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Journal of Experimental Marine Biology and Ecology 341 (2007) 184 – 195

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

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Production of transparent exopolymer particles (TEP) by benthic suspension feeders in coastal systems

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Received 26 September 2006; received in revised form 26 September 2006; accepted 28 September 2006

Abstract

In the marine environment, transparent exopolymer particles (TEP) are ubiquitous and abundant, playing a significant role in carbon cycling and the structuring of food webs. Previous studies have shown that phytoplankton, bacteria, and oysters contribute to the production of TEP through the release of exopolymers. However, little is known about other potential sources of TEP and TEP precursors, especially in coastal systems. It was hypothesized that suspension feeders contribute to the TEP pool in near-shore environments through the release of exopolymers in both the dissolved and particulate form, and tested these hypotheses in both laboratory and field experiments. In the laboratory, the production of TEP by several species of benthic suspension feeders (the blue mussel, *Mytilus edulis*; the bay scallop, *Argopecten irradians*; the slipper snail, *Crepidula fornicata*; and the solitary ascidians, *Ciona intestinalis* and *Styela clava*) was investigated from October to November 2002 and June 2003. Concentrations of TEP and DOC were determined by spectrophotometry after alcian blue staining and high-temperature, catalytic oxidation, respectively. Similar analyses were conducted on water samples from the field in July 2003, collected in close proximity to dense beds of mussels in the Poquonnock River, Connecticut, USA (41°19′ N, −72°02′ W). Laboratory results indicated that actively-pumping blue mussels, bay scallops, slipper snails, and both species of solitary ascidians significantly enhanced TEP concentrations above background levels over a five-hour period. However, only the solitary tunicate *S. clava* significantly enhanced DOC concentrations above background levels over the same period of time. Field samples indicated that TEP and DOC concentrations were high in close proximity to dense beds of mussels. These results imply that a variety of benthic suspension feeders produce TEP during feeding activities which could lead to enhanced flocculation of organic matter and carbon deposition in near-shore waters.

Keywords: Aggregation; Benthic; Dissolved organic carbon (DOC); Mucopolysaccharides; Suspension feeding; Transparent exopolymer particles (TEP)

1. Introduction

Transparent exopolymer particles (TEP) are composed of high-molecular weight (HMW) mucopolysaccharides that can be found in both marine and freshwater systems. In the marine environment, dissolved HMW polysaccharides are often released into the water column by microorganisms (i.e., phytoplankton and bacteria) as extracellular surface-active exopolymers (Alldredge et al., 1998; Passow et al., 2001; Passow, 2002a). This dissolved organic matter (DOM) is transformed into

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0022-0981/$ - see front matter
doi:10.1016/j.jembe.2006.09.019

particulate organic matter (POM) via the microbial loop, and also through abiotic processes (e.g. bubble formation) that result in the formation of TEP.

TEP are operationally defined as individual transparent particles that are formed from acid polysaccharides, retained on polycarbonate filters, and are stainable with alcian blue (Alldredge et al., 1993; Passow, 2002a,b). According to this definition, TEP can be measured by the amount of dye bound to the particles that is acid-extracted and determined colorimetrically (Passow and Alldredge, 1995a). This is a semi-quantitive technique because a weight equivalent of TEP is standardized using gum xanthan (Passow, 2002a,b). Carbon content of TEP can then be estimated from the colorimetric measurements calibrated with this standard (Engel and Passow, 2001).

TEP can be readily scavenged by air bubbles rising through the water column and transported to the sea surface microlayer (Zhou et al., 1998; Kuznetsova et al., 2005). When the bubbles burst, aerosols containing TEP are released into the air. Exopolymers, such as TEP measured by alcian blue, can also have a substantial impact on coagulation efficiency and flocculation of suspended matter into marine snow (Alldredge et al., 1993; Passow, 2002b). TEP can act as a glue that binds together small organic (e.g., detritus, phytoplankton, fecal pellets) and inorganic material (e.g., clay minerals), resulting in the formation of larger aggregates that sink rapidly to the benthos (Alldredge and Silver, 1988; Alldredge et al., 1993; Kiørboe et al., 1994; Passow and Alldredge, 1995a,b). Sinking aggregates are available as a substrate for bacteria (Grossart and Ploug, 2001), and as a potential food source for pelagic and benthic organisms (Alldredge and Silver, 1988). Most of these organisms are able to utilize only the particulate, not the dissolved, form of organic carbon to sustain growth and life processes (Jensen and Søndergard, 1982). Therefore, TEP-mediated transfer of carbon from the dissolved to the particulate phase enhances carbon deposition to the benthos (Kiørboe et al., 1994; Logan et al., 1995), and may provide a significant energy source for benthic suspension and deposit feeders (Alber and Valiela, 1994, 1995).

While phytoplankton and bacteria have been shown to produce TEP in both field and laboratory settings (Decho, 1990; Kiørboe and Hansen, 1993; Passow and Alldredge, 1994, 1995a), TEP production by macroorganisms has not been measured, despite suggestions that other organisms might release TEP and TEP precursors (Decho, 1990; Alldredge et al., 1993). Many marine invertebrates use mucopolysaccharides for various life processes. For example, appendicularians use mucopolysaccharides in the production of their feeding houses (Fenaux, 1985). Corals produce a mucus sheath that aids in antifouling and protection against ultraviolet radiation (Vrolijk et al., 1990). Many species of zooplankton and nekton egest metabolic as fecal pellets enclosed in a mucous sheath (Alldredge and Silver, 1988). Pelagic suspension feeders, such as pteropods, have mucus webs that trap food particles in the water column, and benthic suspension feeders use mucus-covered appendages to trap suspended food particles in a similar manner. In suspension-feeding bivalves, mucus is secreted by the epithelia of pallial organs and is a key component of particle processing (Beninger et al., 1991, 1993). In gastropods, such as the slipper limpet, *Crepidula fornicata*, the gill that strains suspended particles from water entering the mantle cavity secretes a mucous net (Orton, 1912; Jørgensen et al., 1984). A similar mechanism also occurs in solitary tunicates. The pharyngeal basket secretes a mucous net that removes suspended particles from water entering through the buccal siphon (Jørgensen et al., 1984; Monniot et al., 1991). Given the widespread use of mucopolysaccharides by macroorganisms, some of this material is probably released in a dissolved form or as small particles sheared from mucus-covered structures during feeding. In vivo observations of mollusc and tunicate feeding activity have revealed the rejection of mucus-like material and pseudofeces (Ward et al., 1993a,b, 1998; Ward, 1996; Armsworthy et al., 2001). Physiological stress can also cause organisms to slough mucus-covered cells from body linings and feeding structures (MacDonald et al., 1995; Potter et al., 1997). Since these mucins are chemically similar to TEP precursors, they may contribute to the TEP pool. McKee et al. (2005) were the first to quantify the production of TEP by a benthic suspension-feeder (the eastern oyster *Crassostrea virginica*) in field and laboratory studies, and suggested that other benthic suspension-feeding species should be examined.

We hypothesized that mucopolysaccharides released by benthic suspension feeders enhance ambient concentrations of TEP. The chemical composition of TEP implies that they are formed from excretory products released as dissolved organic matter (DOM), and seasonal patterns of DOM released by phytoplankton and TEP are similar (Mari and Burd, 1998; Passow, 2002a,b). Since TEP can form from dissolved precursors, we also hypothesized that dissolved organic carbon (DOC) may serve as an indicator of TEP production by suspension feeders. Therefore, suspension feeders may indirectly enhance the flux of particulate food sources to the benthos through the production of