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PRIMARY RESEARCH PAPER

Effects of food-web structure on the quantity and the elemental quality of sedimenting material in shallow lakes

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Abstract Sedimentation is a key process in lake functioning, and plays an important role in nutrient and carbon cycles at both regional and global scales. Several biological processes have been shown as quantitatively affecting sedimentation, but very few works have tried to relate the structure of aquatic communities and the quality of sinking organic matter. We tested in a mesocosm study how food-web structure affects quantitatively and qualitatively sedimentation in eutrophic systems. We carried out a long-term experiment (14 months) in large replicated enclosures either dominated by planktivorous fish or fishless. Food-web structure modified the specific composition of zooplankton communities and phytoplankton biomass, as expected by the trophic cascade theory. Planktivorous fish had a strong positive effect on gross sedimentation rate, but the fraction of suspended particulate material that sank only slightly differed between treatments. The density of

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transparent exopolymer particles (TEP) was a good descriptor of sedimentation rate, highlighting the key role of these polysaccharidic particles in sinking processes. In fish enclosures, sediment elemental ratios were positively related to seston elemental ratios, suggesting the dominance of algal sedimentation. In fishless mesocosms, N/P ratios of sinking material and of zooplankton showed a strong negative relationship, indicative of a major contribution of zooplankton-egested material to sinking particles. Analyses of free lipids in sediments confirmed the distinct origins of sinking material. Despite the absence of clear elemental composition distinctions between the two types of sediment, food-web structure strongly modified sediment biochemical composition.

Keywords Mesocosm experiment · Zooplankton · Seston · Lipid biomarkers · Transparent exopolymer particles · Consumer-driven nutrient recycling

Introduction

Sedimentation is one of the most important processes affecting not only aquatic ecosystems but also biosphere global functioning, since billions of tons of suspended matter are deposited in these systems each year (Falkowski et al., 2000; Hessen et al., 2004; Cole et al., 2007). At regional and global scales, carbon storage in lake sediments is recognized as a very important component of the carbon cycle (Einsele et al., 2001; Flanagan et al., 2006; Cole et al., 2007). In lakes, sedimentation is also suggested to be an important process regulating epilimnetic phosphorus concentration (Mazumder et al., 1989; Houser et al., 2000) and algal standing biomass (Reynolds & Wiseman, 1982; Bloesch & Bürgi, 1989).

Freshwater sediments often represent large stocks of nutrients that are not directly available for phytoplankton growth. However, the release of nutrients from sediment by chemical processes can represent significant inputs of nutrients for pelagic systems (e.g., Reynolds, 1996). In particular, sediment resuspension and remineralization following agitation events can lead to huge increases in nutrients (Sanford, 1992; Fortino et al., 2009). Even after reduction of nutrient loading in eutrophic lakes, the sediment compartment can act as a source of nutrients able to sustain important algal developments (Marsden, 1989; Søndergaard et al., 2007). To improve the understanding of lake functioning, we need a precise knowledge of biological parameters that affect quantitatively and qualitatively sedimentation in lakes.

Many processes are known to modify sedimentation rates in lakes. In particular, the specific composition of phytoplankton communities and phytoplankton cell sizes can alter the sedimentation rates by changing individual cell settling velocities (Reynolds & Wiseman, 1982; Larocque et al., 1996). For example, diatoms are known to have high settling velocities, whereas green algae are less susceptible to sinking (Sommer, 1984). Biological activity of primary producers and bacteria can also promote the formation of aggregates, mainly through production of exopolysaccharides such as transparent exopolymer particles or TEP (Simon et al., 2002; Engel et al., 2004). After aggregation events with dead or living particulate matter such as algae, particles are transported downward. This process can favor the sedimentation of small algal cells, with low individual settling velocities. Finally, zooplankton can act on the sedimentation process, either through grazing (decrease in algal density) and indirect effects on phytoplankton community composition (Larocque et al., 1996), or by the production of fecal pellets and decaying bodies of zooplankton (Uehlinger & Bloesch, 1987). Although this zooplanktonic material rarely represents a very important fraction of total suspended matter, its effects on sedimentation can be important due to the high sinking velocity of these particles (Sarnelle, 1992).

Several studies have been performed to understand and to predict quantitatively, and less frequently qualitatively, sedimentation in lakes and marine systems (e.g., Bloesch & Bürgi, 1989; Aksnes & Wassmann, 1993; Sarnelle, 1999). In these works, the importance of zooplankton biomass and its effects on phytoplankton have been well recognized. By contrast, the importance of the specific composition of zooplankton communities has rarely been explicitly considered. Elser et al. (1995) and Sarnelle (1999) have shown that an increase in herbivorous zooplankton was susceptible to reduce total sedimentation rates by decreasing total suspended matter despite an increase in mean sinking velocities of particles.

Another important but far less studied issue relative to sedimentation is the understanding of the biological determinants of sedimenting material quality. Elemental ratios of sedimenting material are often considered

as good indicators of sediment degradability (Niggemann, 2005). Elemental composition of each zooplankton species is known to vary in a very restricted range, but this composition can vary much between species (Andersen & Hessen, 1991). Due to these homeostasis constraints, zooplankton might release elements in excess in their food relative to their requirements, either in dissolved or particulate form (Elser & Urabe, 1999). Elemental quality of egested material, which represents a part of sedimenting materials, might thus vary as a function of species composition of zooplankton community. Elser & Foster (1998), followed by Darchambeau et al. (2005), tried to link seston and zooplankton elemental composition to sedimenting material elemental composition in lakes. Both studies revealed a variable but significant negative relationship between sedimenting material and zooplankton elemental compositions. Presence of planktivorous fish, by altering food-web structure via trophic cascades (Carpenter & Kitchell, 1993), can induce shifts in zooplankton community composition (e.g., Bertolo et al., 2000). This could impact the quantity of sedimenting material but also alter its elemental composition through modifications of egested material quality (Elser et al., 2000). Surprisingly, even if several studies have shown that sediment quality can strongly differ within and between aquatic systems (Kristensen et al., 1995; Hulthe et al., 1998; Niggemann, 2005), and despite the fact that laboratory experiments have shown great variability in their degradability (Hulthe et al., 1998), the effects of food-web structure on the quality of sedimented organic matter have rarely been considered.

To test the effects of food-web structure on the quantity and elemental composition of sedimenting material in shallow lakes, we carried out a long-term experiment in large replicated eutrophic enclosures. We modified food-web structure by adding planktivorous fish in half of the enclosures, and the specific and elemental compositions of seston and zooplankton, as well as quantity and elemental composition of sedimenting material, were followed during 14 months.

Materials and methods

Study site and experimental design

This study took place in the meso- to eutrophic (range of 2005 summer chlorophyll concentration: 3–42 µg chl *a* l^{-1}) Lake Créteil (48°46′37″N, 2°26′47″E), a small (42 ha), shallow (mean depth: 4 m, maximal depth: 6 m) sand-pit lake (siliceous parent rock) situated 15 km southeast of Paris, France (for more information on this lake, see Lacroix et al., 1989; Bertolo et al., 1999). Eight large enclosures, made of translucent polyethylene reinforced with nylon mesh, were suspended 25 cm above the lake surface on a floating rectangular pontoon. Enclosures were completely sealed at the bottom, and represented a volume of roughly 40 m^3 (3 × 3, 4.5 m depth). To prevent bird access, they were covered with a thin non-shading nylon net fixed on the pontoon structure. The enclosures were filled with lake water pumped from 1 to 2 m below the surface and filtered through a 1-mm mesh to avoid contamination by large particles. Enclosures were filled in random order by successive steps on 28 and 29 June 2005 to minimize initial heterogeneity between enclosures. To study the effect of food-web structure on stoichiometric constraints and functioning of our mesocosms, we chose to contrast a planktivore-dominated treatment to an herbivore-dominated treatment, each treatment being replicated four times. We used roach (*Rutilus rutilus* Linnaeus), one of the most common planktivorous fish in European temperate lakes. Planktivore-dominated enclosures were stocked with fish on 8 July 2005 to let plankton communities develop after enclosures were filled. At the beginning of the experiment, fish mean ± SE standard length was 42.6 ± 2.7 mm (mean fresh weight: 0.66 ± 0.15 g). We added 40 fishes per enclosure, i.e., 1 fish m^{-3}. Final biomass of roach, i.e., at the end of the second summer, reached 436 ± 355 kg ha^{-1}, which is in the upper range of natural roach biomass in eutrophic lakes (Johansson, 1987; Persson et al., 1988; Lacroix & Lescher-Moutoué, 1991). Fish were initially caught from the native population of the lake using a seine. Another enclosure was deployed within the lake to stock supplementary fishes, for replacement of individuals found dead during the experiment (five individuals throughout the 15-month experiment).

Due to the lack of some planktonic species in lake water at the time of enclosures filling, reduced species diversity could be expected in such long-term experiment carried out in closed systems. To allow colonization by species that were absent during enclosures filling and that occurred naturally in the lake throughout the experiment, we monthly added 4 l of unfiltered

lake water in each enclosure (representing 0.01% of total enclosure volume). This water came from integrative samples of the lake water column. The system was kept under eutrophic conditions by weekly adding inorganic fertilizers. Nutrients were prepared as a liquid mixture of sodium nitrate ($NaNO_3$) and potassium phosphate (KH_2PO_4) with a N:P molar ratio of 20:1, and a phosphorus load of 3 μg P l^{-1} day^{-1}. Inputs of phosphorus were chosen to simulate phosphorus supplied on an annual basis by a rainwater collector in Lake Créteil in the 1980s (Lacroix & Lescher-Moutoué, 1991). The N/P ratio was chosen in order to fall within the typical phytoplankton N:P ratio (15–22), and avoid nitrogen limitation and blooms of cyanobacteria. For more details on the experimental design, see Danger et al. (2008).

Analysis of pelagic compartments

Zooplankton, phytoplankton, and TEP counting

Both zooplankton and phytoplankton samples were collected monthly in each enclosure with a 2-l Friedinger bottle. At each sampling date, a total volume of 32 l was collected in each enclosure from the whole water column at several depths and positions in the mesocosms and then mixed. The samples were filtered through a 50-μm nylon mesh and animals were preserved in 4% formalin–sucrose. Zooplankton from the eight enclosures were identified and counted on four dates (17 October 2005, 20 January 2005, 27 March 2006, and 12 June 2006) under a stereo-microscope on subsamples at different dilutions in Dollfuss chambers. When individuals were rare, the whole sample was counted. Copepods were separated into calanoids and cyclopids. Cladocerans and rotifers were counted at the genus level. For specific composition analyses, density data for each group were converted to dry weights according to Bertolo et al. (1999).

Water for TEP analyses was sampled at four different depths, mixed, and then fixed with 2% (final concentration) formaldehyde. Subsamples of 2–5 ml were stained with the polysaccharide-specific Alcian Blue to enumerate TEP following the method of Passow & Alldredge (1994) adapted by Carrias et al. (2002). Particles analyses were performed with an epifluorescence microscope (Leitz Laborlux) equipped with a 1,250× objective lens, a Sony 3CCD color video camera (model DWC-950P), a Sony video recorder, and a Leica Q500 personal computer. Counts were carried out on video images using the image analysis Leica Qwin software (Carrias et al., 2002).

Counts of phytoplankton cells were made on samples fixed with Lugol's iodine solution under an inverted microscope according to Utermöhl's method as modified by Legendre & Watt (1971–1972). The algal biovolume was estimated from the mean cell volume of each species according to Hillebrand et al. (1999).

Seston and zooplankton biomass and elemental composition

To determine seasonal evolution of seston concentration and elemental composition, water samples were taken monthly from the whole column in the eight enclosures. Samples were pre-filtered on 50 μm filters to eliminate zooplankton, filtered on pre-weighted GF/F glass fiber filters (nominal cut-off: 0.7 μm), and then dehydrated for 12 h in an oven at 60°C. Dry filters were re-weighted to determine mass of seston, and stored in dry conditions until analyses. These filters were then used to quantify the percentages of carbon and nitrogen contained in sestonic matter using a CHN elementary analyzer (NA 1500 Series 2, Fisons). Organic P content was determined after oxidation with sodium persulfate (Ormaza-Gonzales & Statham, 1996). Zooplankton biomass and elemental composition were determined monthly by sampling 96 l of water at different depths and positions in each enclosure with a 2-l Friedinger bottle. The samples were gently passed through a 50-μm filter and animals were gathered in GF/F-filtered water for 4–6 h to let them evacuate their gut content. Then, zooplankton was concentrated on a 50-μm filter, placed on a pre-weighted GF/A filter, and dried at 60°C for 12 h. Dry zooplankton was then grinded, before being analyzed for its elemental composition. Methods for zooplankton elemental analyses were the same as those used for seston. All C:N:P ratios were expressed in molar ratios.

Sampling of sedimenting material

Sedimentation rates of C, N, and P were determined using three sediment traps deployed in each enclosure. Traps consisted of 5 cm diameter and 30 cm long PVC tubes, suspended at 3.5 m depth and hanged near the center of the enclosures to limit potential

contamination by biofilm particles falling down from enclosures walls. During the periods of lake stratification, traps were typically in the non-turbulent hypolimnion. In order to avoid perturbations of our sedimentation measurements by particle resuspension during mixing events, we were cautious about maintaining the lowest parts of the traps 0.5 m above the bottom of the enclosures. Thus, our measurements were probably representative of sedimentation rates in shallow lakes. Traps were deployed for 8- to 15-day intervals during summer and autumn, and for 1 month in winter and spring. The samples collected from the three traps were pooled. In order to concentrate sedimenting material, samples were placed for 48 h at 4°C in transparent glass columns with tips at the bottom. After re-deposition in the temperature-controlled room, sedimenting materials were gently poured in small flasks. This method allowed to separate sedimenting material from the supernatant, and also to visually separate most of the living zooplankton from sedimenting matter, the former remaining in the water column. Sedimenting material was then dried in an oven at 60°C for 24 h before being weighted, grinded to homogenize samples, and stored in dry conditions until analyses. Samples were analyzed for CNP content following the same method described for zooplankton and seston. Gross sedimentation rates were calculated for each element (C, N, and P) from quantities of dry matter divided by the duration of trap deployment, and expressed in g m^{-2} day^{-1}. Relative sedimentation rates represent the fraction of suspended particulate matter in the water column (including both seston and zooplankton) that sedimented each day (% of DW suspended particulate matter day^{-1}), and were also calculated for each element considered (C, N, and P).

Chemical analysis of sedimented matter

At the end of the second summer, we placed specifically six sediment traps per enclosure for 7 days to collect enough fresh material to carry out chemical analyses. Sedimenting material was concentrated as described above and freeze-dried before analyses.

Sugar and protein colorimetric assays

Freeze-dried sedimented matter was extracted with H_2O at 100°C for 18 h. The suspension was filtered through a Whatman GF/F glass fiber filter (nominal cut-off: 0.7 μm), and the filtrate was freeze-dried. The freeze-dried aqueous extracts were dissolved in a known volume of H_2O and assayed for sugars and proteins. Sugar contents were determined by the phenol–sulfuric acid colorimetric method with glucose as standard (Dubois et al., 1956). Absorbances were measured at 490 nm. The protein contents were determined by the colorimetric method of Lowry with bovine serum albumin as standard. Absorbances were measured at 650 nm (Lowry et al., 1951).

Free lipid analysis

Due to elevated costs, analyses of free lipids were only carried out on three sedimenting material replicates coming from fishless enclosures, and two from fish enclosures. Freeze-dried sugar- and protein-free sedimenting materials were extracted with dichloromethane/methanol (2/1 v/v) at room temperature for 18 h. The suspension was filtered through a Millipore FH 0.45-μm filter and solvent was removed under reduced pressure. The lipid fraction was treated with a mixture of anhydrous pyridine/*N*,*O*-*bis*(trimethylsilyl)trifluoroacetamide (BSTFA) (10/1 v/v) for 10 min at 60°C to convert carboxyl and hydroxyl groups to trimethylsilyl (TMS) ester and TMS ether groups, respectively (Evershed, 1993). Lipid components (as TMS esters and TMS ethers) were analyzed by gas chromatography–mass spectrometry (GC–MS) with an Agilent 6890 gas chromatograph coupled to an Agilent 5973N mass spectrometer with electron ionization at 70 eV. Separation was achieved using a fused silica column coated with DB-5MS (30 m, i.d. 0.25 mm, film thickness 0.5 μm) with He as carrier gas. The GC oven was programmed from 100 to 320°C at 4°C min^{-1}. Identification of compounds was made by mass spectral interpretation and comparison with standard spectra (NIST mass spectrum library). Individual component contributions were determined by comparison of the peak areas from GC–MS traces. This method allows a comparison of the relative abundances of components between different sedimenting material samples but does not allow the quantification of individual compounds of the total free lipids. As such, the data should be considered to be qualitative. The chemical analysis of the free lipids extracted from seston (0.7–50 μm fraction) and zooplankton fractions (Allard et al., 2011) indicated that

seston and zooplankton compartments were adequately separated by our screening size.

Statistical analyses

Statistical analyses were performed using the Statistica software program (SAS). We used one-way ANOVAs with time as a repeated measure (RM-ANOVA) to test for the effect of food-web structure and the evolution of this effect with time on zooplankton and seston biomass and elemental compositions, specific composition of zooplankton communities, mean algal biovolume, TEP concentration, gross and relative sedimentation rates, and sedimenting material elemental composition. When necessary, analyses were performed on log-transformed data to homogenize variances. To verify the validity of sphericity assumption necessary to carry out RM-ANOVAs, Mauchly's test was carried out for each analysis. When this assumption was not met, degrees of freedom were adjusted using the Huynh–Feldt correction.

For an unknown reason, zooplankton biomass remained always very low (<100 μg DW l^{-1}) in one fish enclosure since the experiment beginning. Consequently, zooplankton elemental composition measurements were only carried out on the three other replicates. For the same reason, phytoplankton counting and TEP counting from this enclosure were not included in the analyses. To determine the effect of elemental composition of zooplankton and seston on the stoichiometry of sedimenting material, we used simple regressions on N/P ratios of fresh sedimenting material and related them to zooplankton and seston composition at the date of sampling. In these regression analyses, we only considered sedimenting material that was collected in traps deployed for less than 10 days to avoid potential bias due to degradation and excessive bacterial colonization of dead organic matter (Bloesch & Burns, 1980). Thus, regression analyses were carried out on three different dates per enclosure (12 total points for each treatment, i.e., fish and fishless). Consequently, to avoid any pseudoreplication, we verified that N/P ratios were independent of time and enclosure using two-way ANOVAs. Results were always non-significant, i.e., regression patterns cannot be explained by autocorrelations among dates or enclosures. The effect of food-web structure on biochemical quality of fresh sedimenting material (lipids, sugars, and proteins) was analyzed using *t* tests. For all analyses, we chose the $P = 0.05$ significance threshold.

Results

Structure of the pelagic food-web

Food-web structure had a great effect on the biomass of seston (Fig. 1a) and chl *a* concentration (data not shown, see Danger et al., 2008) in the water column. On average, seston biomass was higher in fish treatments, particularly during the second year of the study. In fishless treatments, seston biomass always remained low (1–2 mg DW l^{-1}), whereas it reached up to 11 mg DW l^{-1} in fish enclosures. Algal densities were on average threefold higher in fish treatments ($30.9 \pm 25.4 \times 10^3$ cells ml^{-1}) than in fishless enclosures ($9.3 \pm 2.2 \times 10^3$ cells ml^{-1}, $F_{1,6} = 5.5$, $P = 0.05$). We did not find any significant effect of

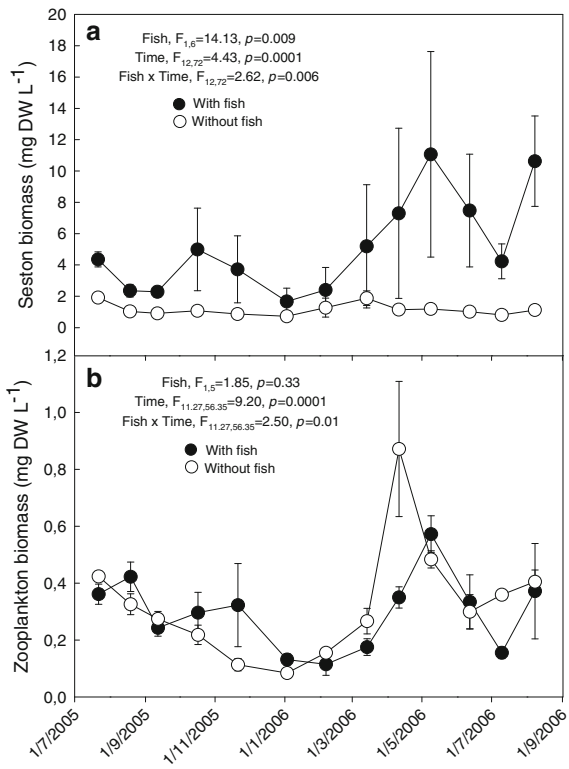

Fig. 1 **a** Seston and **b** zooplankton biomass as a function of time in both treatments. *Vertical bars* correspond to standard errors

Table 1 Mean annual elemental composition of seston, considered as the fraction of suspended matter comprised between 0.7 and 50 μm, in the fish and fishless enclosures

	With fish	Without fish	RM-ANOVA					
	Average ± SD (min–max)	Average ± SD (min–max)	Fish		Time		Fish × time	
			F	*P*	*F*	*P*	*F*	*P*
%N	3.65 ± 0.26	3.48 ± 0.25	1.47	0.27	7.84*	**0.0001**	1.99*	0.09
	(2.61–5.43)	(2.03–5.45)	(1,6)		(5.58,33.51)		(5.58,33.51)	
%P	0.76 ± 0.12	0.75 ± 0.06	1.35	0.29	63.60	**0.0001**	3.60	**0.0008**
	(0.43–1.47)	(0.34–1.58)	(1,6)		(10,60)		(10,60)	
C/N ratio	9.55 ± 1.38	8.67 ± 0.11	1.84	0.22	3.81*	**0.01**	1.53*	0.21
	(7.99–10.67)	(6.75–12.53)	(1,6)		(4.52,27.16)		(4.52,27.16)	
C/P ratio	108.9 ± 10.1	110.9 ± 6.78	0.10	0.76	40.30	**0.0001**	2.50	**0.01**
	(47.9–174.5)	(35.1–178.4)	(1,6)		(10,60)		(10,60)	
N/P ratio	12.01 ± 2.39	13.21 ± 0.93	0.40	0.55	27.11	**0.0001**	1.39	0.20
	(5.45–18.22)	(4.03–22.08)	(1,6)		(10,60)		(10,60)	

For each parameter, maximal and minimal values are shown. Degrees of freedom are indicated under each *F* value. When the assumption of sphericity was not verified, *P* values were calculated using Huynh–Feldt corrected degrees of freedom (see "Materials and methods" section). These corrections are indicated by an asterisk. *P* values in bold indicate significant effects

food-web structure on mean phytoplankton cell biovolume in spite of slight temporal variations (with fish: 192 ± 64 μm^3 $cell^{-1}$; without fish: 181 ± 48 μm^3 $cell^{-1}$, $F_{1,6} = 0.93$, $P = 0.37$). Analyses also revealed great seasonal variations of seston stoichiometry (Table 1). Seston P contents were always higher in winter and early spring (February and March). The significant interaction effect between time and food-web structure on seston C/P ratio illustrated the seasonal dependency of food-web structure effect on seston stoichiometry. Seston C/P ratios were similar for the two treatments during the first part of the experiment (July 2005–April 2006). Then seston C/P ratios became higher in fish treatments up to the end of the experiment (April 2006–July 2006).

Fish effect on zooplankton biomass varied greatly with time, as shown by the significant interaction effect between treatment and time. In both treatments, values decreased during winter and reached a peak in early spring (Fig. 1b). Species composition of zooplankton community was also affected by fish presence (Table 2). The Daphniidae biomass was significantly higher in fishless enclosures. Mean biomass of small cladocerans did not significantly differ between treatments, but the significant interaction with time indicates that the effect of treatment varied with season, in contrast to the biomass of cyclopids, calanoids, and rotifers that were not significantly affected by the presence of fish. The modifications of species dominance in the communities were related to significant modifications of elemental composition of whole zooplankton communities (Table 2). Zooplankton communities of fish enclosures had higher N and C contents, whereas a higher P content characterized fishless ones. This led to significant differences in C/P and N/P ratios, which were lower in fishless enclosures. For both treatments, zooplankton C/N ratios were slightly higher in winter, whereas C/P and N/P ratios showed a slight decrease during this period (data not shown).

Quantitative and qualitative evolution of sedimentation

Mean gross sedimentation rates were three times higher in fish enclosures than in fishless enclosures (Fig. 2a). In both treatments, sedimentation rates strongly decreased in winter (from December to March), and reached a peak in fish enclosures during the second summer of the experiment. Relative sedimentation rates followed the same pattern than gross sedimentation rates and greatly varied as a function of time (Fig. 2b). Relative sedimentation rates of C, N, and P did not differ between fish and fishless treatments (Table 3).

Table 2 Mean annual specific structure and elemental compositions of zooplanktonic communities in the fish and fishless enclosures

	With fish	Without fish	RM-ANOVA					
	Average ± SD (min–max)	Average ± SD (min–max)	Fish		Time		Fish × time	
			F	*P*	*F*	*P*	*F*	*P*
DW Daphniidae	4.3 ± 5.6 (2.1–8.6)	32.9 ± 25.9 (21.9–47.1)	7.49 (1,6)	**0.03**	0.17 (3,18)	0.91	2.08 (3,18)	0.14
DW *Diaphanosoma*	46.0 ± 38.8 (0.0–181.7)	49.8 ± 13.7 (0.1–103.7)	6.14 (1,6)	**0.05**	37.79* (1.48,8.88)	**0.001**	6.10* (1.48,8.88)	**0.03**
DW small cladocerans	7.8 ± 6.9 (1.6–18.3)	3.4 ± 2.3 (0.4–6.4)	0.32 (1,6)	0.59	10.79 (3,18)	**0.0003**	5.53 (3,18)	**0.007**
DW cyclopids	17.3 ± 16.5 (0.7–48.7)	8.5 ± 4.2 (0.7–22.5)	0.02 (1,6)	0.90	13.34 (3,18)	**0.0001**	2.58 (3,18)	0.09
DW calanoids	114.4 ± 79.7 (38.3–293.2)	82.8 ± 32.9 (35.8–148.5)	0.34 (1,6)	0.58	8.34 (3,18)	**0.001**	0.69 (3,18)	0.57
DW nauplii	21.7 ± 15.9 (1.6–40.5)	42.6 ± 18.4 (4.2–106.8)	1.74 (1,6)	0.23	19.40 (3,18)	**0.0001**	1.81 (3,18)	0.18
DW rotifers	15.6 ± 20.8 (3.8–36.9)	7.0 ± 4.6 (3.2–12.2)	0.60 (1,6)	0.47	0.37 (3,18)	0.78	1.55 (3,18)	0.23
C/N ratio	5.55 ± 0.26 (4.65–7.49)	5.64 ± 0.04 (4.85–6.40)	2.44 (1,5)	0.10	6.98 (12,60)	**0.0001**	1.96 (12,60)	**0.04**
C/P ratio	117.4 ± 9.4 (89.0–157.9)	95.2 ± 4.2 (85.2–131.8)	31.57 (1,5)	**0.002**	5.39 (12,60)	**0.0001**	1.20 (12,60)	0.31
N/P ratio	21.09 ± 0.88 (14.63–33.97)	16.89 ± 0.81 (27.32–13.62)	51.85 (1,5)	**0.001**	12.38 (12,60)	**0.0001**	1.62 (12,60)	**0.02**

Zooplankton groups in communities are given in µg DW l^{-1}. *Ceriodaphnia* being in very low abundances, it has been pooled with *Daphnia* in a Daphniidae group. For each parameter, maximal and minimal values are shown. Degrees of freedom are indicated under each *F* value. Huynh–Feldt corrected degrees of freedom are indicated by an asterisk. *P* values in bold indicate significant effects

Food-web structure effect on elemental composition of sedimenting material was very variable with time in the two treatments (Fig. 3). C/N ratios showed no particular trend in time (Fig. 3a). In contrast, C/P and N/P ratios decreased in winter (Fig. 3b, c), reaching minimal values between February and April in both treatments. This decrease was more pronounced in fishless enclosures than in fish enclosures, as revealed by the significant interaction effect between treatment and time.

Biological determinants of sedimentation

To understand the biological determinants of sedimentation under the two food-web structures, we related N/P ratios of fresh sedimenting material (sedimentation time ≤10 days) with N/P ratios of seston and zooplankton. In fishless enclosures, there was no significant relationship between seston and sedimenting material composition (Fig. 4a), while sedimenting material elemental composition was negatively related to the N/P ratio of zooplankton communities ($n = 12$, $R^2 = 0.68$, $P = 0.001$, Fig. 4b). In contrast, in fish enclosures, sedimenting material N/P ratios were positively related to seston N/P ratios ($n = 12$, $R^2 = 0.42$, $P = 0.02$, Fig. 4c), and completely unrelated to zooplankton elemental composition (Fig. 4d).

The abundance of TEP was strongly affected by food-web structure ($2.9 \pm 1.9 \times 10^3$ vs. $1.4 \pm 0.7 \times 10^3$ particles ml^{-1}, $F_{1,5} = 24.8$, $P = 0.004$, in fish and fishless enclosures, respectively). A significant relationship was observed between phytoplankton densities and TEP abundance in the water column ($n = 62$, $R^2 = 0.43$, $P < 0.0001$). In addition, TEP abundance in the water column was positively related to sedimentation rates measured after the counting dates (Fig. 5). This relationship was highly significant

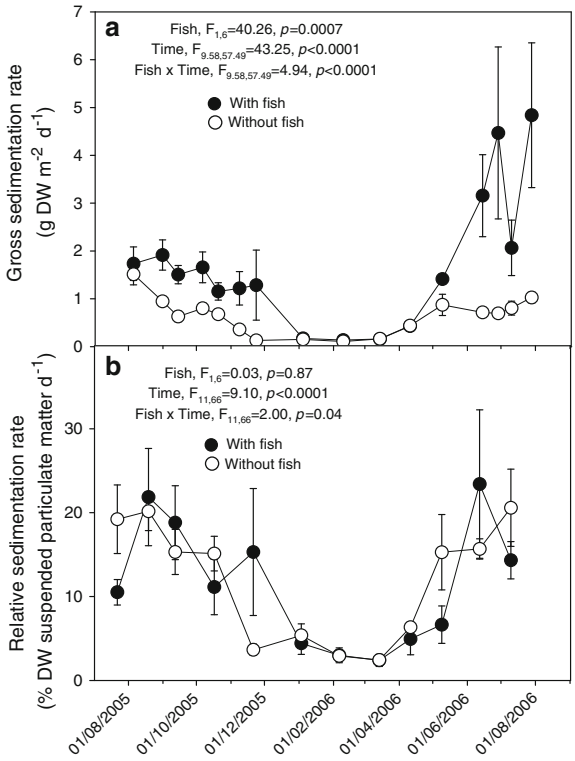

Fig. 2 Seasonal trends of sedimentation rates: **a** gross sedimentation rates and **b** relative sedimentation rates, i.e., fraction of suspended material in the water column that reaches sediment each day. *Symbols* and *vertical bars* as in Fig. 1

($n = 62$, $R^2 = 0.43$, $P < 0.0001$), and TEP explained more variability than algal densities ($n = 62$, $R^2 = 0.11$, $P = 0.003$) or chl a l^{-1} ($n = 62$, $R^2 = 0.13$, $P = 0.009$).

Chemical composition of sedimenting material

Levels of proteins and sugars in fresh sedimenting material varied strongly between the two treatments. Protein and sugar contents were on average twofold higher in fish enclosures than in fishless ones (Table 4). Total lipid extracts accounted for ca. 5% of the sedimenting material from both fish and fishless treatments.

Free lipids of the sedimenting material from both treatments consisted mainly of six sets of compounds: hydrocarbons, *n*-alkanoic acids, *n*-alkan-1-ols, sterols, α,ω-diols and chlorophyll-derived compounds. This latter set was composed of phytol, isomeric phytadienes, and 6,10,14-trimethylpentadecan-2-one, which are usually considered to arise from chlorophyll biodegradation (Rontani & Volkman, 2003). For both treatments, *n*-alkanoic acids largely dominated free lipids. Differences in the relative abundances of several classes of lipids were observed between the sedimenting materials from the two treatments (Fig. 6). This was particularly striking for α,ω-diols

Table 3 Sedimentation rates of C, N, and P in the fish and fishless enclosures

	With fish	Without fish	RM-ANOVA					
	Average ± SD	Average ± SD	Fish		Time		Fish × time	
			F	*P*	*F*	*P*	F	*P*
C sedimentation (g C m^{-2} day^{-1})	0.44 ± 0.05 (0.02–1.69)	0.12 ± 0.02 (0.01–0.26)	28.01 (1,6)	**0.002**	10.67 (15,90)	**0.0001**	6.91 (15,90)	**0.0001**
% Particulate C sedimented day^{-1}	9.1 ± 5.2 (0.9–28.5)	6.8 ± 1.5 (0.9–12.9)	0.70 (1,6)	0.43	7.87* (3.52,21.12)	**0.0006**	1.99* (3.52,21.12)	0.14
N sedimentation (mg N m^{-2} day^{-1})	44.6 ± 6.4 (1.5–191.2)	12.4 ± 1.9 (1.1–27.0)	18.43 (1,6)	**0.005**	10.25* (2.03,12.21)	**0.002**	7.10* (2.03,12.21)	**0.008**
% Particulate N sedimented day^{-1}	6.2 ± 3.1 (0.4–23.3)	3.9 ± 1.0 (0.4–7.5)	1.81 (1,6)	0.23	8.68* (2.59,15.58)	**0.002**	3.01* (2.59,15.58)	0.07
P sedimentation (mg P m^{-2} day^{-1})	11.2 ± 1.4 (0.4–32.8)	3.9 ± 0.4 (0.3–9.9)	52.24 (1,6)	**0.007**	13.00* (2.21,13.26)	**0.0006**	4.64* (2.21,13.26)	**0.02**
% Particulate P sedimented day^{-1}	12.2 ± 6.16 (1.0–52.6)	10.4 ± 2.98 (1.0–42.3)	0.44 (1,6)	0.53	9.68* (4.97,29.82)	**0.0001**	1.78* (4.97,29.82)	0.15

Relative sedimentation rates correspond to the fraction of total suspended matter in the water column that settled down each day. For each parameter, maximal and minimal values are shown. Degrees of freedom are indicated under each *F* value. Huynh–Feldt corrected degrees of freedom are indicated by an asterisk. *P* values in bold indicate significant effects

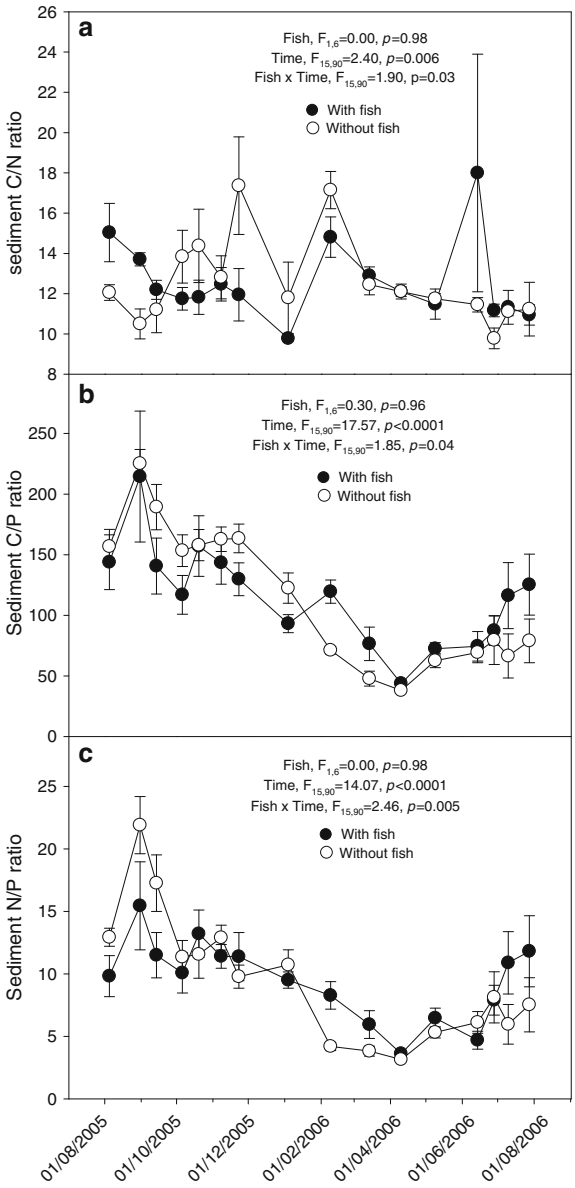

Fig. 3 Seasonal evolutions of fresh sediment elemental ratios: **a** C/N molar ratios, **b** C/P molar ratios, and **c** N/P molar ratios. *Symbols* and *vertical bars* as in Fig. 1

($P < 0.01$, $t = 5.7$, df $= 3$) and chlorophyll-derived products ($P = 0.03$, $t = 3.6$, df $= 3$). *n*-Alkanes and sterols were not significantly different between treatments ($P = 0.28$, $t = -1.3$, df $= 3$, and $t = -0.06$, df $= 3$, respectively). However, cholesterol (hatched parts of sterol bars, Fig. 6) was significantly higher in fishless than in fish enclosures sedimenting material ($P = 0.04$, $t = -3.4$, df $= 3$). Long-chain α,ω-diols occurred in substantial amounts in sedimenting material from fish enclosures while they were hardly detected in sedimenting material from fishless enclosures. Chlorophyll-derived products were detected in higher abundance in sedimenting material from fish than from fishless treatments, while the contrary was observed for *n*-alkanes.

Discussion

Taxonomic structure of the pelagic food-web and elemental compositions

Fish treatment effects on algal densities observed in our experiment are a classic illustration of trophic cascades, increase in phytoplankton occurring indirectly through the predation on microcrustaceans (Carpenter & Kitchell, 1993; Brett & Goldman, 1996). However, it has often been concluded that control by planktivorous fish is mediated by reduction of zooplankton biomass (Brett & Goldman, 1996). In our experiment, the absence of significant difference between mean zooplankton biomasses in the two treatments suggests that the observed top-down effect was mainly driven by changes in specific composition of zooplankton communities, as already found with the same fish species in previous experiments (Bertolo et al., 1999). Roach was able to drive the slow-moving *Daphnia* to low densities. Due to their rapid movements, calanoids can better escape roach predation than cladocerans (e.g., Lacroix & Lescher-Moutoué, 1995). Because of low temperature conditions, zooplankton biomass was the lowest in winter in both treatments. Our study is one of a few replicated long-term experiments available in the literature. In accordance with Bell et al. (2003), this study clearly highlights that strength of trophic cascades remained throughout the duration of the experiment. Some studies have described increases in mean algal size in fishless food-webs, probably due to selective grazing of small algae by large herbivores (e.g., Larocque et al., 1996). Contrary to these studies, we found no significant difference in mean algal cell biovolume between the two treatments. This result was probably due to the strong dominance of small algal species in Lake Créteil (Lacroix et al., 1989; Bertolo et al., 2000).

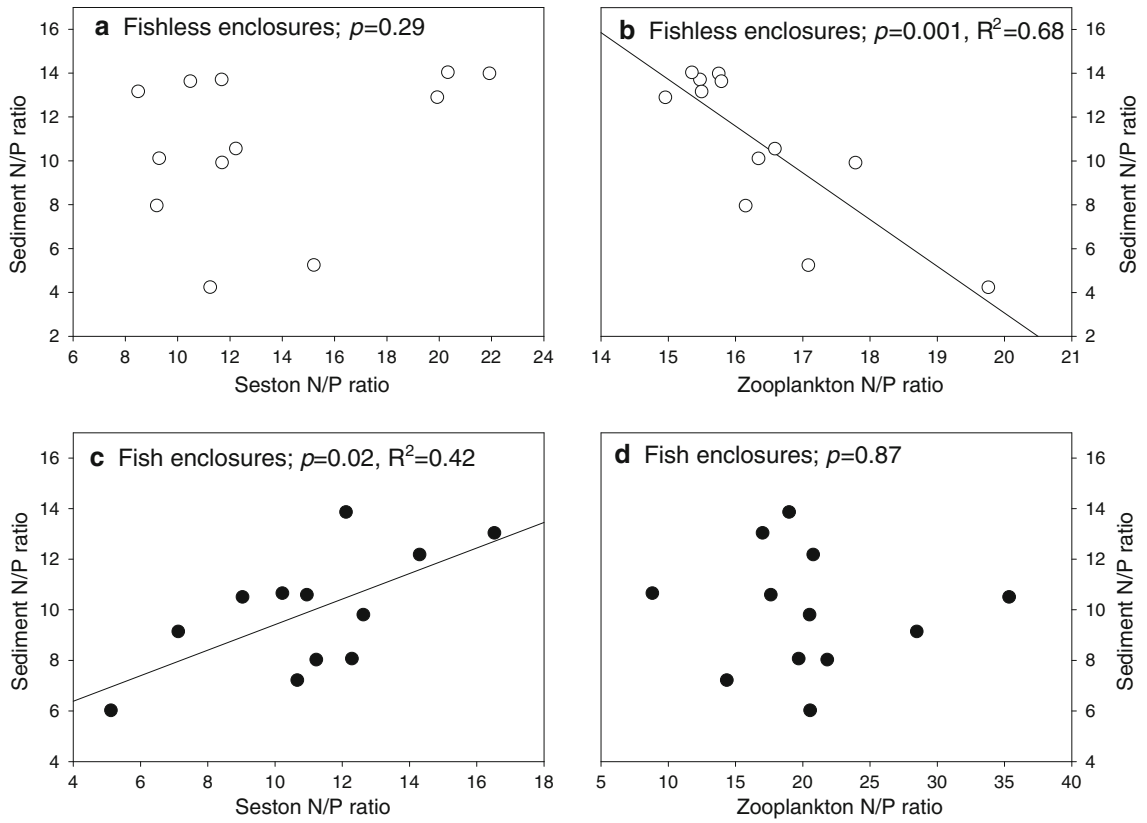

Fig. 4 Relationships between fresh sediment elemental compositions, represented as N/P ratios, and both elemental compositions of zooplankton community and seston under the two food-web structures. Data from sediment traps deployed for more than 10 days were excluded to avoid potential bias due to sediment remineralization (see "Materials and methods" section)

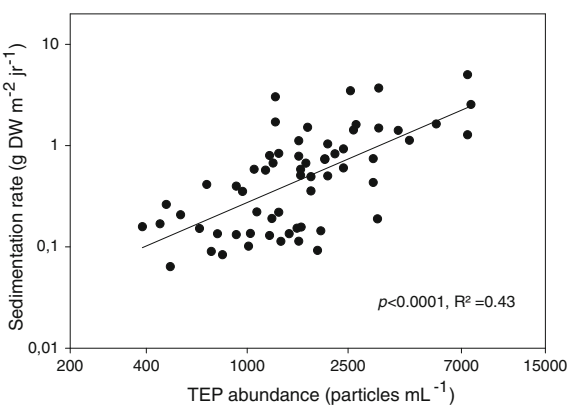

Fig. 5 Relationship between transparent exopolymer particles (TEP) counted in the water column and measured sedimentation rate following sampling dates

Numerous studies have tried to understand how food-web structure affects lakes functioning (e.g., Mazumder et al., 1989; Schindler et al., 1993; Vanni et al., 1997; Elser et al., 2000). Since a few years, developments of ecological stoichiometry theory have proven to be very useful in understanding connections between elemental composition of food-web components and ecosystem functioning (Elser et al., 2000). In this study, we found a great impact of top-down control on the specific composition of zooplankton communities. Zooplankton species are known to have specific elemental compositions (Andersen & Hessen, 1991). As observed by Elser et al. (2000) in biomanipulated lakes, we also found that changes in food-web structure clearly modified elemental composition of zooplankton communities by shifting species dominance. In particular, by reducing P-rich *Daphnia* densities, presence of fish significantly increased mean zooplankton C/P and N/P ratios. However, in contrast to some studies (e.g., Vanni et al., 1997), indirect effects of zooplankton elemental composition (in particular nutrient recycling and storage) on seston elemental composition remained very weak. This result

Table 4 Elements of fresh sediment biochemical quality, expressed as % of sediment dry weight

Sedimenting material biochemical composition	With fish Average ± SD	Without fish Average ± SD	df	*t*	*P* value
% Proteins	25.9 ± 4.0	10.2 ± 2.5	6	6.64	**0.0005**
% Sugars	17.1 ± 4.4	8.2 ± 3.5	6	3.15	**0.02**
% Lipids	5.8 ± 0.3	5.6 ± 3.4	3	0.09	0.93

P values in bold indicate significant effects

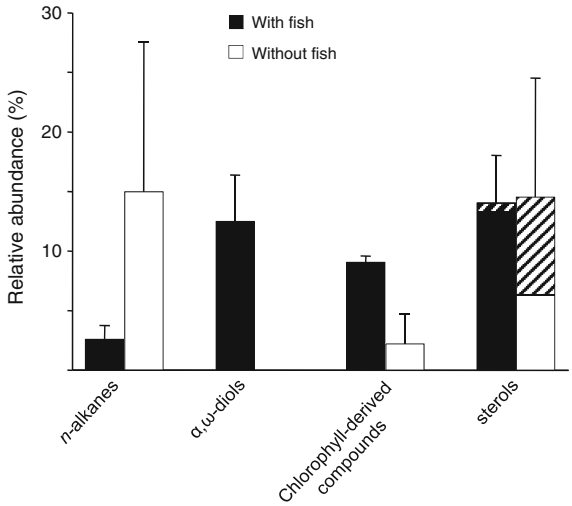

Fig. 6 Relative abundances (% of total free lipids) of some compound classes of the free lipids extracted from the sediment. The hatched parts of sterol bars show the fraction of cholesterol

is not surprising when considering the eutrophic conditions of our enclosures. Measured seston C:nutrient ratios remained always low. This is quite typical of eutrophic lakes (Hessen, 2006). In such conditions, food-web structure has only low effects on the total amount of available nutrients (Evans-White & Lamberti, 2006). In such nutrient-rich systems, the relative importance of consumer-driven nutrient recycling in dissolved form might be strongly reduced compared to egestion of particulate matter. Finally, we found a strong increase in C:nutrient ratios of seston in winter, in low light and low temperature conditions. This very high nutrient content of algae could explain the extreme rapidity of algal development observed in early spring, when environmental conditions become more favorable.

Quantitative evolution of sedimentation

The results of our enclosure experiment show that differences in food-web structure have strong effects on the sedimentation process. Planktivore-dominated systems positively affected gross sedimentation rates. This is in accordance with some previous studies carried out in eutrophic lakes (Sarnelle, 1992, 1999; Vanni et al., 1997), but in opposition to other results obtained in more oligotrophic systems (Bloesch & Bürgi, 1989). Sarnelle (1999) observed that *Daphnia* had a negative effect on sedimentation rates. This author argued that when lake sedimentation is dominated by algal sedimentation, herbivorous zooplankton decreases algal biomass in the water column, and thus decreases the total biomass of material susceptible to sedimentation. He also suggested that negative effects of zooplankton are more likely in eutrophic systems. Our results tend to confirm this hypothesis, and also suggest that the stronger the zooplankton mediated top-down effect on phytoplankton is, the lower the sedimentation rate might be. Our estimates of sedimentation rates are comparable to values found by Bloesch & Bürgi (1989), with great differences between summer (5–10 g DW m^{-2} day^{-1}) and winter (<2 g DW m^{-2} day^{-1}). This clear seasonal pattern points out that sedimentation was mainly due to biological processes in our mesocosms. Moreover, we found very low sedimentation rates in winter, a period of strong agitation in the lake. Thus, the mesocosm walls probably reduced bottom agitation, and sediment resuspension was certainly of minor importance in our sedimentation records.

In many models describing sedimentation processes, it has often been considered that sedimentation constituted a fixed proportion of primary production (Baines & Pace, 1994; Heiskanen & Tallberg, 1999). Other studies have shown that this assumption was not always true and that both the nature of the particles being formed and the water column conditions should be considered (Larocque et al., 1996). Despite very different seston biomasses, the relative sedimentation rates only slightly differed between treatments, but

varied greatly throughout the experiment. This suggests that the intensity of sedimentation was not solely determined by the amount of seston in the water column. It has been shown that 10–30% of phytoplankton standing biomass and up to 7% of zooplankton can sediment per day (Sommer, 1984). Our measurements of seston relative sedimentation varied in the same range of values (2.5–24%). Relative sedimentation rates were minimal in winter and early spring, probably due to a decrease in biological activity. When biological activity is reduced, production of seston and zooplankton fecal material, as well as diverse sinking aggregates, might decrease. The absence of clear negative effect of fish presence on relative sedimentation rates is at odds with the results obtained by Larocque et al. (1996). These authors observed three to five times greater mean length of epilimnetic algae in the fishless enclosures, and suggested that the relative sedimentation rate was mainly related to algal size. In contrast, we observed similar phytoplankton cell sizes between the two treatments, which implies comparable sinking velocities of algae. This might explain the absence of significant fish effect on the relative sedimentation rates in our experiment.

Biological determinants of the elemental composition of sedimenting material

Zooplankton organisms are expected to recycle nutrients at higher levels for elements that are in excess compared to their elemental body requirements (Elser & Urabe, 1999). In such studies, recycled elements were often considered as excreted dissolved nutrients. However, Elser & Foster (1998) followed by Darchambeau et al. (2005) found significant negative relationships between zooplankton and sedimenting material elemental composition in lake investigations. This suggests that organic matter emitted by zooplankton also occurs in the particulate form through egestion. In our study, we found food-web structure effects on sedimenting material elemental composition to be quite variable throughout the experiment. Considering recently deposited material, we found a strong negative relationship between zooplankton N/P ratios and sedimenting material only in the fishless enclosures. In contrast, sedimenting material elemental composition was positively related to seston in fish enclosures, whereas no relationship was found in fishless enclosures. These results suggest that in our planktivore-dominated systems, zooplankton had a minor effect on sedimentation, which was mainly due to sinking of suspended sestonic material. On the contrary, the decrease in seston biomass in fishless mesocosms shifted the enclosures toward systems in which sedimentation was mainly driven by zooplankton. These relationships, suggesting a greater contribution of algae in sedimenting material from fish than from fishless enclosures, were in accordance with chemical analyses carried out on the free lipid extracted from recent sedimenting material. In fishless enclosures, the relative abundance of cholesterol, usually considered to be an animal sterol, was much higher than in fish enclosures. In the fish enclosures, the *n*-alkane distribution dominated by *n*-heptadecane (data not shown), the presence of long-chain α,ω-diols, typically found in several freshwater microalgae from the genus *Scenedesmus* (Allard & Templier, 2000), together with the very low abundance of cholesterol in the sterol fraction strongly suggest a major contribution of phytoplankton to the sedimenting material. The contrast between treatments might have been particularly exacerbated in our experiment because food-web changes had only a very small impact on mean phytoplankton cell size. If algal communities had shifted toward dominance of large cells with high settling velocities in fishless enclosures, this relationship might have been less clear (e.g., Larocque et al., 1996; Elser et al., 2000).

Finally, we found a clear relationship between TEP and sedimentation rates, whereas these rates were less related to phytoplankton. This result emphasizes the major role of such particles in the sedimentation process (de Vicente et al., 2009). In particular, TEP might be extremely important since it could allow massive sedimentation of small particles with low individual settling velocities, such as small algae, after aggregation events (Simon et al., 2002). This result also indicates that TEP could represent a reasonably good predictor of sedimentation in lakes.

Elemental and biochemical quality of sedimenting material

Degradability of sedimenting material is a key factor controlling its potential mineralization by decomposers in lakes. Elemental ratios, such as C/nutrient ratios, are often considered as good indicators of organic

matter degradability, lower ratios being generally synonymous of higher degradability (e.g., Enriquez et al., 1993). In our study, we have shown that sedimenting material had mainly a seston or a zooplankton origin depending on food-web structure. However, despite these distinct origins, no clear differences in sedimenting material C/nutrient ratios were observed. To emphasize the differences in biochemical sedimenting material quality, we quantified three main groups of compounds: sugars, proteins, and lipids. These analyses revealed that protein and sugar levels were nearly twofold higher in sedimenting material from fish treatments than from fishless treatments. By contrast, the total lipid extracts did not differ between the two treatments. However, the relative abundances of some free lipids (particularly *n*-alkanes, α,ω-diols, and chlorophyll-derived compounds) strongly differed. Moreover, the composition of some compound classes strongly depended on the origin of the sedimenting material (see "Biological determinants of the elemental composition of sedimenting material" section). Consequently, despite the absence of marked differences in sedimenting material elemental composition, quality of sedimented organic matter strongly differed between treatments. These differences could have strong effects on sediment mineralization, and led us to hypothesize that sediment degradability, due to biochemical differences, could vary as a function of food-web structure. Such differences in sedimenting material quality related to food-web structure could potentially be a non-negligible process that might determine how and for how long sedimented matter will act as a nutrient source in eutrophic lakes. In particular, for operations of lake restorations involving food-web biomanipulations, changes in sediment quality and degradability could prevent or delay lake recovery (Marsden, 1989; Søndergaard et al., 2007). These results stress the need for further studies aimed at understanding the relationships between biochemical and elemental qualities of sediments and sediment degradability.

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