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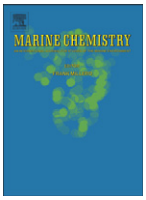

Ballasting effects of smectite on aggregate formation and export from a natural plankton community

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ABSTRACT

Strong correlations between particulate organic carbon (POC) and ballast minerals have been observed in the deep ocean. This has led to the postulation that ballast minerals can enhance POC flux by increasing the density and sinking velocity of ballasted aggregates and/or that ballast minerals protect the aggregated organic matter from degradation. Here we experimentally tested the influence of the ballast mineral smectite on the formation, size, dry weight, size-specific sinking velocity, carbon-specific respiration rate, and total POC flux of marine snow aggregates formed in roller tanks from a natural plankton community isolated from the North Sea. This study shows that the inclusion of smectite offers no protection against degradation of organic matter in freshly produced or aged marine snow aggregates. The main effect of ballasting with smectite was an increase in the density of the aggregates and, therefore 2- to 3-fold higher size-specific sinking velocities. Mineral ballasting had no influence on the total volume of aggregates or the total aggregated amount of POC. Nevertheless, the effect of increased sinking velocities in the ballasted treatment resulted in 2.7 ± 1.6 times larger potential POC fluxes compared to the non-ballasted aggregates. This implies that the incorporation of ballast minerals into sinking organic aggregates can increase the efficiency of the biological pump.

1. Introduction

The biological carbon pump refers to the biologically driven processes that transport particulate organic matter from the surface ocean to the deep sea and sediments (Falkowski et al., 1998). Most of the exported particulate organic matter is transported in the form of organic settling particles such as fecal pellets and macroscopic aggregates (>500 μm diameter) known as marine snow (Fowler and Knauer, 1986). The efficiency of the biological pump is controlled by several factors, including aggregation (e.g. Alldredge and Gotschalk, 1988; Alldredge et al., 1995; Fowler and Knauer, 1986) and disaggregation (e.g. Alldredge et al., 1990) of the settling aggregates, their sinking velocities (e.g. Alldredge and Gotschalk, 1988), microbial remineralization (e.g. Grossart and Ploug, 2001; Iversen and Ploug, 2010; Ploug, 2001), as well as zooplankton consumption (e.g. Iversen et al., 2010; Jackson, 1993; Koski et al., 2005) and transformation (e.g. Dilling and Alldredge, 2000; Iversen and Poulsen, 2007; Lampitt et al., 1990). Additionally, deep ocean sediment trap studies (Deuser et al., 1981) show a strong correlation between fluxes of particulate organic carbon (POC) and minerals such as biogenic silica, calcium carbonate and lithogenic minerals. This has led to the "ballast hypothesis", which suggests that an association between minerals and organic matter within sinking particles controls the export of POC to the deep ocean (Armstrong et al., 2002; Francois et al., 2002; Klaas and Archer, 2002). It has been suggested that the minerals increase the densities of the sinking aggregates and, thus, increase their sinking velocities and/or that the minerals provide protection of the organic matter against remineralization (Armstrong et al., 2002; Engel et al., 2009a; Fischer and Karakas, 2009; Francois et al., 2002; Hedges et al., 2001; Iversen and Ploug, 2010; Klaas and Archer, 2002; Lee et al., 2009a; Passow et al., 2003; Ploug et al., 2008a; Sanders et al., 2010).

The ballast hypothesis has spawned a series of publications investigating the role of ballast minerals for the export of POC. Investigations on the protection of settling aggregates against remineralization via the incorporation of ballast minerals have found evidence supporting both outcomes, not only i) the presence of a protective mechanism (Arnarson and Keil, 2000; Engel et al., 2009a; Le Moigne et al., 2013) but also ii) the lack of an effect on remineralization (Ingalls et al., 2006; Iversen and Ploug, 2010; Ploug et al., 2008a,b). Several studies have confirmed the potential for ballast minerals to increase the density and, thus, the sinking velocity of aggregates (e.g. De La Rocha et al.,

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2008; De La Rocha and Passow, 2007; Engel et al., 2009a; Iversen et al., 2010; Iversen and Ploug, 2010; Ploug et al., 2008a,b; Thomalla et al., 2008). Recent studies have observed that the presence of ballast minerals can enhance POC fluxes, confirming the ballasting effect of minerals (Bressac et al., 2014; Lee et al., 2009b; Sanders et al., 2010; Ternon et al., 2010; Thunell et al., 2007). This shows that the ballasting effect could have important consequences for the future climate, in which it has been suggested that increased desertification and droughts will occur, which could lead to higher dust availability in the atmosphere and ocean (e.g. Mahowald et al., 2009; Prospero and Nees, 1976).

Despite the seemingly clear effect of ballasting toward denser aggregates with larger size-specific sinking velocities, only few studies have been undertaken on the overall effect of ballasting on total export fluxes (Bressac et al., 2014; Ternon et al., 2010). Both studies observed an enhanced export flux in the presence of ballast minerals, but did not combine their results with direct measurements on individual aggregates, i.e. the influence of ballasting on either sinking velocity or degradation of individual aggregates. There is therefore a need to improve our understanding of how ballast minerals can induce enhanced export fluxes on both the scale of individual aggregates and the overall effect on the total aggregated material: i.e. i) will the increase in aggregate abundance typically observed for ballasted aggregates compensate for the mass-loss due to decreased maximum aggregate size (Hamm, 2002; Iversen and Ploug, 2010; Passow and De La Rocha, 2006), and ii) will the increase in excess density cause the smaller aggregates to sink as fast or faster than the large non-ballasted aggregates and, thus, enhance the total POC flux in comparison to non-ballasted aggregates?

This study aims to improve our understanding of the causality of ballast minerals in enhancing POC fluxes by concomitantly measuring ballast effects on individual aggregate parameters such as size, sinking velocity, dry weight, solid hydrated density, particulate organic carbon and nitrogen content, and microbial respiration rate of ballasted and non-ballasted aggregates over time. Additionally, we will follow the total pool of aggregates in terms of abundance of different sizes, total aggregated volume, and total potential POC flux in both a ballasted and a non-ballasted treatment. We chose smectite as ballasting mineral since this is often an important component of desert dust, e.g. Saharan dust (Avila et al., 1996), which has been shown to enhance POC flux in both the Mediterranean (Bressac et al., 2014; Ternon et al., 2010) and in the second largest Eastern Boundary upwelling area off Cape Blanc, Mauritania (Iversen et al., 2010). Additionally, smectite, together with illite, is one of the most abundant minerals in situ (Weaver, 1988) and is the predominant clay mineral in the world's oceans (Cole and Shaw, 1983).

2. Material and methods

2.1. Aggregate formation

100 L of North Sea water (salinity 31.6 and temperature 15 °C) was collected from the coast off Helgoland at the Helgoland Roads Time Series site (54.11°N, 7.54°E) on 29 April 2007 and carefully inverse-filtered through a 100 μm mesh to remove mesoplankton. Sampling coincided with the measured fluorescence maximum at the spring peak, with chlorophyll *a* concentrations of ~5 μg L^{-1}. The in situ chlorophyll *a* concentrations at the sampling site decreased to ~2 μg L^{-1} only a few days after the sampling, suggesting that the plankton community was at a late bloom stage (see Löder et al., 2011 for more information). On 30 April 2007, the <100 μm plankton community was incubated in 35 Plexiglas cylinders, each with a volume of 1.15 L (roller tanks, 14 cm diameter and 7.47 cm height). Qualitative microscopic observations of the <100 μm phytoplankton community showed that it was dominated by diatoms: the most abundant species was *Chaetoceros* sp., while *Skeletonema* sp., *Thalassiosira* sp., and *Coscinodiscus* sp. were also present at high abundances. Smectite clay (Montmorillonite: SW_y-2, Clay Mineral Society, Colorado, USA) was added with a final concentration of 0.5 mg L^{-1} to 15 of the roller tanks to act as a ballast mineral while the remaining 20 roller tanks were non-ballasted. To our knowledge no measurements of surface ocean concentrations of smectite are known. We selected this concentration to imitate mineral input at concentrations similar to previous ballast mineral studies in roller tanks with clay additions in the range of 5 to 100 mg L^{-1} (Hamm, 2002) or 0.007 to 10 mg L^{-1} (Passow and De La Rocha, 2006). A mesocosm study in the Mediterranean Sea added 41.5 g of Saharan dust to 52 m^3 sea water, i.e. 0.8 mg of Saharan dust per L^{-1} (e.g. Bressac et al., 2011, 2014; Guieu et al., 2014). Since 25% of the Saharan dust was composed of clay particles, their clay addition was 0.2 mg L^{-1}, which is similar to the one used in this study. Scanning electron microscope images of the non-ballasted incubations did not show any presence of smectite. All 35 roller tanks were placed on a roller table and rotated with 3 RPM at 15 °C in darkness. The aggregate dynamics were followed throughout the study by counting the number of aggregates within different size classes (<1 mm, 1–2 mm, 2–3 mm, 3–4 mm, 4–5 mm and >5 mm) in each roller tank.

2.2. Sinking velocity

Measurements were carried out at 5 sampling time points: 48, 91, 157, 187 and 380 h after incubation start. On each sampling day, 15 to 25 individual aggregates from each treatment (ballasted and non-ballasted) were gently transferred with a wide bore pipette from the roller tanks to a vertical flow system where the sinking velocity of each aggregate was measured (see Ploug and Jørgensen, 1999). Generally, the aggregates from two randomly selected roller tanks were used for measurements at each sampling time point. This decreased the total number of roller tanks in each treatment by two after each sampling time point. The water in the vertical flow system was GF/F filtered and had the same temperature and salinity as the water in the roller tanks. An upward flow was adjusted to balance the aggregate sinking velocity until the aggregate remained suspended at a distance of one aggregate diameter above the net placed in the middle of the flow chamber (see Ploug et al., 2010). The sinking velocity of an aggregate was calculated from the flow rate divided by the cross-sectional area of the flow chamber. The x-, y-, and z-axes of each aggregate were measured in the flow system using a horizontal dissection microscope with a calibrated ocular. The aggregate volume was calculated by assuming an ellipsoid shape. For comparison with other aggregate shapes we calculated the equivalent spherical diameter (ESD) of each aggregate.

2.3. Oxygen measurements

Oxygen concentrations were measured in 50 μm increments across the aggregate–water interface using a Clark-type oxygen microelectrode with a guard cathode (Revsbech, 1989). The 90% response time of the electrode was <1 s and the stirring sensitivity <0.3%. The oxygen microelectrode was mounted in a micromanipulator and calibrated at air-saturation and at anoxic conditions. The electrode current was measured on a picoamperemeter (Unisense, PA2000) and read on a strip chart recorder (Kipp and Zonen) at high resolution (2 μM O_2 cm^{-1}). The tip diameter of the microsensor was 2 μm. All measurements were done at the steady state of the oxygen gradients. See Iversen and Ploug (2010, 2013) for further details.

2.4. Total microbial respiration rates within the aggregates

Oxygen fluxes to the aggregate and total respiration rates of the microbial community within the aggregates were calculated from the oxygen gradients measured across the aggregate–water interface under steady-state conditions (see Ploug et al., 1997). We used