have separate moving parts or motors which can generate substantial self-noise or flow-noise (*e.g.*, Matsumoto et al., 2011; Klinck et al., 2012). By moving with the current, and having no moving parts, drifters have the potential to generate relatively low levels of self-noise, thus broadening the dynamic range of potential soundscape measurements and the ability to capture low-amplitude sounds previously identified only through stationary recorders. Previously, free-drifting underwater recorders have been used as a tool to detect and localize marine mammals (Laurinolli et al., 2003; Širović and Hildebrand, 2011; Mooney et al., 2013), however, similar instruments rarely been applied in shallow-water environments, or to characterize variation in soundscapes.

Here, we describe the use of passive acoustic drifters in two case studies, applying the approach to a temperate and a tropical system, to highlight the importance of passive acoustic measurements over multiple scales and illustrate the potential value of including a dynamic data collection method in soundscape studies. The objective is to describe an underutilized approach in marine soundscape ecology and to illustrate the utility and potential caveats of applying this technique to measure near-shore marine soundscapes.

Materials and methods

Drifting acoustic recorders

Two types of drifting passive acoustic recorders were used in soundscape characterization efforts described here. The first version of drifting hydrophone units, initially developed in 2012 for use in estuarine habitats, were constructed from a small free-floating water-tight plastic barrel (40 cm length × 15 cm diameter) containing a handheld GPS unit, and an M-audio Microtrack II recorder (48 kHz sampling rate, 24 bit digitization) connected to an external omnidirectional calibrated hydrophone (Sensor Technology SQ-26-08: flat frequency response over the range of 0.1–24 kHz with a sensitivity −169 dB re 1 V/μPa; or High Tech Inc HTI-96-MIN: flat frequency response over the range of 0.02–24 kHz with a sensitivity −165 dB re 1 V/μPa) (Figure 1a). The hydrophone was suspended at 0.75–1 m depth from the surface using a weighted line. Due to the shallow depths present in this estuarine study system, the hydrophone placement depth was chosen to best avoid contact with high relief reef structure within oyster reserves, while minimizing surface and flow noise around a mobile hydrophone.

The second version of drifting acoustic recorders was developed in 2017 for use in Caribbean coral reef systems (Figure 1b). These drifters comprised a weighted surface buoy constructed of a 10 cm diameter × 50 cm long PVC pipe with end caps, surrounded by a syntactic foam jacket, suspending a 4-channel acoustic recorder (SoundTrap 4300, Ocean Instruments NZ) with four hydrophones (High Tech Inc HTI-96-MIN: flat frequency response over the range of 0.02–24 kHz with a sensitivity −165 dB re 1 V/μPa) arranged in a tetrahedral configuration. Reef habitat in this experiment ranged from 4–20 meters depth, allowing the hydrophone array to be placed slightly deeper than the previous

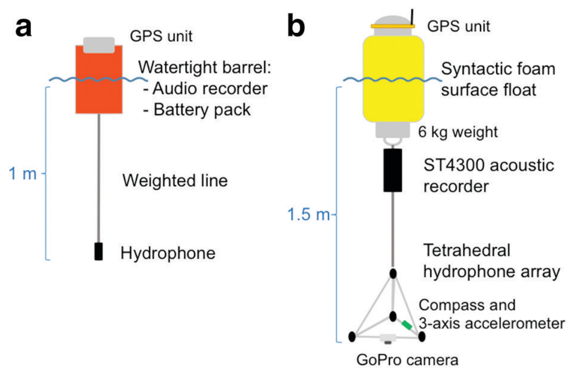

Figure 1. Schematic of drifting underwater acoustic recorder units, showing customizable features.

(a) Original basic design used in shallow estuarine habitats in North Carolina, and (b) modified design for use in coastal Caribbean reefs, including multiple hydrophones, compass, camera, and transmitting GPS.

version, at approximately 1.5–2 m below the water surface. The above-surface module held a GPS device that logged and transmitted drifter locations to a handheld device (Garmin Astro® 320). A compass and 3-dimensional accelerometer measurement device was attached to the hydrophone array to add directional/localization capabilities. Additionally, a GoPro waterproof camera was included in the re-design, allowing video and photo confirmation of the benthic habitats over which the drifter traversed.

Study sites and deployments

Study 1: Estuarine habitats in Pamlico Sound, NC, USA

Pamlico Sound, North Carolina is a large lagoonal estuary located in the Southeastern United States (Figure 2). Oyster reefs in this system provide three-dimensional structured habitat for a variety of finfish and invertebrate species, and host a distinct ecological community compared to off-reef unstructured soft bottom habitats (Boudreaux et al., 2006). Previous acoustic recordings made using stationary hydrophone systems showed that oyster reef habitats in Pamlico Sound, NC consistently had distinct acoustic characteristics compared to simultaneously sampled adjacent off-reef soft bottoms (Lillis et al., 2014a), and experimental work provided evidence that settling oyster larvae can be influenced by the habitat-associated sounds (Lillis et al., 2013). However, variation within reserve sites could not easily be measured with a limited number of stationary hydrophones, and short-term recordings indicated that acoustic characteristics could vary considerably over short distances (<50 m) within reefs. These findings provided the impetus for the development of an additional mobile acoustic measurement approach to capture additional scales of soundscape variation.

Oyster populations in this region declined substantially throughout the 20th century due to overfishing, precipitating recent oyster enhancement efforts in Pamlico Sound that included the creation of subtidal broodstock reserves where oyster harvesting is prohibited. These reserves provide protected habitat where reef communities, including numerous finfish and invertebrates, have become established (Puckett and Eggleston, 2012; Mroch et al., 2012; Pierson and Eggleston, 2014). The reserves, located throughout Pamlico Sound, are typically surrounded by featureless soft bottom habitat. Reserve areas range between 0.02–0.19 km^2 and, within their boundaries, contain discrete patches of reef material in various configurations. Because these reserves are located throughout the large estuary (Figure 2), and are mapped in terms of reef structure and layout, they provided a model system in

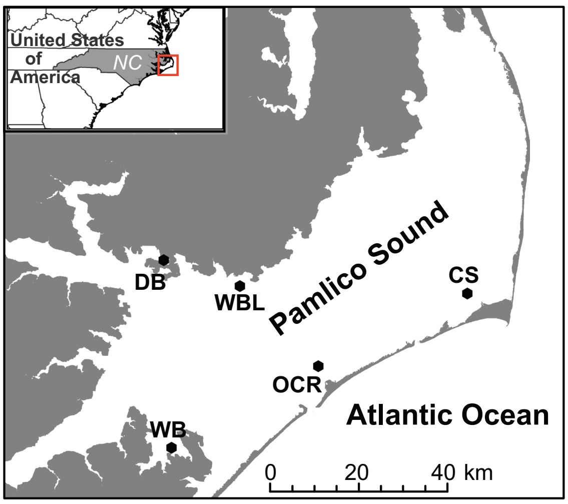

Figure 2. Map of Pamlico Sound, North Carolina with inset showing location within the US.

Oyster reserves sampled by drifter acoustic recorders are labeled: WB = West Bay; DB = Deep Bay; WBL = West Bluff; OCR = Ocracoke; CS = Clam Shoal.

which to evaluate the use of drifting hydrophones to link acoustic patterns to small-scale changes in benthic habitat structure.

Drifter surveys were conducted during daylong site visits to five oyster reserves (labeled in Figure 2) during the summer (July and August 2012). At each site, drifter units were deployed in the water approximately 500–1,000 m upstream of the reserve boundaries in a position projected to produce a drift crossing the reef area. Following deployment, the small boat was moved a sufficient distance to avoid interference with the recordings while maintaining visual contact (~500 m), and the motor was turned off for the duration of a drift. Hydrophones were allowed to drift across the reserve site until they were approximately 500–1,000 m downstream of the reserve, producing drifts ranging from 45–90 minutes depending on current speed. All drifts in this study were conducted during daylight hours and on calm days without substantial wind or wave action; however, current speed and direction differed between days and sites.

Study 2: Coral reef habitats in St. John, US Virgin Islands

St. John, US Virgin Islands (USVI) is a 52 km^2 tropical island in the northeastern Caribbean Sea, part of the archipelago of the Lesser Antilles and Leeward Islands (Figure 3). The coastal waters of St. John include a marine protected area within the Virgin Islands National Park and Biosphere Reserve, where several bays are relatively protected from fishing and anthropogenic disturbance, and a mosaic of coral reefs, seagrass, and sandy bottoms are present. The dynamics of this marine protected area have been studied for several decades, describing reefs with a variety of coral cover and fish abundances, and patches of reef at different points in recovery from disturbance (Edmunds, 2002; Rogers et al., 2008; Edmunds, 2013).

A long-term effort to record underwater soundscapes and associated ecological characteristics of coral reefs within the Virgin Islands National Park commenced in April 2013 with visual surveys and deployments of stationary acoustic recorders at several reef sites (Kaplan et al., 2015). Results of the initial acoustic data collection revealed significant intra- and inter-site variation in sound pressure levels and patterns in sound production, particularly by dominant sound producers such as snapping shrimp, at scales of hundreds of meters (Kaplan et al., 2015; Lillis and Mooney, 2016). Because a major objective of the larger USVI reef study is to examine relationships between soundscape variation, reef characteristics, and larval recruitment, mobile hydrophone deployments offered a useful platform with which to characterize soundscape variation in the study area at scales relevant to changes in benthic habitat composition and larval transport. Drifting hydrophones as in Figure 1b were released within coastal areas on the south side of the island of St. John to collect acoustic data across sandy bottom, coral rubble, and within coral reef habitat (5–15 m depth range) during 1–2 hour deployments. The

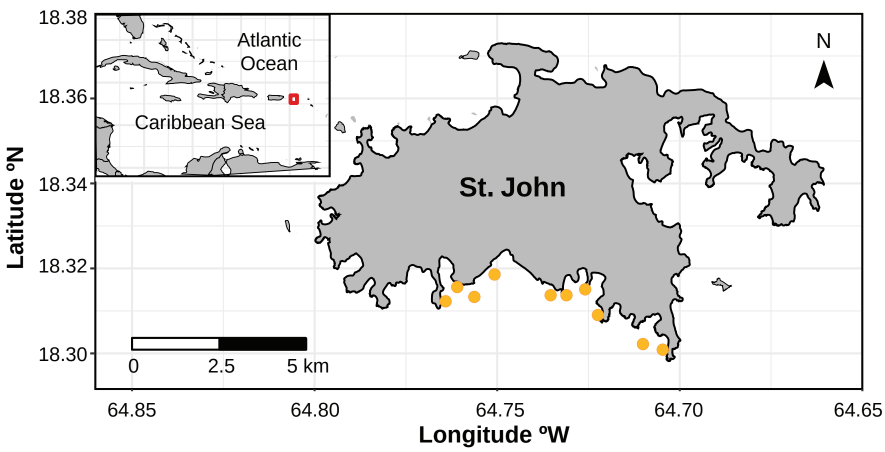

Figure 3. Map of St. John, United States Virgin Islands with inset of the Caribbean.

Reef sites for long-term stationary acoustic monitoring are shown in orange.

experiments were restricted to daytime hours. Deployment methods were adapted from those described above for use in the coastal embayments, with drifters released depending on current direction, and aimed to result in the drifter traversing sandy bottom and coral patches of interest (sites labeled in Figure 3). Following drifter release, the boat was moored ~1 km away and drifter locations were monitored via the handheld GPS receiver.

Data analysis

Acoustic recordings were analyzed with Matlab code written to generate waveforms and spectrograms for the durations of each drift. Prior to analysis, recordings were audited and raw data visually inspected to facilitate removal of the boat noise associated with deployment and retrieval activity. The truncated recordings were then analyzed by filtering the sound to compute the root-mean square (rms) sound pressure levels in a lower (100–2,000 Hz) and higher (2,000–20,000 Hz) frequency band to broadly examine the variation in sound levels attributable to changes in dominant sound sources during a drift. The frequency bands were selected based on previous soundscape characterization studies examining estuarine habitats in Pamlico Sound (Lillis et al., 2014a) and coastal reefs in St. John (Kaplan et al., 2015), that detected habitat-related differences in these bandwidths, which are generally associated with different acoustic sources. Sound in the 100–2,000 Hz band is biologically dominated by fish vocalizations (Ramcharitar et al., 2006; Fay et al., 2008), and contains much of the acoustic energy produced by wind and waves (Wenz, 1962; Urick, 1984), while the higher frequency 2,000–20,000 Hz band is dominated by snapping shrimp *Alpheus* spp. activity (Everest, 1948; Schmitz, 2002). Recordings from St. John 2017 drifts were additionally analyzed specifically for snapping shrimp content, by applying a snap detector (as in Bohnenstiehl et al., 2016) for each 1-minute window of drift audio, to examine snap rates across the duration of drifts.

To further assess the change in frequency composition and sound intensities at different frequencies over the length of each drifter recording, spectrograms were produced using 0.5-second windows with 25% overlap. GPS data were used to generate a map for each drift. For Study 1 (Pamlico Sound, NC), reserve boundaries and reef structure locations (obtained from NC Division of Marine Fisheries) were plotted on drift maps, while available benthic habitat maps (https://maps.coastalscience.noaa.gov/) were used for drift maps in Study 2 (St. John, USVI). Based on these maps, the recording times during which the hydrophone was positioned above reef structure and in proximity to other features was determined, and the acoustic waveforms and spectrograms were directly compared to the drifter positions to evaluate the correspondence of acoustic variation to variation in benthic habitat structure.

The coastal St. John study area is characterized by prevailing easterly winds and currents, and 1–1.5 m wave heights were measured at a nearby oceanographic data buoy (NOAA National Data Buoy Center Station 41052) during drifter deployment periods. As a result, transient mechanical interference was detected on hydrophones intermittently during drifts, as the units moved. Because these sounds contributed unwanted noise to the lower analysis band, and to test if valuable biological data (*e.g.*, fish calls) could still be extracted with this method, recordings were filtered to remove any 1-second samples that contained high-amplitude low-frequency interference, as confirmed by manual inspection of spectrograms and auditing. Although data from multiple hydrophones was collected using a 4-channel recorder on each drifter in the second study, because the objective of the present analysis is to test and illustrate the utility of drifter soundscape measurements in the coastal coral reef environments, here we limit results to single hydrophone data. Future applications will obtain directional information from the hydrophone array and compass features of this drifter design.

Results

Study 1: Estuarine habitats in Pamlico Sound, NC, USA

Twenty-four successful drifter deployments were conducted during 2012 at five study sites (4–6 per site). After initial testing and development, drifter units were straight-forward to use, and unsuccessful deployments were rare, but included instances where drifters did not move across the intended areas due to unpredictable currents or winds, and times when the acoustic recorder or battery pack failed. When possible, two drifter units were deployed in tandem, providing redundancy if a recording failed and most often generating simultaneous replicate drift recordings. A comparison of drifter recordings and concurrent measurements made with a stationary hydrophone indicated that the noise due to flow and wave motion was primarily below 100 Hz and therefore largely excluded from our analysis bands. Drifter speeds varied between 0.12–0.30 m/s, comparable to commonly observed Pamlico Sound surface current speeds (Haase et al., 2012) and therefore provided realistic space-time scales of soundscape variation for the intended application of making inferences about the acoustic experience of planktonic animals.

Drift acoustic recordings revealed variation in the estuarine soundscape at multiple spatial scales. Here we present examples from two reserve sites to highlight the types of observations possible with the drifter method (further examples from this dataset can be found in Lillis et al. (2014b), in the context of larval settlement). Higher sound pressure levels, particularly in the upper frequency band, were detected during transit within oyster reserves compared to the areas outside of reserve boundaries (*e.g.*, West Bay reserve: Figure 4). Measured sound pressures in the low frequency band increased by 5–10 dB over the drifter approach to reef structure, and SPLs in the high frequency band reached 15–30 dB higher during transit within reserve boundaries. The most consistent and detectable sounds forming the daytime oyster reef soundscapes were impulsive broadband signals of snapping shrimp and reef fish vocalizations (*e.g.*, toadfish; Lillis et al., 2014a).

Increases in biologically-associated sound levels were closely associated with proximity to the reef structure within the reserve, as shown by the red shaded areas in Figure 4c, where sound levels were reduced by nearly 5 dB during passage over a small (~30 m) gap in reef material. Replicate drifts at single reserve sites further demonstrate considerable within-habitat variation. The dependence of the acoustic characteristics on the individual drift path is evident by comparing drifter measurements from multiple drifts conducted at single sites; three consecutive drift measurements at West Bay reserve crossed different areas of the oyster reserve, and the magnitude and duration of the reef-associated sound pressure levels varied according to the trajectory of the particular drift (Figure 4).

Sets of simultaneous drifts were conducted at the Ocracoke reserve site (Figure 5), crossing different areas of the reserve and collecting concurrent data that provide additional evidence that the acoustic patterns measured relate to spatial heterogeneity in benthic habitat. Consistent with drift results from other sites, sound levels in the reef-associated upper frequency band increased upon approach to the reserve and a peak sound pressure level was detected above the locations of reef structure in the upper frequency band. Elevated sound pressure levels in the upper frequency band at reserve boundaries were also found during drifts passing in close proximity to reserve marker buoys (Figure 5a, drift 2; Figure 5c: peak at second hashed line, red pulses in spectrogram); these sounds were determined to be 4–5 kHz chain noise from the reserve moorings. A drift that did not transit as close to the reserve markers did not show the same buoy-related acoustic signal (Figure 5b).

Study 2: Coral reef habitats in St. John, US Virgin Islands

Soundscapes of five reef sites on the Southern coast of St. John were sampled at high spatial resolution in June 2017 with 20 drifter deployments. Drifters effectively transited and recorded over benthic areas of interest during 1.5–2 hour deployments, and the instruments were found to be relatively simple to deploy and retrieve from a small boat, and to drift smoothly and predictably in the coastal conditions. Drift data in this system revealed high variability in nearshore soundscapes related to benthic cover, exemplified by the results of data collected by two drifts in Lameshur Bay (Figure 6). Depths ranged from 4–7 m within the embayment, with shallower depths along the coastal margins of the coral reefs. Available benthic habitat maps, combined with GPS data, provided the best approach to compare acoustic results to position and benthic cover, and GoPro photos collected during the drift served to confirm benthic cover in general, but not at a high spatial resolution due to the moving platform (*i.e.*, inconsistent image resolution and angle).

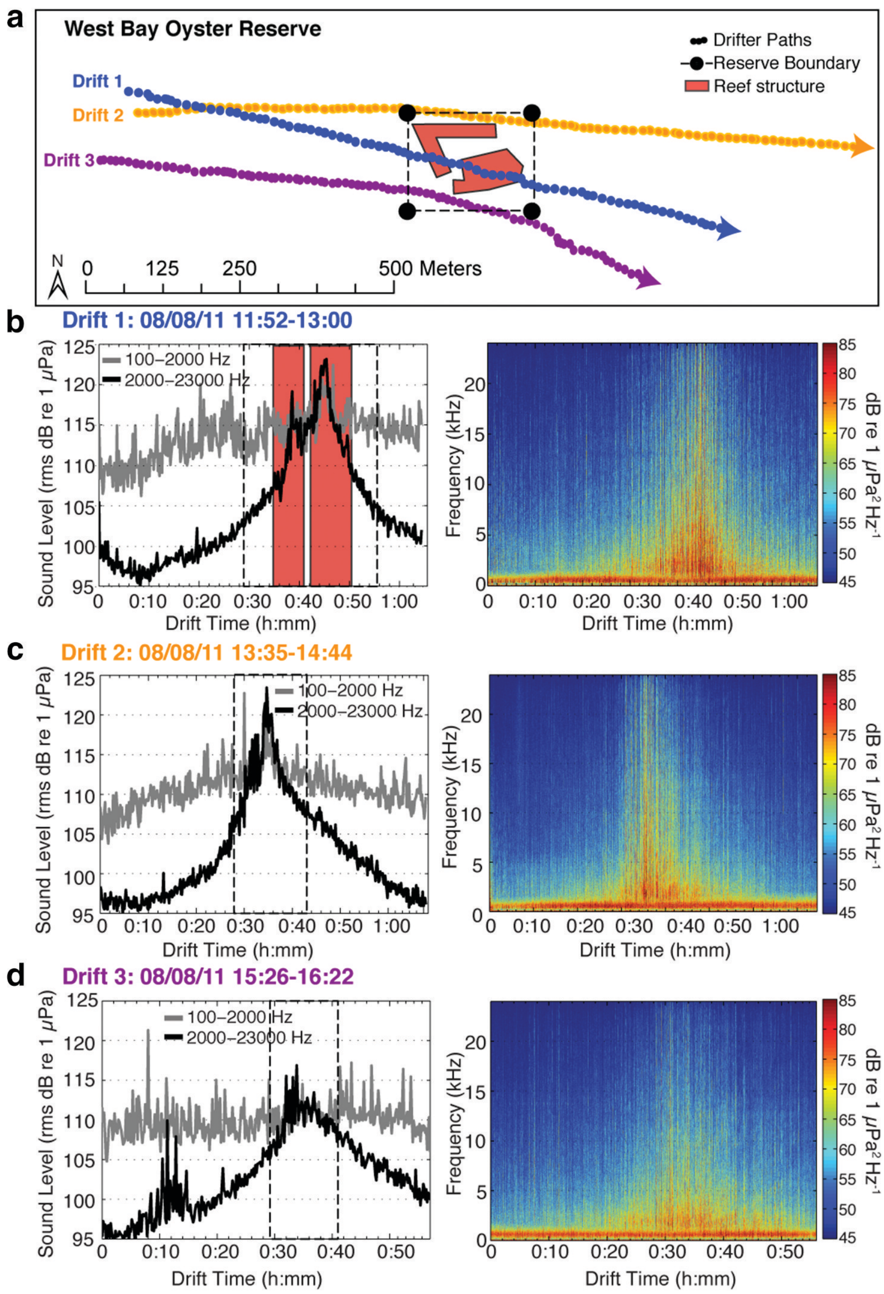

Figure 4. Map of drift at West Bay reserve, crossing the majority of the reef structured area, with time series of sound pressure level for the lower (100–2,000 Hz) and (2,000–23,000 Hz) frequency bands and corresponding spectrograms, for three consecutive drifts (b–d).

Hashed lines show time at which a drifter entered and exited reserve boundaries. The spectrograms were produced using zero-padded 0.5-second duration Hamming windows with 25% overlap. Root-mean-square (rms) pressure was estimated within a series of non-overlapping 10-sec duration windows over the length of the recording. Panel (b) is adapted from Lillis et al. (2014b) Figures 3a and 4a.

Drift 1 started in the waters adjacent to the Tektite reef site, approximately 50 m from shore, and moved westward from the reef over the following 1.5 h (Figure 6, Figure 7a). Acoustic analyses show highest SPLs near the reef (Figure 7), particularly in the higher frequency analysis band, where levels diminished by 5 dB within the first ~50 m of movement from the reef and by 10 dB at 125 m (Figure 7a, b). Correspondingly, snap rates detected were reduced four-fold in the first 20 minutes (50–75 m). Although the SPL measured in the lower frequency analysis band (50–2,000 Hz) did not exhibit the

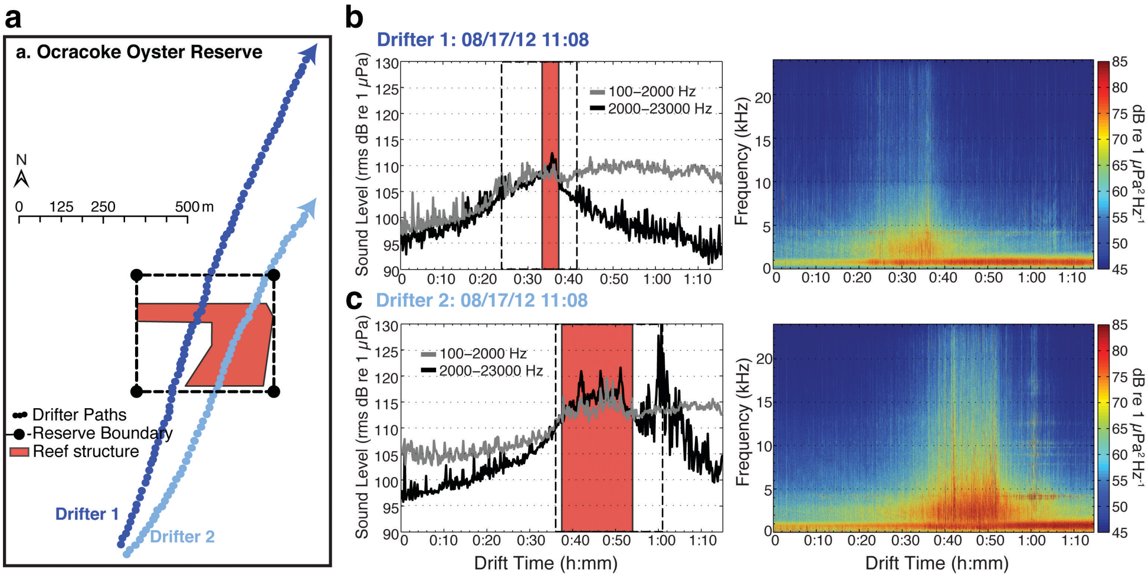

Figure 5. (a) Map of Ocracoke reserve site showing paths for two hydrophone drifters deployed simultaneously. The extent of the reef structure within the reserve boundaries is shown in red. Time-series plots show sound pressure level (rms dB re 1 μPa) in lower and upper frequency bands along with spectrograms, illustrating the changes in sound intensity and frequency composition over the drift measured by the two drifters (b–c).

Corresponding to the map, hashed lines indicate times when a drifter entered and exited the reserve boundary, and red shading indicates times when the drifter was located above reef structure. Sound pressure level was estimated within a series of nonoverlapping 10-sec duration windows over the length of the recording. Spectrograms were produced using zero-padded 0.5-second duration Hamming windows with 25% overlap. (Panel C adapted from Lillis et al., (2014b) Figures 3 and 4 panel D).

same pronounced decrease with distance from the reef, there were higher levels observed nearest to the reef compared to 50–100 m away (Figure 7a, b), and fish calls were detected in the near-reef portion of the drift, but not in the subsequent off-reef period. A diving vessel was visually observed in the Tektite area at 11:50, and the acoustic input of this transient source is clearly evident in the SPL time-series (Figure 7b). While the mechanical interference associated with wave action on the drifter in the latter half of this deployment was largely removed from the SPL time-series by the applied filter, the spectrogram illustrates the presence of this noise (Figure 7c, short-duration red vertical lines up to ~5 kHz), and corresponds to the timing of the drifter entering the less sheltered waters of the opening of the bay.

Drift 2 traversed the Yawzi Point reef site from East to West, providing acoustic data for the middle section of the reef and the adjacent sandy bottoms on either side (Figure 8a). This dataset provided a close examination of the intra-reef soundscape variation along the drift track, showing increased SPL above all reef structure and the highest sound levels and snap rates measured within a ~100 m section of the West-side of the reef (Figure 8). A boat passing by the bay at 13:42 and again at 13:51 caused a spike in the low frequency SPL (Figure 8b). Low frequency sound levels were again more variable and less clearly dependent on proximity to reef, compared to the higher frequency analysis band (Figure 8b). However, inspection of spectrograms at fine temporal resolution, along with listening by expert operators, found that fish vocalizations within the low frequency band could clearly be distinguished in the recording and that calls were prevalent at time-points when the drifter was above structure in the mid-reef and absent from off-reef time-points (Figure 9).

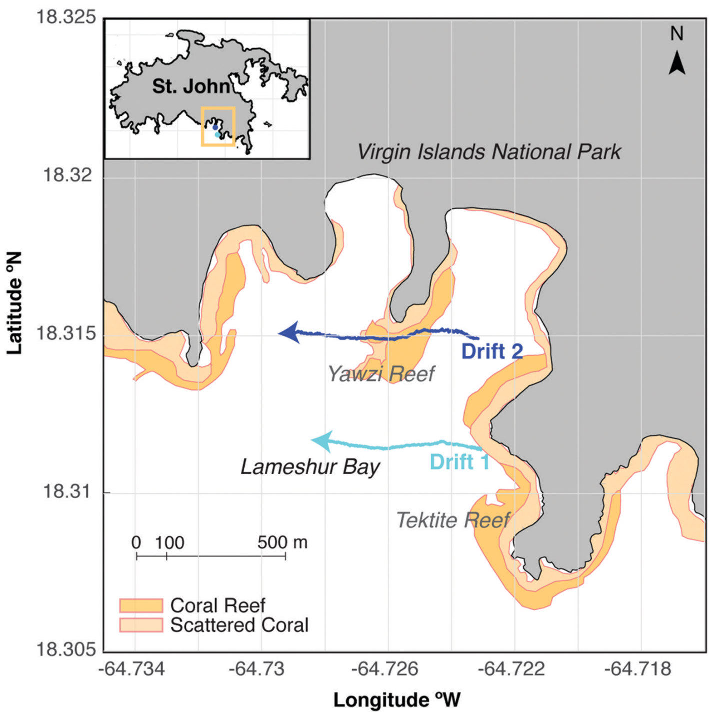

Figure 6. Map of locations of drifting recordings collected in Lameshur Bay, St. John, part of the Virgin Islands National Park.

Inset shows region where Lameshur Bay study area is located on St. John.

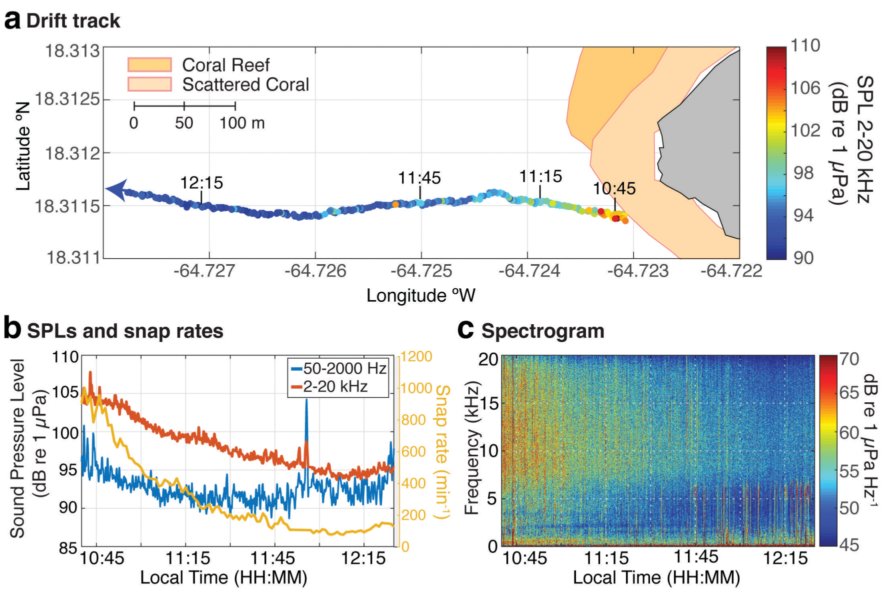

Figure 7. USVI Drift 1.

(a) Map of drifter track showing path of hydrophone drifter deployed adjacent to Tektite Reef. The extent of the coral reef structure based on benthic habitat maps is shown in orange, the remaining areas are sandy bottom with sparse seagrass. Time points in black correspond to time axes in plots b and c, and the colors of the drift path indicate the sound levels measured in the 2–20 kHz frequency band according to the color bar. (b) Time-series plots show sound pressure level (rms dB re 1 μPa) in lower and upper frequency bands along with snap rates (per minute) in yellow. Sound pressure levels were calculated within a series of non-overlapping 1-sec duration windows over the length of the recording, resulting data were smoothed with a 30-point (*i.e.*, 30-sec) moving average. (c) Spectrogram was produced using zero-padded 0.5-second duration Hamming windows with 25% overlap, FFT size: 2,048.

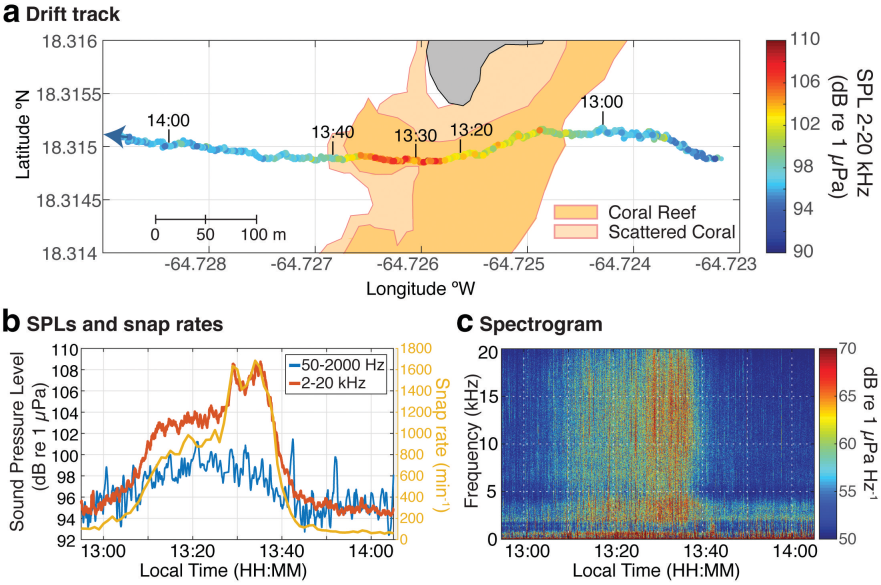

Figure 8. USVI Drift 2.

(a) Map of drifter track showing path of hydrophone drifter deployed and crossing Yawzi Reef. The extent of the coral reef structure based on benthic habitat maps is shown in orange, the remaining areas are sandy bottom with sparse seagrass. Time points in black correspond to time axes in plots b and c, and the colors of the drift path represent the sound levels measured in the 2–20 kHz frequency band according to the color bar. (b) Time-series plots show sound pressure level (rms dB re 1 μPa) in lower and upper frequency bands along with snap rates (per minute) in yellow. Sound pressure levels were calculated within a series of non-overlapping 1-sec duration windows over the length of the recording, resulting data were smoothed with a 30-point (*i.e.*, 30-sec) moving average. (c) Spectrogram was produced using zero-padded 0.5-second duration Hamming windows with 25% overlap, FFT size: 2,048.

Discussion

Drifting hydrophones provide a practical and effective soundscape sampling method, and can produce results that augment information collected by stationary hydrophones. The acoustic variation measured via the drifting hydrophone approach both informs hypotheses regarding the spatial variation and propagation of reef soundscape cues, and also provides important knowledge for future applications of passive acoustics to monitor coastal and estuarine marine reserves. In both the Pamlico Sound estuarine system and the St. John tropical coastal system, drifting hydrophones expanded upon previous results showing differences in sound levels and frequency composition between reef areas and adjacent off-reef habitats. The high spatial resolution acoustic data provided by these studies not only confirmed that a snapping-shrimp dominated frequency range generally defined the soundscapes of reef environments, but showed how closely the peaks in sound levels (particularly in higher frequency bands) correspond to the presence of benthic reef structure over surprisingly small scales. Drifter

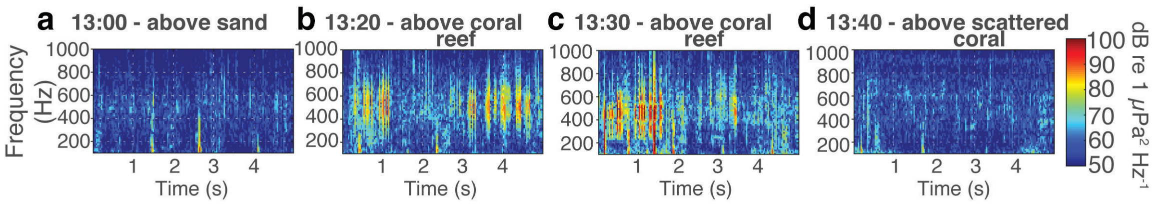

Figure 9. USVI Drift 2 snapshot spectrograms, showing abundant fish calls at timepoints when drifter was above reef structure (b and c), compared to absence of fish call detections at the start and end segments of the drift during passage towards and away from the reef, respectively (a and d).

measurements demonstrated that the method was particularly useful to detect subtle soundscape changes (acoustic gradients and hotspots of fish bioacoustic behavior) within reefs, or where there are many adjacent benthic habitat types. By carrying out these drifter deployments, more sites could be visited and compared, and sampled at higher spatial resolution than in stationary sampling methods (*e.g.*, Lillis et al., 2014a; Kaplan et al., 2015), and this greatly increased the knowledge of the range of variation in soundscape characteristics among and within reefs. The drifter datasets augmented the longer-term acoustic sampling program where a single stationary hydrophone is used to represent the overall soundscape of a given reef site.

Examples from several sites and specific drifts reveal substantial variation at relatively small scales and serve to highlight the utility of the drifter approach in generating ecologically significant acoustic data for use in soundscape ecology and in illuminating reef patterns in general. For example, the drifts across coral habitats in Lameshur Bay point to specific locations within the reefs ("acoustic hotspots") that may warrant further investigation. The finding that drifter acoustic measurements can be used to detect reef fish vocalizations across the reefs further illustrates its potential use as a method to provide a snapshot of within-reef fish presence and activity, and to identify potential variation in benthic fish communities, complementary to conventional visual sampling methods. More broadly, these surveys could help identify areas that potentially warrant further protection. For example, as many fish sounds are associated with vital behaviors such as reproduction and spawning, detecting areas with greater acoustic activity could facilitate specific management such as no-fishing zones or closures to diving. This mobile observation method enabled such observations in a relatively rapid manner. It is important to note that our drifter deployments were all conducted during daylight hours, however, many soniferous animals are known to exhibit crepuscular and nighttime chorusing (Radford et al., 2008; Ricci et al., 2016). Future drifter deployments that occur during crepuscular periods and in darkness will further advance assessments of soundscape variability in relation to ecological processes.

Because a broader context of these works was to understand the role of the soundscape for passively drifting planktonic organisms being transported through the estuarine system, the dynamic measurements of soundscape variation at multiple spatial and temporal scales provided especially insightful information from the larval perspective. Combined with longer stationary recordings and experimental data, the drifter measurements were instrumental to the development of a conceptual model of larval settlement in response to sound, to assess the feasibility of sound as a settlement cue based on the spatiotemporal scales of acoustic cues and animal responses (Lillis et al., 2014b). Given that many organisms of interest to other soundscape ecologists and marine bioacousticians are also mobile (*e.g.*, fish, mammals, larval forms), this dynamic approach gives insight into the soundscape variation these mobile creatures could experience.

The results presented also indicate that conventional hydrophone measurements are unlikely to capture relevant small-scale (*i.e.*, tens of meters) variation present in many heterogeneous coastal and estuarine systems, where habitats typically form a patchwork of benthic environments, or a habitat-type may vary greatly in its composition within an area. Studies of habitat soundscapes often use few hydrophones and relatively short (*e.g.*, minutes) recordings to represent an entire reef or habitat-type — a practice that warrants further investigation in light of the potential small-scale variation revealed in our higher-resolution drifter data. These datasets indicate that sound levels and frequency composition can differ substantially over only tens of meters, an important consideration for soundscape studies where recordings are typically made from a recording unit stationed 20–50 m from the target habitat. To prevent mis-characterizing the acoustics of a site, initial investigations of a given study area using drifting hydrophones would help assess the small-scale spatial variation and determine the need for within site replication and the appropriate placement of stationary hydrophones. By using multiple drogues, a high number of simultaneous and consecutive deployments can be carried out at a site to rapidly generate high-resolution soundscape data. Drifter-captured soundscape measurements also revealed important small-scale anthropogenic sources (*e.g.*, buoy chains) that could go undetected or be a considerable artifact, depending on placement of a stationary hydrophone.

The drifters and deployments described herein were tailored to our particular focus on habitat-related soundscapes as a larval fish and invertebrate settlement cue, however, the results demonstrate great potential for drifter use in obtaining fine-scale measurements that could fit numerous applications. To collect ecologically meaningful soundscape data, hydrophones and recorders can also be attached to existing surface drifters or other devices already made to measure animal behaviors (*e.g.*, Irisson et al., 2009). In high sea-state environments, it may be necessary to further decouple the hydrophone from the surface float using bungee material (*e.g.*, Kaplan and Mooney, 2016) or in deeper water locations a buoyancy controlled subsurface float may be used as a drifter platform (*e.g.*, Simons et al., 2009; Matsumoto et al., 2013). Overall, the success of these initial drifter soundscape surveys should encourage the development and application of this type of approach to enhance stationary soundscape measurements and to investigate the spatiotemporal variation in soundscapes patterns that may be relevant to important ecological processes such as recruitment and habitat complexity.

Funding sources

National Science Foundation, USA, Grants OCE-1234688 to DBE and DRB, ISO-1210292 to AL, DBE and DRB, OCE-1536782 to TAM and JKL, and funding to AL from Woods Hole Oceanographic Institution's Interdisciplinary Award and Postdoctoral Scholar Programs.

Competing interests

All authors declare that they have no conflict of interest.

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