Vol. 509: 57–70, 2014
doi: 10.3354/meps10917

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published August 27

Soundscape variation from a larval perspective: the case for habitat-associated sound as a settlement cue for weakly swimming estuarine larvae

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ABSTRACT: Settlement is a critical phase in the life history of most benthic marine organisms and has important implications for their survival and reproductive success, and ultimately for population and community dynamics. Larval encounter with settlement habitats is likely facilitated through the use of habitat-specific physical and chemical cues, but the scales over which particular habitat-related environmental cues may operate are rarely measured. In Pamlico Sound, North Carolina, USA we used passively drifting acoustic recorders to measure the variation in habitat-related underwater sound, a potential broad-scale settlement cue, at spatiotemporal scales relevant to dispersing bivalve larvae in the estuary. Sound levels increased by up to 30 dB during passage over oyster reefs compared to off-reef soft bottom areas, and sound level fluctuations in the 2000 to 23 000 Hz frequency range closely corresponded to the presence of oyster reef patches below drifters, indicating that sound characteristics could reliably provide a signal of benthic habitat type to planktonic larvae. Using these soundscape measurements and the known descent capabilities of oyster larvae, we demonstrate with a conceptual model that response to habitat-related sound cues is a feasible mechanism for enhanced larval encounter with settlement substrate.

KEY WORDS: Soundscape ecology · Larval habitat cues · Acoustic patterns · Hydrophone drifters · Oyster reefs · Passive acoustics

INTRODUCTION

The majority of marine invertebrate species that reside on the seafloor as adults begin their lives as dispersing planktonic larvae (Mileikovsky 1971). Spatiotemporal patterns of larval delivery and subsequent recruitment to benthic habitats can influence population and community-level ecological processes and patterns (Gaines & Roughgarden 1985, Kinlan & Gaines 2003, Allen & Marshall 2010). Understanding the biophysical interactions that drive the dispersal and settlement of larvae is a significant focus in marine ecology. Given that many benthic animals attach permanently to the substrate at settlement, and often have narrow habitat requirements, their survival probability and reproductive success depend heavily on settlement in favorable locations. A central question in larval ecology is, how do the larvae of benthic species locate often patchily distributed settlement habitats (e.g. coastal areas, isolated reefs) following pelagic dispersal periods of days to months?

Planktonic larvae acquire information from their environment using multiple sensory modes, and, although their movement over broad geographical scales is largely bound by physical oceanographic processes, their ultimate settlement site can be the outcome of behavioral and physiological responses to a suite of biotic and abiotic signals (Kingsford et al. 2002, Sponaugle et al. 2002, Levin 2006, McManus & Woodson 2012). Despite their relatively weak swimming capabilities, the larvae of many marine inverte-

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brates are not entirely passive propagules and may exert considerable control over their dispersal trajectory and subsequent settlement location via vertical positioning in response to environmental cues (Mileikovsky 1973, Chia et al. 1984, Butman 1987, Kingsford et al. 2002, Levin 2006). There are several mechanisms by which larval responses to their environment are proposed to influence settlement patterns at various spatial scales: (1) larvae 'partially navigate' by directing their vertical positioning in the water column in response to hydrodynamic, light, or salinity cues, exploiting tidal currents or circulation patterns to control retention or export (e.g. Epifanio 1988, DiBacco 2001, Morgan et al. 2012); (2) larvae respond to habitat-related environmental cues in the water column by sinking or diving, thus facilitating encounter with settlement substrate (e.g. Fuchs et al. 2004, 2010); (3) larval competency and metamorphosis is induced by certain environmental cues or delayed in their absence (e.g. Coon et al. 1990, Fitzgerald et al. 1998, Stanley et al. 2010, Gaylord et al. 2013); and/or (4) following encounter with a potential settlement location, larvae accept (i.e. metamorphose) or reject (i.e. re-enter plankton) the substrate based on fine-scale habitat properties (e.g. Hadfield 1986, Butman 1987, Eckman 1996).

Settlement and post-settlement success is likely enhanced by a combination of these mechanisms and the hierarchical integration of multiple cues (Kingsford et al. 2002). The relative importance of various environmental cues in driving settlement patterns is subject to the sensory adaptations, swimming capabilities, and habitat requirements of an individual or species, as well as the scales over which cues can operate. Substrate-associated chemical and hydrodynamic inducers of larval settlement and metamorphosis at small scales (millimeters to meters) have typically been emphasized in behavioral studies of larval invertebrates and are clearly important signals for larvae once viable habitat has been reached (Bourget 1988, Pawlik 1992, Rittschof et al. 1998). However, for the larvae of organisms with narrow habitat requirements, particularly those that must locate discrete patches of structurally complex habitats that are not widespread (e.g. reefs, hydrothermal vents), a major challenge is to first encounter settlement substrate over larger scales (meters to kilometers). To facilitate the orientation to and encounter with such patchy settlement substrate, it is likely that these larvae have adapted to utilize sensory cues that are distinctive, conservative, and detectable at habitat-scales. Environmental gradients that have been proposed as potentially useful habitat cues include chemical stimuli emanating from habitats (i.e. odor plumes), changes in turbulence due to flow over benthic structure, and variation in ambient sound (Kingsford et al. 2002, Levin 2006).

There is growing evidence that underwater sound meets the criteria to serve as a reliable and information-rich sensory cue to the dispersing larvae of many fish and invertebrate taxa (Rogers & Cox 1988, Simpson et al. 2005, Montgomery et al. 2006, Radford et al. 2007, 2010, Lillis et al. 2013). Variation in acoustic sources present in an environment (the 'soundscape'), determined by the spatial mosaic of physical and biological characteristics, provides a sensory context for organisms to locate spatially and temporally heterogeneous resources (Farina et al. 2011, Pijanowski et al. 2011). As a potential cue for larval settlers, sound is distinct compared to dissolved chemical cues in that its fluctuations and propagation are not influenced by rapid changes in hydrodynamics. In contrast to turbulence, which could indicate changes in the rugosity of benthic habitat below larvae in the water column (Fuchs et al. 2004, 2013), habitat-related sounds do not rely on tidal currents or water flow to operate, and are also capable of traveling greater distances. Moreover, acoustic spectral characteristics can convey detailed information that uniquely reflects the biological and physical features (e.g. presence and abundance of soniferous predator and/or prey species, feeding activity, depth, substrate type and structure) of the benthic habitat over which planktonic larvae are being transported. Compared to other environmental cues, habitat-related soundscapes could have certain advantages, including their temporal predictability, but it is important to note that the potential for masking by transient noises, such as weather events or anthropogenic noise inputs, might impede their efficacy.

Although sound has rarely been considered as a sensory signal for larval invertebrates, mechanosensory systems found in a range of marine invertebrate taxa could act as sound receptors (Budelmann 1989). The 2 primary candidates for marine invertebrate auditory function are (1) epidermal cells with cilia sensitive to deformation or deflection by acoustic vibrational stimuli and local water movements, and (2) internal statocyst receptor systems (Budelmann 1989, 1992). Statocysts are probable sound-detecting organs because they can, based on their structure, serve as linear accelerometers that detect fluid particle motion (Rogers & Cox 1988). Particle accelerations produced by a sound wave can be detected when a stimulus displaces the relatively heavy mass (statolith) that deflects the mechanosensory hairs that line the internal surface of the statocyst (Budelmann 1992). Statocyst hearing mechanisms have been demonstrated for crustacean and mollusk species by measuring neurological responses to acoustic and acceleration stimuli (Lovell et al. 2005, Mooney et al. 2010). Larval invertebrate auditory reception is essentially unstudied, but documented behavioral and settlement responses to soundscape properties provide convincing evidence that larval-stage animals can detect acoustic stimuli (Branscomb & Rittschof 1984, Radford et al. 2007, Stanley et al. 2011, 2012), and the presence of statocyst structures in the larval stages of many marine invertebrates suggests that they have this sensory capability (Budelmann 1992). Many bivalve species develop statocyst structures in the pediveliger (pre-settlement) stage (Cragg & Nott 1977, Gosling 2003).

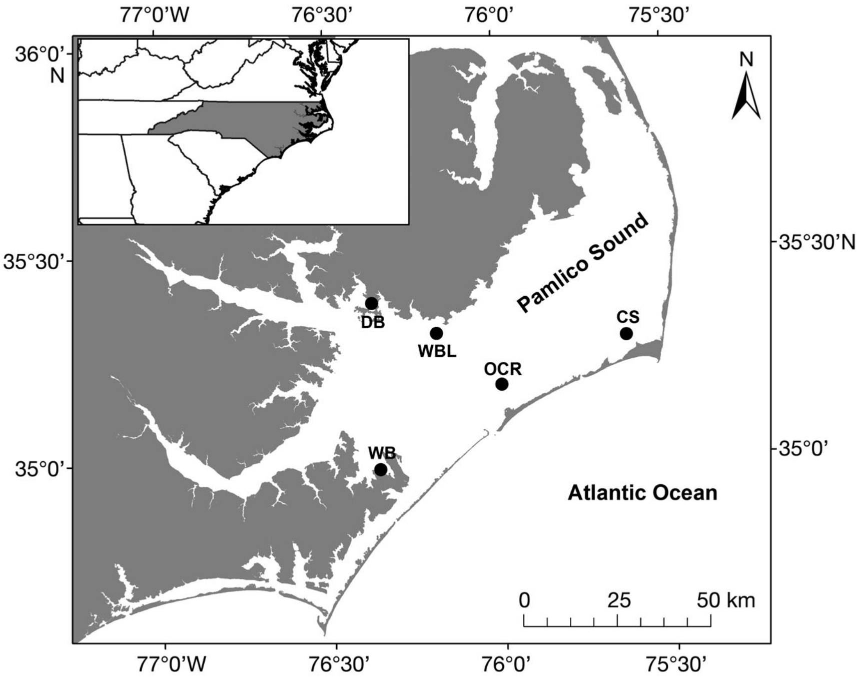

Fig. 1. Pamlico Sound, North Carolina, USA showing locations of oyster reserves acoustically sampled by drifting hydrophone (DB = Deep Bay, WBL = West Bluff, CS = Clam Shoal, OCR = Ocracoke, WB = West Bay)

Current knowledge of the use of acoustic cues by larval forms is limited. There is clearly a selective advantage for larvae that can respond to the unique acoustic properties of their settlement habitat and enhance the likelihood of successful encounter and selection of favorable attachment sites. Our recent soundscape measurements of oyster reef and off-reef habitats in Pamlico Sound, North Carolina have established that these estuarine habitats are consistently acoustically distinct, where oyster reefs form 'hotspots' of acoustic diversity with localized elevated levels of sound primarily in the 1.5 to 23 kHz snapping shrimp-dominated range, as well as the sounds of soniferous reef fish (Lillis et al. 2014). These results suggest that acoustic cues could be a reliable indicator of oyster reef habitat, and that the ability for larvae of reef-seeking organisms to respond to the soundscape would be highly adaptive. Complimentary laboratory and field experiments found increased settlement of Eastern oyster *Crassostrea virginica* larval cultures in response to oyster reef sounds compared to off-reef soft bottom sounds, indicating that the bivalve larvae can distinguish and respond to the soundscape characteristics of their settlement habitat (Lillis et al. 2013). Though the spatiotemporal scales over which a potential acoustic cue may operate are still unknown, and specific behavioral responses (e.g. diving, sinking) for oyster larvae to particular sound characteristics (i.e. frequencies, sound levels) are untested, the initial findings provide a compelling case for oyster reef sound as a broad-scale cue that could function to enhance habitat encounter and settlement success for the larvae of reef-dwellers. Therefore, the specific objectives of this study were to (1) measure variation in soundscape characteristics from the perspective of planktonic larvae dispersing in an estuary, and (2) develop a conceptual model of the spatiotemporal scales over which drifting bivalve larvae might respond to habitat-specific soundscapes.

MATERIALS AND METHODS

To capture habitat-related variation in acoustic characteristics that drifting organisms may encounter in an estuary, resulting from spatiotemporal changes in both physical and biological factors, drifting acoustic recorder surveys were conducted over subtidal oyster reefs and unstructured soft bottom in Pamlico Sound, North Carolina, USA (Fig. 1). Pamlico Sound is a shallow (mean depth = 4.5 m), wind-driven estuary with little tidal influence and stable salinities, and provides habitat for diverse fish and invertebrate populations (Paerl et al. 2001). We worked within a network of 10 subtidal oyster re-

Table 1. Oyster reserves in Pamlico Sound, NC, sampled by drifting acoustic recorders

Oyster reserve	Depth (m)	Area of hard substrate (m^2)	Construction material	Year created	Reef dimensions and configuration
West Bay	3.5	2725	Limestone marl, oyster shell	1996	160 × 20 × 1 m high reef; 75 × 20 × 1 m high reef; 6 mounds (2 m tall, 10 m diameter)
West Bluff	3.8	5325	Limestone marl	2005	75 discrete mounds (2 m tall, 10 m diameter) with 30 m inter-patch distance
Deep Bay	2.4	6278	Limestone marl, oyster shell	1996	190 × 20 × 1 m high reef; 5 mounds (1 m tall, 10 m diameter)
Ocracoke	5.8	4384	Limestone marl	2004	75 discrete mounds (2 m tall, 10 m diameter) with 30 m inter-patch distance
Clam Shoal	3.4	5783	Limestone marl	1996	241 discrete mounds (2 m tall, 10 m diameter) with 30 m inter-patch distance

serves that were established by the North Carolina Division of Marine Fisheries (NCDMF) from 1996 to 2013 to aid in the recovery of severely reduced oyster populations. Limestone boulders and oyster shell were used to construct the reefs, providing suitable settlement substrate for oyster larval settlement and subsequent development of diverse fish and invertebrate assemblages (Puckett & Eggleston 2012, Pierson & Eggleston 2014). The oyster reserves, located throughout Pamlico Sound, range in size between 0.03 and 0.19 km^2 and each contain between 1300 and 37 000 tons of substrate material. Oyster reefs within this network can vary substantially in their physical characteristics (e.g. salinity, exposure, depth, dissolved oxygen), oyster demographic rates (Mroch et al. 2012, Puckett and Eggleston 2012) and fish assemblages (Pierson & Eggleston 2014).

Drifting acoustic recorders were deployed in August 2011 and 2012 at multiple reserve sites (Fig. 1) to continuously measure small-scale changes in sound as oyster reef habitats were crossed. A total of 5 reserve sites were chosen that covered the entire southern half of Pamlico Sound and represented a range in reef characteristics (Table 1), with the intent of capturing variation in the soundscapes that drifting oyster larvae might experience. Drifting hydrophone deployments were conducted during August because (1) oyster larvae are dispersing in the estuary during this time (Ortega & Sutherland 1992, Mroch et al. 2012), and (2) it is a bioacoustically active season with differences previously detected between reef and off-reef habitat types (Lillis et al. 2014).

Drifting acoustic recording units consisted of a free-floating barrel containing an M-Audio Microtrack II recorder (48 kHz sampling rate, 24 bit, zero recorder gain), battery pack and handheld GPS unit, and a calibrated omni-directional hydrophone (Sensor Technology SQ-26-08, flat frequency response 0.03 to 30 kHz, sensitivity −169 dB re 1 V/µPa; or High Tech HTI-96-MIN, flat frequency response 0.02 to 30 kHz, sensitivity −164 dB re 1 V/µPa) weighted and suspended at 0.5 m from the water surface. This hydrophone placement depth was selected both to avoid hydrophone contact with reef structure during transit above high-relief portions of reserves and minimize surface and water flow noise around the moving hydrophone. West Bay, Clam Shoal and West Bluff reserves were sampled in 2011, and West Bay, Clam Shoal, Deep Bay and Ocracoke reserves were sampled in 2012 (Fig. 1). For each drifter trial, 2 drifters were deployed ~100 m apart and ~500 m upstream from a reserve boundary (Fig. 2). The drifters were released at locations projected to produce a drift path that crossed through the oyster reserve. Following drifter deployment, the boat was moved a sufficient distance to not interfere with the recordings, yet to maintain visual contact, and the motor was shut off. Drifters were collected once they had travelled approximately 500 m off the downstream edge of a reserve. Drift trials were repeated at a given site throughout a sampling day as many times as logistics and drift speed would allow. All drifts were conducted during daytime between 09:00 and 18:00 h because drifter units could not be visually monitored at night. Drifts were not carried out during dawn or dusk periods when temporal shifts in bioacoustic activity were most likely to occur (Radford et al. 2008). For reference, local sunrise and sunset times in mid-August 2011 and 2012 occur at ~06:20 and ~20:05 h, respectively.

Acoustic data were visually inspected and recordings truncated to remove noise from the research vessel motor. To examine the general acoustic dynamics during each drift, spectrograms of the full bandwidth recording were generated and the sound pressure levels (SPL) in 2 frequency ranges of interest

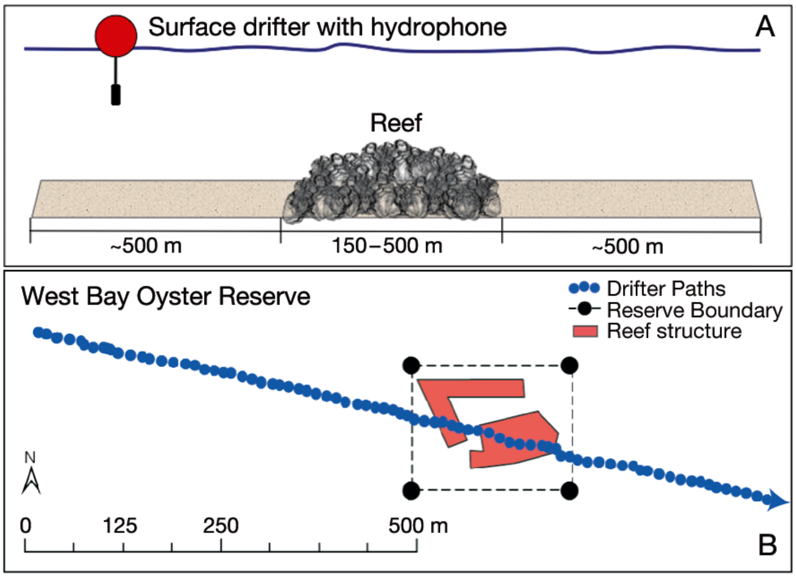

Fig. 2. (A) Schematic of drifting hydrophone method and (B) example drifter track across an oyster reserve, showing the boundaries of the reserve site and the configuration of reef structure (limestone boulders or shell) within the reserve

(100 to 2000 Hz and 2000 to 23 000 Hz) were computed for the duration of drifts. These frequency ranges were defined based on previous oyster reef sound characterization that showed these bands to be the most distinct between the subtidal habitats, particularly in the upper frequency range associated with invertebrate-generated sounds (Lillis et al. 2014). A comparison of drifter recordings and concurrent measurements made with a stationary hydrophone indicates that the drifter self-noise (due to flow and wave motion) is primarily below 100 Hz and therefore largely excluded from these analysis bands. GPS data were used to plot the courses of each drift and to determine the time points when the drifters were within the reserve boundaries and above reef structure based on NCDMF maps of original oyster reef configurations. This allowed for evaluation of the correspondence of acoustic characteristics with drifter positions in relation to benthic habitat type. Reef extent data were only available for the times of original reef creation, but provided an estimate of the reef shape and positioning within each reserve.

RESULTS

Habitat-related soundscape variability

At each location, multiple drifts were conducted throughout a given sampling day, producing a total of 24 drift recordings (4 to 6 successful drifter deployments per site) for unique trajectories across different parts of reserve sites containing oyster reefs and unstructured bottom. Weather, sea state, and current conditions varied between sampling days, and therefore between sampling of sites; however, no drifts were conducted during days with substantial wind or a sea state higher than 3 on the Beaufort scale. Capturing a range of variation in these physical variables was intended for this study, as the objective was to measure a range of variation in soundscape that drifting larvae experience, and not to control for or directly relate these factors to the soundscape measurements. Importantly, over the course of single drifts trials (~1 h duration) substantial changes in environmental conditions were not observed that would account for intra-drift on reef vs. off-reef acoustic patterns. Drift speed ranged from 0.12 to 0.30 m s^{-1} with an average speed of 0.23 m s^{-1}. This range is consistent with current speeds previously observed for Pamlico Sound waters, but the mean drift speed is slightly higher than the reported mean daily current speeds range of 0.1 to 0.2 m s^{-1} (Haase et al. 2012) and is probably due to surface wind influence on the drifter buoy.

All drifts showed higher broadband sound levels while crossing oyster reefs than during their transit over unstructured bottom (Figs. 3 & 4; representative drift for each site). Spectrograms of representative drifts consistently demonstrate higher acoustic power levels concentrated in the 1000 to 5000 Hz frequency range, and more impulsive broadband sounds from snapping shrimp (Au & Banks 1998) within reserve boundaries (Fig. 3). Similar to our prior stationary measurements of reef soundscapes (Lillis et al. 2014), recordings during transit over the oyster reef habitats were characterized primarily by these high intensity snapping shrimp sounds, and also contained vocalizations of common reef fish such as weakfish, black drum and toadfish. These reef-associated fish species produce grunts, knocks and croaks with dominant sound energy in the 100 to 1600 Hz range (Fine 1978, Ramcharitar et al. 2006). Changes in geophonic contributions to acoustic energy in this lower frequency band (e.g. wind noise, the sounds of bubbles and breaking wavecrests, Cotter 2008; as well as bottom

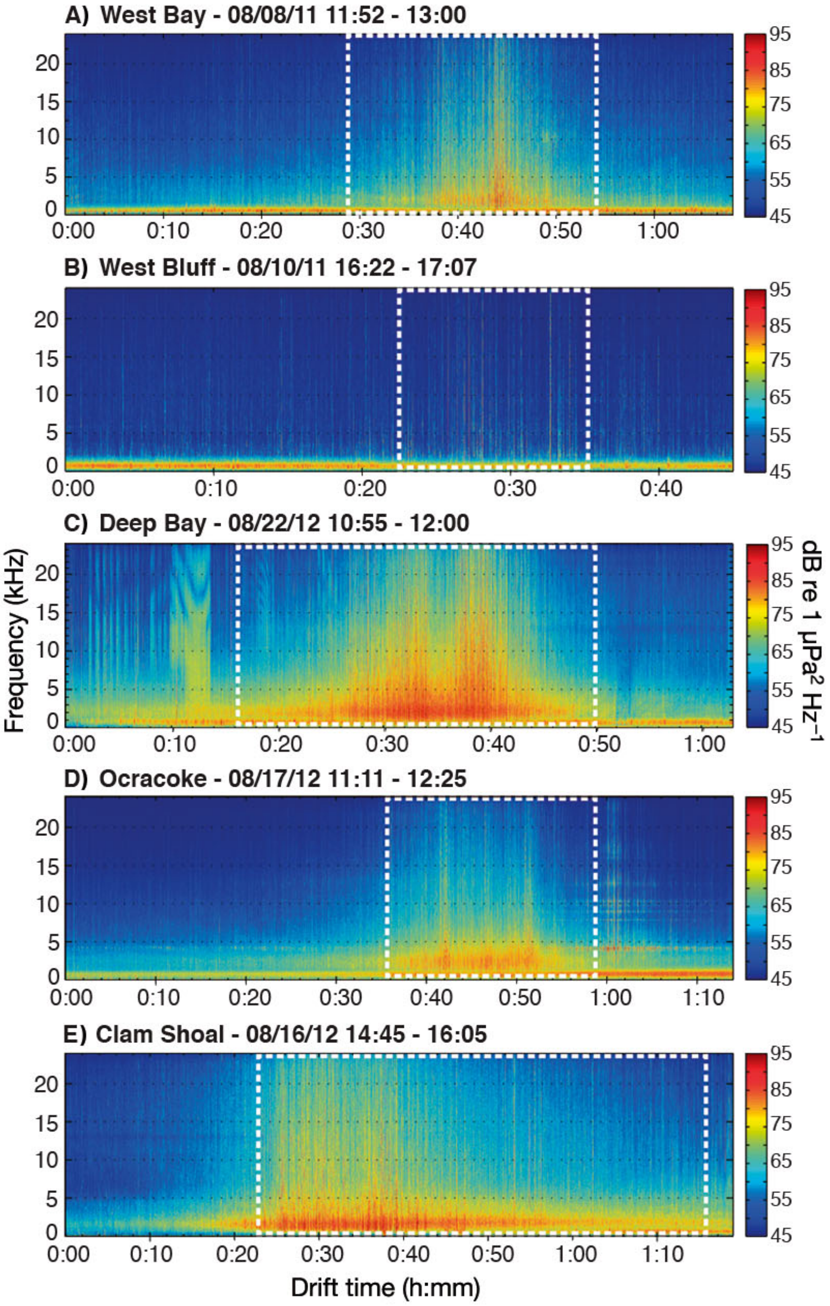

Fig. 3. Spectrograms of a representative drift crossing the reef for each sampled reserve site. Spectrograms indicate the sound intensity across frequencies over time. Dashed white lines represent time at which the drifter entered and exited reserve boundaries. Spectrograms were produced using zero-padded 0.5 s duration Hamming windows with 25% overlap. Dates are mm/dd/yy

turbulence, Urick 1983) are more difficult to detect in drifter recordings and were not clearly associated with benthic habitat differences during drifts.

By partitioning the data into lower and upper frequency bands (Fig. 4), the consistent association of the frequencies above 2000 Hz with the reef environment is clearly visible. Within reserve boundaries, the 2000 to 23 000 Hz frequency band increased in intensity to levels 20 to 30 dB re 1 µPa higher than outside of reserves. Increases of 15 to 25 dB re 1 µPa in the lower frequency band (100 to 2000 Hz) were measured within several reserves (Deep Bay, Ocracoke, Clam Shoal; Fig. 4C–E), but were less reliably associated with reef structure. For instance, at West Bay and West Bluff reserves, the low-frequency sound levels were consistent across the habitat types, with little increase within the reserves (Fig. 4A,B). At the Ocracoke site, the sound levels in the lower frequency bandwidth remained elevated upon exiting the reserve (Fig. 4D). Examination of spectrograms in the 100 to 2000 Hz band indicates that these patterns were due to repetitive biophonic signals in the 200 to 800 Hz range, and are most likely associated with fish aggregations that appear to occur in the off-reef areas at certain sites. The narrow peak in the upper frequency sound levels as the drifter exits the reserve (*t* = 1 h) at Ocracoke is most likely due to a 3 to 4 kHz noise produced by the reserve boundary marker buoy chain (Fig. 4D).

The strength of the reef signal varied between sites sampled, but was clearly distinguishable for drifts at West Bay, Deep Bay, Ocracoke and Clam Shoal (Fig. 3A,C–E). While less pronounced in West Bluff drifts, there was still a detectable increase in broadband snaps and sound levels in the higher frequency range (2000 to 23 000 Hz) within the West Bluff reserve boundaries (Figs. 3B & 4B). Reef characteristics differ among reserve sites (Table 1), but there are no clear single factors that predict the inter-site acoustic variation. Oyster reef demographic data are not available for these years; however, oyster densities and sizes were not previously found to significantly differ between West Bluff and the other reserves (Mroch et al. 2012) and relatively high fish abundances have been measured at this site (Pierson & Eggleston 2014). Deep Bay, Clam Shoal and West Bay, the reserves where the highest

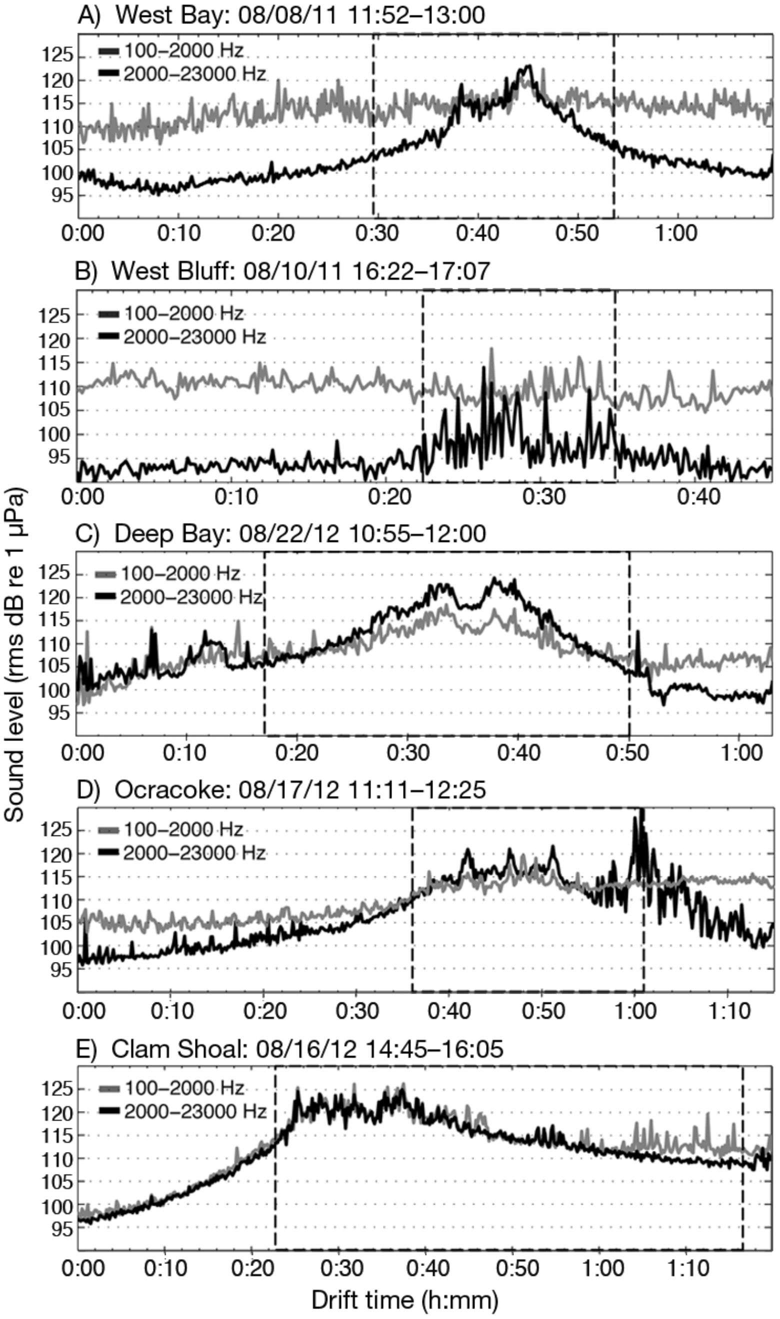

Fig. 4. Sound pressure levels in the 100 to 2000 Hz and 2000 to 23 000 Hz frequency bands for the duration of a drift crossing an oyster reef at each sampled reserve site. Dashed lines show time at which a drifter entered and exited reserve boundaries. Root-mean-square (rms) pressure was estimated within a series of non-overlapping 10 s duration windows over the length of the recording. Dates are mm/dd/yy

sound levels were observed, are also the shallowest sites (Table 1). Deep Bay and West Bay are also the most sheltered sites within embayments, and have a lower relief reef structure compared to the others. However, the deepest and most exposed site with high relief mound structures, Ocracoke, also showed a comparably distinct reef signal with high sound levels above reef structure. Interestingly, Deep Bay is the only site previously measured to have significantly lower oyster density compared to the other 4 sites (Mroch et al. 2012).

Closer examination of drifter recordings in relation to reserve configurations demonstrates the unique acoustic signal produced within the oyster reserves is highly localized to the reef features; soundscape variation within reserve boundaries is related to the benthic habitat structure immediately below the drifter. For example, the Clam Shoal reserve can be divided into 2 regions that differ in reef patch density: high density (~30 000 tons of limestone boulders) versus low density (~1500 tons) (Fig. 5A). The soundscape measured by a drift across the reserve was clearly affected by this reef configuration, with increased broadband sound levels within the high reef-density area, and reduced broadband sound levels in the low reef-density area (Fig. 5B). Sound levels increase steeply by 30 dB re 1 μPa over the 400 m approach to the reserve edge containing a high concentration of reef material, then are maintained at a high level within that area, followed by a ~15 dB re 1 μPa decrease during transit through the part of the reserve with little reef material (Fig. 5C).

The dependence of soundscape pattern on drift path, and therefore the variation in sound to which a planktonic larva may be exposed, is further illustrated by comparing multiple drifts at a single site. For example, 2 drifts conducted at the Deep Bay reserve demonstrate a strong reef acoustic signature highly localized to the reef structure below the drifters (Fig. 6). By combining band-pass filtered SPL data with GPS data to identify the times the drifters were in different parts of the reserve, we can detect substantial changes over relatively small space–time scales and relate them to benthic habitat structure. Because of the arrangement of reef structure at this site and the path that Drift 2 traveled, the close association of sound to the reef is underscored

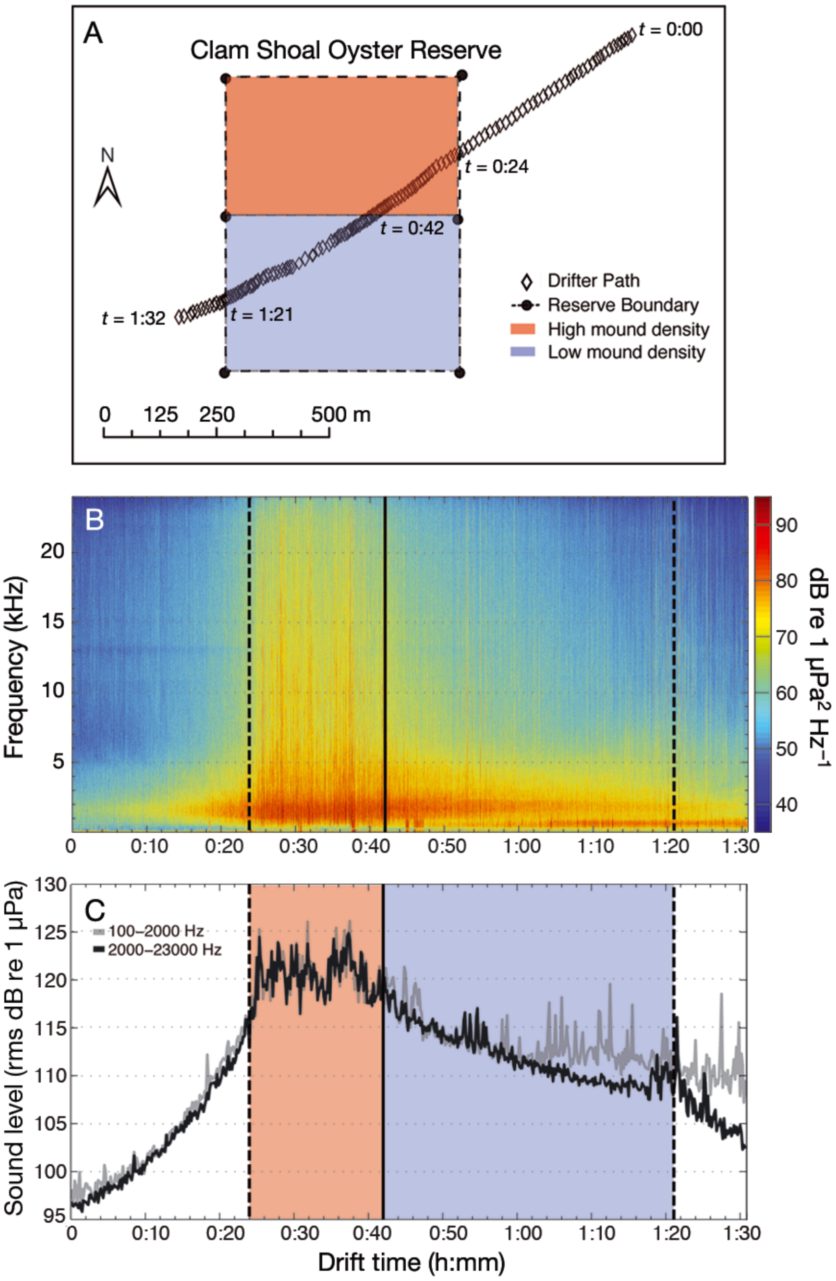

Fig. 5. (A) Sample drifter track for the Clam Shoal reserve, indicating portions of the reserve area that contained high and low densities of reef material. (B) Spectrogram and (C) sound levels bandpass-filtered into lower and upper frequency bands over the duration of the drift (generated as described in Figs. 3 & 4). The dashed line denotes when the drifter was within reserve boundaries, and shading indicates the times the drifter was transiting the 2 areas

by a rapid ~5 dB re 1 μPa drop in sound level over the 30 to 40 m gap in the reef material (i.e. when drifter is briefly over unstructured bottom) (Fig. 6B,C). The Deep Bay drifts also demonstrate non-biological and habitat-unrelated contributions to soundscape variability (Fig. 6). In Drift 1, peaks in the upper frequency band at *t* = 00:05 and *t* = 00:54 h are consistent with light rainfall (Nystuen 1996) from a short rain shower (Fig. 6A). A rain shower was also detected at *t* = 00:10 to 00:15 h in Drift 2 (Fig. 6B). A broadband signal at *t* = 01:08 h in Drift 1 was produced by the distant passage of a fishing vessel (Fig. 6A). These data highlight how meteorological and human input can contribute to the variable soundscape which larvae experience, and provide insight into the potential for masking or interference with biological soundscape components. For instance, larval detection of habitat-related soundscape cues may be hindered during periods of rainfall or heavy boating activity.

Conceptual model of soundscape variation as a settlement cue

The data from this study on the 'larval perspective' of the estuarine soundscape, combined with related work showing enhanced oyster larval settlement in response to the sounds of oyster reefs (Lillis et al. 2013), allow for the development of a conceptual model to address the question: Is it realistic for weakly swimming larvae, such as those of *Crassostrea virginica*, to sense and respond to the unique sound characteristics of oyster reefs under realistic flows and sinking velocities in a manner that would facilitate their encounter with preferred settlement substrate? The aim of this exercise is 2-fold: to assess the feasibility of sound as a habitat-scale settlement cue, and to provide a framework for future hypothesis testing.

We use Eastern oyster and hard clam *Merceneria merceneria* as model organisms to make contrasting predictions for the responses of a reef-dwelling (oyster) and a non-reef-dwelling (clam) bivalve species to habitat-related sounds. In this model, we first assume that late-stage larvae are located in the water column and transported by currents across heterogeneous substratum in the estuarine environment (Fig. 7: Stage 1). As larvae approach an oyster reef, the

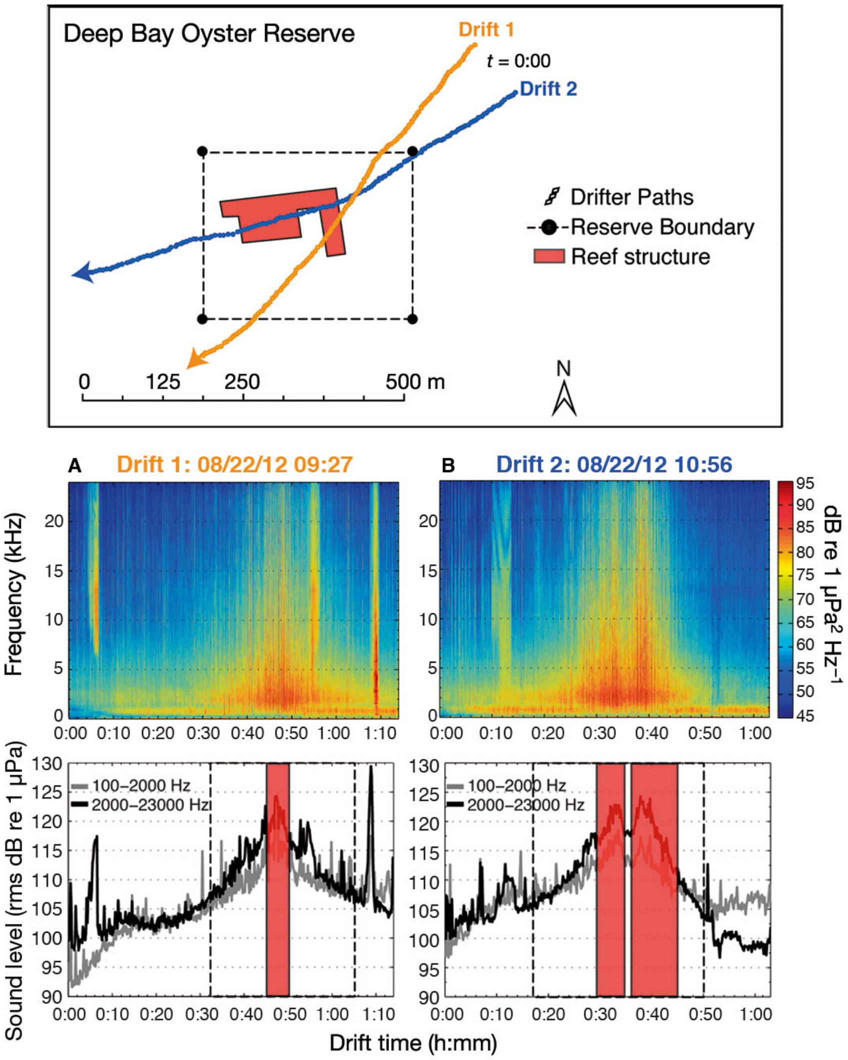

Fig. 6. Comparison of 2 drifting hydrophone deployments at Deep Bay reserve. Map depicts reserve boundaries, reef configuration and the paths of 2 drifts. Spectrograms are shown above plots of sound pressure levels in lower and upper frequency bands are shown for the duration of (A) Drift 1 and (B) Drift 2. Dashed lines and red shaded areas correspond to periods in which the drifters were within reserve boundaries and positioned above reef structure, respectively. Spectrograms and waveform rms SPLs were calculated as described in Figs. 3 & 4. Dates are mm/dd/yy

acoustic stimuli associated with the habitat (elevated sound levels and frequencies) are encountered (Fig. 7: Stage 2). In this scenario, we hypothesize that clam larvae will have no response (i.e. continue drifting) to reef sound characteristics (Fig. 7: Stage 2a). In contrast, the changing soundscape of oyster reefs is expected to elicit an adaptive behavioral response of downward vertical sinking or swimming by oyster larvae (Fig. 7: Stage 2b). Oyster pediveligers can, on average, sink at rates between 0.3 and 0.5 m min^{-1} in still water (Hidu & Haskin 1978), and recent work has found that oyster larvae can rapidly dive at speeds up to ~10 m min^{-1} in turbulence (Fuchs et al. 2013). If we use the most conservative sinking speed (0.3 m min^{-1}) to estimate the total time for larvae to reach the seafloor within oyster reserves where depths range from 2.4 to 5.8 m, we predict that larvae can descend to the bottom from the surface within 8 to 19 min after initiating sinking behavior in response to oyster reef sound. Following substrate encounter, possibly facilitated by turbulence and/or reinforced by detection of appropriate chemical cues near the substrate (Tamburri et al. 1992, Finelli & Wethey 2003, Fuchs et al. 2013), oyster larvae select their final attachment site based on cues such as texture, hydrodynamics, chemical exudates, biofilms, and, potentially, acoustic characteristics (Fig. 7: Stage 3). We expect clam larvae to sink or swim to the benthos to settle in the absence of reef sound in soft sediment bottoms (Fig. 7: Stage 4), utilizing local chemical and physical factors to select microhabitats in which to metamorphose (Keck et al. 1974).

The exposure time of planktonic larvae to a reef sound cue, and thus the ability to encounter substrate via a behavioral response, will vary depending upon the drifting speed, reef shape and size, as well as specific dispersal path. We can apply the drifter survey results from this study to estimate 'acoustic cue windows' and evaluate the feasibility of sound as a settlement cue in this system. For example, although behavioral response thresholds and detection frequencies for oyster larvae are currently unknown, oyster settlement responses were detected for oyster reef sounds between 118 and 124 dB re 1 µPa (Lillis et al. 2013), levels reached or exceeded for drifters above the reef structure at all sites except West Bluff. Drifter surveys indicate that the time period when larvae were directly above reef structure and exposed to these peak reef sound levels ranged from 5 to 20 min. If we assume that larvae can detect the reef-associated sound level increase at lower than peak levels, and begin descent in response to changes in the soundscape upstream of the reef edge, this could

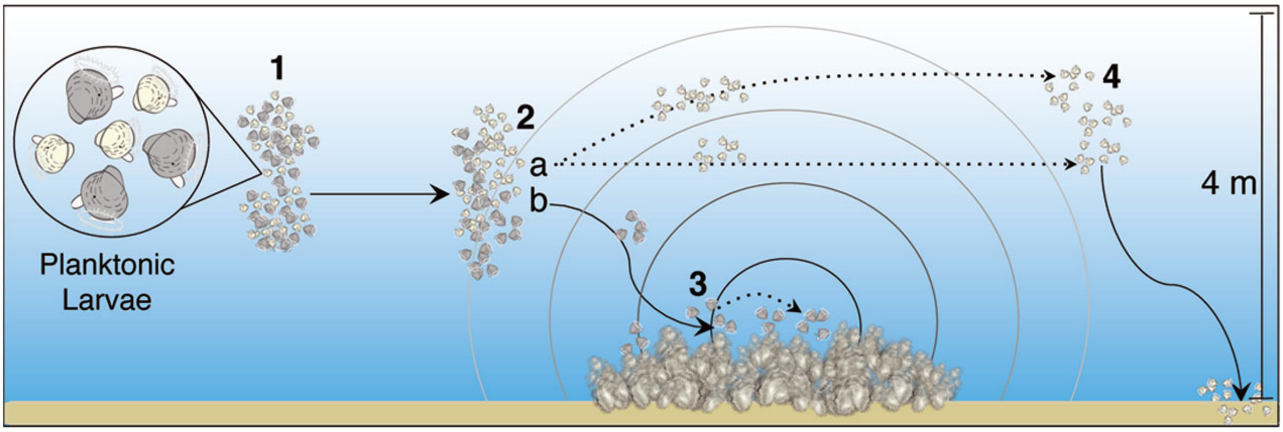

Fig. 7. Schematic depicting how habitat-related sound could operate to facilitate larval encounter with settlement substrate in an estuarine system. Oyster larvae (which prefer to settle on other oysters) are depicted in gray, clam larvae (which prefer to settle on muddy-sand bottoms) are white

expand the acoustic cue window range to approximately 10 to 45 min for our drifts. Given that late-stage larvae are unlikely to be at the near surface (Dekshenieks et al. 1996, Carriker 2001, Baker & Mann 2003), and larvae are capable of actively propelling themselves downward much faster than 0.3 m min^{-1} (Finelli & Wethey 2003, Fuchs et al. 2013), it is conceivable that the time window in which larvae could take advantage of an acoustic cue could be much less than the 8 to 19 min estimate above, and in most cases well within the acoustic window measured by the drifters. Note also that the drifters are imperfect larval dispersal mimics, influenced by surface wind and waves, and likely underestimate the time scales over which larvae may be exposed to habitat sounds. Therefore, under many realistic field scenarios of current speed and reef configurations, oyster larvae should have adequate time to respond to reef-associated sound characteristics by moving toward the bottom. Larval response to reef-associated sound is a reasonable mechanism by which larvae can enhance their encounter with preferred settlement habitat.

DISCUSSION

This study is among the first to characterize the ecologically relevant spatiotemporal scales over which habitat-associated acoustic characteristics can vary during the transport of a planktonic larva. The soundscape measurements collected by drifting acoustic recorders confirm that acoustic characteristics closely vary with benthic habitat type and support the hypothesis that reef sounds provide a distinct habitat indicator at scales relevant to larval transport over heterogeneous seafloor structure. Soundscape changes were observed for each drift in association with transit over reef habitat, where sound levels increased by up to 30 dB re 1 µPa. These changes are primarily and most consistently observed at higher frequencies (2000 to 23 000 Hz), in agreement with our prior reef versus off-reef habitat characterization (Lillis et al. 2014). Variation in the strength of the reef sound signal among sites was detected (e.g. West Bluff reserve showed a relatively small increase in sound levels over reef compared to other sites), as was variation in overall reef signal composition. For instance, the reef-associated acoustic signature at certain sites (e.g. Deep Bay, Clam Shoal) included elevated sound levels in the lower frequency band (100 to 2000 Hz) in addition to upper frequencies. At reserve sites where these lower frequency sounds were not closely associated with reef structure (e.g. West Bay, West Bluff), there may be nearby habitats (e.g. seagrass) that harbor soniferous fish. The variety and unpredictability of lower frequency sound sources reinforces the idea that the broadband, invertebrate-generated soundscape components, or sounds distinctly produced by a sedentary reef-dwelling fish species, are most closely associated with reef structure and are therefore the best candidate for habitat-specific settlement cues (Lillis et al. 2013).

Soundscapes are a complex phenomenon, integrating myriad physical and biological factors, and the observed inter-site variation in the reef signal likely relates to a combination of differences among the reserves. Certain differences detected in the reef signal strength between sites could relate to reef variables such as depth, reef structure or reef community demographics; however, available community-level data are limited for the reserves, and correlating specific environmental factors to acoustic variables was outside the specific objectives of this study. It is also important to note that these drifts were only carried out over single days at each location and do not necessarily define the acoustics of a site or the differences between sites, but rather demonstrate the amount of heterogeneity possible, as well as highlight the need for further investigation to identify the drivers of inter-reef variability (Lillis et al. 2014).

Irrespective of inter-site variation in the sounds produced by oyster reefs, the conceptual model developed in this study suggests that passively dispersing oyster larvae could enhance their chances of encountering preferred settlement substrate by responding to the changing soundscape under realistic current speeds, reef patch sizes, water depths, and larval descent speeds. Behavioral responses to oyster reef sound have not yet been determined, and quantifying the bivalve larval responses (e.g. sinking or diving) to different sound levels and frequencies is a key next step to test and refine our conceptual model. The drifter-collected acoustic data provide ecologically relevant levels of variation for future larval experiments. Logistical limitations of the drifter technique prevented the collection of these data overnight, therefore missing potential diel variation in soundscape dynamics. However, the reef-related elevated sounds were comparable in composition and level to previous dusk and night recordings (Lillis et al. 2014), and evidence that snapping shrimp, the major sound source in this study, have a reliable diel pattern in this estuarine system is not strong (A. Lillis unpubl. data). Even so, if the reef sound increases at night due to increases in animal foraging and activity, the reef signal would be stronger than our conceptual model estimates and provide a stronger orientation and settlement cue than posited in our conceptual model. Forthcoming analysis of oyster reef temporal patterns in noise will aid in assessing the importance of diel, and other temporal variation to the soundscape cue.

Drifting hydrophone recordings also revealed interesting variation in anthrophonic (e.g. buoy noise, boating activity) and geophonic (e.g. rainstorms) inputs to the larval soundscape experience that should be considered in future investigations of larval response to acoustic stimuli. The high amplitude transient sound sources (e.g. boat motors, storms) could be relevant to biological activities such as larval settlement because if they spectrally overlap with habitat-related sounds they may interfere with the detection of soundscape cues by marine organisms (Slabbekoorn & Bouton 2008, Clark et al. 2009). Sounds produced by anthropogenic structures (e.g. buoys, windmills, vessels) that share acoustic characteristics with settlement cues could attract larval settlers (e.g. Wilkens et al. 2012), and have implications for biofouling management or artificial reef establishment. Ongoing long-term monitoring of our reef and off-reef study sites will provide more information about the impact of weather events and anthropogenic sources, as well as temporal variability at multiple scales, on habitat-related soundscape patterns. As our understanding of the role of sound in ecological processes such as larval settlement grows, comprehensive measurements of the ambient soundscape could be particularly valuable in addressing questions of anthropogenic noise impacts on marine ecosystems (Cotter 2008, Slabbekoorn & Bouton 2008, Slabbekoorn et al. 2010).

Compared to conventional fixed hydrophone recordings, drifter-collected acoustic data give new insight into the potential larval experience within a dynamic acoustic environment. Most aquatic animals, however, including non-arthropod larvae, are likely sensitive to fluid particle motions of sound waves as opposed to differential pressure (Budelmann 1992). With this in mind, it is worthy to note that our hydrophone-based measurements may somewhat underestimate the true change in acoustic stimuli (particularly at low frequencies) experienced by larvae near the reef. Although pressure changes are proportional to the acoustic particle velocities at far-field ranges, in the acoustic 'near-field', particle motions may be influenced by hydrodynamic flow, and at ranges less than ~1/4 wavelength from the (dipole) source this local component cannot be considered negligible (Kalmijn 1988). Efforts to directly measure particle motions in the field are advancing (MacGillivray & Racca 2005, Wahlberg et al. 2008, Radford et al. 2012) and future development of technology and approaches to quantify particle motions will improve our ability to make increasingly ecologically relevant soundscape recordings.

Larval invertebrates can respond rapidly to cues by changing their behavioral mode (Hadfield & Koehl 2004, Koehl & Hadfield 2010) and molluscan veliger larvae can regulate their vertical movements in response to environmental variables through fine-scale ciliary coordination, contraction of velar lobes, and rapid withdrawal of the velum and foot (Murakami & Takahashi 1975, Mackie et al. 1976, Arkett et al. 1987). Late-stage oyster larvae exhibit active downward propulsion greatly exceeding the capabilities of the larvae of other mollusks (Finelli & Wethey 2003, Fuchs et al. 2013), and possess statocysts that have been implicated in the detection and response to turbulence-driven accelerations (Fuchs et al. 2013). These larval characteristics, combined with the relatively patchy distribution of their preferred settlement habitat, suggest that larval oysters may be particularly suited to use soundscape cues as part of their settlement process in oyster reef patches. In addition to the need for tests of oyster behavioral responses to a range of acoustic stimuli, the present study highlights the need for investigation of other basic aspects of larval settlement ecology. For example, even for relatively well-studied species such as the eastern oyster, our knowledge of key elements of their dispersal and settlement behavior that may affect their use of soundscape cues is limited (e.g. vertical distributions, diel or tidal timing of settlement). An investigation of the depth distribution of late-stage *Crassostrea virginica* larvae at a single location in the Chesapeake Bay found larvae concentrated in the lower half of the well-mixed water column, and suggested that this distribution was the result of active behavior that increases their ability to encounter near-bottom cues (Baker & Mann 2003). Additional studies of larval vertical distributions in other locations and stratification types, as well as investigations of settlement timing (e.g. day vs. night), are needed to better understand the oyster settlement process and evaluate the role of environmental variables such as sound.

Because productive natural subtidal oyster reefs are not present in the study region, the reef soundscapes measured for this study were all collected at restored oyster reefs that were created by deployment of material suitable for oyster settlement, which may not exactly represent the natural reef soundscape, but to which we would expect organism responses to be adapted. However, in the case of the Pamlico Sound oyster reserves used for this study, it is reasonable to assume that the present soundscapes of the artificially created reefs are similar to historical natural reef soundscapes, based on the successful establishment of the reef communities (and therefore biophonic components) over the past 10 to 15 yr (Powers et al. 2009, Puckett & Eggleston 2012, Pierson & Eggleston 2014), and the original use of materials (shell and limestone marl) with similar properties to natural reef structure. Given that reef community structure and the types of sound producers on the restored reefs are comparable to those of natural reefs, it is likely that the soundscape variation captured in this study is representative of oyster reefs in general. A small-scale study to compare natural and artificial oyster reef soundscapes found no consistent differences in snapping shrimp snap counts between natural and restored reefs, but both reef types had higher sound production and number of snaps compared to bare bottom (Becerra 2012).

This study establishes ecologically relevant scales of soundscape variation across distinct estuarine habitats and identifies a likely role of sound as part of the overall ‘cuescape’ for weakly swimming, estuarine bivalve larvae. A compelling area for future investigation will be to resolve the relative importance and sequence of multiple settlement cues over various spatiotemporal scales and under different environmental conditions. Because investigation into sound as a settlement cue for larval invertebrates is at an early stage, adequately characterizing the putative stimulus from a larva's point of view is central to generating testable hypotheses and determining suitable experimental treatments for future work. Our characterization of soundscape variation and the development of a conceptual framework build capacity for the investigation of sound as a larval settlement cue. Although we illustrate the concept of sound as a settlement cue using bivalve larvae, it could be applied to larvae of other reef- and non-reef-dwelling organisms. Detailed examination of the sound levels and frequencies that elicit larval responses, and incorporation of empirical behavioral data into modeling efforts, is fundamental to improving the biophysical models used to predict larval recruitment patterns and connectivity.

Acknowledgements. We thank field assistants J. Peters, G. Plaia, R. Dunn, H. Eggleston and B. Gericke for help with drifter deployments. We are grateful to T. Wolcott for assistance and use of equipment for acoustic recorder calibration, and to J. Luczkovich and D. Kamykowski for valuable feedback on this study. We also thank 3 anonymous reviewers for providing comments that improved the original manuscript. Funding for the early stages of this project was generously provided by a National Shellfisheries Association Student Research Grant, a PADI Foundation Grant (#5145), and American Academy of Underwater Sciences Scholarship to A.L. in support of PhD research. This study was further supported by National Science Foundation Grants OCE-1234688 and Doctoral Dissertation Improvement Grant to A.L. (ISO-1210292).

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Editorial responsibility: Nicholas Tolimieri, Seattle, Washington, USA

Submitted: February 4, 2014; Accepted: June 11, 2014
Proofs received from author(s): August 14, 2014