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The role of sinking phytodetritus in structuring shallow-water benthic communities

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ABSTRACT

Sinking phytodetritus from surface waters represents a prime source of high-quality food supply for marine benthic organisms. Despite its obvious relevance, the structuring role it plays in shallow sedimentary communities is surprisingly poorly studied. In this article we review the contribution of natural sources of organic food supply to abundance, composition, and diversity of shallow-water macrobenthic communities. We then present a case study that tests how the addition of spring bloom-levels of diatom phytodetritus to a 20-m deep sedimentary habitat contributes to variation in benthic community structure in coastal Newfoundland. *In situ* patches of otherwise undisturbed sediment were enriched by syringing high and low concentrations of phytodetritus onto their surface. After one week and five weeks, macrofauna in the patches were sampled and compared with ambient sediments where no phytodetritus was added. The experiment was conducted during the summer and then repeated in the fall in order to evaluate how seasonal variation in colonizers might influence infaunal response. Despite significant temporal changes in macrofaunal abundance and composition within and between experiments, the only response that could be attributed to the phytodetritus addition was a rapid response during the first week of the summer experiment. Multiple measures of diversity (species richness, rarefaction, Margalef's index) indicated reduced diversity with phytodetritus addition. These responses did not persist through the five weeks of the summer experiment and were not observed during the fall experiment, suggesting that the effect of food supply is short term and strongly dependent on seasonal timing. In both experiments, the organic material was largely undetectable even after one week. The rapid utilization of phytodetrital patches in shallow-water environments, in concert with higher background levels of phytodetrital flux, may represent a key difference in structuring of shallow-water and deep-sea sedimentary communities.

1. Introduction

With increased consumption of fossil fuels and associated carbon dioxide emissions, the fate of carbon in the global ecosystem has become a major environmental issue (Hopkinson and Vallino, 2005). As much as one hundred million tons of carbon in the form of carbon dioxide is consumed by primary producers in the world's oceans each day, and most of this is sequestered into the marine ecosystem by sinking particles (Behrenfeld et al., 2006). As increased amounts of carbon dioxide are absorbed by the ocean the functioning of this massive ecosystem is at risk of major changes (Schmittner, 2005; Buesseler et al., 2007). Sinking particulate organic matter serves as a high quality food source for many forms of marine life, including benthic sedimentary communities (Gray, 1981; Parrish, 1998; Widbom and Frithsen, 1995). Food supply is therefore a potentially important structuring mechanism for benthic communities that has gained some attention (Graf, 1987; Josefson and Conley, 1997; Galeron et al., 2000) but surprisingly, has been addressed by only a small number of studies to date.

The significance of food supply for macrobenthic communities is far from well understood, in part because their effects vary widely among habitats, depths, and locations (cf. Grebmeier et al., 1988; Gould and Gallagher, 1990; Ambrose and Renaud, 1997; Stocks and Grassle, 2001; Kelly, submitted for publication). In fact, the organic matter that the benthos receives can have very different effects depending on concentration and timing of delivery (Widbom and Frithsen, 1995; Widdicombe and Austen, 2001). Too much organic matter can have an adverse effect on benthic communities, as described in classic models of anthropogenic organic enrichment (Pearson and Rosenberg, 1978). For example, there is already strong evidence that large organic loads combined with low physical disturbance yield lower than expected diversities (Widdicombe and Austen, 2001). Similarly, numerous eutrophication studies consistently show that high levels of organic enrichment, carbon or other nutrients such as nitrogen or phosphorous generally lead to increases in a few opportunistic species, while decreasing diversity and abundance of other less opportunistic species (Oviatt et al., 1986; Widbom and Frithsen, 1995; Gray et al., 2002).

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In extreme cases, eutrophication can cause such intense oxygen stress that macrofauna can be almost wiped out entirely during warm summer months (Rabalais, 2004). These areas must subsequently undergo large-scale recolonization during the winter months (Tagliapietra et al., 1998). Although food limitation is expected to affect shallow-water benthic organisms (Jumars and Wheatcroft, 1989; McMahon et al., 2006), examples from shallow-water habitats in close proximity to the photic zone are rare in the literature (Josefson and Rasmussen, 2000). At the other extreme, deep-sea sedimentary communities are kilometers below the depth of light penetration and generally depend on sinking pulses of organic matter from surface waters. In these cases, multiple studies have shown that community diversity and abundance is clearly influenced by food availability and/or related disturbances (Grassle and Morse-Porteous, 1987; Snelgrove et al., 1994; Snelgrove and Smith, 2002). The role that sinking phytodetritus is expected to play in shallow boreal communities has been inferred largely from observations (Kelly, submitted for publication) and from spatial or temporal correlations (see mini review below). However, more experimental studies are required in order to understand the causal mechanisms that drive this aspect of pelagic-benthic coupling.

A few studies on tidal flats and saltmarsh ecosystems have focused on the response of shallow-water macrofauna to the supply of phytodetrital organic matter (Kendall et al., 1995; Josefson and Conley, 1997; Stocks and Grassle, 2001; Kelaher and Levinton, 2003). Ironically, more specific studies that have examined the role of organic composition in faunal response have focused primarily on the deep sea (Snelgrove et al., 1992, 1996). Only recently have studies addressed natural organic flux in shallow subtidal systems, and a brief compilation of what is currently known for such habitats is therefore both timely and necessary. In this article we present such a review and explore the contribution of organic flux to patterns of shallow macrobenthic individuals, populations, and communities. We then present a specific case study that examines the effect of quantity of sinking phytodetritus on sedimentary fauna in a shallow, soft-sediment fjordic system. In this study, we use in situ experiments to determine if the quantity of sinking organic matter (phytodetritus) has measurable effects on benthic community structure. More specifically, we assess whether the experimental addition of high concentrations of good-quality phytodetritus triggers a macrofaunal response in terms of composition, abundance, or species diversity. We compare this treatment with lower levels of enrichment (half the phytodetrital addition described above) and with no addition (ambient/control).

2. Mini-review: Phytodetritus flux and its structuring role

2.1. Definitions and scope

Different authors have defined phytodetritus and phytodetrital flux to the seafloor in a variety of ways. In this brief review, we follow Brown and Parsons (1972) as adopted by Beaulieu's (2002) overview: Phytodetritus encompasses sinking particulate matter derived from phytoplankton cells clumped together by bacteria and organic slimes. Our definition deliberately excludes detritus derived from macrophytes or vascular plants (seagrass, mangroves), a material that is usually highly refractory with little or no nutritive value to benthic organisms (Grant and Hargrave, 1987). Although macrophyte detritus is often better represented than phytodetritus in the sinking particles that reach shallow bottoms associated with the photic zone (Graf, 1989), the scenario changes dramatically with increased distance from shore where phytodetritus represents the primary source of organic input. The influence of phytodetritus on benthic communities is also complicated by the many different definitions of community structure that are used in the literature. We use a classical definition of structure here that includes species composition, species number, and relative abundance of species within an assemblage. This mini-review focuses on the changes in these measures of community structure that result from the natural input of sinking phytodetritus.

In contrast to the often sporadic nature of the organic matter that reaches deep-sea environments, coastal sediments are usually seen as habitats with a constant, though seasonally variable, supply of phytodetritus (Ambrose and Renaud, 1995). Nonetheless, a large proportion of the organic matter in coastal environments is refractory (Grant and Hargrave, 1987) and not surprisingly then, shallow benthic communities are generally considered to be food limited (Jumars and Wheatcroft, 1989; McMahon et al., 2006), and they should therefore exhibit measurable responses to organic-rich particle supply from the water column above. Although this type of pelagic-benthic link likely applies to some extent to the entire marine realm (Graf, 1992; Moodley et al., 2005), it should be more evident at relatively high latitudes, where organic subsidies from the water column are more ubiquitous in time and space (Ambrose and Renaud, 1995; Polis et al., 1997; Cattaneo–Vietti et al., 1999). We extend our brief overview to encompass natural phenomena associated with unusually high organic flux (upwelling and related phenomena; cf. Thiel, 1982), but deliberately omit organic enrichment related to anthropogenic activity (euthrophication and related phenomena). The multiplicity of stressors typically associated with anthropogenic organic loading confounds their applicability to the objectives of this review, and this topic has been already addressed thoroughly by comprehensive reviews by Gray (1982, 1992), Gray et al. (2002) and others (e.g. Pearson and Rosenberg, 1978; Diaz and Rosenberg, 1995; Rosenberg, 2001).

2.2. Individual and population responses to flux of organic matter

The arrival of fresh organic material on the seafloor has been shown to modify one or more aspects of the growth, reproduction, and behaviour of benthic invertebrates. Bivalve populations have frequently been used as model organisms to detect and monitor life history responses in short- (Maire et al., 2006) and long-term (Ambrose et al., 2006) studies. For instance, Boon et al. (1998) related growth of three distinctive bivalve cohorts to seasonal changes in phytopigment concentrations of the water overlying North Sea bottom habitats. Similarly, growth and secondary productivity of populations of the protobranchs *Yoldia notabilis* in the western Pacific (Nakaoka, 1992) and *Yoldia hyperboria* in coastal Newfoundland (Stead and Thompson, 2003, 2006) have been linked to seasonal phytoplankton blooms. In other regions growth in the clam *Arctica islandica* (Witbaard et al., 1994) and the intensity of sediment bioturbation by *Abra abra* (Maire et al., 2006) have both been causually related to sinking phytodetritus. Blooms also drive the timing of reproduction and gonado-somatic indices in clams and scallops (Cattaneo–Vietti et al., 1999; Jaramillo, 2001), as well as growth and rates of arm regeneration in infaunal brittle stars (Skold and Gunnarsson, 1996). Changes in population mean body sizes such as those depicted in classic organic enrichment studies (Pearson and Rosenberg, 1978; Grizzle and Penniman, 1991) have been also linked to deposition of organic matter. Smaller body sizes observed in abyssal polychaete populations exposed to organic enrichment events (Paterson et al., 2006) suggest that this pattern is likely to be ubiquitous in sedimentary invertebrates.

The sinking of enriched phytodetritus have been causally related to the occurrence and intensity of deposit feeding in spionid (Kihslinger and Woodin, 2000; Riordan and Lindsay, 2002) and in capitellid (Taghon and Jumars, 1984; Linton and Taghon, 2000) polychaetes, as well as in emergence and active deposit feeding of maldanid polychaetes and echyuran worms (Jaccarini and Schembri, 1977; Hughes et al., 2004). Moreover, recent work has documented individual species' preferences for naturally- or artificially-enriched patches of sediment (Hudson et al., 2005) although these preferences are not necessarily consistent among sites and species (Uthicke and Karez, 1999). The physiological and behavioural responses described above extend to life-history characteristics. Natural increases in organic matter concentration drive recruitment of capitellid and opheliid populations on the North Carolina