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Loïc Harrault, Béatrice Allard, Jacques Mériguet, David Carmignac, Sylvain Huon, Benoît Gauzens, Gérard Lacroix

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## Bottom-up effects of lake sediment on pelagic compartments: a mesocosm study

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3 **1 Bottom-up effects of lake sediment on pelagic compartments: a mesocosm study**  
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9 3 Loïc Harrault<sup>1,2,3,#</sup>, Béatrice Allard<sup>1</sup>, Jacques Mériquet<sup>3</sup>, David Carmignac<sup>3</sup>, Sylvain Huon<sup>1</sup>,  
10  
11 4 Benoit Gauzens<sup>3,4</sup> and Gérard Lacroix<sup>5,6</sup>  
12  
13

14 <sup>1</sup> Université Pierre et Marie Curie, UMR CNRS 7618 - Bioemco, 4 place Jussieu, 75252 Paris  
15  
16 Cedex05, France  
17  
18

19 <sup>2</sup> Université Rennes 1, UMR CNRS 6118 - Géosciences Rennes, Campus de Beaulieu, 35042  
20  
21 Rennes Cedex, France  
22  
23

24 <sup>3</sup> Ecole Normale Supérieure, UMR CNRS 7618 - Bioemco, 46 rue d'Ulm, 75005 Paris,  
25  
26 France  
27  
28

29 <sup>4</sup> Université Rennes 1, UMR CNRS 6553 ECOBIO, Campus de Beaulieu, 35042 Rennes  
30  
31 Cedex, France  
32  
33

34 <sup>5</sup> CNRS, UMR iEES - Paris, Institute of ecology and environmental sciences - Paris,  
35  
36 Université Pierre et Marie Curie, 7 quai St.-Bernard, 75005 Paris, France  
37  
38

39 <sup>6</sup> Ecole Normale Supérieure, UMS CNRS 3194 - CEREEP – Ecotron IleDeFrance, 78 rue du  
40  
41 Château, 77140 St-Pierre-lès-Nemours, France  
42  
43  
44

45  
46 17

47  
48 □ corresponding author : loic.harrault@gmail.com  
49

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51  
52 nutrient release, mesocosms, pelagic compartments  
53  
54

55 21

56  
57 **Abbreviated title:** Influence of lake sediment on pelagic compartments  
58  
59  
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1  
2  
3 23 **Summary**  
4

5 24 1. Sediment plays a key role in organic matter (OM) and internal nutrient cycling in  
6  
7 25 lakes. The role of sediment as a source of OM, and its potential bottom-up effects on  
8  
9 26 the pelagic food web have been rarely studied. Particularly, the influence of the  
10  
11 27 biochemical composition of sediment OM on pelagic compartments remains largely  
12  
13 28 unknown.

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15  
16  
17 29 2. In a five-months experiment, we studied the influence of two different sediments  
18  
19 30 added at the bottom of large replicated mesocosms on the biomass, the elemental and  
20  
21 31 the lipid compositions of seston and zooplankton. The influence of sediment  
22  
23 32 treatments on sedimentation rates, elemental and biochemical compositions and  
24  
25 33 potential biodegradability of recently sedimented OM (ca. 1 week) was also examined.  
26  
27 34 The two added sediments ( $S_1$  and  $S_2$ ) presented very contrasted elemental and  
28  
29 35 biochemical compositions and potential biodegradabilities. According to their contents  
30  
31 36 in organic carbon, nitrogen, proteins, sugars and polyunsaturated fatty acids,  $S_2$   
32  
33 37 appeared to be much more biodegradable than  $S_1$ . Therefore, the  $S_2$  sediment was  
34  
35 38 expected to release more nutrients and OM to the water column than  $S_1$ , leading to  
36  
37 39 changes in communities, stoichiometry and lipid compositions of pelagic  
38  
39 40 compartments.  
40  
41  
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43

44 41 3. Probably due to its very poor content in labile compounds, the presence of  $S_1$  at the  
45  
46 42 bottom of the mesocosms did not induce changes in the biomass of seston and  
47  
48 43 zooplankton. Only few changes in the stoichiometry of these compartments were  
49  
50 44 observed. On the contrary,  $S_2$  sediment released more phosphorus and dissolved OM  
51  
52 45 in the water column than  $S_1$ . As a result,  $S_2$  treatment induced an increase in seston  
53  
54 46 biomass and therefore, in zooplankton biomass *via* herbivory.  
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3 47 4. None of the sediment treatments affected the lipid composition of seston and  
4  
5 48 zooplankton. Moreover, neither S<sub>1</sub> nor S<sub>2</sub> induced changes in the sedimentation rates,  
6  
7 49 elemental and lipid compositions, and potential biodegradability of recent sediments.  
8  
9  
10 50 Our mesocosm experiment suggests that differences in the quality of lake sediment  
11  
12 51 lead to moderate changes in the pelagic communities in the absence of planktivorous  
13  
14 52 or omnivorous fish.  
15  
16  
17 53 5. Our results might explain the efficiency of biomanipulations for improving water  
18  
19 54 quality of eutrophic lakes despite potential nutrient release from sediment. Finally, our  
20  
21 55 results provide additional support for the ecological significance of mesocosms for  
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23 56 studying processes occurring at larger scales.  
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## 58 Introduction

59 Since a few decades, the role of sediment in the biological and biogeochemical processes in  
60 lacustrine ecosystems has received an increased attention. Lipid composition of sedimented  
61 organic matter (SOM) has been widely used to assess, via specific biomarkers, i)  
62 autochthonous vs allochthonous origin of sediment (Canuel & Martens, 1993; Bechtel &  
63 Schubert, 2009; Castaneda & Schouten, 2011), ii) transfers of energy and nutrients between  
64 primary producers, herbivores and other consumers within aquatic food webs (Müller-  
65 Navarra *et al.*, 2000; Masclaux *et al.*, 2009) or iii) inter-specific differences (Volkman *et al.*,  
66 1988; Cranwell *et al.*, 1990). The sediment geochemistry has also been used to study the  
67 carbon balance in lacustrine ecosystems and its contribution to the global carbon cycle (Alin  
68 & Johnson, 2007; Cole *et al.*, 2007). The net heterotrophy of lakes (CO<sub>2</sub> source for  
69 atmosphere) is the most commonly observed carbon fate in concerned studies (del Giorgio *et al.*,  
70 1997; Cole *et al.*, 2000). It has been shown that this balance can be influenced by food-  
71 web structure, nutrient concentration (Schindler *et al.*, 1997), or climate (Kosten *et al.*; 2010),  
72 which, in turn, modifies sedimentation (Flanagan *et al.*, 2006). Furthermore, several recent  
73 studies in both marine mesocosms (Canuel *et al.*, 2007; Spivak *et al.*, 2007) and freshwater  
74 mesocosms (Allard *et al.*, 2011; Danger *et al.*, 2012), have shown that the biochemical  
75 composition (e.g. organic carbon, protein, sugar and lipid contents) of recently deposited  
76 sediments depends on food-web structure.

77         Once sedimented, OM is subject to transformation and biodegradation by benthic  
78 macroinvertebrates (Mermillod-Blondin *et al.*, 2003; Nogaro *et al.*, 2008) and  
79 microorganisms (Gächter *et al.*, 1988; Hargreaves, 1998). Biodegradation depends on several  
80 parameters, such as dissolved oxygen concentration at the sediment-water interface, binding  
81 on mineral matrix (Wakeham & Canuel, 2006), physical resuspension (Sanford, 1992), or OM  
82 composition (Hulthe *et al.*, 1998). This latter has been largely used to provide information on

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3 83 the degradation state and the biodegradability of the sediment, due to the large range of  
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5 84 lability covered by the different components of OM (Meckler *et al.*, 2004; Schubert *et al.*,  
6  
7 85 2005). During its degradation, the sediment can release into the water column nutrients and  
8  
9 86 dissolved organic matter (DOM; Reynolds, 1996; Klump *et al.*, 2009), which will support  
10  
11 87 both primary and bacterial productions (del Giorgio & Cole, 1998). As phytoplankton and  
12  
13 88 bacteria are the basal resources for aquatic food webs, release of nutrients and OM from  
14  
15 89 sediment might strongly impact food-web communities via a bottom-up forcing. Whereas the  
16  
17 90 bottom-up effects of inorganic nutrients or light on aquatic ecosystems are well known (see  
18  
19 91 for example, Urabe *et al.*, 2002; Cebrian & Lartigue, 2004; Hessen *et al.*, 2004; Dickman *et*  
20  
21 92 *al.*, 2006; Spivak *et al.*, 2007), those of SOM have been more rarely studied. In natural lakes,  
22  
23 93 it has been shown that the temporal dynamics of bacterioplankton communities are strongly  
24  
25 94 dependent on the DOM origin and amount (Berdjeb *et al.*, 2011), suggesting a bottom-up  
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27 95 forcing from DOM. As DOM can originate from sediment biodegradation, one may wonder if  
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29 96 sediment could be responsible for a bottom-up control for the whole food web, through the  
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31 97 availability of resources for basal organisms (e.g. phytoplankton and bacterioplankton).  
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33 98 Moreover, as the sediment biodegradability seems to be linked to its OM composition (Allard  
34  
35 99 *et al.*, 2011; Danger *et al.*, 2012; Harrault *et al.*, 2012), an interesting issue is whether  
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37 100 different sediment compositions could lead to different bottom-up forcing on aquatic food  
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39 101 webs.  
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46 102 In this paper, we report results of a lake mesocosm study examining how the presence  
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48 103 and the OM composition of sediment can exert a bottom-up effect on the composition of  
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50 104 seston, zooplankton and recently deposited (ca. 1 week) sediment. Three treatments were  
51  
52 105 compared: enclosures without added sediment ( $S_0$ ), enclosures with carbon-poor sediment  
53  
54 106 ( $S_1$ ), and enclosures with carbon-rich sediment ( $S_2$ ). Sediment  $S_1$  was taken in the bottom of  
55  
56 107 Lake Créteil (Lacroix & Lescher-Moutoué, 1995), while  $S_2$  came from a previous mesocosm  
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3 108 experiment (Danger *et al.*, 2008, 2012) and was composed of OM from pelagic origin, settled  
4  
5 109 down during a few years in large pelagic enclosures. The compounds that are preferentially  
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7 110 degraded by bacteria, such as polyunsaturated fatty acids (PUFAs, Cranwell, 1981), and  
8  
9 111 sugars and proteins (Weiss & Simon, 1999), were much more abundant in S<sub>2</sub> than in S<sub>1</sub> (Table  
10  
11 112 1). This strongly suggested that S<sub>2</sub> was much more biodegradable than S<sub>1</sub>. Indeed, S<sub>1</sub> had been  
12  
13 113 formed over several decades in a shallow gravel-pit lake with a clear tendency to  
14  
15 114 oligotrophication since the end of its exploitation (Garnier, 1992). In contrast, the  
16  
17 115 composition of S<sub>2</sub> was typical of sediments found in hypereutrophic conditions (Søndergaard,  
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19 116 1988), in aquaculture areas (Yokoyama *et al.*, 2009), and in extensive fish ponds (Banas *et*  
20  
21 117 *al.*, 2008).

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26 118 During 5 months, the biomass and the elemental composition of pelagic compartments  
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28 119 were determined. At the end of the experiment, the lipid composition of the biotic  
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30 120 compartments was determined. According to the results of Spivak *et al.* (2007), Allard *et al.*  
31  
32 121 (2011), Danger *et al.* (2012) and Harrault *et al.* (2012), we hypothesised that:

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36 122 (i) a positive bottom-up forcing from sediment would increase the biomass of seston  
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38 123 (direct effect through the ingestion of released OM and/or nutrients) and the biomass  
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40 124 of zooplankton (indirect effect through the ingestion of increased seston biomass);  
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43 125 (ii) the strength of this bottom-up effect would depend on the OM composition of the  
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45 126 bottom sediment:  $S_0 < S_1 < S_2$  (i.e. the more biodegradable a sediment, the greater the  
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47 127 bottom-up forcing);  
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50 128 (iii) this effect could change the stoichiometry and/or the lipid biomarker composition of  
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52 129 pelagic compartments by modifying nutrient balances.  
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131 **Methods**

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133 Study site, experimental design and choice of bottom sediments

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135 This study took place in Lake Créteil (48°46'37''N, 2°26'47''E), a small (42 ha),  
136 shallow (mean depth 4 m) sandpit lake 15 km southeast of Paris, France (for more  
137 information on this lake, see Danger *et al.*, 2008). Twenty-four translucent polyethylene  
138 enclosures, sealed at the bottom, were suspended above the lake surface on a floating  
139 pontoon. The volume of each enclosure was ca. 13.5 m<sup>3</sup> (2 × 1.5 × 4.5 m depth). At the end of  
140 November 2009, enclosures were randomly filled in successive steps with pumped lake water.  
141 To study the bottom-up effects of initial sediment on pelagic compartments and on recently  
142 deposited sediment, two contrasted sediments were set down at the bottom of the enclosures.  
143 Enclosures without added sediment were used as a control (S<sub>0</sub>). Each treatment was replicated  
144 eight times. The first sediment (S<sub>1</sub>) was collected randomly in Lake Créteil with an Uwitec  
145 bottom sampler and consisted of a dark grey sandy material. The second sediment (S<sub>2</sub>) was  
146 collected in enclosures used in a previous study (Danger *et al.*, 2008, 2012). S<sub>1</sub> and S<sub>2</sub> were  
147 chosen to simulate contrasted bottom-up treatments in enclosures. Both autochthonous and  
148 allochthonous sources contributed to S<sub>1</sub>. This sediment had been accumulated and exposed to  
149 microbial and benthic reworking over several decades. In contrast, S<sub>2</sub> was sampled in  
150 enclosures sealed at their bottom and largely preserved from allochthonous inputs, and  
151 therefore mainly of autochthonous origin. Moreover, this sediment is relatively young since it  
152 was collected in experimental mesocosms set up in 2005 (Danger *et al.*, 2008) and has been  
153 exposed to degradation over a shorter period than the sediment of the lake. The difference in  
154 the initial sediment quality was estimated using the sugar, protein and PUFA contents (Table

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3 155 1). The difference in the degradation state of the initial sediments was estimated using their  
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5 156 bacterial fatty acid (BACTFA),  $\alpha$ - and  $\beta$ -hydroxy fatty acid (OH-FA) and stanol contents  
6  
7 157 (Supplementary Table 1).  
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10 158 Once collected, sediments (ca. 600 L each) were pooled into 200-L tanks for homogenisation.  
11  
12 159 Trays ( $2 \times 1.5$  m), filled with ca. 70 L of homogenized sediment (ca. 2.4 cm depth layer),  
13  
14 160 were lowered very slowly at the bottom of each enclosure to minimize sediment resuspension  
15  
16 161 and subsequent dissolution of nutrients and OM. Empty trays were put in the control  
17  
18 162 enclosures. To allow sedimentation of suspended material in S<sub>1</sub> and S<sub>2</sub> enclosures, we started  
19  
20 163 samplings on February 2010.  
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27 165 Orthophosphates, ammonium and nitrates analyses  
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33 167 Orthophosphate, ammonium and nitrate concentrations were determined for water sampled in  
34  
35 168 May and June 2010 using the phosphorus-ammonium molybdate and the indophenol blue  
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37 169 spectrometric methods, respectively (AFNOR, 1990, 2004).  
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43 171 Dissolved organic carbon analysis  
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49 173 Water samples collected in May 2010 were filtered through a Whatman GF/F filter. Dissolved  
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51 174 organic carbon (DOC) concentration was determined using a total organic carbon analyser  
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53 175 (TOC-5000A, Shimadzu, Kyoto, Japan).  
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3 177 Seston and zooplankton sampling  
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9 179 Seston biomass and elemental composition were determined monthly. Water was sampled  
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11 180 monthly from February to June 2010 at different depths and locations with a 2-L sampling  
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13 181 bottle (Uwitec) in each enclosure. Water samples were filtered through a 50- $\mu\text{m}$  nylon filter to  
14  
15 182 remove zooplankton, and then filtered through a pre-weighted Whatman GF/F glass-fiber  
16  
17 183 filter (nominal cut-off: 0.7  $\mu\text{m}$ ) in order to gather seston (particulate matter between 0.7 and  
18  
19 184 50  $\mu\text{m}$ ). Filters were dried overnight at 60°C and weighted to determine seston biomass. Dry  
20  
21 185 filters were stored in the dark at room temperature until elemental and lipid analyses.  
22  
23

24 186 Zooplankton biomass was determined monthly by sampling 60 L of water at different depths  
25  
26 187 and locations in each enclosure with a 12-L Schindler plankton trap equipped with a 50- $\mu\text{m}$   
27  
28 188 filter. Zooplankton was gathered in GF/F-filtered water for several hours to allow evacuation  
29  
30 189 of gut content. Zooplankton was concentrated on a 50- $\mu\text{m}$  filter, washed with deionized water  
31  
32 190 to remove particles and dissolved matter bound to their shell, placed on a pre-weighted  
33  
34 191 Whatman GF/A glass-fiber filter (nominal cut-off: 1.6  $\mu\text{m}$ ), and dried overnight at 60°C. Dry  
35  
36 192 zooplankton was ground and stored in the dark at room temperature until elemental and lipid  
37  
38 193 analyses.  
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46 195 Zooplankton counting  
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49 196  
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51

52 197 Zooplankton composition was determined in February and May 2010 by filtering 60 L of  
53  
54 198 water at different depths and locations in three enclosures of each treatment with a 12-L  
55  
56 199 Schindler plankton trap equipped with a 50- $\mu\text{m}$  filter. Zooplankton was preserved in 4%  
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3 200 formaldehyde. Zooplankton taxa were identified and counted under a Leica stereo-microscope  
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5 201 on subsamples at different dilutions in Dollfuss chambers. Copepods were separated into  
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7 202 cyclopidae, calanoida and nauplii. Cladocera were separated into *Daphnia*, *Ceriodaphnia*, and  
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9 203 Chydoridae. Rotifers were counted globally.

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15 205 Sampling of recent sediment

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22 207 Recently deposited sediments were sampled in May and June 2010. Sedimentation rates were  
23  
24 208 determined using six sediment traps deployed in each enclosure. Traps consisted of 5-cm  
25  
26 209 diameter and 30-cm long PVC tubes, suspended at 4 m depth. Suspended 0.5 m above the  
27  
28 210 bottom of the enclosures, sediment traps were preserved for bottom sediment resuspension.  
29  
30 211 Traps were deployed for 7- to 9-day intervals. Material collected from the six traps was  
31  
32 212 pooled in a collection flask and allowed to sediment overnight at 4°C. The supernatant and  
33  
34 213 zooplankton therein was removed. Sediment was freeze-dried, weighted, ground and stored in  
35  
36 214 the dark at room temperature until analyses. Sedimentation rates were calculated as the mass  
37  
38 215 of dry matter divided by the duration of the trap deployment and the total surface of the six  
39  
40 216 traps, and expressed in  $\text{g m}^{-2} \text{ day}^{-1}$ .

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47 218 Elemental composition of seston, zooplankton, initial and recent sediment

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54 220 Carbon and nitrogen contents of dried samples were determined using a CHN elementary  
55  
56 221 analyzer (FlashEA 1112 series, Thermo Fisher Scientific) with acetanilide as standard. Initial  
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3 222 and recent sediment organic carbon contents (OC) were determined after removal of inorganic  
4  
5 223 carbon (IC) from sediment by successive additions of 1 M HCl (Hedges & Stern, 1984).  
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10  
11 225 Sugar and protein colorimetric assays of sediments  
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17 227 Freeze-dried sediments were extracted with H<sub>2</sub>O at 100°C for 2 h. The mixture was filtered  
18  
19 228 through a Whatman GF/F filter, and the filtrate was freeze-dried. The freeze-dried aqueous  
20  
21 229 extract was dissolved in a known volume of H<sub>2</sub>O and assayed for sugars and proteins. Sugar  
22  
23 230 contents were determined using the phenol–sulfuric acid colorimetric method with glucose as  
24  
25 231 standard (Dubois *et al.*, 1956). The protein contents were determined using the colorimetric  
26  
27 232 method of Lowry with bovine serum albumin as standard (Lowry *et al.*, 1951). Sugar and  
28  
29 233 protein contents were expressed as percentages of the sediment dry weight (DW).  
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36 235 Lipid analysis  
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42 237 All chemicals used were of analytical grade.  
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45 238 Apart from initial sediments S<sub>1</sub> and S<sub>2</sub>, analyses of lipids were carried out on three  
46  
47 239 replicates of each treatment for seston, zooplankton and recent sediment sampled in May  
48  
49 240 2010.  
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52 241 The filter with collected seston was extracted with a dichloromethane  
53  
54 242 (DCM)/methanol (MeOH) (2/1, v/v) mixture at room temperature for 18 h. The mixture was  
55  
56 243 filtered through a Whatman GF/F glass-fiber filter and solvent was removed under reduced  
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3 244 pressure. Extracts were saponified at 80°C for 2 h with 1 M KOH in MeOH. The pH of  
4  
5 245 saponified extract was brought to 2 by addition of 6 M HCl and lipids extracted with DCM.  
6  
7 246 The organic phase was washed with deionized water until neutral pH, dried over Na<sub>2</sub>SO<sub>4</sub> and  
8  
9 247 DCM removed under reduced pressure. Saponified lipids were treated with ca. 4 M HCl in  
10  
11 248 MeOH at 80°C for 1 h to convert carboxyl groups into their methyl ester derivatives.  
12  
13 249 Esterified extract was then treated with a mixture of anhydrous pyridine/N,O-  
14  
15 250 Bis(trimethylsilyl)trifluoroacetamide (BSTFA) (10/1, v/v) for 10 min at 60°C to convert  
16  
17 251 hydroxyl groups into trimethylsilyl (TMS) ether groups. Lipid components (as methyl esters  
18  
19 252 and TMS ethers) were analysed by gas chromatography-mass spectrometry (GC-MS) with an  
20  
21 253 Agilent 6890 gas chromatograph coupled to an Agilent 5973N mass spectrometer with  
22  
23 254 electron ionization at 70 eV. Separation was achieved using a fused silica column coated with  
24  
25 255 RTX5SilMS (30 m, i.d. 0.25 mm, film thickness 0.5 µm) with helium as carrier gas. The GC  
26  
27 256 oven was programmed from 100 to 320°C at 4°C min<sup>-1</sup>. Unsaturated fatty acids were analysed  
28  
29 257 using gas chromatography-flame ionization detector (GC-FID) and identified by comparison  
30  
31 258 with standards (Larodan, Malmö, Sweden) using fused silica column coated with DB23 (60  
32  
33 259 m, i.d. 0.25 mm, film thickness 0.25 µm) with helium as carrier gas. The GC oven was  
34  
35 260 programmed from 100 to 170°C at 6.5°C min<sup>-1</sup>, then to 215°C at 2.75°C min<sup>-1</sup> and to 230°C at  
36  
37 261 40°C min<sup>-1</sup>. Individual component contributions were determined by comparison of the peak  
38  
39 262 areas from GC-MS traces. This method allowed a comparison of the relative abundance of  
40  
41 263 each compound between the different samples analysed, but did not allow the quantification  
42  
43 264 of individual compounds within the total lipids. Dried zooplankton samples were extracted  
44  
45 265 and lipids analyzed as described for seston. The amounts of extracted lipids were too low to  
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47 266 allow an accurate weight determination.  
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3 267 Freeze-dried sugar- and protein-free sediment samples were extracted with a  
4  
5 268 chloroform/MeOH (2/1, v/v) mixture for 2 h at 80°C. Lipid extracts were analysed as  
6  
7 269 described for seston.  
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12  
13 271 Statistical analyses  
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18  
19 273 Statistical analyses were performed using R software ([www.r-project.org](http://www.r-project.org)). A linear mixed-  
20  
21 274 effects model (LME) with sediment treatment, time and cross-effect as explanatory variables  
22  
23 275 and replicates as a random effect was used to test the individual and the combined effects of  
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25 276 sediment treatment (S<sub>0</sub>, S<sub>1</sub> and S<sub>2</sub>) and time on the biomass of seston and zooplankton (from  
26  
27 277 February to June), zooplankton composition (February and May), sedimentation rates (May  
28  
29 278 and June), elemental compositions of seston, zooplankton (from February to June) and recent  
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31 279 sediment (May and June), and orthophosphate, ammonium and nitrate concentrations of water  
32  
33 280 (May and June). For response variables analysed only in May (DOC and lipid biomarkers),  
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35 281 effects of sediment treatment were tested with a LME with sediment treatment as explanatory  
36  
37 282 variable and replicates as a random effect. Post-hoc Tukey's tests (Tukey) were performed to  
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39 283 compare one treatment to another. Data were log-transformed when necessary to homogenize  
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41 284 distributions and variances.  
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49 286 Technical constraints  
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55 288 The design of this experiment had been initially planned to last for almost 2 years and not for  
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57 289 5 months as presented here. With the design initially conceived, regular sampling on various  
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3 290 biotic and abiotic parameters were planned from May 2010 to December 2011. Unfortunately,  
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5 291 extreme climatic events have damaged the enclosures, forcing us to stop the experiment on  
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7 292 July 2010 with an incomplete and heterogeneous set of data. As a consequence, phosphorus  
8  
9 293 analyses in the various compartments of the mesocosms were not possible, and other analyses  
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11 294 (nutrients, DOC, particles, zooplankton taxonomy) were conducted only on one or two  
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13 295 sampling dates.  
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## 20 297 **Results**

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26 299 Water: nutrient and DOC concentrations  
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32 301 In May and June, sediment treatment had a significant effect on orthophosphate concentration  
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34 302 of water (Table 2). Orthophosphate concentration from S<sub>2</sub> enclosures was significantly higher  
35  
36 303 than those from S<sub>0</sub> and S<sub>1</sub> enclosures, which did not differ significantly each other.  
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39 304 Sediment treatment had no significant effect on the concentrations of ammonium and  
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41 305 nitrates and on the inorganic nitrogen (sum of ammonium and nitrate  
42  
43 306 concentrations)/orthophosphates ratio (IN/P, Table 2). Despite this absence of significant  
44  
45 307 effect, a IN/P ratio from S<sub>2</sub> enclosures (5) much lower than that from both S<sub>0</sub> and S<sub>1</sub> (16 and  
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47 308 18, respectively) was observed.  
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51 309 In May, sediment treatment had a significant effect on DOC concentration (Table 2).  
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53 310 DOC concentration in S<sub>2</sub> enclosures was significantly higher than that in S<sub>1</sub> enclosures. In  
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3 311 contrast DOC concentration in S<sub>0</sub> and S<sub>1</sub> enclosures did not differ significantly and DOC  
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5 312 concentration in S<sub>2</sub> enclosures did not differ significantly from that in S<sub>0</sub> enclosures.  
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11 314 Seston: biomass and elemental composition  
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17 316 Biomass and elemental compositions of seston (particulate matter between 0.7 and 50 µm)  
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19 317 from the different treatments were reported in Table 2.  
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22 318 Sediment treatment had a significant effect on seston biomass (Fig. 1a) since, on  
23  
24 319 average, seston biomass in S<sub>0</sub> and S<sub>1</sub> enclosures did not differ significantly but were lower  
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26 320 than those from S<sub>2</sub> enclosures. Seston biomass was higher during winter than during spring.  
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30 321 The C content of seston did not differ significantly among treatments and was slightly  
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32 322 higher on April than for the other dates (Fig. 2a). The N content of seston was affected by  
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34 323 sediment treatment: it did not differ between S<sub>0</sub> and S<sub>1</sub> enclosures but was lower in S<sub>0</sub>  
35  
36 324 enclosures compared to S<sub>2</sub> enclosures, without any time effect (Fig. 2b). The C/N ratio of  
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38 325 seston from S<sub>0</sub> treatment was higher than that of seston from S<sub>1</sub> and S<sub>2</sub> treatments but this  
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40 326 difference was only observed in February and March (Fig. 2c). The C/N ratio of seston was  
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42 327 lower in February than during the following months.  
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49 329 Zooplankton: biomass, specific and elemental compositions  
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55 331 Biomass and elemental compositions of zooplankton from the different treatments were  
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57 332 reported in Table 2.  
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3 333 Sediment treatments had a very significant effect on zooplankton biomass (Fig. 1b).  
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5 334 On average, zooplankton biomass did not differ significantly between S<sub>0</sub> and S<sub>1</sub> enclosures  
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7 335 but was higher in S<sub>2</sub> enclosures than in S<sub>0</sub> and S<sub>1</sub> ones, especially in March and April (Fig.  
8  
9 336 1b). Zooplankton biomass increased from February to April and then decreased up to June.

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11  
12 337 Species composition of zooplankton communities was weakly affected by sediment  
13  
14 338 treatments since only the concentration of Chydoridae was significantly higher in the S<sub>2</sub>  
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16 339 enclosures than in S<sub>0</sub> and S<sub>1</sub> ones (Table 4). On average, the number of individuals was lower  
17  
18 340 in February than in May, especially for nauplii of copepods ( $7.3 \pm 3.4$  and  $180.9 \pm 77.7$   
19  
20 341 individuals L<sup>-1</sup>, for February and May, respectively. C and N contents and C/N ratio of  
21  
22 342 zooplankton from S<sub>0</sub>, S<sub>1</sub> and S<sub>2</sub> treatments did not differ significantly (Table 2). The C  
23  
24 343 content of zooplankton slightly increased from February to March and then slightly decreased  
25  
26 344 until June (Fig. 3a). The N content of zooplankton sampled in February was lower than that  
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28 345 sampled on the other dates (Fig. 3b). The opposite trend was observed for the C/N ratio of  
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30 346 zooplankton (Fig. 3c).

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38 348 Recent sediment: sedimentation rates, elemental compositions and sugar and protein contents

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44 350 Recent sediments were sampled in May and in June. Sedimentation rates and elemental  
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46 351 composition of recent sediments were reported in Table 2.

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48  
49 352 Sediment treatments and time did not significantly affect the sedimentation rates (Fig.  
50  
51 353 1c), although sedimentation rates tended to be higher in S<sub>1</sub> and S<sub>2</sub> than in S<sub>0</sub> enclosures.

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55 354 Sediment treatments affected the C, OC and N contents of recent sediments since  
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57 355 those from S<sub>1</sub> enclosures were lower than those from S<sub>0</sub> and S<sub>2</sub> ones (Fig. 4a and 4b). The

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3 356 C/N ratio of recent sediment from S<sub>1</sub> treatment was higher than that from S<sub>0</sub> and S<sub>2</sub> treatments  
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5 357 (Fig. 4c). In contrast, the OC/N ratio was not significantly affected by the sediment treatment.  
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8 358 The amount of sugar and protein contents of recent sediments did not differ  
9  
10 359 significantly between the different treatments (Table 2).  
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16 361 Lipid compositions of seston, zooplankton and recent sediments  
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22 363 Mean lipid distributions of the three pelagic compartments were reported in Table 3.  
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25 364 Except for chlorophyll-derived compounds in recent sediments (LME:  $p = 0.026$ ,  $F_{2,6}$   
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27 365 = 7.13), sediment treatments had no significant effect on the relative amounts of the different  
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29 366 lipid classes of seston, zooplankton and recent sediments (data not shown). Chlorophyll-  
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31 367 derived compounds were more abundant in recent sediments from S<sub>2</sub> ( $4.7 \pm 1.7$  % of total  
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33 368 lipids) enclosures than in recent sediments from S<sub>0</sub> ( $1.8 \pm 0.7$  % of total lipids, Tukey:  $p =$   
34  
35 369 0.033) and S<sub>1</sub> ( $2.0 \pm 0.5$  % of total lipids, Tukey:  $p = 0.048$ ) enclosures. FAs largely  
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37 370 dominated their lipid distributions, followed by alkanols. Sterols, hydroxy acids and  
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39 371 chlorophyll-derived compounds were present in lower relative abundances.  
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44 372 Sediment treatments had no effect on the FA distributions (Supplementary Tables 1  
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46 373 and 2). For all treatments saturated fatty acids (SAFAs) dominated the distribution, followed  
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48 374 by monounsaturated fatty acids (MUFAs), PUFAs (long-chain PUFAs, carbon number  $\geq 20$ ,  
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50 375 accounting for ca. 1, 27 and 8% of total PUFAs for seston, zooplankton and recent sediments,  
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52 376 respectively) and BACTFAs.  
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3 377 Sterol distributions did not depend on sediment treatment (Table 3). For all treatments,  
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5 378 24-ethyl-cholest-5-enol ( $C_{29}\Delta^5$ ) and cholesterol ( $C_{27}\Delta^5$ ) largely dominated the sterol  
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7 379 distribution of recent sediments, with stanols accounting for less than 2% of total sterols.  
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### 11 12 13 381 **Discussion**

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16 382 All the criteria used for the selection of the bottom sediments suggest that the potential  
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18 383 biodegradability of  $S_2$  could have been one order of magnitude higher than that of  $S_1$ . The  
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20 384 pool of OM, which represented the total stock of resources potentially used by bacteria,  
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22 385 proteins and sugars, essential for bacterial growth, and PUFAs, preferentially degraded by  
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24 386 bacteria, were clearly more abundant in  $S_2$  than in  $S_1$ .  
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31 388 Effects of bottom-up forcing on pelagic compartments  
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37 390 According to the characteristics of  $S_1$  and  $S_2$ , a release of nutrients and OM in the water  
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39 391 column in the order  $S_0 < S_1 < S_2$  was expected. We hypothesized that this would lead to an  
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41 392 enhanced bottom-up forcing on the basal organisms of the food web, resulting in an increase  
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43 393 of seston biomass. By consuming seston, zooplankton was also expected to increase its  
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45 394 biomass with addition of sediment of increasing biodegradability. The phosphate and DOC  
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47 395 concentrations in the water column as well as the biomass values of seston and zooplankton,  
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49 396 all higher in  $S_2$  treatment than in  $S_1$  and  $S_0$  treatments, partially corroborated this hypothesis.  
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54 397 The sediment of  $S_2$  enclosures, which was typical of eutrophic to hypertrophic lakes  
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56 398 and fishponds (Søndergaard, 1988; Banas *et al.*, 2008), clearly fostered pelagic compartments.  
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3 399 This result confirms that eutrophic ecosystems are subject to internal nutrient loading, and  
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5 400 that released nutrients may be taken up by aquatic food webs (Søndergaard *et al.*, 2003,  
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7 401 2007). Interestingly, the experiment was run from December to June, when dissolved oxygen  
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9 402 remained oversaturated in all enclosures, even near sediments (data not shown). This  
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11 403 strengthens the statement of Nürnberg (2009) that “phosphorus release is not restricted to and  
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13 404 does not require anoxia in the overlaying water”. As for dissolved oxygen, we did not find  
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15 405 any significant treatment effect on the pH values in the water column, which were high and  
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17 406 ranged between 8.1 and 8.5 (data not shown). Such values are considered to favour  
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19 407 phosphorus release from sediment (Koski-Vahala & Hartikainen, 2001). Other processes may  
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21 408 have favoured nutrient transfer into the overlaying water of S<sub>2</sub> enclosures. Activity of benthic  
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23 409 micro- and macroinvertebrates is probably one of these mechanisms, as suggested by the  
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25 410 higher abundance of Chydoridae in microinvertebrate samples and by the frequent  
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27 411 observation of Chironomids in the S<sub>2</sub> enclosures (direct observations). Moreover, a higher  
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29 412 microbial mineralisation of the highly biodegradable S<sub>2</sub> SOM was expected (Gächter &  
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31 413 Meyer, 1993; Pettersson, 1998). The observed changes in dissolved nutrients in water and  
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33 414 associated biomass of seston suggest a limitation of planktonic primary producers by  
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35 415 phosphorus in S<sub>0</sub> and S<sub>1</sub> enclosures, and a reduction of such P-limitation, accompanied by a  
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37 416 higher primary productivity, in S<sub>2</sub> enclosures. It would be interesting to conduct long-term  
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39 417 experiments in order to verify how internal nutrient loading associated to sediment-water  
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41 418 exchanges may change nutrient limitation of phytoplankton in a seasonal context.  
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48 By contrast, no difference was observed in the nutrient and DOC concentrations, and  
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50 420 in the biomass of seston and zooplankton between S<sub>1</sub> and S<sub>0</sub> treatments. This absence of  
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52 421 significant difference between S<sub>1</sub> and S<sub>0</sub> suggests that the potential bottom-up effect  
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54 422 associated to OM degradation and nutrient release from the sediment of Lake Créteil was  
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56 423 limited. As highlighted previously (Lacroix *et al.* 1989), the lack of OM accumulation in the  
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3 424 sediment of this shallow sand-pit lake, despite high lake productivity, suggests an efficient  
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5 425 OM transfer within the pelagic food web and an efficient nutrient recycling within the water  
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7 426 column. The low initial abundance of very labile compounds, such as proteins, sugars and  
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9 427 PUFAs in S<sub>1</sub> sediment confirmed this recycling efficiency. Moreover, it is very probable that  
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11 428 the natural mineral matrix of Lake Créteil sediment (such mineral matrix was negligible in S<sub>2</sub>  
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13 429 enclosures) contained much more P-binding elements, such as iron oxides, which should have  
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15 430 favoured a higher retention of phosphorus in the well-oxygenated conditions of the  
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17 431 experiment (Mortimer, 1941).

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21 432 Whatever the treatments, the highest biomass of seston was observed in February and  
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23 433 in March, when the biomass and abundance of zooplankton were the lowest. This seasonal  
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25 434 trend, previously observed (Danger *et al.*, 2012), agrees with the low grazing activity of  
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27 435 zooplankton in late winter, which results in a weak top-down control on phytoplankton. On  
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29 436 the other hand, the enhanced grazing activity of zooplankton in spring probably resulted in a  
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31 437 more important top-down control on phytoplankton (Sarnelle, 1999).

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35 438 The bottom-up effect observed for S<sub>2</sub> treatment did not strongly influence the structure  
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37 439 of the zooplankton community. The only effect was observed within Cladocera. The typically  
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39 440 pelagic daphniidae tended to be less abundant, while the benthic and littoral Chydoridae  
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41 441 attained higher densities in the S<sub>2</sub> enclosures. The observed increase in the abundance of  
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43 442 Chydoridae in the S<sub>2</sub> enclosures, characterized by their OM-rich sediment, is consistent with  
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45 443 the ability of Chydoridae to ingest detritus (de Eyto & Irvine, 2001). Indeed, some  
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47 444 Chydoridae, such as *Chydorus* sp., present in the enclosures, are able to use both benthic and  
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49 445 open-water food sources (de Eyto & Irvine, 2001). Finally, after a strong increase in the  
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51 446 beginning of spring, the biomass of zooplankton from S<sub>2</sub> treatment slowly decreased in the  
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53 447 end of spring, suggesting that phytoplankton became rapidly limiting for zooplankton growth  
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55 448 in spite of the initial positive bottom-up effect from this sediment. This result supports the  
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3 449 hypothesis that competition for food might be important for herbivorous zooplankton in such  
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5 450 experimental systems when external nutrient loading is absent.  
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8 451 The occurrence of a bottom-up effect of S<sub>2</sub> treatment is also supported by the  
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10 452 elemental composition of seston. The higher N content of seston observed in S<sub>2</sub> treatment,  
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12 453 compared to S<sub>0</sub> and S<sub>1</sub> ones, suggests a release of N from this “labile” sediment. The lower  
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14 454 C/N ratio of seston from S<sub>2</sub> enclosures, probably indicative of a higher nutritional value  
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16 455 (Jones *et al.*, 2002), could have contributed to the higher biomass of zooplankton observed in  
17  
18 456 these enclosures. By contrast, zooplankton C/N ratios did not depend on treatments and were  
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20 457 quite similar to those obtained by Danger *et al.* (2012). Since species composition of  
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22 458 zooplankton was only slightly affected by sediment treatments, this constant C/N ratio is in  
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24 459 agreement with the homeostasis constraints on zooplankton stoichiometry. Indeed,  
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26 460 zooplankton species have specific elemental compositions (Hessen, 1990; Andersen &  
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28 461 Hessen, 1991). Moreover, the decrease in zooplankton C/N ratio with time observed in the  
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30 462 enclosures is in agreement with the increase in copepods within the community. As a  
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32 463 conclusion, changes in seston stoichiometric ratios do not necessarily induce changes in the  
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34 464 structure of the zooplankton community. In a previous study, Danger *et al.* (2012) had shown  
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36 465 that changes at the top of the food web affected elemental composition of zooplankton  
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38 466 communities by shifting species dominance, but did not affect seston stoichiometric ratios.  
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40 467 This suggests that stoichiometric changes are not necessarily transferred up or down along  
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42 468 food chains within pelagic food webs.  
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49 469 Although addition of sediment influenced seston stoichiometry, we did not observe  
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51 470 any significant influence of the sediment treatments on its lipid composition. On the other  
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53 471 hand, previous studies (Allard *et al.*, 2011, Danger *et al.*, 2012) showed that changes in  
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55 472 biochemical composition of seston could occur despite similar elemental ratios. This  
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57 473 strengthens the conclusion of these authors that both elemental and biochemical compositions  
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3 474 of OM might provide useful information for understanding links between food-web structure  
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5 475 and functioning of aquatic ecosystems.  
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8 476 Even if controversies do exist about the importance of internal nutrient loading and the  
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10 477 various mechanisms that allow the release of resources from sediments to the overlaying  
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12 478 water (see Nürnberg, 2009), our results show that:  
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15 479 (i) sediments with a high abundance of labile OM, which are more typical of eutrophic  
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17 480 ecosystems, may clearly foster the pelagic food webs even after the reduction of  
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19 481 allochthonous inputs and even in absence of anoxia (Søndergaard *et al.*, 2007);  
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23 482 (ii) sediments with low OM contents and biodegradability, typical of oligo-mesotrophic  
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25 483 ecosystems, are necessary for reducing (at least in absence of anoxia) delayed bottom-up  
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27 484 forcing of sediment on the pelagic compartments.  
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33 486 Effects of bottom-up forcing on recent sediments  
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39 488 The higher biomass of both seston and zooplankton observed in S<sub>2</sub> enclosures did not induce  
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41 489 significant higher sedimentation rates in these enclosures. This might be due to low  
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43 490 production of sinking material from seston and zooplankton in pelagic systems characterized  
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45 491 by the absence of fish. Indeed, the values obtained in this study are in agreement with those  
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47 492 from previous studies carried out in zooplankton-dominated systems (Sarnelle, 1999; Danger  
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49 493 *et al.*, 2012). These studies showed that the sedimentation rates are lower in systems  
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51 494 dominated by zooplankton than in presence of fish. As a consequence, even if differences in  
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53 495 sedimentation rates may have existed, they were probably low and hardly detectable in such  
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55 496 fishless and shallow systems.  
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3 497 In our enclosures, the biomass of seston was higher than that of zooplankton.  
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5 498 Moreover, phytoplankton, which constitutes up to 40% of seston (Hessen *et al.*, 2003), is  
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7 499 known to sink much more than zooplankton (Sommer, 1984). Thus, changes in the elemental  
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9 500 composition of seston observed in the different treatments are expected to result in similar  
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11 501 changes in recent sediment. This hypothesis was not supported by the stoichiometric analyses  
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13 502 since the elemental composition of recent sediment from S<sub>2</sub> treatment was similar to that from  
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15 503 S<sub>0</sub> treatment. Surprisingly, the elemental composition of recent sediment from S<sub>1</sub> treatment  
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17 504 differed from that of recent sediment from S<sub>0</sub> and S<sub>2</sub> treatments. At the present time, no  
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19 505 explanation can be put forward for these results.  
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24 506 Apart from chlorophyll-derived compounds, no differences in the relative amounts of  
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26 507 lipid classes of recent sediment were observed between the treatments. The higher relative  
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28 508 abundances of chlorophyll-derived compounds in recent sediment from S<sub>2</sub> treatment probably  
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30 509 indicate a higher contribution of phytoplankton to this sediment. The relative abundances of  
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32 510 both FAs and sterols in the recent sediment ranged between those observed for seston and  
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34 511 zooplankton. These results suggest that both seston and zooplankton noticeably contributed to  
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36 512 recent sediment. The relative contribution of each pelagic compartment is difficult to  
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38 513 estimate. As the relative abundances of long-chain PUFAs of recent sediments were quite  
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40 514 low, and more similar to those observed for seston than to those observed for zooplankton,  
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42 515 this suggest a rather low contribution of zooplankton to recent sediment. However, PUFAs  
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44 516 are highly sensitive to bacterial degradation (Cranwell, 1981) and likely do not survive  
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46 517 unaltered for a long time in the water column. Consequently, on the basis of PUFA  
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48 518 concentrations, zooplankton contribution to recent sediment could be underestimated.  
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53 519 The low amounts of bacterial FAs suggest a rather low contribution of bacteria to  
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55 520 recent sediments. Nevertheless, stanols were present in higher relative amounts in recent  
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57 521 sediments than in seston and in zooplankton. This indicates that the degradation of settling  
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3 522 organic matter occurred even at the very short time scales (ca. 1 week) of this experiment.  
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5 523 However, the relative amounts of unsaturated fatty acids, the most reactive compounds  
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7 524 towards biodegradation, were rather high in recent sediments. This suggests that microbial  
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9 525 reworking was limited for these very recent sediments.  
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12 526 Lipid biomarkers such as PUFAs and bulk parameters such as sugar and protein  
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14 527 contents have been used to estimate and compare the quality of sediments (Canuel *et al.*,  
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16 528 2007; Allard *et al.*, 2011). In the present study, these indicators did not reveal any relationship  
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18 529 between the quality of the added sediment and that of the recently deposited one. Finally, the  
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20 530 comparison between this study and those dealing with top-down effects (Canuel *et al.*, 2007;  
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22 531 Allard *et al.*, 2011; Danger *et al.*, 2012) suggests that the quantity and the quality of settling  
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24 532 organic matter in aquatic ecosystems are less affected by bottom-up forces (linked to  
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26 533 sediment quality) than by top-down forces (linked to food-web structure) and calls for a  
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28 534 factorial approach on these two parameters.  
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## 36 536 **Conclusion**

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42 538 This mesocosm experiment demonstrates that the origin and the quality of lake sediment can  
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44 539 result in changes in the pelagic compartments. The release of nutrients and OM from the  
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46 540 sediment to the water column can induce a bottom-up forcing transferred from seston to  
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48 541 zooplankton by means of trophic interactions. However, this effect is substantial only when  
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50 542 sediment OM is highly biodegradable and typical of eutrophic systems with high abundances  
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52 543 of omnivorous and planktivorous fish (Banas *et al.*, 2008; Yokoyama *et al.*, 2009). This  
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54 544 strengthens the suggestion of Harrault *et al.* (2012) that maintaining over a sufficiently long  
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56 545 period a top-down control of phytoplankton biomass, for example through the  
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3 546 biomanipulation of fish communities, should not only induce a more efficient grazing on  
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5 547 primary producers, but should also reduce the quantity and biodegradability of SOM,  
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7 548 ultimately decreasing internal nutrient cycling. The progressive reduction of internal recycling  
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9 549 might explain the acknowledged efficiency of biomanipulations for improving water quality  
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11 550 (Jeppesen *et al.*, 2007).  
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15 551 Finally, microcosms and mesocosms have been frequently criticized for their lack of  
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17 552 realism (Carpenter, 1996; Schindler, 1998). Our results suggest that the absence of initial  
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19 553 sediment in most realized mesocosm experiments did not necessarily induce major biases in  
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21 554 the functioning of pelagic systems, and tend to confirm the ecological significance of the  
22  
23 555 effects identified by such manipulations (Spivak & Vanni, 2011). However, it should be kept  
24  
25 556 in mind that other benthic processes, such as redox and pH conditions controlling phosphorus  
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27 557 release, or sediment as a source of planktonic organisms and macroinvertebrates, might also  
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29 558 strongly impact biogeochemical cycles (Søndergaard *et al.*, 2003). Their importance could be  
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31 559 underestimated in most mesocosm experiments.  
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49 566 complies with the current French laws.  
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**Table 1:** Selection criteria for the choice of the initial sediments. Elemental and biochemical composition (n = 1)

	C <sup>a</sup>	OC <sup>a</sup>	N <sup>a</sup>	OC/N	Sugars <sup>a</sup>	Proteins <sup>a</sup>	PUFAs <sup>b</sup>
S <sub>1</sub>	5.7	0.9	0.1	9.0	0.1	0.1	4.9
S <sub>2</sub>	23.1	9.7	2.4	4.0	0.7	1.5	12.6

<sup>a</sup> % of dry weight

<sup>b</sup> % of total fatty acids.

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**Table 2** Nutrient ( $\mu\text{g/L}$ ) concentrations of water sampled in May and June 2010 and DOC ( $\text{mg/L}$ ) concentrations of water sampled in May. Biomass ( $\text{mg L}^{-1}$ ), elemental and biochemical compositions (% of dry weight) of seston, zooplankton (sampled from February to June 2010). Sedimentation rates ( $\text{g DW m}^{-2} \text{d}^{-1}$ ), elemental and biochemical compositions (% of dry weight) of recent sediments (sampled in May and June 2010). Significant effects are in bold. Tukey's post-hoc tests were performed when the effect of sediment treatment was significant with the LME test.

	Means $\pm$ SD			Statistics								
	Treatment			Sediment						Time	Sediment $\times$ Time	
				LME			Tukey (P values)			P values	P values	
	S <sub>0</sub>	S <sub>1</sub>	S <sub>2</sub>	P values	DF <sup>a</sup>	F values	S <sub>0</sub> -S <sub>1</sub>	S <sub>0</sub> -S <sub>2</sub>	S <sub>1</sub> -S <sub>2</sub>			
<b>Water</b>												
Ammonium	28.5 $\pm$ 22.7	22.9 $\pm$ 22.1	32.7 $\pm$ 22.7	0.39	2, 21	0.98	-	-	-	<b>0.001</b>	0.52	
Nitrates	4.6 $\pm$ 3.8	4.1 $\pm$ 2.2	4.5 $\pm$ 3.5	0.90	2, 21	0.10	-	-	-	< <b>0.001</b>	0.34	
Phosphates	3.1 $\pm$ 5.3	3.8 $\pm$ 5.5	11.3 $\pm$ 10.3	<b>0.01</b>	2, 21	5.21	0.96	<b>0.01</b>	<b>0.02</b>	0.35	0.62	
IN/P <sup>b</sup>	16 $\pm$ 21	18 $\pm$ 21	5 $\pm$ 5	0.24	2, 21	1.52	-	-	-	< <b>0.01</b>	0.35	
DOC	4.6 $\pm$ 0.9	4.3 $\pm$ 0.9	5.8 $\pm$ 1.2	<b>0.02</b>	2	5.01	0.80	0.07	<b>0.02</b>	-	-	
<b>Seston</b>												
Biomass	1.18 $\pm$ 0.63	1.40 $\pm$ 1.03	2.14 $\pm$ 1.49	< <b>0.005</b>	2, 21	6.92	0.57	<b>0.001</b>	<b>0.03</b>	< <b>0.0001</b>	0.11	
C	30.3 $\pm$ 8.6	29.3 $\pm$ 8.8	32.2 $\pm$ 8.6	0.27	2, 21	1.39	-	-	-	< <b>0.001</b>	0.76	
N	4.6 $\pm$ 1.9	4.7 $\pm$ 1.4	5.5 $\pm$ 1.5	<b>0.03</b>	2, 21	4.12	0.89	<b>0.02</b>	0.07	0.80	0.18	
C/N ratio	6.6 $\pm$ 1.1	6.2 $\pm$ 1.0	5.9 $\pm$ 1.3	< <b>0.005</b>	2, 21	8.06	<b>0.03</b>	< <b>0.0001</b>	0.12	< <b>0.0001</b>	< <b>0.0001</b>	
<b>Zooplankton</b>												
Biomass	0.27 $\pm$ 0.16	0.29 $\pm$ 0.19	0.51 $\pm$ 0.34	<b>0.002</b>	2, 21	8.87	0.99	< <b>0.0001</b>	< <b>0.0001</b>	< <b>0.0001</b>	<b>0.002</b>	

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C	42.8 ± 8.8	42.7 ± 4.6	44.3 ± 4.2	0.52	2, 21	0.67	-	-	-	< 0.01	0.84
N	7.9 ± 2.6	8.9 ± 2.0	8.0 ± 1.7	0.66	2, 21	0.43	-	-	-	< 0.0001	0.23
C/N ratio	5.4 ± 2.1	5.3 ± 1.4	5.3 ± 1.2	0.94	2, 21	0.06	-	-	-	< 0.0001	0.06
<b>Recent sediment</b>											
Sedimentation rate	0.77 ± 0.40	1.42 ± 0.96	1.17 ± 0.53	0.13	2, 21	2.25	-	-	-	0.09	0.65
C	24.8 ± 2.7	15.5 ± 3.7	26.9 ± 2.6	<b>0.0001</b>	2, 21	14.22	< 0.001	0.43	< 0.0001	<b>0.03</b>	0.10
N	2.8 ± 0.7	1.5 ± 0.5	3.3 ± 0.4	< 0.0001	2, 21	22.61	< 0.005	0.12	< 0.0001	0.97	0.65
C/N ratio	9.1 ± 2.4	10.3 ± 1.8	8.0 ± 1.1	< 0.005	2, 21	8.41	<b>0.04</b>	0.37	< 0.001	0.17	0.95
OC <sup>c</sup>	23.9 ± 2.6	14.4 ± 5.8	27.3 ± 2.2	<b>0.02</b>	2	8.93	<b>0.05</b>	0.58	<b>0.01</b>	-	-
OC/N <sup>c</sup>	8.9 ± 1.1	9.6 ± 5.8	8.0 ± 0.8	0.94	2	0.06	-	-	-	-	-
Sugars <sup>c</sup>	3.3 ± 0.3	2.7 ± 1.2	3.2 ± 0.8	0.36	2	1.22	-	-	-	-	-
Proteins <sup>c</sup>	2.2 ± 0.3	1.8 ± 0.6	3.2 ± 0.9	0.78	2	0.25	-	-	-	-	-

<sup>a</sup> Degrees of Freedom<sup>b</sup> Inorganic Nitrogen (sum of ammonium and nitrates)/Phosphates ratio<sup>c</sup> analyses were performed only on sediments sampled in May 2010

**Table 3** Mean lipid composition of seston, zooplankton and recent sediment sampled in May 2010. Statistical analyses were performed on the mean of the three sediment treatments for each compartment (mean  $\pm$  SD; n = 9 for seston, zooplankton and recent sediment). Bold values indicate significant differences between seston, zooplankton and/or recent sediment. Total was expressed as % of total lipids. Sub-classes of fatty acids and sterols were expressed as % of total fatty acids and sterols, respectively.

Mean	FAs					Sterols				OHs	OH-FAs	CHLOs
	Total	SAFA	MUFA	PUFA	BACTFA	Total	C <sub>27</sub> $\Delta^5$	C <sub>29</sub> $\Delta^5$	Stanols	Total	Total	Total
Seston	<b>75.4 <math>\pm</math> 9.3</b>	<b>74.2 <math>\pm</math> 5.4</b>	<b>11.9 <math>\pm</math> 4.4</b>	<b>4.2 <math>\pm</math> 2.8</b>	<b>9.7 <math>\pm</math> 1.5</b>	5.2 $\pm$ 2.0	<b>23.5 <math>\pm</math> 10.8</b>	<b>57.2 <math>\pm</math> 16.0</b>	<b>0.9 <math>\pm</math> 0.6</b>	<b>14.5 <math>\pm</math> 6.9</b>	<b>4.2 <math>\pm</math> 1.2</b>	<b>0.5 <math>\pm</math> 0.1</b>
Zooplankton	<b>87.3 <math>\pm</math> 7.0</b>	<b>52.8 <math>\pm</math> 5.3</b>	<b>21.5 <math>\pm</math> 5.3</b>	<b>19.4 <math>\pm</math> 4.9</b>	<b>6.4 <math>\pm</math> 1.2</b>	6.0 $\pm$ 4.6	<b>68.1 <math>\pm</math> 11.0</b>	<b>21.5 <math>\pm</math> 11.0</b>	<b>1.2 <math>\pm</math> 0.8</b>	<b>3.9 <math>\pm</math> 2.9</b>	<b>1.3 <math>\pm</math> 0.6</b>	<b>1.3 <math>\pm</math> 0.8</b>
Recent sediment	<b>75.0 <math>\pm</math> 7.7</b>	<b>56.2 <math>\pm</math> 3.2</b>	<b>24.0 <math>\pm</math> 2.2</b>	<b>11.1 <math>\pm</math> 2.5</b>	<b>8.7 <math>\pm</math> 1.9</b>	6.8 $\pm$ 4.1	<b>34.1 <math>\pm</math> 7.1</b>	<b>43.9 <math>\pm</math> 9.5</b>	<b>2.3 <math>\pm</math> 0.9</b>	<b>10.5 <math>\pm</math> 3.7</b>	<b>4.6 <math>\pm</math> 1.1</b>	<b>2.8 <math>\pm</math> 1.7</b>

FAs: fatty acids, SAFA: saturated fatty acid, MUFA: monounsaturated fatty acid, PUFA: polyunsaturated fatty acid, BACTFA: bacterial fatty acid =  $\Sigma 15:0 + \Sigma 17:0 +$  branched-chain FAs, OHs: *n*-alkanols, OH-FAs: sum of  $\alpha$ -,  $\beta$ - and  $\omega$ -hydroxy acids, CHLOs: chlorophyll-derived compounds.



**Table 4** Mean specific composition of zooplankton communities (Individual L<sup>-1</sup>) sampled in February and May 2010. Mean ± SD. For each treatment and each date, counting was only performed on triplicates. Significant effects are in bold.

	Means ± SD			Statistics							
	Treatment			Sediment						Time	Sediment × Time
				LME			Tukey (P values)			P values	P values
	S <sub>0</sub>	S <sub>1</sub>	S <sub>2</sub>	P values	DF <sup>a</sup>	F values	S <sub>0</sub> -S <sub>1</sub>	S <sub>0</sub> -S <sub>2</sub>	S <sub>1</sub> -S <sub>2</sub>		
<b>Rotifers</b>	2.8 ± 2.8	1.7 ± 1.2	7.2 ± 15.4	0.86	2, 6	0.15	-	-	-	0.23	<b>0.002</b>
<b>Cladocerans</b>											
<i>Daphnia</i>	23.4 ± 22.2	11.4 ± 13.7	3.4 ± 4.2	0.11	2, 6	3.27	-	-	-	<b>0.066</b>	<b>0.24</b>
<i>Ceriodaphnia</i>	1.1 ± 2.2	0.1 ± 0.3	0.0 ± 0.1	0.18	2, 6	2.33	-	-	-	<b>0.0008</b>	<b>0.0054</b>
<i>Bosminidae</i>	1.3 ± 1.7	2.2 ± 3.9	2.2 ± 4.4	0.95	2, 6	0.05	-	-	-	< <b>0.0001</b>	0.94
Chydoridae	5.6 ± 6.2	2.8 ± 3.7	16.5 ± 23.3	<b>0.016</b>	2, 6	8.87	<b>0.76</b>	<b>0.02</b>	< <b>0.005</b>	< <b>0.0001</b>	< <b>0.0001</b>
<b>Copepods</b>											
Cyclopids	13.0 ± 14.0	7.5 ± 11.0	12.1 ± 12.5	0.33	2, 6	1.34	-	-	-	< <b>0.0001</b>	0.67
Calanoids	16.6 ± 10.8	10.3 ± 16.5	15.7 ± 18.6	0.41	2, 6	1.04	-	-	-	<b>0.0001</b>	<b>0.0008</b>
Nauplii	111.9 ± 111.5	61.0 ± 65.1	99.2 ± 124..0	0.11	2, 6	2.22	-	-	-	0.066	0.24

<sup>a</sup> Degrees of Freedom

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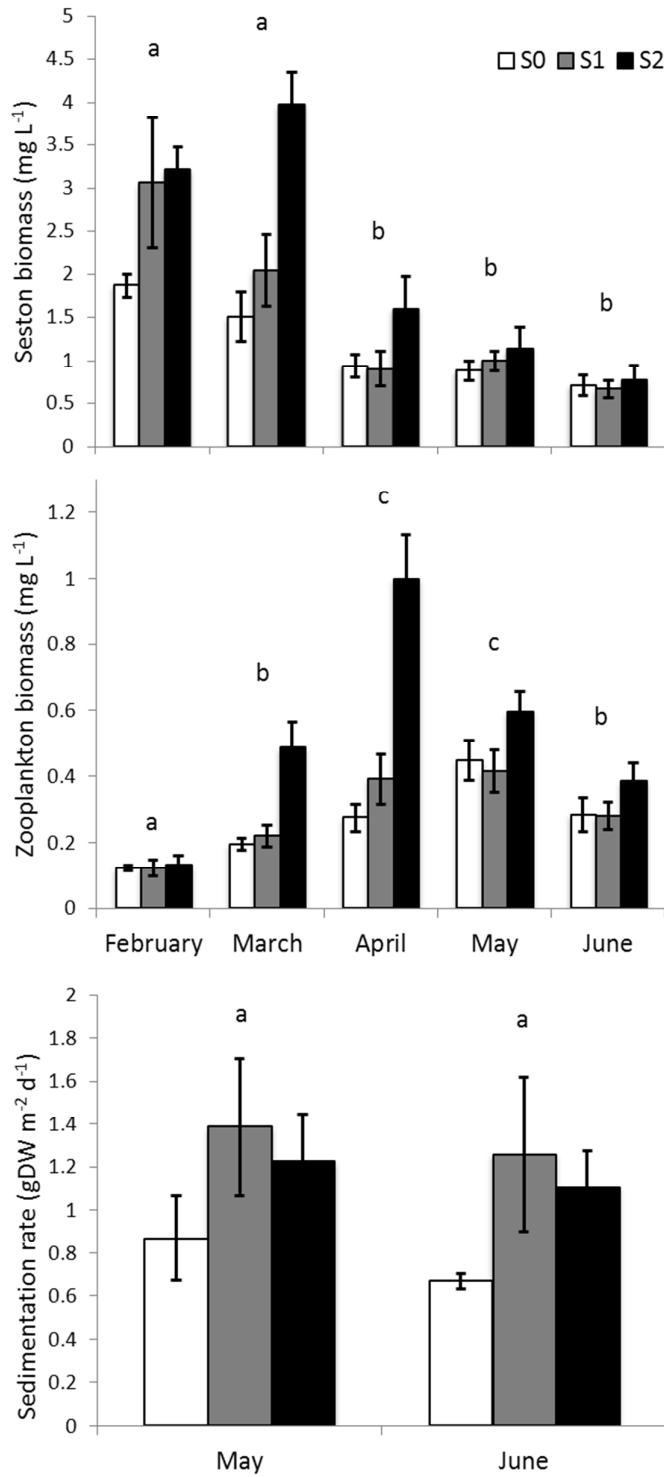
3 Figure 1: Seasonal variations of seston (a) and zooplankton (b) biomass and sedimentation  
4 rates (c) (mean  $\pm$  SE). White, grey and black bars represent the control treatment (S<sub>0</sub>), S<sub>1</sub> and  
5 S<sub>2</sub> treatments respectively. Significant effects of time are represented by different letters.

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7 Figure 2: Seasonal variations of carbon (a) and nitrogen (b) contents and C:N ratio (c) of the  
8 seston (mean  $\pm$  SE). White, grey and black bars represent the control treatment (S<sub>0</sub>), S<sub>1</sub> and S<sub>2</sub>  
9 treatments respectively. Significant effects of time are represented by different letters.

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11 Figure 3: Seasonal variations of carbon (a) and nitrogen (b) contents and C:N ratio (c) of the  
12 zooplankton (mean  $\pm$  SE). White, grey and black bars represent the control treatment (S<sub>0</sub>), S<sub>1</sub>  
13 and S<sub>2</sub> treatment respectively. Significant effects of time are represented by different letters.

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15 Figure 4: Variations of carbon (a) and nitrogen (b) contents and C:N ratio (c) of the short-term  
16 sediment (mean  $\pm$  SE). White, grey and black bars represent the control treatment (S<sub>0</sub>), S<sub>1</sub> and  
17 S<sub>2</sub> treatment respectively. Significant effects of time are represented by different letters.

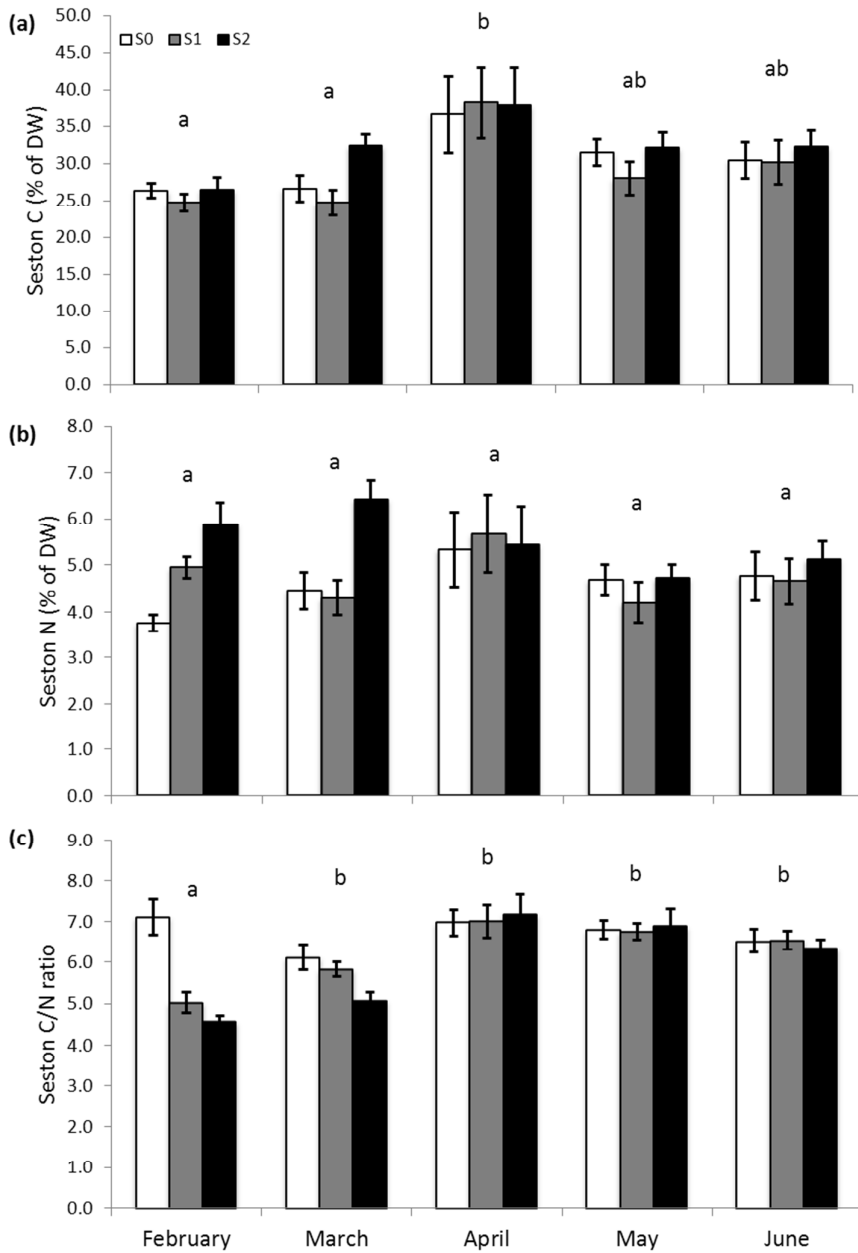
19 Figure 1



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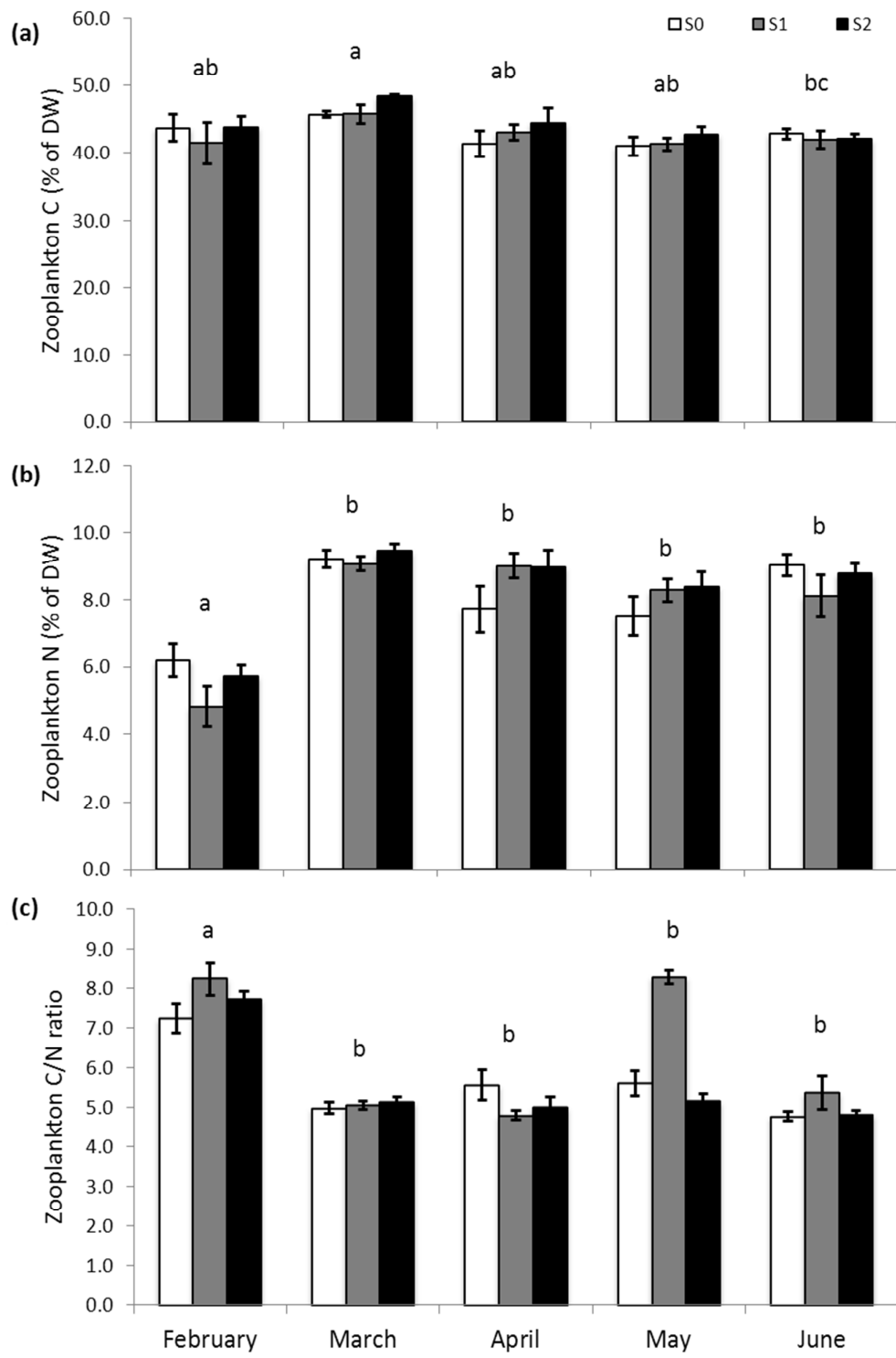


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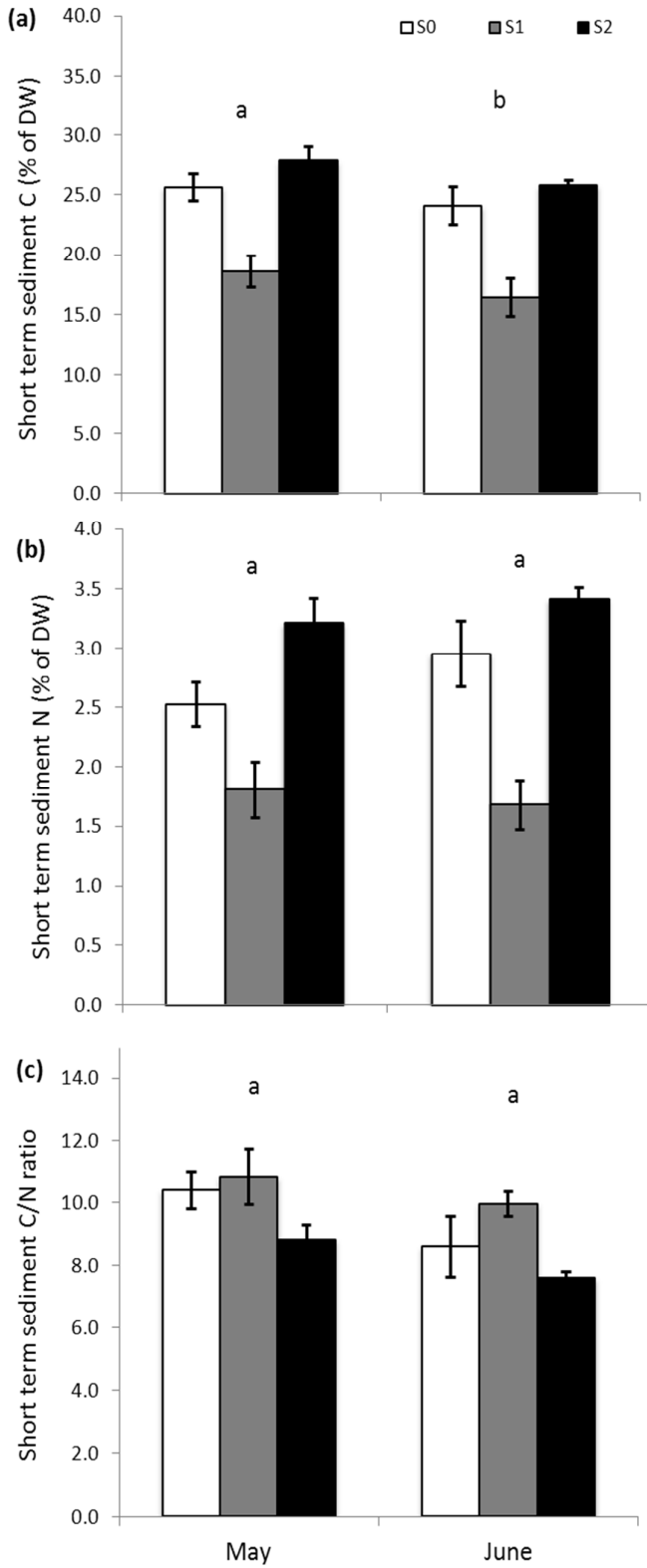
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**Supplementary Table 1** Lipid composition of the initial sediments. Total was expressed as % of total lipids. Sub-classes of fatty acids, sterols, alkanols and hydroxy acids were expressed as % of total fatty acids, sterols, alkanols and hydroxy acids, respectively.

	FAs					Sterols				OHs			OH-FAs			CHLOs
	Total	SAFA	MUFA	PUFA	BACTFA	Total	$\Sigma\Delta^5$	$\Sigma\Delta^7$	stanols	Total	SC	LC	Total	$\alpha + \beta$	$\omega$	Total
S <sub>1</sub>	36.4	74.2	13.9	4.9	6.6	16.0	61.2	ND	38.8	26.3	5.1	94.9	8.5	71.4	26.9	4.5
S <sub>2</sub>	48.2	64.9	17.6	12.6	3.9	19.0	30.1	24.6	28.2	13.4	1.7	98.3	2.4	100.0	ND	9.8

FAs: fatty acids, SAFA: saturated fatty acid, MUFA: monounsaturated fatty acid, PUFA: polyunsaturated fatty acid, BACTFA: bacterial fatty acid =  $\Sigma 15:0 + \Sigma 17:0 +$  branched-chain FAs,  $\Sigma\Delta^5$ : sum of  $\Delta^5$ -sterols,  $\Sigma\Delta^7$ : sum of  $\Delta^7$ -sterols, OHs: alkanols, SC: short-chain alkanols (carbon number  $\leq 18$ ), LC: long-chain alkanols (carbon number  $\geq 20$ ), OH-FAs: hydroxy acids,  $\alpha + \beta$ : sum of  $\alpha$ - and  $\beta$ -hydroxy acids,  $\omega$ :  $\omega$ -hydroxy acids, CHLOs: chlorophyll-derived compounds, ND: non detected.

The quality (potential biodegradability) of the initial sediments was estimated using their contents in the constituents which were preferentially degraded by bacteria i.e., proteins, sugars and PUFAs. The degradation state of these sediments was estimated using their contents in compounds related to the presence of bacteria i.e. BACTFAs (Wakeham & Beier, 1991; Budge & Parrish, 1998) or to the bacterial activity i.e.  $\alpha$ - and  $\beta$ -OH-FAs (Cranwell, 1981), and stanols, the saturated homologues of sterols (Gaskell & Eglinton, 1975).

The high relative abundance of  $\Delta^7$ -sterols in S<sub>2</sub> is consistent with the high contribution of Chlorophyceae to S<sub>2</sub> observed previously (Danger *et al.*, 2012). Indeed, these sterols are abundant in many Chlorophyceae (Volkman, 1986), and have been proposed as indicators of these algae (Cranwell, 1982). In contrast,  $\Delta^7$ -sterols were not detected in S<sub>1</sub>. 24-methyl- and 24-ethyl-cholest-5-enols, present in high amounts in S<sub>1</sub>, are abundant in algae and in vascular plants as well. So, the sterol distribution of S<sub>1</sub> cannot allow to discriminate between autochthonous and allochthonous inputs. The higher relative abundances of chlorophyll-derived compounds in S<sub>2</sub> than in S<sub>1</sub> corroborate also a higher phytoplanktonic contribution to S<sub>2</sub>. Indeed, such chlorophyll-derived compounds are usually considered as arising from the biodegradation of the phytol side-chain of chlorophyll (Rontani & Volkman, 2003).

The higher relative amounts of BACTFAs in S<sub>1</sub> than in S<sub>2</sub> suggest that S<sub>1</sub> was in a more advanced degradation state than S<sub>2</sub>. This is supported by higher amounts of  $\alpha$ - and  $\beta$ -OH-FAs and stanols in S<sub>1</sub> than in S<sub>2</sub>. Indeed,  $\alpha$ - and  $\beta$ -OH-FAs are usually related to microbial input in sediment (Cranwell, 1981), and stanols, the saturated homologues of sterols, are usually considered as formed through in situ microbial reduction of sterols (Gaskell & Eglinton, 1975).

**Supplementary Table 2** Fatty acid composition (% of total fatty acids) of the initial sediments S<sub>1</sub> and S<sub>2</sub> (n = 1).

<b>SAFA</b>	S <sub>1</sub>	S <sub>2</sub>	<b>MUFA</b>	S <sub>1</sub>	S <sub>2</sub>	<b>PUFA</b>	S <sub>1</sub>	S <sub>2</sub>	<b>BACT</b>	S <sub>1</sub>	S <sub>2</sub>
14:0	1.3	0.8	16:1 $\omega$ x	tr	tr	16:3 $\omega$ 3	ND	0.4	14:0 br	0.0	0.2
16:0	12.4	10.7	16:1 $\omega$ 7	5.1	1.7	16:2 $\omega$ x	ND	0.9	15:0 <sup>a</sup>	2.9	2.0
18:0	8.4	3.2	18:1 $\omega$ 9	4.8	9.5	18:3 $\omega$ 6	0.0	0.3	16:0 br	0.4	0.4
20:0	3.2	1.0	18:1 $\omega$ 7	3.0	2.8	18:4 $\omega$ 3	0.0	0.3	17:0 <sup>a</sup>	3.2	1.3
21:0	0.7	0.2	18:1 $\omega$ x	0.0	0.7	18:2 $\omega$ 6 (LIN)	1.0	1.6			
22:0	5.4	6.1	20:1 $\omega$ 9	0.9	1.2	18:3 $\omega$ 3 (ALA)	1.6	7.8			
23:0	1.8	0.5	22:1 $\omega$ x	0.0	0.2	20:4 $\omega$ 6 (ARA)	0.9	0.3			
24:0	12.6	9.7	24:1 $\omega$ x	0.0	0.5	20:5 $\omega$ 3 (EPA)	1.4	0.9			
25:0	1.6	0.7	26:1 $\omega$ x	0.0	0.8	22:5 $\omega$ 6	tr	0.1			
26:0	10.7	17.1				22:6 $\omega$ 3 (DHA)	tr	0.1			
27:0	1.2	0.9									
29:0	0.5	0.0									
30:0	2.9	1.5									
Subtotal	74.2	64.9		13.9	17.6		4.9	12.6		6.6	3.9
$\Sigma$ short-chain	22.1	14.7				$\Sigma$ short-chain	2.6	11.2			
$\Sigma$ long-chain	52.1	50.2				$\Sigma$ long-chain	2.3	1.4			



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x: unknown position of double bounds. br: branched-chain FA. tr: traces, LIN: linoleic acid, ALA:  $\alpha$ -linolenic acid, ARA: arachidonic acid, EPA: eicosapentaenoic acid, DHA: docosahexaenoic acid. <sup>a</sup> Sum of branched and linear FAs.

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**Supplementary Table 3** Fatty acid composition (% of total FAs) of seston, zooplankton and recent sediment sampled in May 2010 (mean  $\pm$  SD; n = 3).

FA	Seston			Zooplankton			Recent sediment		
	S <sub>0</sub>	S <sub>1</sub>	S <sub>2</sub>	S <sub>0</sub>	S <sub>1</sub>	S <sub>2</sub>	S <sub>0</sub>	S <sub>1</sub>	S <sub>2</sub>
<b>SAFA</b>									
12:0	0.4 $\pm$ 0.2	0.4 $\pm$ 0.1	0.4 $\pm$ 0.1	0.3 $\pm$ 0.1	0.2 $\pm$ 0.1	0.2 $\pm$ 0.0	0.3 $\pm$ 0.1	0.2 $\pm$ 0.1	0.4 $\pm$ 0.2
14:0	4.1 $\pm$ 1.8	5.3 $\pm$ 2.5	3.2 $\pm$ 0.4	6.0 $\pm$ 5.1	7.2 $\pm$ 5.3	3.6 $\pm$ 1.4	2.4 $\pm$ 0.6	3.1 $\pm$ 1.5	3.0 $\pm$ 1.7
16:0	41.6 $\pm$ 3.3	40.6 $\pm$ 3.6	40.7 $\pm$ 2.7	32.1 $\pm$ 1.3	34.6 $\pm$ 2.0	36.7 $\pm$ 2.5	35.6 $\pm$ 1.7	33.5 $\pm$ 4.0	34.0 $\pm$ 2.3
18:0	17.5 $\pm$ 0.4	17.1 $\pm$ 4.0	19.3 $\pm$ 2.5	8.7 $\pm$ 0.7	11.3 $\pm$ 1.3	9.3 $\pm$ 0.8	11.6 $\pm$ 1.2	12.0 $\pm$ 0.9	9.6 $\pm$ 1.6
20:0	1.6 $\pm$ 0.1	1.6 $\pm$ 0.4	1.9 $\pm$ 0.2	0.5 $\pm$ 0.1	0.8 $\pm$ 0.2	0.5 $\pm$ 0.1	0.9 $\pm$ 0.8	1.6 $\pm$ 0.1	1.0 $\pm$ 0.2
21:0	0.5 $\pm$ 0.1	0.6 $\pm$ 0.2	0.6 $\pm$ 0.0	0.1 $\pm$ 0.0	0.1 $\pm$ 0.1	0.1 $\pm$ 0.0	0.2 $\pm$ 0.2	0.3 $\pm$ 0.0	0.2 $\pm$ 0.1
22:0	3.1 $\pm$ 0.0	3.6 $\pm$ 1.8	4.0 $\pm$ 0.2	0.8 $\pm$ 0.3	1.4 $\pm$ 0.5	0.7 $\pm$ 0.1	1.5 $\pm$ 1.5	3.2 $\pm$ 1.1	1.6 $\pm$ 1.1
23:0	0.7 $\pm$ 0.0	0.9 $\pm$ 0.5	0.9 $\pm$ 0.1	0.2 $\pm$ 0.0	0.3 $\pm$ 0.1	0.1 $\pm$ 0.0	0.3 $\pm$ 0.3	0.4 $\pm$ 0.2	0.3 $\pm$ 0.2
24:0	1.2 $\pm$ 0.2	1.5 $\pm$ 1.0	1.6 $\pm$ 0.3	0.3 $\pm$ 0.1	0.5 $\pm$ 0.4	0.2 $\pm$ 0.1	0.9 $\pm$ 0.9	1.2 $\pm$ 0.6	0.8 $\pm$ 0.4
25:0	0.3 $\pm$ 0.1	0.5 $\pm$ 0.4	0.5 $\pm$ 0.2	0.1 $\pm$ 0.0	0.1 $\pm$ 0.1	0.1 $\pm$ 0.0	0.2 $\pm$ 0.2	0.2 $\pm$ 0.1	0.1 $\pm$ 0.1
26:0	0.3 $\pm$ 0.2	0.4 $\pm$ 0.4	0.4 $\pm$ 0.2	0.1 $\pm$ 0.1	0.2 $\pm$ 0.2	0.1 $\pm$ 0.1	0.5 $\pm$ 0.7	0.6 $\pm$ 0.5	0.5 $\pm$ 0.4
27:0	0.1 $\pm$ 0.0	0.1 $\pm$ 0.1	0.1 $\pm$ 0.1	0.0 $\pm$ 0.0	0.1 $\pm$ 0.0	0.0 $\pm$ 0.0	0.1 $\pm$ 0.1	0.1 $\pm$ 0.1	0.1 $\pm$ 0.1
28:0	0.5 $\pm$ 0.4	0.7 $\pm$ 0.8	0.9 $\pm$ 0.7	0.1 $\pm$ 0.1	0.3 $\pm$ 0.3	0.1 $\pm$ 0.1	1.2 $\pm$ 1.1	0.2 $\pm$ 0.1	0.4 $\pm$ 0.4
30:0	0.5 $\pm$ 0.6	0.7 $\pm$ 0.9	0.7 $\pm$ 0.8	0.1 $\pm$ 0.1	0.3 $\pm$ 0.4	0.1 $\pm$ 0.1	1.3 $\pm$ 1.4	0.5 $\pm$ 0.8	1.8 $\pm$ 3.0
32:0	0.2 $\pm$ 0.1	0.2 $\pm$ 0.2	0.3 $\pm$ 0.3	0.0 $\pm$ 0.0	0.1 $\pm$ 0.1	0.0 $\pm$ 0.0	0.1 $\pm$ 0.1	0.2 $\pm$ 0.2	0.1 $\pm$ 0.1

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4										
5	Subtotal	72.6 ± 3.8	74.3 ± 9.5	75.6 ± 2.5	49.3 ± 2.8	57.3 ± 7.0	51.8 ± 2.4	57.2 ± 2.0	57.5 ± 2.2	54.1 ± 4.5
6										
7	Σshort-chain	63.6 ± 5.0	63.4 ± 3.8	63.7 ± 5.0	47.1 ± 3.3	53.2 ± 8.5	49.8 ± 3.1	49.9 ± 2.8	48.8 ± 6.4	47.1 ± 3.9
8										
9	Σlong-chain	9.0 ± 1.6	10.9 ± 6.6	12.0 ± 2.7	2.2 ± 0.8	4.1 ± 2.2	2.0 ± 0.7	7.3 ± 4.4	8.8 ± 4.2	7.0 ± 5.8
10										
11	<b>MUFA</b>									
12										
13	15:1ωx	0.5 ± 0.2	0.4 ± 0.2	0.3 ± 0.2	0.2 ± 0.1	0.4 ± 0.3	0.5 ± 0.1	0.2 ± 0.1	0.4 ± 0.1	0.6 ± 0.5
14	16:1ω7	3.6 ± 1.3	4.1 ± 2.9	3.3 ± 0.8	4.1 ± 0.6	3.9 ± 1.5	5.2 ± 2.4	4.4 ± 0.3	4.8 ± 1.9	5.1 ± 1.7
15	16:1ωx	0.2 ± 0.3	0.1 ± 0.1	0.3 ± 0.2	0.4 ± 0.1	1.0 ± 0.5	1.2 ± 0.4	1.5 ± 0.3	1.5 ± 0.6	2.5 ± 0.5
16										
17	17:1ωx	0.3 ± 0.5	0.1 ± 0.1	0.0 ± 0.0	0.4 ± 0.1	0.3 ± 0.2	0.4 ± 0.3	0.6 ± 0.2	0.6 ± 0.2	1.2 ± 0.6
18										
19	18:1ω9	6.4 ± 1.6	2.3 ± 1.6	5.2 ± 0.7	10.0 ± 2.8	9.8 ± 2.1	9.4 ± 2.0	8.1 ± 0.9	10.6 ± 0.9	8.5 ± 0.7
20										
21	18:1ω7	2.2 ± 2.0	0.9 ± 0.7	1.5 ± 1.3	5.2 ± 1.5	4.0 ± 2.4	6.2 ± 2.5	6.5 ± 0.8	4.3 ± 1.3	4.2 ± 0.6
22										
23	18:1ωx	0.3 ± 0.4	1.7 ± 2.8	0.6 ± 1.1	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.1	0.4 ± 0.1	0.4 ± 0.1	2.9 ± 1.8
24										
25	20:1ωx	0.2 ± 0.1	0.3 ± 0.2	0.2 ± 0.0	0.4 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.3 ± 0.0	0.5 ± 0.3	0.4 ± 0.1
26										
27	20:1ω9	0.1 ± 0.1	0.0 ± 0.1	0.2 ± 0.0	0.1 ± 0.0	0.0 ± 0.0	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.0
28										
29	22:1ωx	0.1 ± 0.2	0.2 ± 0.4	0.0 ± 0.1	0.0 ± 0.1	0.0 ± 0.1	0.0 ± 0.1	0.7 ± 0.9	0.3 ± 0.3	0.1 ± 0.1
30	Subtotal	13.9 ± 3.2	10.2 ± 7.3	11.8 ± 1.8	21.1 ± 4.4	19.9 ± 5.7	23.5 ± 7.0	22.9 ± 1.5	23.5 ± 0.4	25.6 ± 3.2
31										
32	<b>PUFA</b>									
33										
34	16:xω3	0.1 ± 0.1	0.2 ± 0.2	ND	0.2 ± 0.1	0.1 ± 0.0	0.2 ± 0.1	0.4 ± 0.1	0.3 ± 0.1	0.3 ± 0.0
35	16:3ω3	0.1 ± 0.1	0.1 ± 0.1	ND	0.3 ± 0.1	0.2 ± 0.1	0.5 ± 0.0	0.3 ± 0.0	0.4 ± 0.2	0.7 ± 0.2
36	16:2ωx	0.0 ± 0.1	0.1 ± 0.1	ND	0.1 ± 0.0	0.2 ± 0.0	0.1 ± 0.1	ND	ND	ND
37										
38	18:3ω6	ND	ND	ND	0.3 ± 0.1	0.1 ± 0.0	0.2 ± 0.1	0.2 ± 0.0	0.2 ± 0.1	0.1 ± 0.0
39										
40										
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18:2 $\omega$ 3	0.5 $\pm$ 0.2	0.3 $\pm$ 0.2	0.1 $\pm$ 0.2	1.9 $\pm$ 0.6	1.0 $\pm$ 0.4	1.5 $\pm$ 1.1	0.8 $\pm$ 0.2	0.5 $\pm$ 0.2	0.4 $\pm$ 0.1	
18:2 $\omega$ 6 (LIN)	1.5 $\pm$ 1.0	0.9 $\pm$ 0.6	0.8 $\pm$ 0.2	6.1 $\pm$ 1.7	5.4 $\pm$ 1.0	2.9 $\pm$ 0.7	5.7 $\pm$ 0.9	4.6 $\pm$ 1.5	3.4 $\pm$ 0.2	
18:3 $\omega$ 3 (ALA)	1.7 $\pm$ 1.2	2.9 $\pm$ 3.5	1.4 $\pm$ 0.8	7.6 $\pm$ 2.5	4.6 $\pm$ 1.2	6.7 $\pm$ 1.7	3.5 $\pm$ 0.4	3.7 $\pm$ 1.8	4.1 $\pm$ 1.5	
18:2 $\omega$ x	0.3 $\pm$ 0.1	0.8 $\pm$ 0.5	0.7 $\pm$ 0.4	1.1 $\pm$ 1.0	0.4 $\pm$ 0.3	0.7 $\pm$ 0.2	0.4 $\pm$ 0.1	0.4 $\pm$ 0.2	0.4 $\pm$ 0.1	
20:4 $\omega$ 6 (ARA)	0.1 $\pm$ 0.1	ND	0.0 $\pm$ 0.1	1.4 $\pm$ 0.3	1.1 $\pm$ 0.1	0.6 $\pm$ 0.1	0.2 $\pm$ 0.1	0.2 $\pm$ 0.1	0.2 $\pm$ 0.1	
20:5 $\omega$ 3 (EPA)	0.0 $\pm$ 0.1	ND	0.0 $\pm$ 0.0	2.4 $\pm$ 0.7	1.6 $\pm$ 0.6	2.1 $\pm$ 1.1	0.2 $\pm$ 0.1	0.4 $\pm$ 0.1	0.3 $\pm$ 0.1	
20:2 $\omega$ x	ND	ND	ND	0.6 $\pm$ 0.1	0.4 $\pm$ 0.1	0.2 $\pm$ 0.1	ND	ND	0.1 $\pm$ 0.1	
20:3 $\omega$ 3	ND	ND	ND	0.2 $\pm$ 0.1	0.1 $\pm$ 0.1	0.3 $\pm$ 0.0	0.1 $\pm$ 0.1	0.1 $\pm$ 0.1	0.1 $\pm$ 0.1	
20:3 $\omega$ x	ND	ND	ND	0.2 $\pm$ 0.0	0.1 $\pm$ 0.1	0.1 $\pm$ 0.1	0.0 $\pm$ 0.0	0.1 $\pm$ 0.1	0.1 $\pm$ 0.1	
22:5 $\omega$ 6	ND	ND	ND	0.3 $\pm$ 0.1	0.2 $\pm$ 0.1	0.2 $\pm$ 0.1	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0	
22:6 $\omega$ 3 (DHA)	ND	ND	ND	1.3 $\pm$ 0.4	0.8 $\pm$ 0.5	1.0 $\pm$ 0.7	0.1 $\pm$ 0.1	0.0 $\pm$ 0.1	0.1 $\pm$ 0.0	
22:5 $\omega$ 3	ND	ND	ND	0.2 $\pm$ 0.1	0.2 $\pm$ 0.1	0.1 $\pm$ 0.0	ND	ND	ND	
Subtotal	4.2 $\pm$ 2.2	5.3 $\pm$ 4.7	3.1 $\pm$ 1.1	24.1 $\pm$ 3.1	16.6 $\pm$ 2.0	17.3 $\pm$ 5.5	12.0 $\pm$ 1.4	10.9 $\pm$ 4.1	10.2 $\pm$ 1.6	
$\Sigma$ short-chain	4.1 $\pm$ 2.0	5.3 $\pm$ 4.7	3.0 $\pm$ 1.0	17.6 $\pm$ 2.3	12.1 $\pm$ 0.9	12.7 $\pm$ 3.3	11.3 $\pm$ 1.5	10.0 $\pm$ 3.8	9.3 $\pm$ 1.9	
$\Sigma$ long-chain	0.1 $\pm$ 0.2	0.0 $\pm$ 0.0	0.1 $\pm$ 0.1	6.5 $\pm$ 0.9	4.6 $\pm$ 1.3	4.5 $\pm$ 2.2	0.8 $\pm$ 0.1	0.9 $\pm$ 0.3	0.9 $\pm$ 0.3	
<b>BACTFA</b>										
14:0 br	0.2 $\pm$ 0.1	0.1 $\pm$ 0.0	0.3 $\pm$ 0.1	0.2 $\pm$ 0.1	0.2 $\pm$ 0.0	0.2 $\pm$ 0.1	0.3 $\pm$ 0.1	0.3 $\pm$ 0.1	0.3 $\pm$ 0.2	
15:0 br	1.9 $\pm$ 0.6	2.3 $\pm$ 1.4	1.8 $\pm$ 0.2	1.8 $\pm$ 0.2	1.5 $\pm$ 0.2	2.2 $\pm$ 0.3	2.0 $\pm$ 0.3	2.3 $\pm$ 1.3	4.0 $\pm$ 1.8	
15:0	2.0 $\pm$ 0.6	2.0 $\pm$ 0.1	1.9 $\pm$ 0.2	0.9 $\pm$ 0.1	1.3 $\pm$ 0.7	1.2 $\pm$ 0.2	1.4 $\pm$ 0.3	1.5 $\pm$ 0.4	1.9 $\pm$ 0.6	
16:0 br	0.2 $\pm$ 0.0	0.2 $\pm$ 0.2	0.2 $\pm$ 0.2	0.3 $\pm$ 0.1	0.2 $\pm$ 0.2	0.3 $\pm$ 0.1	0.5 $\pm$ 0.0	0.3 $\pm$ 0.1	0.5 $\pm$ 0.1	

17:0 br	1.0 ± 0.2	1.1 ± 0.4	1.0 ± 0.4	0.7 ± 0.1	0.8 ± 0.3	1.2 ± 0.7	1.5 ± 0.9	1.2 ± 0.0	1.2 ± 0.2
17:0	3.4 ± 0.1	4.2 ± 0.4	3.8 ± 0.1	1.6 ± 0.1	2.0 ± 0.7	2.1 ± 0.7	2.1 ± 1.0	2.1 ± 0.2	1.8 ± 0.0
19:0	0.4 ± 0.2	0.3 ± 0.0	0.4 ± 0.1	0.1 ± 0.0	0.1 ± 0.1	0.1 ± 0.0	0.2 ± 0.0	0.3 ± 0.2	0.3 ± 0.1
Subtotal	9.3 ± 1.2	10.3 ± 2.7	9.5 ± 0.1	5.5 ± 0.1	6.1 ± 1.5	7.5 ± 1.0	7.9 ± 1.1	8.1 ± 1.7	10.1 ± 2.4

ND non detected. x: unknown position of double bounds. br: branched-chain FA

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