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The contribution of marine snow to the particle food supply of the benthic suspension feeder, *Mytilus edulis*

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Abstract

In order to examine the importance of the settling of large particles to the food supply and feeding behavior of a benthic culture of the blue mussel, *Mytilus edulis*, we investigated the tidal dynamics of large (>0.5 mm diameter) marine aggregates, commonly known as marine snow, during three tidal cycles in July 1998 at a shallow, subtidal, low current flow regime site along the coast of Maine (Shorey Cove, Roque Island, Englishman's Bay, Maine).

In situ, optically measured marine snow showed a distinct tidal signal displaying an increase in size and abundance through high tide with a peak on the early ebb tide as it settled to the bottom. Marine snow volume ranged an order of magnitude through the tidal cycle, from under 8 to over 80 $mm^3\ l^{-1}$. An increase in the in situ marine snow volume corresponded with an increase in benthic mussel feeding activity (from 20% to 60% of maximum exhalant siphon area, which is an estimate of pumping rate) and maximum rates of pseudofeces production by the mussels during periods of low tidal current speeds. In contrast, mussels from the same population feeding on surface waters in shipboard chambers produced no pseudofeces and had high pumping rates (80–100% maximum exhalant siphon area) over the whole tidal period. A second peak in benthic mussel pumping rates also occurred during flood tide.

Food quality was lower in the bottom waters due to significantly higher particulate inorganic matter (PIM, >2 mg l^{-1}) when compared with the surface waters. PIM accounted for 95% of the total settled mass flux of 3.4 g m^{-2} day^{-1} measured in sediment traps deployed 1 m off the bottom, with organic carbon representing only 2.5% of the mass flux during the mid-summer conditions. At low-current sites such as Shorey Cove, Roque Island, Maine, the settling of marine snow provides an important additional source of food, albeit of low quality, to benthic populations of blue mussels.

Keywords: Exhalant siphon area; Flow modeling; Marine snow; *Mytilus edulis*; Pseudofeces production; Suspension-feeding

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1. Introduction

In recent years, investigations of the physical factors controlling the food availability to benthic suspension-feeders have focused on the role of current velocity in enhancing the supply of particles removed by the suspension-feeders in the benthic boundary layer (Wildish and Kristmanson, 1979, 1984; Fréchette and Bourget, 1985; Muschenheim, 1987; Peterson and Black, 1987; Wildish et al., 1987; Fréchette et al., 1989; Calahan et al., 1989; Monismith et al., 1990; Cole et al., 1992; Butman et al., 1994; O'Riordan et al., 1995). Fréchette et al. (1989) and O'Riordan et al. (1995) described the food supply to benthic filter feeders as a function of horizontal advection, turbulent diffusion and settling, but they assumed that the settling rate of natural particulates was not important to the food supply of suspension-feeders when compared with advection and turbulent diffusion. The expectation was that the majority of the settling particles consisted of slowly settling phytoplankton cells and tiny organic and inorganic particles. Supporting the assumption above were the slow settling rates of heterogenous, temperate phytoplankton populations of 0.003–0.02 mm s^{-1} (Bienfang, 1981) and chain-forming centric diatoms such as *Skeletonema costatum* of 0.01 mm s^{-1} (Smayda, 1970). Fréchette et al. (1989) also considered the food supply to a mussel bed in shallow water to be individual phytoplankton of 10–30 μm diameter rather than flocs of algal matter and inorganic material. It is now known that particles in coastal to open-ocean systems often exist as components of larger, organic-rich aggregates called marine snow, which are over 0.5 mm long and which have much higher settling rates than their individual particle components. These large particles are primarily responsible for the mass flux of material through the water column (McCave, 1975). Marine aggregates may be a significant food source for bivalves such as blue mussels, and especially important in shallow, low current regime, soft sediment locations where the tidal advection of phytoplankton-rich waters may limit bivalve productivity.

Reported measurements of in situ settling rates of marine snow averaged 0.2–1 mm s^{-1} m (Asper, 1987; Pilskaln et al., 1998; Alldredge and Gotschalk, 1988) in oceanic environments. Eisma and Li (1993) analyzed the size of large particles during a tidal cycle in the turbid Dollard estuary in Europe. Using an in situ camera, they observed a tidal cycle in both fine and coarse particle concentrations due to resuspension from maximum tidal current speeds, followed by the appearance of large (>0.128 mm) particles. Major pulses of large sinking particles occurred around slack high water. They reported that over 10 $mm^3\ l^{-1}$ of particles larger than .064 mm were observed on the late flood tide, declining to less than 1 $mm^3\ l^{-1}$ at slack low tide as the large particles settled to the bottom. Van Leussen and Cornelisse (1993) observed an increase in the number of particles 0.4–1.1 mm after the maximum flood velocity, with settling velocities of 1–7 mm s^{-1}. Typical aggregates 0.2–0.5 mm long had settling rates of 0.5–2.0 mm s^{-1}. Syvitski et al. (1995) found that large particles of a mean diameter of 0.6 to 1.9 mm comprised 36–100% of the suspended particulate matter in Halifax Inlet, Nova Scotia. The mean size of the individual aggregates was more than 100 times the mean size of the constituent particle material, and the mass flux was about 4 g m^{-2} day^{-1} for particles with a diameter of about 0.5 mm (Syvitski et al., 1995) during winter conditions.

The flux of settling particles may be estimated from optical measurements of particle size. McCave (1984) revised his settling rates vs. particle size based on more recent data about the decrease in excess particle density with increasing particle size. Using data presented in McCave (1984), Newell et al. (1998) estimated the times required for various particle sizes to reach the bottom of a 5 m water column typical of the subtidal mussel beds in Maine. For settling to occur during a tidal stage (about 3 h), particles would need to be 0.2 mm in diameter or larger. If particles above 0.2 mm are abundant in coastal waters, they are likely to be important in the tidal supply of food to benthic suspension-feeders such as blue mussels. In the present study, the in situ particle sizes observed (0.25–5 mm) would be expected to reach the bottom in 1 to 2 h after high tide. At low flow, soft sediment sites where horizontal advection and turbulent eddy diffusion are low, the settling flux of marine snow could be an important component of the diet of benthic filter feeders such as blue mussels, especially as it has been observed that decreased growth occurs in the middle of high density mussel clumps (Newell, 1990; Svane and Ompi, 1991) as a result of depleted