Tidal Modulation of Nocturnal Vertical Migration from the Benthos: A High-Resolution Acoustic Analysis

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Abstract- Emergence-trap sampling has shown that several species living primarily on or in the sediment emerge nightly into the water column. A TRACOR acoustic profiler, TAPS, was mounted on the sea bottom, looking upwards in approximately 10 m of water in the Damariscotta River Estuary, Walpole, Maine. TAPS emits high-frequency (265-3000 kHz) sonar pulses and each minute measures backscatter from 12.5-cm range bins in the water column. TAPS data showed a distinct increase in backscatter in the water column most evenings, beginning near or after dusk and terminating before dawn. Emergence-trap samples suggest that the acoustic signal was dominated by *Neomysis americana* and *Crangon septemspinosa, a possum and decapod shrimp, respectively.* In addition, there appeared to be a second emergence event per night. A higher-density emergence event occurred shortly after the first peak in tidal speed after dark, as the tidal currents were decelerating. Although "emergence" of hyperbenthic organisms has only been documented as occurring at night, a similar increase in backscatter was observed during the day at a similar stage of the tide as nocturnal emergence events. The backscatter increase measured during the day, however, was significantly smaller than at night. Our acoustic results suggest that emergence in the Damariscotta River Estuary is tidally modulated. They also suggest that emergence in an environment with strong tidal velocities may be more temporally complex than previous studies by non-acoustic means have been able to resolve.

I. INTRODUCTION

Numerous species of macrofauna living in, on or near the sediment (infaunal, epi- or hyperbenthic organisms) in some coastal and estuarine systems emerge nightly into the water column (e.g. [10, 7]). This regular migration resembles the better-studied vertical migration of some open-ocean zooplankton. In the open ocean, migrating zooplankton have been visualized by examining acoustic backscatter. The large groups of migrating zooplankton that cause extensive backscatter in the open ocean are collectively called the deep scattering layer. This study used acoustic methods to resolve analogous migration patterns of hyperbenthic animals in shallow water, a phenomenon recently dubbed the "shallow scattering layer [5].

Acoustic methods have proven effective in measuring such vertical migrations in a lake [9] and in a shallow marine setting at West Sound, Orcas Island, Washington [5]. Acoustic methods are particularly effective at monitoring near-bottom plankton, which are notoriously difficult to sample using conventional methods. Most importantly, acoustic methods of observation provide excellent spatial and temporal resolution.

This project addresses several questions. First, can a pattern resembling vertical migration be resolved using acoustics in an environment with strong currents? Can the high resolution observations provided by acoustic technology enable us to quantify the timing and magnitude of benthic emergence? Finally, can we detect the influence of the tides on the acoustically observed pattern?

II. METHODS

For this project, a TRACOR acoustic profiler (TAPS-6 from BAE SYSTEMS, San Diego, CA), abbreviated as TAPS, was deployed in the Damariscotta River estuary during the summers of 2001 and 2002. The Damariscotta River estuary, located in mid-coast Maine, is tidal, well mixed, and receives very little freshwater input. Its tides are semi-diurnal with velocities on the order of 25 cm s^{-1}. Substrate in the study area was a sandy silt.

TAPS as we deploy it is a multi-frequency (265, 420, 720, 1100, 1865, and 3000 kHz), moored, inverted echosounder. TAPS was placed by divers in ~ 10 m of water 50-100 m from the pier at the Darling Marine Center, Walpole, ME. Power was supplied to TAPS from the pier through a 500-m, multi-conductor cable. Once every minute, each transducer of TAPS emitted 24 sets of high-frequency sonar pulses and measured backscatter from 12.5-cm range bins in the water column directly above TAPS. Within TAPS, the backscatter measurements of each set were averaged. All 24 averages were then summed to produce an output representing the backscatter for one minute. This value was transmitted to a laptop computer on the pier through the conductor cable.

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A multi-frequency inversion was performed, to obtain volume estimates from backscatter measurements [2, 3, 4, 6].

One of the most difficult tasks in this study of benthic emergence was objective definition of an emergence event. An algorithm was devised that uses both the magnitude of increased abundance and the duration of the increase to define an event. For a given time period, this algorithm searches a strip from 2-5 m above TAPS to find the initiation time of the longest-lasting, highest-density event. This algorithm was used in examination of nighttime (1900-0700 hours) and daytime (0700-1900 hours) periods. The emergence algorithm identifies observations above a threshold value in biovolume (mm^3 m^{-3}). This threshold can vary from depth to depth or night to night. The algorithm searches each depth for observations above an arbitrarily low threshold. If there are more than 240 observations (min) above the selected value, the threshold is raised. Then the depth is searched again. The process repeats until ≤ 240 observations fall above the threshold. The median threshold value used to find emergence for a given time period (over all depths searched) estimates the "magnitude" of the event.

During summer and fall of 2001 and 2002, four emergence traps were deployed in the area around TAPS an average of four times per week. Traps were deployed for approximately 24-h beginning around 1300 hours EDT. The basic trap design is pyramidal with a 1-m^2 base made of aluminum angle stock that penetrates into the sediment. The faces of the pyramid are covered with 1-mm Nitex™ mesh. At the top of the trap is a 2-cm diameter tube leading into a collection bottle. The collection bottle has a mesh-covered hole at the top to allow ambient water to circulate into the bottle and prevent hypoxia. Emerging animals from the one-meter square beneath the trap will be funneled into the collection bottle if they continue to migrate vertically through the orifice. Although the traps are imperfect, e.g. they change the water flow regime above the sediment and may modify an animal's behavior, they provide baseline taxonomic and size information.

III. RESULTS

Trap samples indicate that the primary emergers in the Damariscotta River estuary are the mysid or possum shrimp *Neomysis americana* and the decapod shrimp *Crangon septemspinosa*. Other species of mysids, cumaceans, amphipods, decapods and copepods were also captured in our emergence traps. Nocturnal emergence can be resolved by TAPS beginning in late June. The emergence behavior persists through October. Emergence events are seen on both incoming and outgoing tides.

The emergence pattern observed acoustically in the Damariscotta estuary site does not follow previously documented patterns. From previous studies, using both acoustic and trap sampling methods [5, 8, 7], we expected mysids to engage in primarily one, coherent daily emergence event. TAPS data from the Damariscotta estuary site, however, show two (or more) nightly emergence events (e. g. Figure 1).

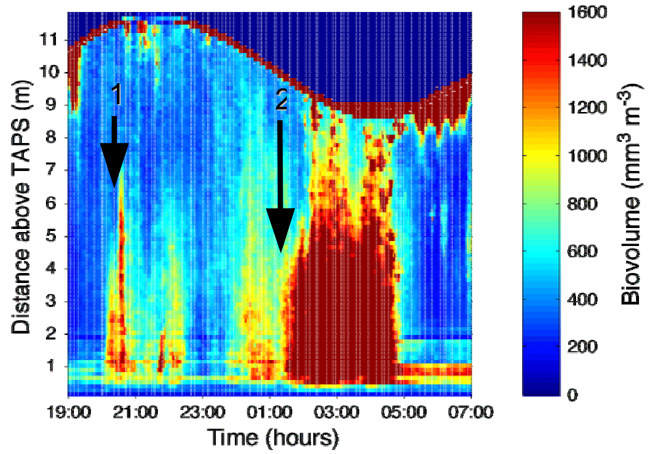

Fig 1. Multiple emergence events can be observed in one night. The first increase in biovolume (1) is around sunset. The highest-density emergence event (2) occurs shortly after the first peak in tidal velocity after dark.

One emergence event, beginning shortly after dusk, resembles the conventionally observed pattern. The strongest event of the night, however, occurs at a fixed tidal phase. The two emergence patterns may be in or out of phase depending upon the time of sunset and the tidal cycle.

The larger, high-density emergence event frequently occurred at the same phase of the tide. There is a strong linear relationship between the estimated time of slack tide in Boothbay Harbor (used here as a proxy for phase of the tide) and the initiation time of the high-density emergence event. This relationship can be seen in data collected in both 2001 (R^2 = 0.81) and 2002 (R^2 = 0.84) (Figure 2).

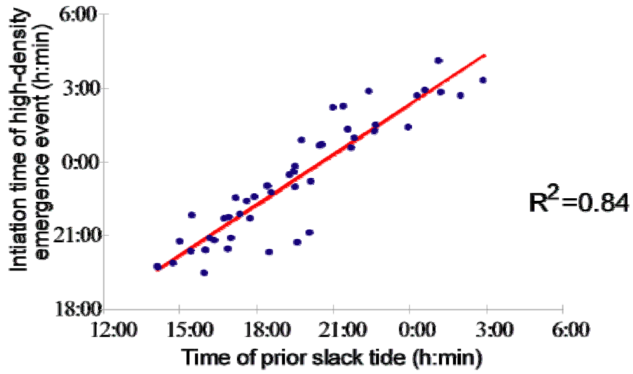

Fig 2. In 2002, there is a significant linear relationship between the time of slack tide in Boothbay Harbor (a proxy for phase of the tide) and the initiation time of a nocturnal high-density emergence event.

Generally, emergence began between 3.5 and 4 h after local slack tide, when the local tidal currents were decelerating.

While emergence has generally been conceived as an event occurring after dark, the close relationship between tidal phase and initiation of emergence provoked questions about the pattern of backscatter at the same phase of the tide during the day.

Applying the emergence algorithm to daytime observations highlighted an “emergence” event during the day near the same phase of the tide as the preceding night’s emergence event (Figure 3). The magnitude of the daytime events was substantially smaller (max~550 mm^3 m^{-3}) than events occurring at night (max~1600 mm^3 m^{-3}).

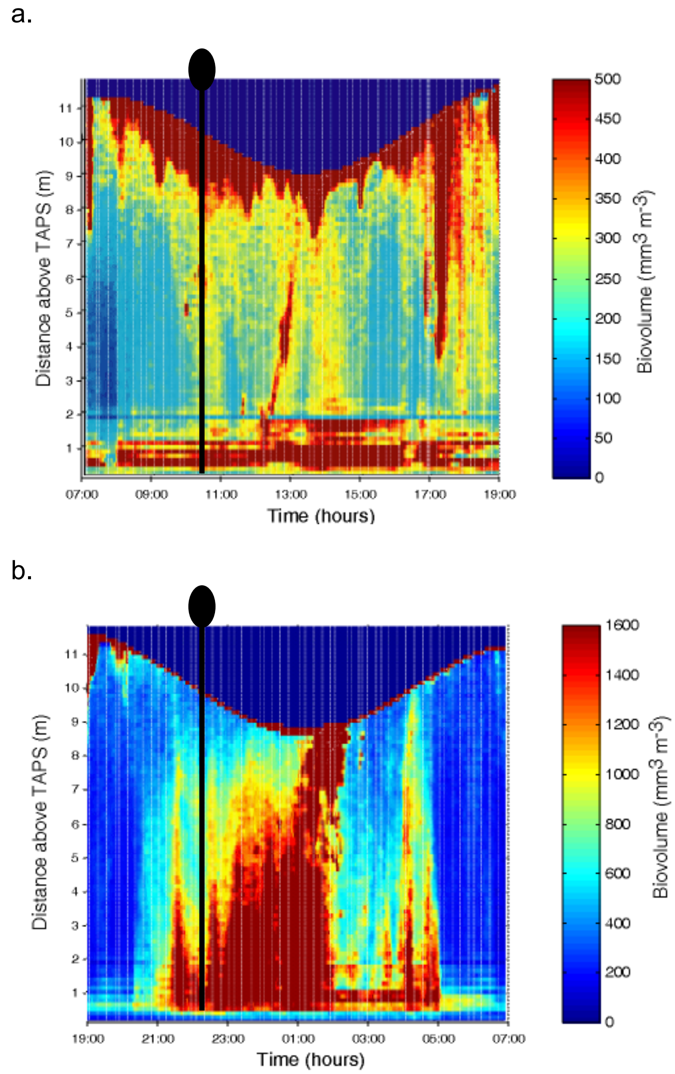

Fig 3. An increase in backscatter is seen during the day (black bar in a) near the same phase of the tide that an emergence event was initiated the previous night (black bar in b).

During the day, as well as the night, here is a significant linear relationship between the phase of the tide and the initiation time of a backscatter event as detected by the emergence algorithm (Figure 4).

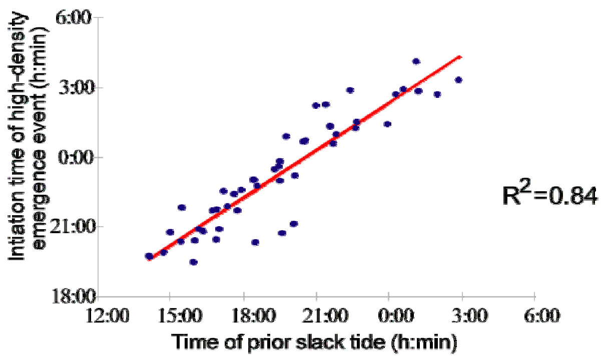

Fig 4. In 2002, there is a significant linear relationship between the time of slack tide in Boothbay Harbor (a proxy for phase of the tide) and the initiation of a daytime high-density emergence event.

IV. DISCUSSION

One of the problems with acoustic analysis is that backscatter patterns cannot yet be assigned to taxa (although that is an ultimate goal of acousticians). It is certain neither what particles are responsible for the backscatter patterns described in this paper nor what organisms might be responsible for the emergence events. Emergence trapping suggests that mysids and *Crangon* are responsible for the nocturnal emergence, but those animals have never been caught during the day. It is possible that mysids are responsible for both the diurnal and the nocturnal emergence. Mysids might emerge during the day but not enter emergence traps when there is light. Although trap avoidance selectively in daylight has never been documented, mysids are notoriously good at evading plankton nets (e.g. [1]).

It is also possible that mysids emerge during the day only under conditions of starvation. The bulk of mysids may emerge only at night. Yet, mysids that have desperately low lipid stores may risk an excursion into the water column during daylight hours.

Another hypothesis is that at least two participants create the pattern. One constituent emerges at a certain time of tide, day and night. Only at night does the second constituent emerge in concert with the first. It may be that benthic copepods emerge both day and night but are only fed on by emerging mysids during the night. The smaller magnitude of daytime emergence events suggests that the first constituent (e.g. copepods) may be smaller or less abundant than the other constituent (likely mysids). However, the greater magnitude of nocturnal emergence could be the result of the combined biovolume of two constituents.

At present, it is unclear what makes a certain phase of tide a desirable time at which to initiate an emergence event. It is possible that animals select a time of moderate and decelerating tidal velocities to enter the water column in order to avoid strongest tidal velocities that might result of large displacement. If the tide is decelerating when an animal emerges, the animal's first moments in the water column could have the strongest tidal velocities it would encounter.

Additionally, decelerating tidal currents indicate the approach of slack tide and tidal direction change. Depending upon the duration of emergence, an animal could spend some time in the water column traveling in one direction along the estuary, followed by some time traveling the other direction. In this way, an animal could avoid large excursions from its point of departure from the benthos.

V. CONCLUSION

This study demonstrates that emergence can be consistently identified in an environment with high tidal velocities. Our acoustic results suggest that emergence in the Damariscotta River Estuary is tidally modulated. In the Damariscotta River, high-density emergence events at night and during the day start at a fixed phase of the tide (during deceleration, approximate 3.5 to 4 h after local slack tide). Our results also suggest that emergence in an environment with strong tidal velocities may be richer in structure temporally than previous studies by non-acoustic means have been able to resolve.

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