Vertical movement of *Mytilus edulis* larvae in the eastern Gulf of Maine

Weinstock, J.B.[1*]; Morello, S.L.[2]; Yund, P.O.[2]

[1]Smith College, Northampton, MA 01063 (jweinstock@smith.edu); [2]Downeast Institute, Beals, ME

Introduction

Background

- Many invertebrate larvae cannot swim fast enough to overcome horizontal advection, but vertical movement (VM) can significantly alter larval dispersal trajectories
- In laboratory studies bivalve larvae move through the water column (e.g. Bayne 1964) at swimming speeds of around 10^{-4} m/s (Cragg 1980)
- Field studies have identified shifts in the vertical distribution of larvae that have been interpreted as reflecting behavioral movement (Raby et al. 1994, Knights et al. 2006)
- However, this interpretation assumes vertical velocities are negligible, which may not be the case

Mussel Larvae

- Tidally timed VM is thought to facilitate either dispersal or local retention (Knights et al. 2006, Peteiro & Shanks 2015), while ascension at night has been linked to nocturnal feeding (Raby et al. 1994, Garland et al. 2002)
- *Mytilus spp.* are thought to descend in the water column on ebb tides (Knights et al. 2006)
- The Gulf of Maine (GOM) has 2 high and low tides each day, with one ebb tide falling during the night when bivalves may ascend to feed
- Therefore, larval responses to the tidal vs. diel cycle may conflict (Figure 1)

Goal: We conducted two studies to evaluate *M. edulis* (1) tidal and (2) diel migration patterns in the GOM and assess whether these patterns are due to behavioral or oceanographic processes

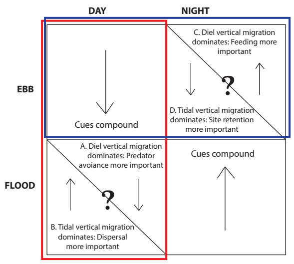

Figure 1. Diagram of hypothesized larval vertical distributions based on sampling conditions. Bivalves are thought to descend in the water column on ebb tides, but to ascend at night. We evaluated behavior on daytime ebb and flood tides and on nighttime ebbs.

Methodology

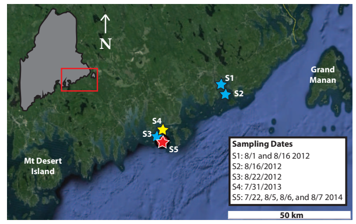

Figure 2. Map showing study sites. Samples were collected from five study sites in two bays off the coast of northern Maine during the summers of 2012 (blue stars), 2013 (yellow star), and 2014 (red star).

Sampling

- Larval vertical distributions were sampled at 5 sites over 3 years (Figure 2)
- Samples were collected each summer after *M. edulis* populations spawned (Figure 2 inset) during the middle of day ebb and day flood tides. Night ebb tides were also sampled in 2014
- Sampling regimes summarized in Figure 3
- Conductivity, temperature, and depth (CTD) casts were taken before and after sampling to quantify physical structure of the water column
- Vertical velocities during 2014 samples were evaluated via a high-resolution coastal circulation model (FVCOM)

Post-Processing

- Bivalve veligers sorted and counted at 40x
- Aliquot (33 per sample) identified with Scanning Electron Microscope (SEM) to family level via hinge teeth morphology (Figure 4)
- Mytillids classified to genus (*Modiolus* vs. *Mytilus*) based on relationship between size and # of hinge teeth (as in Lutz & Hidu 1979)
- % *M. edulis* per depth from SEM applied to total veliger counts to yield # *M. edulis* per depth
- Numbers summed across depths to estimate total # *M. edulis* in water column
- Depth center of *M. edulis* abundance (*D*) calculated as in Hoffle et al. 2013:

$$D = \frac{\sum M_j * W_j * A_j}{\sum W_j * A_j}$$

M_j = midpoint of stratum j
W_j = width of stratum
A_j = abundance of larvae

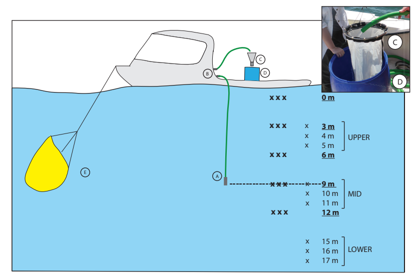

Figure 3. Diagram of sampling techniques. Samples from 2012 and 2013 were collected from five water depths (0, 3, 6, 9, and 12 m), with three replicates collected at each depth (shown as bold x's). Sampling occurred during daytime flood and ebb tides. Samples collected in 2014 were collected from three consecutive depths in each bin [upper (3, 4, and 5 m), mid (9, 10, and 11 m), and lower (15, 16, and 17 m)]. For all samples, seawater was pumped via a suction hose (A) at each depth into the boat (B) through a 50 μm plankton net (C) into a bucket to measure a total of 100 L seawater filtered (D). Water retained in the hose was pumped out before sample collection at each subsequent depth. A sea anchor (E) was deployed in order to minimize vessel movement in relation to the water body being sampled. Collected samples were backwashed into plastic jars and preserved in ethanol.

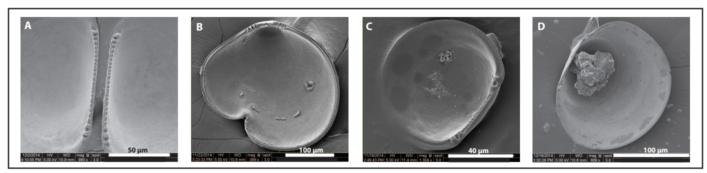

Figure 4. Typical bivalve larvae found in the GOM. (A) *Mytilus edulis.* Many hinge teeth, continuously distributed, shorter on the ends and in the middle. Looks similar to *Modiolus modiolus* but has more hinge teeth for any given shell length. (B) *Anomiidae*. Approx. 4 hinge teeth on hinge sides and none in the middle, notched valves. (C) *Ostreidae*. Pair of hinge teeth on either side, possible ridges in between. (D) *Pholadidae*. Single hinge tooth on either side. Other typical bivalves (not shown) include: *Pectinidae*. Approx. 4 hinge teeth on hinge sides and none in the middle; no notch in valves. *Veneridae*. Multiple teeth that differ in size and distribution. *Cardiidae*. No defined teeth, but small bumps on center of hinge. *Hiatellidae*. Smooth hinge, no teeth.

Results

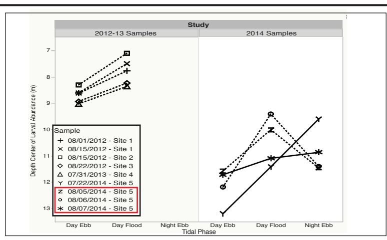

Figure 5. Vertical Distribution of *M. edulis* in Relation to Tidal Phase. Two-way and three-way pairwise comparisons (paired t-tests with Bonferroni corrections for three-way comparisons) were used to determine the relationship between average larval abundance (*D*) and tidal phase for 2012-13 and 2014 samples, respectively. In all nine sample sets, the distribution of larvae shifted upward between the day ebb and flood tides (2012-13, $p = 0.0006$; 2014, $p = 0.0109$). Night ebb tides showed no overall difference from either day flood or day ebb tides (day flood vs. night ebb, $p = 0.7677$; day ebb vs. night ebb, $p = 0.1717$). In two of the 2014 sample sets, larvae moved downward on the night ebb tide, while in the other two they showed continued upward movement. Red box denotes sampling sessions in which vertical velocities were modeled in Figure 6.

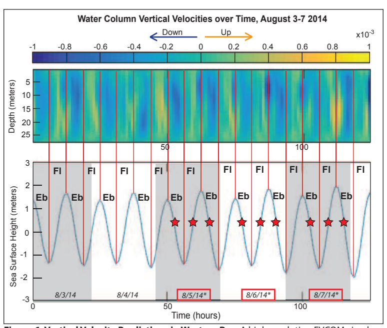

Figure 6. Vertical Velocity Predictions in Western Bay. A high resolution FVCOM circulation model was used to predict the vertical velocities at site 5 before and during the 2014 August sampling period. Vertical velocities were estimated to be on the order of 10^{-4} to 10^{-3} m/s, the same or faster than typical bivalve swimming speeds, with positive values associated with flood tides and negative with ebb. This pattern breaks down on 8/7/14, which is consistent with the larval distribution data in Figure 5. Sampling times shown as red stars.

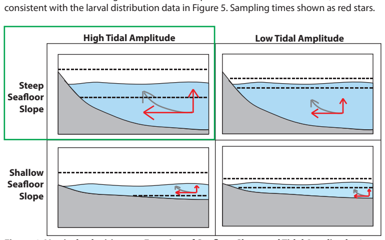

Figure 8. Vertical velocities as a Function of Seafloor Slope and Tidal Amplitude. As the tide ebbs and floods, the base of the water column is forced to move in accordance with ocean floor bathymetry, either cascading down or ramping up the sea floor. This causes positive and negative vertical velocities that can be the same magnitude or faster than bivalve swimming speeds (green box). The GOM falls in this category. Flood-oriented water movement is shown with grey arrows. Horizontal and vertical components shown in red. High and low tide marks shown with dashed lines.

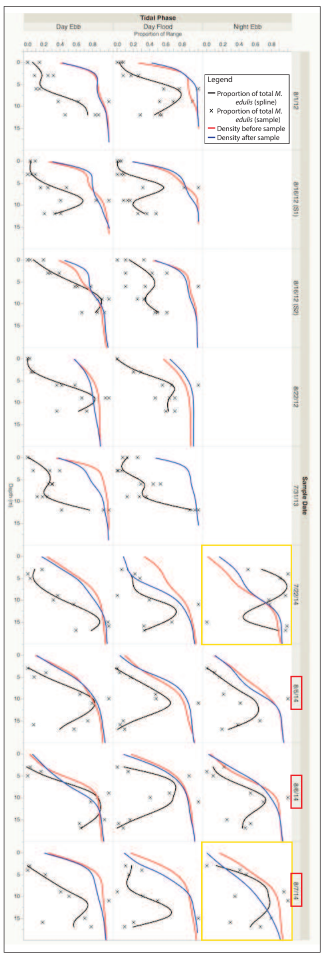

Figure 7. Proportions of *M. edulis* as a function of water depth. Black lines show *M. edulis* abundance distribution throughout water column, represented as proportion of the sampling range within each date/tide combination. Sample points represented as x's. Pycnocline data from before (red) and after (blue) CTD casts represented, also plotted as proportion of range. Red boxes denote sampling sessions in which vertical velocities were modeled in Figure 6. Yellow boxes highlight samples where larvae cross into or beyond pycnocline, implying a behavioral component to vertical shift.

Discussion

- *M. edulis* larvae displayed consistent tidally timed shifts in vertical distribution (Figure 5)
- A coastal circulation model estimated water column vertical velocities for those sample dates on the order of 10^{-4} to 10^{-3} m/s, equal to or faster than bivalve swimming speeds (Figure 6), with positive velocities generally associated with flood tides and negative velocities with ebb tides
- Downward diel movement was observed on two of four night samples (8/5/14 and 8/6/14), while ascension occurred on the remaining two (7/22/14 and 8/7/14; Figure 5)
- Vertical velocity data predicted a breakdown of the positive-flood negative-ebb pattern on 8/7/14 (Figure 6). This breakdown was not, however, observed on 7/22/14
- Breakdowns in velocity pattern could explain some variation in larval distribution pattern (ex- 8/7/14 samples), but remaining variation is likely due to behavioral mechanisms, in particular on nights when larvae crossed pycnocline (Figure 7)
- Our results highlight the need to assess vertical velocities when examining shifts in larval vertical distribution. Rather than an active process of swimming higher or lower in the water column, larvae could be passively carried to the same depths through purely physical processes, depending on the seafloor slope and tidal amplitude (Figure 8)

Conclusions

- *M. edulis* larval distributions in the GOM shift upwards in the water column on flood tides and lower in the water column on ebb tides.
- This shift may be due to physical processes, rather than the typical behavioral interpretation
- The pattern sometimes breaks down at night and may reflect behavioral mechanisms
- Further research should involve empirical measurement of vertical velocities and evaluation of spring/neap tidal influences on larval dispersal

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Acknowledgements

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