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Review

Transparent exopolymer particles: Effects on carbon cycling in the ocean

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ABSTRACT

Transparent Exopolymer Particles (TEP) have received considerable attention since they were first described in the ocean more than 20 years ago. This is because of their carbon-rich composition, their high concentrations in ocean's surface waters, and especially because of their ability to promote aggregation due to their high stickiness (i.e. biological glue). As large aggregates contribute significantly to vertical carbon flux, TEP are commonly seen as a key factor that drives the downward flux of particulate organic carbon (POC). However, the density of TEP is lower than that of seawater, which causes them to remain in surface waters and even move upwards if not ballasted by other particles, which often leads to their accumulation in the sea surface microlayer. Hence we question here the generally accepted view that TEP always increase the downward flux of POC via gravitational settling. In the present reassessment of the role of TEP, we examine how the presence of a pool of non-sinking carbon-rich particulate organic matter in surface waters influences the cycling of organic carbon in the upper ocean at daily to decadal time scales. In particular, we focus on the role of TEP in the retention of organic carbon in surface waters versus downward export, and discuss the potential consequences of climate change on this process and on the efficiency of the biological carbon pump. We show that TEP sink only when ballasted with enough high-density particles to compensate their low density, and hence that their role in vertical POC export is not solely linked to their ability to promote aggregation, but also to their contribution to the buoyancy of POC. It follows that the TEP fraction of POC determines the degree of retention and remineralization of POC in surface waters versus its downward export. A high TEP concentration may temporally decouple primary production and downward export. We identify two main parameters that affect the contribution of TEP to POC cycling; TEP stickiness, and the balance between TEP production and degradation rates. Because stickiness, production and degradation of TEP vary with environmental conditions, the role of TEP in controlling the balance between retention versus export, and hence the drawdown of atmospheric CO_2 by the biological carbon pump, can be highly variable, and is likely to be affected by climate change.

Contents

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1. Introduction

1.1. Transparent exopolymer particles in the ocean: a new approach

Transparent exopolymer particles (TEP; Alldredge et al., 1993) range in size from <1 to >100 μm, are ubiquitous in aquatic systems, and are found in high concentrations in a variety of marine environments (Passow, 2002a). TEP are very sticky, and it is generally thought that their principal fate is to aggregate with other suspended particles, resulting in the formation of sinking marine snow (Engel et al., 2004a). Indeed, TEP are required to be present in surface waters for phytoplankton blooms to sink (e.g. Logan et al., 1995; Passow et al., 2001). The expression "surface waters" in this text refers to the euphotic zone, i.e. the upper part of the water column where underwater irradiance is high enough to sustain phytoplankton net production. Another class of gel-like particles is the protein-containing particles that can be stained with Coomassie Blue (CSP; Long and Azam, 1996). Since CSP were first described, few studies have been conducted on these particles and information about their characteristics and behavior remains very limited. However, contrary to TEP, CSP do not seem to significantly impact aggregation processes (Prieto et al., 2002; Cisternas-Novoa et al., 2015). Therefore, CSP may not play the same pivotal role in carbon cycling as TEP do. Considering the lack of information about CSP and their seemingly low implication in aggregation processes, this class of gel-like particles is not specifically addressed in this paper.

A lesser-known property of TEP may lead to a modification of the generally accepted view that the main effect of TEP on vertical fluxes is always to enhance the downward particle flux. Indeed, Azetsu-Scott and Passow (2004) showed that TEP have a density much lower than that of seawater (i.e. 700–840 versus 1020–1030 kg m^{-3}). As a consequence of this property, TEP rise in the water column, and accumulate in the sea surface microlayer (SML, operationally defined as the top 50–100 μm of the ocean surface) (e.g. Wurl et al., 2009). This idea was part of the conceptual model of TEP cycling in the ocean of Wurl et al. (2011). Because the density of TEP is lower than that of seawater, the relative proportions of (light) TEP and (denser) solid particles control the buoyancy of organic aggregates (Engel and Schartau, 1999; Azetsu-Scott and Passow, 2004) and hence determine if particulate organic carbon (POC) is exported downward or retained in surface waters. In the present review, we develop the hypothesis that *in situ* TEP-rich organic aggregates that linger in surface waters may form frequently. It is only when the relationship between TEP and solid particles changes that they may sink. Such a change in the ratio of TEP to ballasting particles may be due to addition of particles denser than seawater or to preferential degradation of TEP relative to the non-TEP fraction. We explore the consequences for carbon cycling of the existence of such a pool of non-sinking carbon that may temporally decouple production and sinking.

The above hypothesis rests on three lines of evidence, which increasingly focus on TEP. Firstly, there have been reports in the literature for more than two decades of a non-sinking or ascending pool of particulate organic matter in surface waters. Secondly, it is now increasingly recognized that TEP make up a C-rich POC pool in surface waters that does not readily sink. Thirdly, the SML is known to be enriched in TEP. In the remainder of the present introductory section, we examine in turn each of these three lines of evidence.

1.2. Evidence of a non-sinking or ascending pool of particulate organic matter in surface waters

In the early 1990s, measurements of the concurrent drawdown of dissolved inorganic carbon (DIC), nitrate and phosphate during both the spring phytoplankton bloom (Sambrotto et al., 1993) and summer nutrient-depleted conditions (Michaels et al., 1994) showed that the amount of DIC removed from surface waters largely exceeded that predicted from the removal of nitrate or phosphate using the corresponding Redfield molar ratios of C:N = 6.6:1 or C:P = 106:1. Sambrotto et al. (1993) concluded that the amount of carbon removed during the blooms was 40–80% greater than the carbon uptake linked to the production of phytoplankton biomass (with C:N = Redfield ratio), and concluded that there must be a large pool of organic matter that cycled through the system with an anomalously high C:N ratio. Interestingly, the discrepancy between the removal of DIC and the downward flux of POC observed over a 5-year period in the Sargasso Sea also supported the idea that the downward POC flux was too low compared to the amount of POC that should have been produced based on the removal of DIC (Michaels et al., 1994). Other studies showed that during nitrate-limited conditions, the phytoplankton C:N uptake ratio was twice the Redfield ratio (Codispoti et al., 1986; Ward et al., 1989; Michaels et al., 1994; Banse, 1994; Bates et al., 1996; Marchal et al., 1996; Hansell and Waterhouse, 1997; Copin-Montégut, 2000).

One hypothesis proposed to explain the non-Redfield production of organic matter, which was called carbon overconsumption (Toggweiler, 1993), was the formation of a large standing stock of C-rich organic matter unnoticed until then, cycling through the system with an anomalous C:N ratio, i.e. "*A second example of preferential recycling calls for the build-up of a carbon-rich detrital pool that does not sink. For this scheme to work, a large standing stock of*