Effects of shorebird predation and snail abundance on an intertidal mudflat community

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ABSTRACT

Top-down effects of predation are well documented in a variety of ecological communities, including marine soft-sediment systems. It has been proposed that intertidal mudflats in the upper Bay of Fundy, Canada, which host a large population of foraging shorebirds each summer, may exhibit this community dynamic. Biofilm (consisting mainly of diatoms) forms the base of the mudflat community food web, which is dominated by the amphipod *Corophium volutator*. To assess the potential for a trophic cascade, we conducted a manipulative field experiment examining individual and combined effects of the shorebird *Calidris pusilla*, a primary predator of *C. volutator*, and the eastern mudsnail (*Nassarius obsoletus*), an intraguild predator, on community structure (including macrofauna and large meiofauna retained by a 250-μm screen). Snails exhibited density-dependent top-down effects, primarily from strong negative interactions with juvenile and adult *C. volutator*, likely due to interference, consumption and emigration. Medium and high densities of snails reduced chlorophyll *a* concentration (a measure of diatom abundance), likely through consumption and disturbance of the sediment. When present at higher densities, snails also increased variability in community structure. Shorebirds were less influential in determining community structure. They reduced *C. volutator* biomass through consumption, but there was no resulting effect on primary production. Top-down effects of snails and birds were cumulative on *C. volutator*, but did not generate a trophic cascade. We suggest that a combination of omnivory and intraguild predation by shorebirds and snails, coupled with relatively low grazing pressure by *C. volutator*, prevented transmission of top-down effects.

1. Introduction

Ecological communities are structured by a combination of top-down and bottom-up forces, coupled with indirect effects stemming from interactions among species, and abiotic influences (Hooper et al., 2005; and references therein). While bottom-up input is important, an understanding of top-down forces is essential to predict the effect of a change in predator regimen (Estes et al., 2011). In its simplest form, a top-down trophic cascade occurs when carnivores reduce the abundance of herbivores, which leads to an increase in primary production (Hairston et al., 1960). Although trophic cascades are well documented in aquatic systems (e.g., Estes and Palmisano, 1974; Silliman and Bertness, 2002), cascades can be blocked and communities stabilized by indirect effects, such as compensation (e.g., Best and Stachowicz, 2012; Pace et al.,

1998) and intraguild predation (predation of potential competitors) (Finke and Denno, 2005). Furthermore, multiple predators can enhance or dampen top-down effects (e.g., Soluk, 1993).

In intertidal mudflat communities, microphytobenthic biofilm forms the base of the food web (MacIntyre et al., 1996), in addition to enhancing sediment stability and encouraging invertebrate settlement (summarized in Pillay et al., 2007). Invertebrate assemblages inhabiting these mudflats are often relatively simple (Hamilton et al., 2006), with a limited number of consumer taxa present at each trophic level, making mudflat communities good candidates for a trophic cascade (sensu Pace et al., 1999; Strong, 1992). Indeed, top-down effects of grazing on biofilm have frequently been noted (e.g., Armitage and Fong, 2006; Armitage et al., 2009; Hagerthey et al., 2002); however, examples of compensation that blocks trophic cascades do exist (e.g., Hamilton et al., 2006). Furthermore, complex interactions, including multiple indirect effects, are common and important in understanding the structure of soft-sediment systems (reviewed in Thrush, 1999).

Intertidal mudflats in the upper Bay of Fundy, Canada, are productive (Hargrave et al., 1983), supported by a biofilm composed primarily of diatoms, with limited presence of other microphytobenthos (cyanobacteria and euglenophytes) (Trites et al., 2005). Densities of

diatoms are within the range of those observed on mudflats in other geographic regions (Trites et al., 2005). Based on a review of the literature (Consalvey et al., 2004), diatoms are at their highest density near the substrate's surface (i.e., μm and mm scales), but can be found several cm deep. In the region of our study, the diatom assemblage during summer is composed primarily of tychoplankton, which occupy interstitial spaces between grains, and to a lesser degree epipelon (Trites et al., 2005), which migrate vertically within the sediment in response to diel and tidal cycles (Consalvey et al., 2004; Guarini et al., 2000). We found little variability in chlorophyll *a* concentration (a measure of diatom biomass; MacIntyre et al., 1996) in the top 2 mm of sediment over a tidal cycle (seconds to hours after tidal recession on multiple replicate days; J. Murray, M.A. Barbeau and K. Haralampides, unpubl. data), suggesting that diatom density in the top layer of sediment may be less variable on a short temporal scale than in mudflats dominated by epipelic diatoms (e.g., Consalvey et al., 2004; Hagerthey et al., 2002).

Deposit-feeding and grazing invertebrates that consume the mudflat biofilm include amphipods, polychaetes, nematodes and harpacticoid copepods (Gerdol and Hughes, 1994a; Jensen and André, 1993; Rieper, 1982; Riera et al., 1996). In the upper Bay of Fundy, the tube-dwelling amphipod *Corophium volutator* often dominates the infaunal biomass and can exceed densities of 60,000 ind. m^{-2} (Peer et al., 1986). Fish (Gilmurray and Daborn, 1981; McCurdy et al., 2005) and migratory shorebirds (Hicklin and Smith, 1984, 1979; Quinn and Hamilton, 2012) are recognized predators of infauna. Mawhinney et al. (1993) estimated that roughly 1 to 2 million Semipalmated Sandpipers (*Calidris pusilla*) use the upper Bay of Fundy as a staging ground during their annual fall migration (though in recent years populations have declined; Gratto-Trevor et al., 2012). While in the region, the sandpipers forage in dense aggregations on abundant mudflat invertebrates, including *C. volutator* (Hicklin and Smith, 1984; Wilson, 1990). This raises the possibility of substantial top-down effects in this system. The influence of sandpipers on *C. volutator* behavior and population structure is well documented (e.g., Boates and Smith, 1989; Boates et al., 1995; Matthews et al., 1992; Wilson, 1989), but community-wide effects are less clear (Hamilton et al., 2006), and studies of shorebirds foraging in similar systems elsewhere have generated variable results (e.g., Quammen, 1984; Raffaelli and Milne, 1987).

The eastern mudsnail (*Nassarius obsoletus* (= *Ilyanassa obsoleta*)) is also a prominent species on mudflats during summer and fall (Cranford, 1988); it is patchily distributed at low tide, often aggregating in tide pools at densities up to 1000 ind. m^{-2} (Coffin et al., 2008; Wilson, 1988). The mudsnail is an obligate omnivore known to consume diatoms (Curtis and Hurd, 1979; Feller, 1984), and a bioturbator. At low density, mudsnails can increase nutrient cycling, enhancing diatom abundance, whereas at high density, snails can reduce diatom abundance by excess stirring and overgrazing (Connor et al., 1982). A well-documented negative relationship exists between mudsnails and *C. volutator* in the upper Bay of Fundy (Drolet et al., 2009; Hamilton et al., 2006, 2003). Mudsnails increase *C. volutator* mortality through interference competition and predation (Coffin et al., 2012; Wilson, 1988), and cause *C. volutator* to retreat deeper into the sediment (Coulthard and Hamilton, 2011) or emigrate (Drolet et al., 2013a, 2009).

Daborn et al. (1993) suggested that shorebird predation on upper Bay of Fundy mudflats generated a trophic cascade by reducing the abundance of *C. volutator*, leading to an increase in biofilm, perhaps enhancing sediment stability due to the extra-cellular mucopolysaccharide matrix produced by diatoms (Grant et al., 1986; Underwood and Paterson, 1993). Conversely, Hamilton et al. (2006) did not observe a cascade, and speculated that it was blocked because mudsnails consumed the excess biofilm made available by the decline in *C. volutator*. However, their experiment did not manipulate mudsnail density, and was conducted on a mudflat where snails were abundant (Hamilton et al., 2006, 2003). Mudsnail effects are density-dependent (Coffin et al., 2012; Coulthard and Hamilton, 2011; Drolet et al., 2009), raising the possibility that results may be different in an environment with

fewer snails. To investigate top-down processes in a mudflat community (including macrofauna and large meiofauna retained by a 250-μm screen), and the extent to which density-dependent effects of mudsnails interact with bird predation to enhance or block top-down effects, we conducted a manipulative field experiment on a mudflat with fewer mudsnails. Specifically, our experiment allowed us to test the competing hypotheses that the mudflat community (a) exhibits a trophic cascade due to the cumulative top-down effects of shorebirds and mudsnails on *C. volutator*, resulting in an increase in diatom abundance or (b) that a cascade is blocked through compensation if the consumption of diatoms by snails and shorebirds, both intraguild predators, exceeds *C. volutator* grazing. A clear understanding of how mudsnails affect mudflat systems would be useful and anticipatory. On some mudflats, large increases in mudsnail density have been noted in recent years (Supplement S1), which, coupled with the documented strong effects of mudsnails in a range of environments (e.g., Kelaher et al., 2003; Pascal et al., 2013), raises the potential for altered community dynamics.

2. Materials and methods

2.1. Study area

Work was conducted from June to September 2007 in the upper Bay of Fundy at the Grande Anse mudflat, Johnson's Mills, New Brunswick, Canada (45°48′15″ N, 64°29′46″ W). The mudflat extends up to ~2.5 km from shore at the widest across-shore distance, covers ~1100 ha and has a tidal range averaging ~12.1 m (range 9.7 to 13.9 m; Fisheries and Oceans Canada). The angle of repose of the mudflat surface is shallow and fairly consistent between a distance of 0 and ~1000 m from shore (~2.8 m change in elevation; Hicklin et al., 1980). The sediment consists of an unconsolidated aerobic layer on the surface (2–10 cm in depth), with compact anaerobic sediment underneath. Volume-weighed mean particle size of the sediment is 17.8 μm, with the 10th, 50th and 90th percentile being 3.9, 11.9 and 40.6 μm. We conducted our experiment in an area 300 to 330 m from shore (shore being the transition from the gravelly beach to the mudflat) and 500 m wide alongshore. This location was far enough from shore to avoid near-shore effects (e.g., road run-off, wave action, terrestrial wildlife), while ensuring adequate exposure time and distance from shore to facilitate sampling.

2.2. Experimental design

The experiment consisted of 10 spatial blocks (hereafter termed sites), each with six treatments present. Sites were established in two rows of five, ~300 and 330 m from shore, with consistent exposure times. Each site was positioned 30–50 m from its nearest neighbor and contained the following treatments: an open plot (B,S, meaning that both birds and mudsnails had access), a bird exclosure (−B,S, meaning that snails had access but birds were excluded), a complete exclosure (−B,−S) and three snail enclosures containing low (LS, nominally 50 m^{-2}), medium (MS, nominally 125 m^{-2}) and high (HS, nominally 250 m^{-2}) snail densities. These densities are within the range observed on mudflats in the region (Supplement S1), and the lower two were used in a related study (Coulthard and Hamilton, 2011), allowing comparison with that work. Mudsnails placed in enclosures were collected from the surrounding area.

Within each site, the six treatments were randomly allocated into two rows of three, with 3 m separating treatment plots (Fig. 1). All treatments covered a 1.0 m × 1.0 m area of the mudflat. Open plots were un-manipulated mudflat, designated by four bamboo stakes. Snail enclosures and exclosures were bamboo frames covered with clear plastic mesh (6-mm apertures), selected to minimize effects of shading, limit disruption of water flow and permit migration of invertebrates while restricting access by shorebirds, fish and mudsnails. The mesh