

**Enhanced rates of
POM remineralization
by microzooplankton**

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Enhanced rates of particulate organic matter remineralization by microzooplankton are diminished by added ballast minerals

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Abstract

To examine the potentially competing influences of microzooplankton and calcite mineral ballast on organic matter remineralization, we incubated diatoms in darkness in rolling tanks with and without added calcite minerals (coccoliths) and microzooplankton (rotifers). Concentrations of particulate organic matter (POM), suspended or in aggregates, of dissolved organic matter (DOM), and of dissolved inorganic nutrients were monitored over 8 days. The presence of rotifers enhanced the remineralization of ammonium and phosphate, but not dissolved silicon, from the biogenic material, up to 40 % of which became incorporated into aggregates early in the experiment. Added calcite resulted in rates of excretion of ammonium and phosphate by rotifers that were depressed by 67 % and 36 %, respectively, demonstrating the potential for minerals to inhibit the destruction of POM in the water column by zooplankton. Lastly, the presence of the rotifers and added calcite minerals resulted in more rapid kinetics of aggregation, although not a greater overall amount of aggregation during the experiment.

1 Introduction

The biological pump exports 5 to 10 GtCyr⁻¹ to the deep ocean as dissolved and particulate organic matter (Falkowski et al., 1998; Henson et al., 2011). Without such transfer of carbon to the deep, pre-industrial concentrations of atmospheric carbon dioxide (CO₂) would have been almost twice as high as they were (Broecker and Peng, 1982; Parekh et al., 2006) and a greater portion of annual anthropogenic CO₂ emissions would remain in the atmosphere, accelerating the growth of atmospheric CO₂ (Le Quére et al., 2010). The processes controlling the efficiency of particulate organic matter (POM) export by the biological pump are thus critical with respect to global climate change.

A long-known correlation between fluxes of minerals (i.e. biogenic calcite, biogenic opal, and lithogenic material like clays) and of particulate organic carbon (POC) sinking

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into sediment traps in the deep sea (Deuser et al., 1981) has been recently revisited as the “ballast hypothesis” that suggests sinking fluxes of minerals control the export of POC to the deep sea (Armstrong et al., 2002; Francois et al., 2002; Klaas and Archer, 2002). Minerals could provide organic matter with protection from remineralization and/or excess density that increases sinking velocities, increasing POC export efficiency (Armstrong et al., 2002; Francois et al., 2002; Klaas and Archer, 2002; Passow et al., 2003; Ploug et al., 2008; Engel et al., 2009b; Fischer and Karakaş, 2009; Lee et al., 2009; Sanders et al., 2010).

Subsequent research has shown that while addition of mineral ballast to aggregates can increase their sinking velocity (De La Rocha and Passow, 2007; De La Rocha et al., 2008; Ploug et al., 2008; Thomalla et al., 2008; Engel et al., 2009b; Lee et al., 2009; Iversen and Ploug, 2010; Sanders et al., 2010; Riley et al., 2012), little evidence has emerged for minerals protecting organic matter in the water column from remineralization or solubilization (Ingalls et al., 2006; Engel et al., 2009a; Iversen and Ploug, 2010). In the only reported case, aggregates of a calcifying strain of *Emiliana huxleyi* degraded more slowly relative to those of a non-calcifying strain (Engel et al., 2009a), but the underlying mechanisms, undetermined, could have been exclusion of bacteria or ectoenzymes from the coccolith-laden aggregates, or differences in the physiological condition or composition of the two strains of *E. huxleyi*. Conversely, experiments that directly investigated carbon-specific respiration rates of aggregates (Iversen and Ploug, 2010) have not found differences related to the presence of ballast minerals. No study has yet examined whether mineral ballast reduces the rate of remineralization driven by grazing by marine zooplankton, especially with respect to aggregates, although suspended particles of clay and calcite are known to interfere with feeding by *Daphnia* sp. in freshwater systems (Vanderploeg et al., 1987; Kirk 1991).

To address whether incorporation of calcite into aggregates affects rates of solubilization and remineralization mediated by bacteria and/or microzooplankton, we allowed diatoms to aggregate in the presence and absence of calcite minerals and

microzooplankton (rotifers) and then monitored nutrients, POM, and DOM in the tanks over 8 days.

2 Materials and methods

2.1 Experimental setup

5 Experiments were carried out in cylindrical tanks kept in rotation on motorized tables to allow particles to sink freely throughout the experiment (Shanks and Trent, 1980; Passow and De La Rocha, 2006; De La Rocha et al., 2008). Twelve 4.5-L tanks were set up, covering three replicates of four different treatments: phytoplankton only (P), phytoplankton + minerals (PM), phytoplankton + microzooplankton (PZ), and phyto-
10 plankton + microzooplankton + minerals (PMZ). Tanks were kept in darkness at 15 °C in rotation at 1.5–3 rpm.

All tanks contained a mixture of seawater filtered through a 0.6 µm polycarbonate filter to remove phytoplankton and microzooplankton but not bacteria and an equal volume mixture of two diatom cultures, *Skeletonema marinoi* and *Chaetoceros gracilis*,
15 grown in a modified *f/2* medium ($\text{Si(OH)}_4 = 50 \mu\text{M}$; $\text{PO}_4 = 4 \mu\text{M}$; $\text{NO}_3 = 64 \mu\text{M}$, and vitamins and trace elements in *f/2* quantities). Calcite was added to tanks 3, 7, and 11. Microzooplankton (the marine rotifer *Brachionus* sp.) were added to tanks 2, 6, and 10. Microzooplankton and minerals were added to tanks 4, 8, and 12. Approximately 6200 rotifers per liter were added to all rotifer containing tanks except T10, which received
20 only 4400 rotifers per liter.

The calcite was prepared from Cretaceous (Maastrichtian) chalk from the cliffs of Rügen, Germany. The chalk was disaggregated, gently ground, soaked overnight in bleach, and then rinsed with deionized distilled water (Milli-Q). The calcite was then suspended in artificial sea water ($1.68 \text{ g L}^{-1} \text{ NaHCO}_3$, $71.25 \text{ g L}^{-1} \text{ MgSO}_4$ and
25 $321.25 \text{ g L}^{-1} \text{ NaCl}$) and those particles remaining in suspension after several minutes were used in the experiment. A similar suspension used by De La Rocha et al. (2008)

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consisted of coccoliths and smaller calcium carbonate debris. The final experimental concentration of calcite was 1.3 mgL^{-1} .

The experiment lasted 8 days, with tanks sampled on days 0, 2, 4, and 8. Aggregates were gently removed with a 10-mL disposable pipette whose tip had been cut off. The aggregates were combined and subsampled for various parameters and the now aggregate-free “background” water in the tanks was sampled for the material remaining in suspension.

2.2 Bacteria counts and ectoenzyme activity

Background water samples were fixed with 2% formalin, flash frozen in liquid nitrogen, then stored at -80°C until preparation for counting. Tween 80 was added to detach bacteria from POM (Yoon and Rosson, 1990). Samples were sonicated in an ice bath, stained with SYBR gold (Invitrogen), and then mounted on black polycarbonate filters ($0.22 \mu\text{m}$) using a 1 : 1 mixture of phosphate buffer solution and glycerol and 0.01% *p*-phenylenediamine as a preservative during storage at -20°C until further counting. More than 200 bacteria were typically counted per sample using an Olympus epifluorescence microscope.

Aminopeptidase activity was measured using L-leucinemethyl coumarinyl amide (Leu-MCA) in methyl Cellosolve as substrate analogue (Hoppe et al., 1988). Samples were incubated in duplicate across a range of leucine concentrations and with sterile-filtered and boiled seawater controls (Hoppe et al., 1988). Fluorescence was measured in a FP-1520 spectrofluorometer (JASCO) at a 364 nm excitation wavelength and a 445 nm emission wavelength. Final results are expressed in terms of maximal velocities (V_{max}) from fitting a Michaelis-Menten curve through the resulting data using the curve fitting routine in SigmaPlot.

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2.3 Nutrients and dissolved organic matter

Silicate, nitrate + nitrite, and phosphate were measured using a Bran + Luebbe AAll auto-analyser as described by Aminot and Kerouel (2007). Ammonium was measured manually by spectrophotometry (Shimadzu UV 1700) as described by Koroleff (1969).

5 Samples for dissolved organic carbon (DOC), nitrogen (DON), and phosphorus (DOP) were filtered through pre-combusted (450 °C, 4 h) Whatman GF/F filters into acid cleaned HDPE bottles and stored frozen (−20 °C) until analysis. DOC and total dissolved nitrogen (TDN) were measured using a Shimadzu TOC VCSH Total Organic Carbon Analyzer with the TNM-1 Total Nitrogen detector, according to methods of Pan
10 et al. (2005). DON concentrations were calculated as the difference between TDN and dissolved inorganic nitrogen (the sum of nitrate, nitrite, and ammonium). For DOP, filtered samples were frozen at −20 °C in precombusted borosilicate vials until analysis via a segmented flow automated method with on-line photo-oxidation (Aminot and Kerouel, 2001).

15 2.4 Particulate matter

Particulate organic carbon (POC) and nitrogen (PON) were filtered onto pre-combusted (450 °C, 4 h), pre-weighed Whatman GF/F filters, rinsed with MilliQ water, and dried at 60 °C. Filters were fumed with HCl to remove inorganic carbon before measurement with a Flash 1112 series elemental NC analyser ThermoQuest as described in Lor-
20 rain et al. (2003). Total particulate phosphorus (TPP) was filtered onto pre-combusted (450 °C, 4 h) Whatman GF/F filters and rinsed with filtered seawater. Filters were dried at 60 °C then frozen. Defrosted filters were rinsed with 0.17 M Na₂SO₄ and placed in precombusted borosilicate vials with 17 mM MnSO₄, covered with aluminum foil, dried at 95 °C, and stored in a desiccator. Vials were combusted at 450 °C for 2 h and then
25 digested with 0.2 NHCl at 80 °C for 30 min before phosphate measurement via the standard molybdate method (Aminot and Kerouel, 2007).

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Particulate inorganic carbon (PIC) was filtered onto 0.4 μm Millipore polycarbonate filters, rinsed with MilliQ water, dried, and then digested in 0.4 M nitric acid. Ca and Na were determined using a PerkinElmer Optima 4300 DV inductively coupled plasma optical emission spectrometer (ICP-OES) as described in (Poulton et al., 2006). PIC was calculated assuming that all PIC was CaCO_3 . Low Na concentrations indicated lack of sea salt Ca on the filters. Biogenic silica (bSiO_2) was filtered onto 0.4 μm polycarbonate filters (Millipore) and dried at 60 $^\circ\text{C}$ then dissolved in 4 mL of 0.2 M NaOH at 100 $^\circ\text{C}$ for 60 min (Ragueneau et al., 2005), neutralized with 1 M HCl, and determined colorimetrically as dissolved silicon.

2.5 Photosynthetic parameters

Measurements of the quantum yield of photosynthesis F_v/F_m , were made for suspended cells and cells in aggregates via pulse amplitude modulated (PAM) fluorometry (AquaPen-C AP-C 100). Samples were dark adapted for 10–15 min before measurement of F_m (maximum chlorophyll fluorescence) and F_t (instantaneous chlorophyll fluorescence, which, in dark adapted cells, is equivalent to F_o , emission by excited chlorophyll *a* in photosystem II antennae). F_v , the maximum capacity for photosynthetic quenching, was calculated as the difference between F_m and F_o (i.e. $F_v = F_m - F_o$).

3 Results

3.1 Formation of aggregates

Aggregates > 1 mm formed overnight in all but the P treatment (Figs. 1–4). By the day 2 sampling day, a higher proportion of POM and bSiO_2 had been incorporated into aggregates in the PM and PZM treatments than in the PZ treatment (Fig. 5). By day 4, the P tanks also contained aggregates > 1 mm (Figs. 1–4), although they represented a smaller fraction of the total POM than in the PZ, PM, and PZM treatments (Fig. 5). These differences between the treatments disappeared by the end of the experiment.

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The different kinetics of aggregation were likely related to the presence of zooplankton and added minerals. There were not differences in phytoplankton physiology (exemplified by F_v/F_m ; Fig. 6) or in concentrations of transparent exopolymer particles (TEP) (Laurenceau, personal communication) or bacteria (Fig. 7) because all experimental tanks were filled at the same time from the same large reservoir of phytoplankton and seawater. Further examination of the aggregation will be given in another manuscript.

3.2 Decline in the condition of the phytoplankton

The phytoplankton were initially relatively healthy, showing quantum efficiency of photosystem II (F_v/F_m) of 0.6 on day 0 (Parkhill et al., 2001) (Fig. 6), but F_v/F_m declined dramatically during the incubation, not due to any lack of nutrients (Fig. 8), but to the dark conditions of the incubation. By day 2, F_v/F_m had dropped to ~ 0.4 in all treatments (Fig. 6), indicating cells under stress. By day 4, F_v/F_m had dropped below 0.1 for cells in aggregates in the P, PM, and PZM tanks, indicating cells in extreme stress while F_v/F_m remained ~ 0.3 for non-aggregated cells in all tanks and for cells in aggregates in the PZ tank.

3.3 Bacterial abundance and aminopeptidase activity

Bacteria occurred in both the water in the tanks (Fig. 7), at typical concentrations of 1.5×10^6 to 3.5×10^6 cells per mL, and within the aggregates (their abundance within the aggregates was not ascertained). The number of bacteria suspended in the water in the tanks did not vary systematically between treatments or over time, except within the range of error of the counts.

Aminopeptidase activities show that the bacteria were active in the tanks (Fig. 9). On day 0, the pattern for aminopeptidase activity is the same in all of the treatments, with a maximum velocity (V_{\max}) for leucine hydrolysis of $227 \pm 10 \text{ h}^{-1}$ and a half saturation constant (K_s) of $192 \pm 18 \mu\text{M}$ ($r^2 = 0.99$). By day 8, V_{\max} and K_s had decreased in all tanks, although the decrease in V_{\max} was smaller in the two mineral containing

treatments, which also experienced the greater decrease in K_s (Fig. 9). The divergence in V_{max} and K_s values among the different treatments may reflect shifts in the bacterial population in each tank or to the response of the bacterial community to changes in the composition of DOM in the different treatments.

3.4 Dissolved and particulate matter

Concentrations of suspended particulate matter decreased during the experiment (Figs. 1–4), with 30–40 % of the initial POC, PON, TPP, and bSiO₂ remaining in suspension at the end of the experiment. Overall, ~ 44 % of the loss of suspended POC and PON and ~ 36 % of the loss of suspended bSiO₂ and TPP could be attributed to incorporation into aggregates. The rest of the loss had to be due to oxidation (reminer-

alization) and solubilization (DOM production). Concentrations of most nutrients increased during the experiment, indicating net remineralization of organic matter and silica. DSi, indicative of biogenic silica dissolution, increased by ~ 4 μM to an average end concentration of $22.0 \pm 0.4 \mu\text{M}$ (Fig. 8), effectively equalling the total recorded loss of $6 \mu\text{mol L}^{-1}$ bSiO₂ (Fig. 4). Nitrite (indicative of nitrification) increased on average from $0.27 \pm 0.02 \mu\text{M}$ at day 0 to $0.70 \pm 0.08 \mu\text{M}$ on day 8 (Fig. 8). Ammonium (Fig. 8) roughly doubled in the P and PM tanks and increased five- to tenfold in the PZ and PZM tanks. Phosphate (Fig. 8) increased by ~ 0.5 μM in the P and PM treatments and by ~ 0.9 μM in the PZ and PZM treatments.

Nitrate was the only nutrient not to show a general increase during the experiment, remaining relatively close to 23 μM in the P and PM tanks and not rising above 27 μM , even in the zooplankton-containing tanks (Fig. 8). This is unsurprising as during the relatively short duration of the experiment (8 days), significant quantities of nitrate would not be expected to be formed from nitrite and ammonium via nitrification (Von Brand et al., 1942).

Between the beginning and end of the experiment, concentrations of dissolved organic nitrogen (DON) generally increased and those of dissolved organic phosphorus (DOP) and dissolved organic carbon (DOC) did not change very much (aside from

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the exceptionally elevated DOC values on day 8 in the PM and PZM tanks which may reflect contamination). The pools of DOM represent a balance between inputs through solubilization and outputs through oxidation, suggesting that the microzooplankton drove enhanced net production of DON and DOP between day 0 and 8 (although not between day 0 and 4) (Figs. 2–3). Added minerals had no clear impact on DON and DOP concentrations. If the two elevated end values of DOC in the two mineral-containing treatments are to be believed, then between day 0 and day 8, the presence of added calcite resulted in an enhanced net production of DOC (Fig. 5).

4 Discussion

The efficiency of POM export from the upper ocean is determined by the balance between the sinking rate of this material, some of which forms large, rapidly sinking aggregates, and the oxidation rate back to inorganic nutrients and CO₂. The controls over the rate of destruction of sinking particles (aggregates), both in terms of conversion to non-sinking organic matter like small particles and DOM and of remineralization to inorganic nutrients and CO₂, lie largely with zooplankton of various size classes and bacteria, with different contributions from each at different times, places, and depths (e.g., Iversen et al., 2010). Unfortunately, our understanding of the links between food web structure and the efficiency of export (and of destruction) of POM lags behind our understanding of aggregation and sinking. Results presented here suggest that microzooplankton and ballast minerals influence sinking fluxes by accelerating aggregation kinetics. In addition, added minerals may diminish the enhanced regeneration of ammonium and phosphate driven by microzooplankton, probably by interfering with their grazing on POM.

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4.1 The influence of zooplankton and minerals on nutrient regeneration

During the experiment, rotifers and added calcite had no effect on the regeneration of DSi (Fig. 8c) from bSiO₂ nor on the net production of nitrite (Fig. 8b), but they influenced the regeneration of NH₄⁺ and phosphate (Fig. 8d, e) from organic matter.

By the end of the experiment, the increase in NH₄⁺ concentrations was 4–7 times greater in the PZ and PZM treatments than in the treatments lacking added rotifers, accounting for 7% of the loss of PON in the P and PM treatments, 36% of the loss in the PZ treatment (n.b. in the day 8 tank of which had 30% fewer zooplankton than the other zooplankton-containing tanks), and 41% of the loss in the PZM treatment. A net 2.83 μmol L⁻¹ of NH₄⁺ regeneration in the PZ treatment and 1.38 μmol L⁻¹ in the PZM treatment can be ascribed to excretion by rotifers as they fed on diatoms. An NH₄⁺ excretion rate (*E*) per rotifer biomass can be calculated for the 8-day duration of the experiment (Δt) using the number of rotifers (*n*) added to the PZ tank (4400 individuals per liter) and to the PZM tank (6200 individuals per liter) sampled on day 8 and the average dry weight per individual *Brachionus* sp. (*DW_B*) of 0.16 μg (Theilacker and McMaster, 1971):

$$E = \left(\frac{([\text{NH}_4]_{\text{d8}} - [\text{NH}_4]_{\text{d0}}) - \text{NRR}}{(n \times \text{DW}_B)} \right) \div \Delta t \quad (1)$$

after subtracting the 0.48 ± 0.10 μmol L⁻¹ of “non-rotifer” regeneration (NRR) of NH₄⁺ in the treatments lacking added microzooplankton presumably associated with phytoplankton cell lysis as their physiological condition deteriorated. This yields an NH₄⁺ excretion rate of 0.3 μg N mg⁻¹ rotifer h⁻¹ in the PZ treatment and of 0.1 μg N mg⁻¹ rotifer h⁻¹ in the PZM treatment, revealing that the added calcite had an inhibitory effect on feeding by the rotifers. Carrying out this calculation using the quantity of NH₄⁺ plus nitrite (assuming that the increase in nitrite during the experiment was fueled by the nitrification of NH₄⁺ and thus nitrite represents an NH₄⁺ sink) yields equivalent rates.

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Similarly, the increase in phosphate concentration by the end of the experiment is 2 times greater in the two rotifer-containing treatments ($0.88 \pm 0.10 \mu\text{M}$) than in the two treatments lacking rotifers ($0.46 \pm 0.07 \mu\text{M}$). This regeneration accounts for 60 % of the loss of TPP in the P and PM treatments and for 80 % of the loss of the TPP in the PZ and PZM treatments. Adapting equation 1 for phosphate yields a phosphate excretion rate of $0.11 \mu\text{g P mg}^{-1} \text{ rotifer h}^{-1}$ in the PZ treatment and $0.07 \mu\text{g P mg}^{-1} \text{ rotifer h}^{-1}$ in the PZM treatment, further suggesting that the added calcite inhibited rotifer feeding.

These values are a minimum estimate of phosphate excretion because phosphate uptake clearly occurred between days 0 and 2 (Fig. 4e) and may have carried on throughout the experiment. Bacteria are known to take up phosphate and the diatoms may have retained sufficient energy for phosphate uptake, at least for a few days. Judging from the decrease in phosphate in the two treatments lacking zooplankton, the net uptake was $0.15 \mu\text{M}$ between days 0 and 2. Accounting for this in the calculation of phosphate uptake increases the excretion rates to $0.14 \mu\text{g P mg}^{-1} \text{ rotifer h}^{-1}$ in the PZ treatment and $0.09 \mu\text{g P mg}^{-1} \text{ rotifer h}^{-1}$ in the PZM treatment.

The added calcite had no further visible impact on nutrient regeneration during the experiment beyond their inhibitory effect on the regeneration of ammonium and phosphate by the rotifers, most likely related to physically interfering with grazing.

4.2 The partitioning of carbon between dissolved and particulate phases

Differences in the kinetics of aggregation between treatments (Figs. 1–5) would have resulted in different patterns of export. More suspended material became more quickly incorporated into aggregates in the mineral-containing treatments (PM and PZM), meaning that for a few days, more of the POM was present in the form of aggregates in the mineral containing treatments than in the two treatments lacking minerals (Fig. 5). Because the aggregates sank an average of 180–380 m per day (Laurenceau, personal communication, 2013) but suspended (non-aggregated) POM did not, the treatments that formed aggregates sooner and faster would have exported more POM earlier than the others. For example, by day 2, the P treatment, lacking visible aggregates, would

have exported no POC while 6 % of the POC in the PZ treatment and approximately 20% of the POC in the PM and PZM treatments would have been sinking with an average speed greater than 240 m d^{-1} (Laurenceau, personal communication, 2013).

By the end of the experiment the differences between treatments in the extent of aggregation disappeared. Thus, over this time frame (8 days), and within the closed system represented by the rolling tanks, the presence of minerals and/or rotifers had no impact on the percent of POC that was incorporated into aggregates (Fig. 5). Previous studies with clays, calcium carbonate, and/or silica which have shown that the presence of large quantities of suspended mineral particles speeds up the aggregation of diatoms (Hamm, 2002) and alters the size and compactness of the aggregates (Hamm, 2002; Passow and De La Rocha, 2006; De La Rocha et al., 2008; Engel et al., 2009b) did not determine whether or not the minerals increased the total amount of POC incorporated into aggregates.

The rotifers and added calcite minerals had no effect on the partitioning of organic carbon between dissolved and particulate phases (Fig. 5). Although the fraction of the total organic carbon that occurred as DOC increased from $51 \pm 0.5 \%$ to $65 \pm 1 \%$ between day 0 and day 8 for all the treatments due to a decrease in the amount of POC, throughout the experiment the differences between treatments were negligible. Thus neither the rotifers nor the added calcite resulted in enhanced scavenging of DOC into the particulate phase, nor increased the relative amount of production of DOC from POC.

4.3 Was it suspended POM, aggregates, or DOM that remineralized?

Increases in nutrient concentrations during the experiment due to remineralization appear to have been related to losses of particulate matter rather than DOM because concentrations of DOM tend to either increase over time or remain roughly the same (Figs. 1–3).

Taking the most simple case of regeneration from aggregates versus suspended matter, the per day increase in DSI concentrations increased during the first 4 days

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of the experiment, from an average of $0.15 \pm 0.06 \mu\text{M d}^{-1}$ between days 0 and 2 to $0.70 \pm 0.19 \mu\text{M d}^{-1}$ between days 2 and 4. It remained at $0.65 \pm 0.06 \mu\text{M d}^{-1}$ between days 4 and 8. This increase in the rate of DSi regeneration is tied likely to the decline in the health of the diatoms indicated by the decline in F_v/F_m (Fig. 6). In fact, there is a strong negative correlation between the F_v/F_m of suspended plankton and the increase in DSi concentration, with DSi increasing by $3.0 \mu\text{M d}^{-1}$ for each unit of decrease in F_v/F_m ($r^2 = 0.82$; $n = 12$; $p < 0.01$). Given that there were large differences in the kinetics of aggregate formation between treatments, the overall similarity in DSi regeneration (Fig. 8c) suggests that the dissolution of biogenic silica occurred equitably between suspended diatoms and diatoms in aggregates. Beyond that, it is difficult to say to what extent remineralization was driven by the decomposition of suspended matter versus the decomposition of material in aggregates. If any loss of matter from aggregates occurred, it was masked by the process of aggregation during the experiment.

4.4 Probable feeding behavior of the rotifers

The rotifers were capable of feeding on the aggregates that formed during the experiment. Rotifers are selective feeders able to home in on concentrated patches of food (Ignoffo et al., 2005). Marine species such as *Brachionus* sp. can feed on diatoms and are known to graze on coccolith-containing coccolithophorids (Harris, 1994), meaning that the POM in this experiment should have been available to them. Rotifers are also known to graze on aggregates (Zimmermann-Timm et al., 1998) and were observed associated with the aggregates during the experiment (Fig. 10). The rotifers were of course too small to feed on entire aggregates, but the individual diatoms present within the aggregates were well within the range of the 5 to 12 μm equivalent spherical diameter (ESD) preferred by *Brachionus* sp. (Rothhaupt, 1990). Although *Brachionus* sp. may have also fed on suspended POM, observations of them grazing on the periphery

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of the aggregates during the experiment (Fig. 10) confirms that they fed at least partly on aggregates.

5 Conclusions

This work has demonstrated, in a simplistic way, that food web structure influenced the remineralization of nutrients from a population of diatoms, at least 40 % of which were associated with aggregates for more than half the duration of the experiment. In this case, the presence of rotifers resulted in enhanced remineralization of NH_4^+ and phosphate, but not of DSi, during the 8 days of the experiment. More interestingly, the presence of added calcite minerals diminished the enhanced rates of NH_4^+ regeneration and phosphate regeneration related to grazing by microzooplankton (rotifers) by 67 % and 36 %, respectively, although the estimate for phosphate regeneration is an underestimate due to phosphate uptake by phytoplankton and/or bacteria during the experiment. Lastly, the presence of the microzooplankton and of the added calcite increased the kinetics of aggregation, although they did not result in an overall greater amount of POM incorporated into aggregates in the different treatments by the end of the experiment. Because of the high sinking speeds of the aggregates, this would have resulted in earlier export of organic matter from these systems in the treatments containing zooplankton and minerals.

Acknowledgement. We thank H. Stibor, Oceanopolis Brest, P. Pondaven, A. C. Baudoux, R. Corvaisier, A. Masson, C. Liourzou (IUEM), E. Achterberg, C. Dumousseau, Z. Chowdhury, (NOC), C. Labry (IFREMER) for technical support, discussions, and/or advice. This work was supported by the CalMarO FP7 Marie Curie Initial Training Network (www.calmaro.eu, grant agreement no. 215157), Region Bretagne and the EURO-BASIN FP7 Integrated Project.

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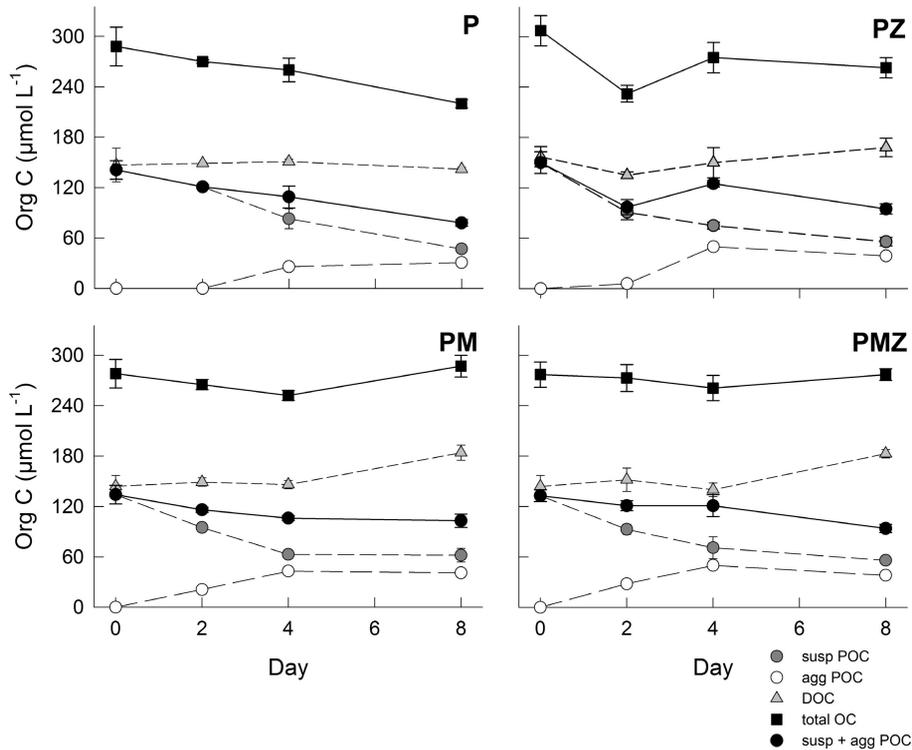


Fig. 1. Concentrations of DOC, total POC, suspended POC, and POC in aggregates in the 4 treatments during the experiment.

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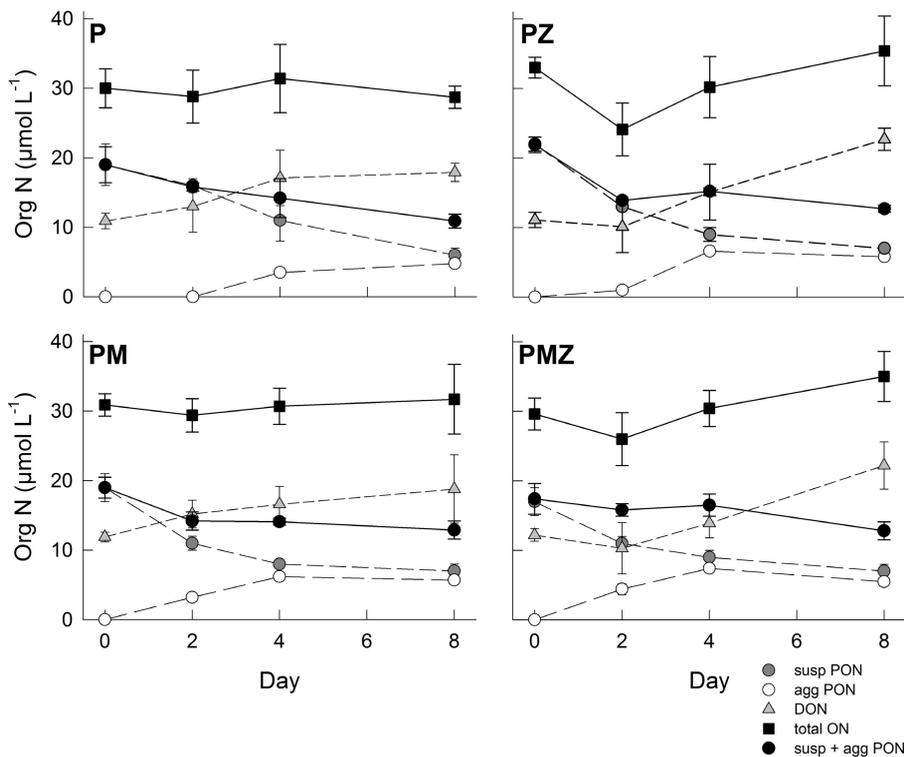


Fig. 2. Concentrations of DON, total PON, suspended PON, and PON in aggregates in the 4 treatments during the experiment.

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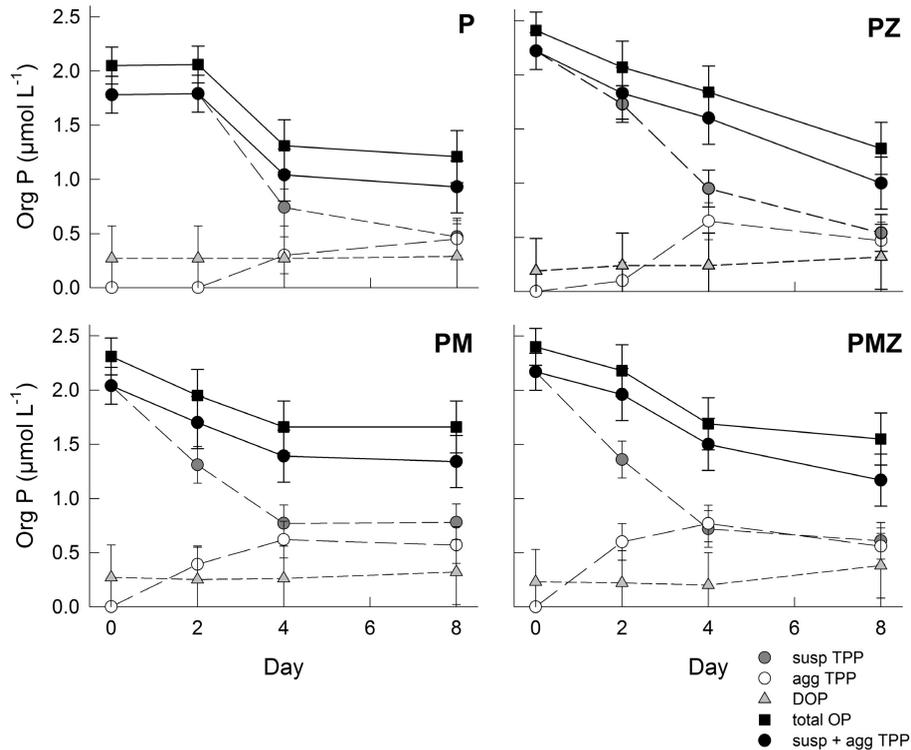


Fig. 3. Concentrations of DOP, total TPP, suspended TPP, and TPP in aggregates in the 4 treatments during the experiment.

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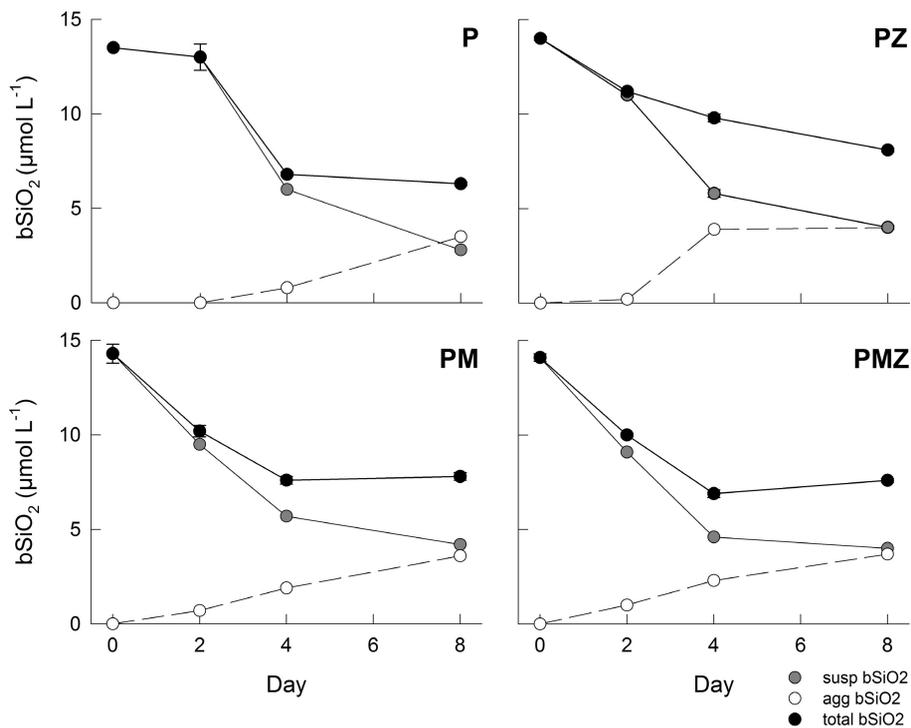


Fig. 4. Concentrations of total bSiO₂, suspended bSiO₂ and bSiO₂ in aggregates in the 4 treatments during the experiment.

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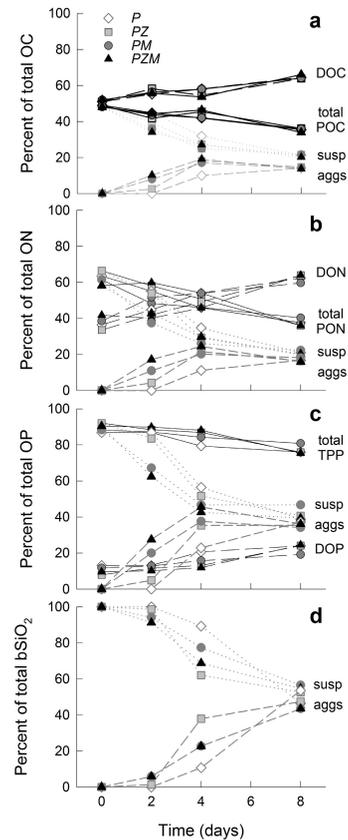


Fig. 5. The percent of the total **(a)** organic carbon, **(b)** organic nitrogen, **(c)** organic phosphorus, and **(d)** biogenic silica that is in the dissolved organic, total particulate organic (or biogenic), suspended particulate, or aggregate form.

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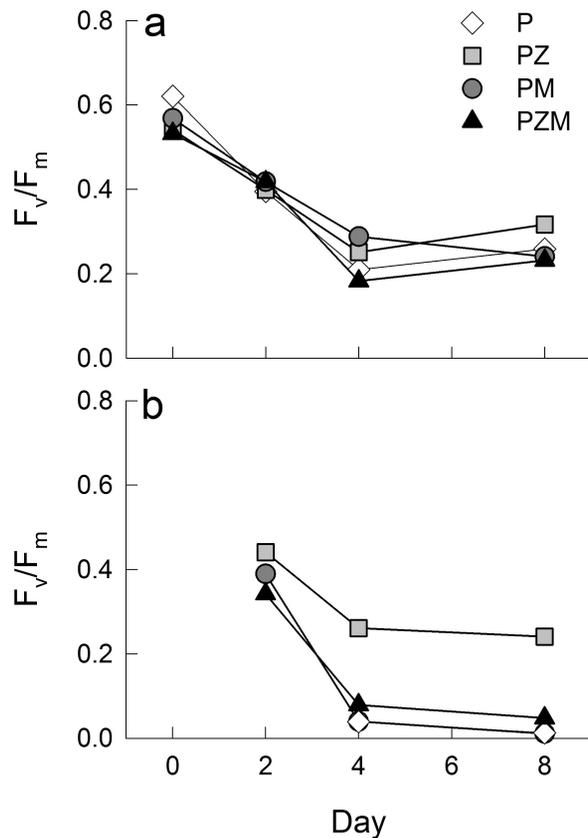


Fig. 6. Photosynthetic efficiency (F_v/F_m) of phytoplankton in **(a)** the background water and **(b)** associated with aggregates.

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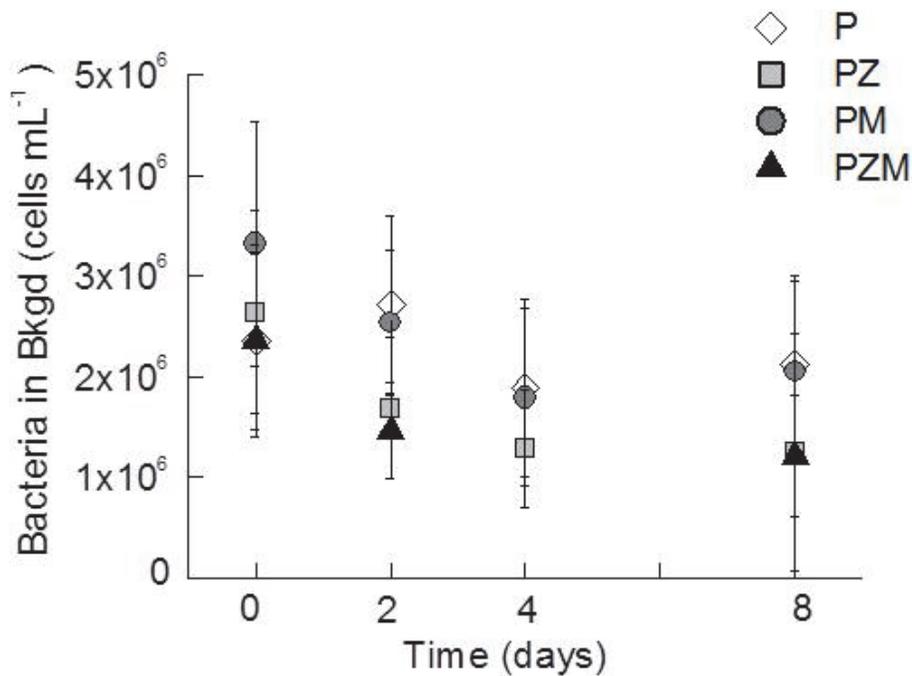
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**Fig. 7.** Abundance of bacteria in the suspended in the background water.[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[◀](#)[▶](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

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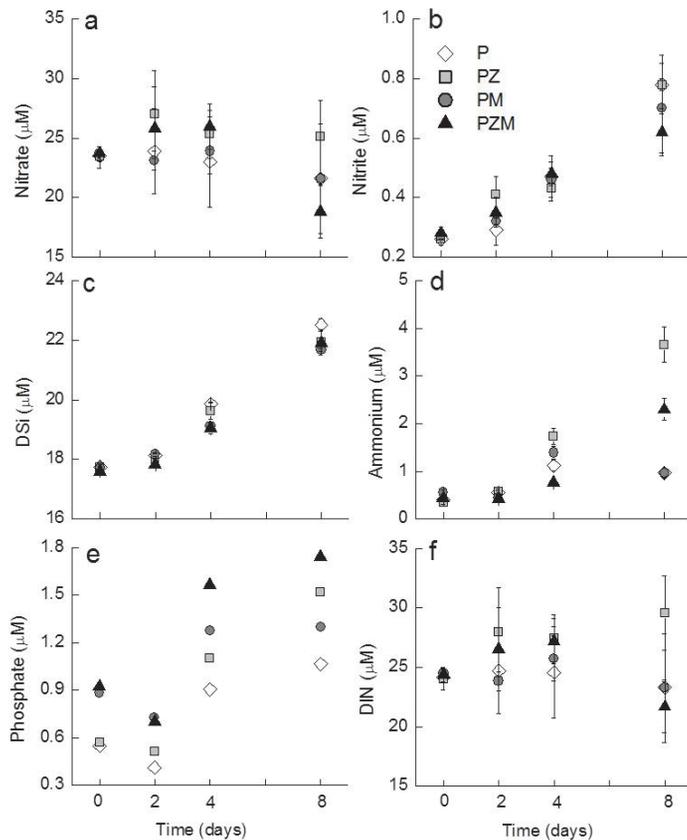


Fig. 8. Concentrations of (a) nitrate, (b) nitrite, (c) DSi, (d) ammonium, (e) phosphate, and (f) DIN (nitrate + nitrite + ammonium) in the tanks.

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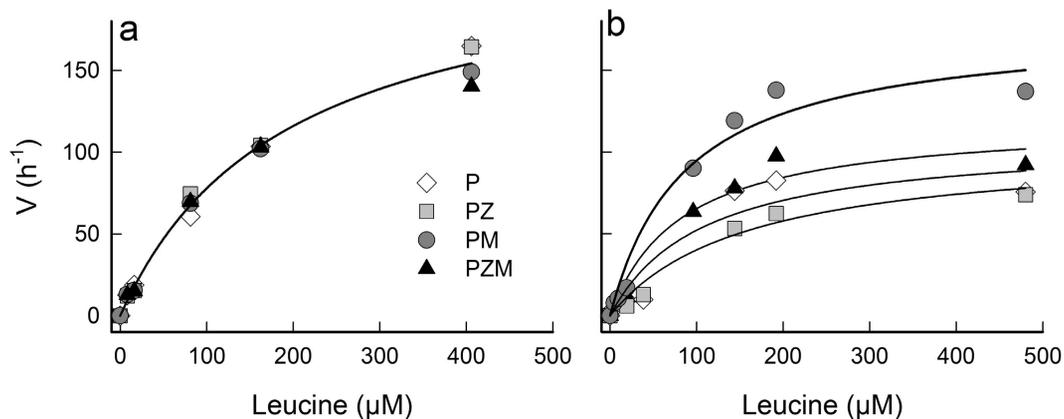


Fig. 9. Aminopeptidase activity in the background water of the tanks on days 0 **(a)** and 8 **(b)** as determined from the hydrolysis of leucine. The values of V_{\max} and K_s for the curve shown in panel **(a)** are $227 \pm 10 \text{ h}^{-1}$ and $192 \pm 18 \mu\text{M}$ ($r^2 = 0.99$). In panel **(b)**, the highest curve (the one for PM) has a V_{\max} of $177 \pm 19 \text{ h}^{-1}$ and a K_s of $87 \pm 28 \mu\text{M}$ ($r^2 = 0.97$), while the lowest curve (the one for PZ) has a V_{\max} of $103 \pm 14 \text{ h}^{-1}$ and a K_s of $157 \pm 50 \mu\text{M}$ ($r^2 = 0.98$).

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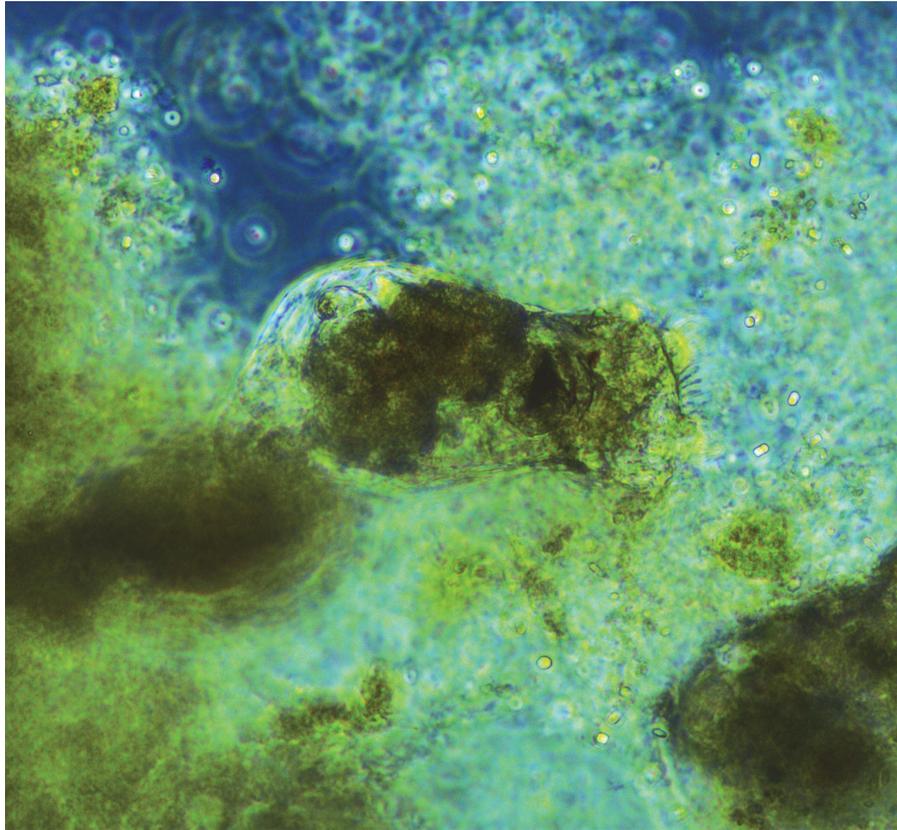


Fig. 10. Image of rotifer associated with (and actively feeding on) an aggregate during the experiment.

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