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Effect of the filter feeder *Daphnia* on the particle size distribution of inorganic colloids in freshwaters

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ABSTRACT

To quantify the effect of the filter feeder *Daphnia* on the aggregation of mineral particles, temporal changes in the particle size distribution of inorganic colloids were experimentally determined both in the presence and in the absence of *Daphnia* in water samples of Lake Brienz, Switzerland, an oligotrophic lake rich in suspended inorganic colloids. The results obtained show that daphnids favour the aggregation of mineral colloids, but only for particle sizes above the *Daphnia* filter mesh size. However, the number concentration of particles smaller than the *Daphnia* filter mesh size simultaneously increases in the presence of the filter feeder, suggesting either the break-down of existing aggregates or the aggregation of particles with initial sizes below the measured size range. The density of daphnids in this lake is currently too low to have any significant effect on the fate of inorganic colloidal particles as compared with aggregation due to physical processes of particle collision. However, in more productive water bodies where *Daphnia* is more abundant, they may play a significant role.

1. Introduction

Due to their small size, colloids—particles with a size between 1 nm and 1 μm at least in one dimension (Everett, 1972)—have a long settling time in water, typically ranging from days to months. As a result of their slow sedimentation, combined with their highly specific surface, they have a significant influence on the transport and bioavailability of nutrients and pollutants, as well as on the optical properties of surface waters. Colloid aggregation, resulting in increased particle size and thus increased particle settling velocity, regulates colloid removal. It is usually assumed that coagulation in natural waters is based on physical processes of particle collision (Weilenmann et al., 1989; Jackson, 1990; Hofmann and Filella, 1999; Hofmann et al., 2001). However, formation of fecal pellets by zooplankton has also often been invoked as an important aggregation mechanism in surface waters but their real significance in freshwaters is unknown because: (i) most of the existing studies are devoted to particulate organic matter fluxes and (ii) most of them have focused on marine (Fowler and Knauer, 1986; Alldredge and Silver, 1988; Turner, 2002) rather than freshwater systems.

Although a number of studies have been devoted to the effect of high turbidity levels on *Daphnia* (Koenings et al., 1990; Kirk, 1992; Rellstab and Spaak, 2007), the effect of *Daphnia* on the aggregation of inorganic colloidal particles has never been specifically investigated. Only Gliwicz (1986) concluded that *Daphnia* played an important role in the dynamics of

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inorganic turbidity in a large tropical reservoir. Since daphnids filter the surrounding water, they ingest not only algae but also inorganic suspended particles, and it is thus highly probable that they influence inorganic colloid fate in natural waters. It must be mentioned, however, that while copepods produce large, compact pellets covered by a peritrophic membrane (Wotton and Malmqvist, 2001), cladocerans, such as the filter feeder *Daphnia*, produce loose feces that disaggregate easily after release (Olsen et al., 1986; Lampert, 1987; Evans et al., 1998).

In the present study, the effect of *Daphnia* filtering on the size distribution of inorganic particles in the colloidal size range has been quantified for the first time to our knowledge. Both *Daphnia* and the inorganic colloids came from an ultra-oligotrophic, glacial lake (Lake Brienz, Switzerland). In summer, melting water originating from the glaciers present in its catchment area makes the lake extremely rich in suspended inorganic colloids and particles (Sturm and Matter, 1978; Finger et al., 2006; Anselmetti et al., 2007). The size and mineralogical composition of Lake Brienz inorganic colloids as well as their coagulation properties have been the subject of extensive studies (Chanudet and Filella, 2007a, b). Simultaneously, Lake Brienz daphnids have also been extensively characterized (Rellstab et al., 2007). This lake is therefore an ideal system for quantitatively measuring any possible effect of *Daphnia* on inorganic colloid aggregation in surface waters.

2. Materials and methods

Lake water (5 m depth) was sampled twice on 5 October 2005, once in the morning (Exp. 1) and once in the afternoon (Exp. 2). Experiments were run immediately after sampling. Both were performed by using identical procedures and can be considered as replicates. Several ancillary parameters were measured: temperature, pH, conductivity, chlorophyll, dissolved organic carbon (DOC), particulate organic carbon (POC), refractory organic matter (ROM) and total suspended solids (TSS). The mineralogical composition of inorganic colloids was assessed by transmission electronic microscopy (TEM) coupled with energy dispersive spectroscopy (EDS) and selected area electron diffraction (SAED) after non-perturbing onsite preparation of the specimen grids (Chanudet and Filella, 2006).

The particle size distribution (PSD) of the inorganic colloids was measured with a single-particle counter (SPC) in the range of 50–2000 nm. The instrument used (Particle Measuring Systems, Boulder, CO) is composed of two single-particle counters: a high-sensitivity liquid *in-situ* monitor (HSLIS) Model M50 and a volumetric spectrometer LiQuilaz-S02. These two systems are based on the principle of light scattering by single particles (Rossé and Loizeau, 2003). The water did not require any pre-treatment other than removal of the daphnids.

For the two experiments, large adult females of a clonal culture of *Daphnia hyalina* originating from Lake Brienz were used. *D. hyalina* is the most common taxon in this lake (Rellstab, unpublished results) and is typical of large oligotrophic lakes in Europe (Keller, 2006). Prior to the experiment, daphnids were grown in Greifensee water (a lake in central Switzerland with no glacial turbidity) and fed chemostat-grown *Scenedesmus obliquus*. In order to avoid the presence of colloids smaller than 2 μm being released from the gut of daphnids and ingested before the experiment, daphnids were exposed to filtered (0.45 μm) Greifensee water containing 10 μm standard latex beads (Coulter CC Size Standard L10) for 12 h before the experiments. The effect of these beads on the size distribution of colloids smaller than 2 μm was also tested.

In both experiments, six aliquots of 130 mL prefiltered (95 μm) Lake Brienz water were placed in glass jars and put in a thermostated bath (14 °C), then 80 daphnids were added to three of them. The three jars that did not contain any daphnids were treated in the same way. PSD measurements were taken just before the experiments (t_0), and after 60 (t_1), 180 (t_2) and 310 (t_3) min. Immediately before measuring the PSD, daphnids were collected in a 95 μm net and their body size (top of the eye to the base of the spine) was determined in order to calculate the theoretical filtration rate (after Jones et al., 1979). The duration of the experiment was chosen so that the full amount of water in the jars was theoretically filtered at time t_3.

3. Results

Table 1 shows the values of the different measured parameters in Lake Brienz water samples used for the experiments. The concentration of natural organic matter (NOM) was remarkably low. The mineral particles present were mainly composed of illite (38%), albite (19%) and orthose, Ti-rich biotite, biotite and chlorite (each $<10\%$). Oxides accounted for about 2%.

Latex beads had no significant effect on the size distribution of the colloids (results not shown here). The average lengths of the daphnids for experiment 1 (Exp. 1) were 1.64 mm ± 0.04 SE (t_1), 1.67 mm ± 0.04 SE (t_2) and 1.68 mm ± 0.04 SE (t_3), which correspond to theoretical total volumes of filtered water of 41 (t_1), 128 (t_2) and 224 mL (t_3) per jar

Table 1 – Characteristics of the lake water samples used for the experiments

Parameter	Exp. 1	Exp. 2
T (°C)	11.5	11.7
pH	8.25	8.40
Conductivity at 25 °C (μS cm^{-1})	155.9	156.2
DOC[a] (mg L^{-1})	0.42	0.51
POC[b] (mg L^{-1})	0.25	0.25
ROM[a,c] (mg L^{-1})	0.15	0.15
Chlorophyll (μg L^{-1})	1.01	1.15
TSS[d] (mg L^{-1})	3.5	3.5

[a] Filtered at 1.2 μm.
[b] Filtered at 0.45 μm (Whatman glass microfibre filters).
[c] Determined as described in Chanudet et al. (2006). 1 SD = 0.01 mg L^{-1}.
[d] Filtered at 0.45 μm (cellulose nitrate filters, 50 mm, from Schleicher and Schuell, Dassel, Germany).