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Effect of immersion at low tide on distribution and movement of the mud snail, *Ilyanassa obsoleta* (Say), in the upper Bay of Fundy, eastern Canada

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ABSTRACT

Habitat heterogeneity often affects movement behaviours of animals, and consequently their spatial distribution. We evaluated the effect of immersion at low tide on the distribution, fine-scale movement patterns and daily movement patterns of the mud snail *Ilyanassa obsoleta* on a mudflat in the upper Bay of Fundy, Canada. Mud snails migrate onto intertidal mudflats in the summer, and our field survey showed that their density was higher inside tide pools relative to adjacent areas that are exposed at low tide. Using time-lapse videography, we evaluated the effect of snail size, snail density, and immersion at low tide on fine-scale movement patterns of *I. obsoleta*. Time until snails stopped moving and burrowed was unaffected by snail size, but snails at low and high densities burrowed somewhat faster than those at intermediate densities. Snail size and snail density had no detectable effect on displacement speed or linearity of displacement. Immersion affected snail movement: snails within tide pools delayed burrowing and traveled in more convoluted paths compared to those on exposed mud. Snails increased their turning angles within tide pools, which is probably the mechanism by which aggregations are formed. We also performed a mark-recapture experiment to compare daily movement patterns of snails released inside and outside tide pools. Snails released in tide pools moved shorter distances, but did not orient themselves differently than snails released outside tide pools. Both groups exhibited significant directionality, moving against the mean water current direction over 24 h. In sum, immersion at low tide affected the behaviour and spatial distribution of snails, resulting in snail aggregations within tide pools. These snail aggregations, in turn, may be a major factor influencing spatial dynamics on mudflats, including causing changes in distribution patterns of the burrowing amphipod *Corophium volutator*, a dominant inhabitant and key species in the food web of mudflats.

1. Introduction

Naturally occurring populations are most often distributed contagiously rather than randomly or uniformly (Legendre and Fortin, 1989). Organisms often aggregate as a response to heterogeneity in some feature of the environment. These aggregations may simply be a consequence of differential movement of organisms in different patch types. For example, movement may be slower or turning angles may be sharper within a preferred microhabitat than in a less desirable microhabitat (Turchin, 1991, 1998). By understanding how environmental factors affect movement patterns of individuals, and ultimately distribution patterns at the population level, one can determine where and when the influence of a species will be observed. This is especially important for species with a strong influence on community structure and that live in heterogeneous environments.

One of the most obvious, yet relatively unstudied, sources of heterogeneity in intertidal soft-sediment environments is the presence of tide pools (or depressions) that remain covered by water at low tide. Fluctuations in environmental conditions such as temperature and salinity are dampened in tide pools relative to adjacent areas that are emerged at low tide (Metaxas and Schiebling, 1993). Accordingly, communities in tide pools differ relative to areas exposed at low tide. Presence of tide pools has been shown to influence distribution and movement of the burrowing amphipod *Corophium volutator* (Drolet and Barbeau, submitted), and cursory observation suggests that a similar effect may occur with the mud snail *Ilyanassa obsoleta*.

The neogastropod *Ilyanassa obsoleta* occurs commonly in soft-sediment intertidal environments throughout the Atlantic coast of North America, with densities peaking at over 1000 individuals m^{-2} (Curtis, 2005). *I. obsoleta* is an obligate omnivore that feeds selectively on biofilm composed of diatoms, bacteria, and on a wide variety of plant and animal detritus (Curtis and Hurd, 1979; Connor and Edgar, 1982; Feller, 1984). *I. obsoleta* affects diatom populations by both stimulating and hindering population growth, depending on snail density. When in low densities, snails improve nitrogen cycling through bioturbation, defecation, and production of mucus trails, resulting in increased diatom population

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growth. As snail densities increase, grazing eventually outstrips positive effects and diatom populations decline (Connor et al., 1982). Mud snails negatively affect several species of invertebrates, including polychaetes (Kelaher et al., 2003), nematodes (Curtis, 2005) and amphipods (DeWitt and Levinton, 1985), as well as bivalve settlement and recruitment (Hunt et al., 1987), although the mechanisms behind these effects remain poorly understood. *I. obsoleta* exhibits seasonal migration; snails spend summers on the intertidal mudflat and winters in the subtidal (Cranford, 1988). They have been observed to move at a speed of about 2 mm s^{-1} by use of their pedal cilia (Dimock, 1985; Dewitt and Levinton, 1985) and to move from 5 to 50 m over a 5-day period, with large snails moving faster than small ones (Batchelder, 1915). Their ability to move relatively long distances in a short period of time is observed infrequently; most snails remain within a small area (Hamilton, 1978). Movement of *I. obsoleta* is affected by excess amounts of organic material, such as animal matter, diatom blooms or algae (Crisp, 1969). They usually move toward these food sources, most likely detecting food presence through chemodetection, as is observed for other gastropod species (e.g. Lemaire and Chase, 1998). *I. obsoleta* also follow mucus trails left by conspecifics (Trott et al., 1978; Bretz et al., 1983) to conserve energy, either by consuming or recycling their mucus (Hutchinson et al., 2007).

The dominant macro-invertebrate, by mass and number, within the mudflats of the upper Bay of Fundy is the burrowing amphipod *Corophium volutator*, which can reach densities exceeding 50 000 individuals m^{-2} (Peer et al., 1986). *C. volutator* is the main food source for over 70% of the world's population of migrating Semipalmated Sandpipers, *Calidris pusilla*, during their only stop before a direct flight to South America (Hicklin and Smith, 1979). Recently, densities of *C. volutator* as well as *I. obsoleta* have been used as predictors of foraging area selection by Semipalmated Sandpipers (Hamilton et al., 2003). It is thought that *I. obsoleta* negatively affects *C. volutator* populations. Wilson (1988), Hamilton et al. (2003, 2006) and Drolet et al. (submitted) reported negative correlations between mud snail and *C. volutator* densities at spatial extents ranging from less than a meter to 10's of meters. Exploitative and interference competition exists between *C. volutator* and mud snails, but its exact nature is not clear (Hamilton et al., 2006). Drolet et al. (submitted) found that an experimentally increased density of snails leads to decreased density of *C. volutator* through an effect on amphipod survival as well as emigration rates. Since *C. volutator* aggregate in tide pools (Drolet and Barbeau, submitted), information on the effect of immersion at low tide on distribution patterns as well as movement behaviour of *I. obsoleta* is essential for a full understanding of the mudflat ecosystem.

The objective of this study was to evaluate the effect of tide pools on distribution and movement of *I. obsoleta* on an intertidal soft-sediment environment in the upper Bay of Fundy. First, we surveyed densities of *I. obsoleta* inside and outside tide pools. Second, we examined the effect of immersion at low tide on fine-scale movement patterns of snails using time-lapse videography. Finally, we performed a large-scale mark-recapture experiment to determine the effect of presence of tide pools on snail movement (distance and direction) over a 24-h period. Given the documented negative effect of *I. obsoleta* on many competing species, and the fact that movement patterns are a key determinant of spatial distribution, information on movement in this species will ultimately determine where and when its influence will be observed.

2. Materials and Methods

2.1. Study Site

Work was conducted on an intertidal mudflat at Pecks Cove, New Brunswick, Canada (45° 48' N, 64° 28' W), near the mouth of the Cumberland Basin in the upper Bay of Fundy between 25 June and 6 September 2006. The mudflat is roughly 3.5 km wide and extends 850 m seaward from the high tide line (see Peer et al., 1986 for a map of the area). This mudflat has a patchy surface with many drainage channels and tide pools present at low tide. Migration of mud snails, *Ilyanassa obsoleta*, into the intertidal zone starts in June and is nearly complete by July, and their return to the subtidal does not occur until well after September (Cranford, 1988).

2.2. Effect of presence of tide pools on distribution of I. obsoleta

We measured density of *I. obsoleta* inside and outside tide pools to determine whether immersion at low tide influences snail distribution. Sampling was done from 1 to 3 h after the tide receded on 16 August 2006 on seven 550-m transects (separated by 300 m) running perpendicular to the low water line. Before sampling, we randomly pre-selected (using a random number generator) three distances along each transect. The tide pool closest to each of these distances was then selected for sampling. We counted the number of snails in three quadrats (25 cm × 25 cm) randomly located inside each tide pool and three quadrats outside each tide pool. Density of snails was analyzed using a mixed-model ANOVA with Pool treatment (2 levels: inside and outside tide pools) as a fixed factor, and Transect (7 levels) and Location (3 locations nested within transect) as random factors. Variance components of the random sources of variance were also calculated (Quinn and Keough, 2002; Searle et al., 1992) to determine the proportion of the variation explained by each random source of variation. The assumption of homogeneity of variances was tested using Cochran's test, and data were square root transformed prior to analysis to meet this assumption.

2.3. Effects of presence of tide pools, snail size and snail density on fine-scale movement of I. obsoleta

We conducted an experiment using time-lapse videography to evaluate the effect of varying sized tide pools, snail size and conspecific density on fine-scale movement patterns of mud snails. Snails were released during low tide in the centre of 1-m^2 quadrats located 300-400 m from shore on one of seven possible transects. Exact release points were preselected using a random number generator within the 300-400 m margin. Once the point was established a quadrat was thrown haphazardly and then oriented parallel to shore. Quadrat areas were filmed for a maximum of 1 h and individual snails were followed for the duration of the period or until they burrowed or left the quadrat area. The 1-h film time was arbitrarily set prior to filming but proved to be more than ample considering most snails burrowed in the first 20 min and rarely emerged once burrowed. Each quadrat location contained a tide pool that covered 0 to 75% of the

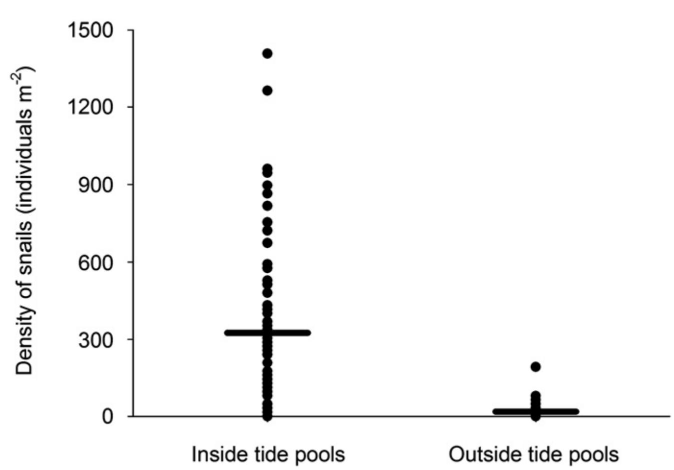

Fig. 1. Density of *Ilyanassa obsoleta* inside and outside tide pools at Pecks Cove. Dots represent replicate measurements and the solid line represents the mean (n = 63 for both inside and outside tide pools).