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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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50 **Keywords:** sediment biodegradability, organic matter, lipid biomarkers, stoichiometry,
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52 nutrient release, mesocosms, pelagic compartments
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57 **Abbreviated title:** Influence of lake sediment on pelagic compartments
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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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17 29 2. In a five-months experiment, we studied the influence of two different sediments
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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.
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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
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52 45 in the water column than S_1 . As a result, S_2 treatment induced an increase in seston
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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
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5 48 zooplankton. Moreover, neither S₁ nor S₂ induced changes in the sedimentation rates,
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7 49 elemental and lipid compositions, and potential biodegradability of recent sediments.
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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
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14 52 or omnivorous fish.
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17 53 5. Our results might explain the efficiency of biomanipulations for improving water
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19 54 quality of eutrophic lakes despite potential nutrient release from sediment. Finally, our
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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 (CO₂ 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

1
2
3 83 the degradation state and the biodegradability of the sediment, due to the large range of
4
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
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9
10 86 dissolved organic matter (DOM; Reynolds, 1996; Klump *et al.*, 2009), which will support
11
12 87 both primary and bacterial productions (del Giorgio & Cole, 1998). As phytoplankton and
13
14 88 bacteria are the basal resources for aquatic food webs, release of nutrients and OM from
15
16 89 sediment might strongly impact food-web communities via a bottom-up forcing. Whereas the
17
18 90 bottom-up effects of inorganic nutrients or light on aquatic ecosystems are well known (see
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20 91 for example, Urabe *et al.*, 2002; Cebrian & Lartigue, 2004; Hessen *et al.*, 2004; Dickman *et*
21
22 92 *al.*, 2006; Spivak *et al.*, 2007), those of SOM have been more rarely studied. In natural lakes,
23
24 93 it has been shown that the temporal dynamics of bacterioplankton communities are strongly
25
26 94 dependent on the DOM origin and amount (Berdjeb *et al.*, 2011), suggesting a bottom-up
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28 95 forcing from DOM. As DOM can originate from sediment biodegradation, one may wonder if
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30 96 sediment could be responsible for a bottom-up control for the whole food web, through the
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32 97 availability of resources for basal organisms (e.g. phytoplankton and bacterioplankton).
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34 98 Moreover, as the sediment biodegradability seems to be linked to its OM composition (Allard
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36 99 *et al.*, 2011; Danger *et al.*, 2012; Harrault *et al.*, 2012), an interesting issue is whether
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38 100 different sediment compositions could lead to different bottom-up forcing on aquatic food
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40 101 webs.
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46 102 In this paper, we report results of a lake mesocosm study examining how the presence
47
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
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54 106 (S_1), and enclosures with carbon-rich sediment (S_2). Sediment S_1 was taken in the bottom of
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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
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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_2 than in S_1 (Table
10
11 112 1). This strongly suggested that S_2 was much more biodegradable than S_1 . Indeed, S_1 had been
12
13 113 formed over several decades in a shallow gravel-pit lake with a clear tendency to
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15 114 oligotrophication since the end of its exploitation (Garnier, 1992). In contrast, the
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17 115 composition of S_2 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*
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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.*
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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 m³ (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 (S₀). Each treatment was replicated
144 eight times. The first sediment (S₁) was collected randomly in Lake Créteil with an Uwitec
145 bottom sampler and consisted of a dark grey sandy material. The second sediment (S₂) was
146 collected in enclosures used in a previous study (Danger *et al.*, 2008, 2012). S₁ and S₂ were
147 chosen to simulate contrasted bottom-up treatments in enclosures. Both autochthonous and
148 allochthonous sources contributed to S₁. This sediment had been accumulated and exposed to
149 microbial and benthic reworking over several decades. In contrast, S₂ 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), α - and β -hydroxy fatty acid (OH-FA) and stanol contents
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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.
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12 159 Trays (2×1.5 m), filled with ca. 70 L of homogenized sediment (ca. 2.4 cm depth layer),
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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
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18 162 enclosures. To allow sedimentation of suspended material in S₁ and S₂ enclosures, we started
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20 163 samplings on February 2010.
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28 165 Orthophosphates, ammonium and nitrates analyses
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33 167 Orthophosphate, ammonium and nitrate concentrations were determined for water sampled in
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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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41 170
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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- μm 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 μm) in order to gather seston (particulate matter between 0.7 and
18
19 184 50 μm). Filters were dried overnight at 60°C and weighted to determine seston biomass. Dry
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21 185 filters were stored in the dark at room temperature until elemental and lipid analyses.
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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- μm
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- μm 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 μm), and dried overnight at 60°C. Dry
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36 192 zooplankton was ground and stored in the dark at room temperature until elemental and lipid
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38 193 analyses.
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46 195 Zooplankton counting
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52 197 Zooplankton composition was determined in February and May 2010 by filtering 60 L of
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54 198 water at different depths and locations in three enclosures of each treatment with a 12-L
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56 199 Schindler plankton trap equipped with a 50- μm 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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21 207 Recently deposited sediments were sampled in May and June 2010. Sedimentation rates were
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23 208 determined using six sediment traps deployed in each enclosure. Traps consisted of 5-cm
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25 209 diameter and 30-cm long PVC tubes, suspended at 4 m depth. Suspended 0.5 m above the
26
27 210 bottom of the enclosures, sediment traps were preserved for bottom sediment resuspension.
28
29 211 Traps were deployed for 7- to 9-day intervals. Material collected from the six traps was
30
31 212 pooled in a collection flask and allowed to sediment overnight at 4°C. The supernatant and
32
33 213 zooplankton therein was removed. Sediment was freeze-dried, weighted, ground and stored in
34
35 214 the dark at room temperature until analyses. Sedimentation rates were calculated as the mass
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37 215 of dry matter divided by the duration of the trap deployment and the total surface of the six
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39 216 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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53 220 Carbon and nitrogen contents of dried samples were determined using a CHN elementary
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55 221 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
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5 223 carbon (IC) from sediment by successive additions of 1 M HCl (Hedges & Stern, 1984).
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11 225 Sugar and protein colorimetric assays of sediments
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17 227 Freeze-dried sediments were extracted with H₂O at 100°C for 2 h. The mixture was filtered
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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 H₂O 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
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27 232 method of Lowry with bovine serum albumin as standard (Lowry *et al.*, 1951). Sugar and
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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 S₁ and S₂, analyses of lipids were carried out on three
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47 239 replicates of each treatment for seston, zooplankton and recent sediment sampled in May
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49 240 2010.
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52 241 The filter with collected seston was extracted with a dichloromethane
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54 242 (DCM)/methanol (MeOH) (2/1, v/v) mixture at room temperature for 18 h. The mixture was
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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
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5 245 saponified extract was brought to 2 by addition of 6 M HCl and lipids extracted with DCM.
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7 246 The organic phase was washed with deionized water until neutral pH, dried over Na₂SO₄ and
8
9 247 DCM removed under reduced pressure. Saponified lipids were treated with ca. 4 M HCl in
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11 248 MeOH at 80°C for 1 h to convert carboxyl groups into their methyl ester derivatives.
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13 249 Esterified extract was then treated with a mixture of anhydrous pyridine/N,O-
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15 250 Bis(trimethylsilyl)trifluoroacetamide (BSTFA) (10/1, v/v) for 10 min at 60°C to convert
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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
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25 255 RTX5SilMS (30 m, i.d. 0.25 mm, film thickness 0.5 µm) with helium as carrier gas. The GC
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27 256 oven was programmed from 100 to 320°C at 4°C min⁻¹. Unsaturated fatty acids were analysed
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29 257 using gas chromatography-flame ionization detector (GC-FID) and identified by comparison
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31 258 with standards (Larodan, Malmö, Sweden) using fused silica column coated with DB23 (60
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33 259 m, i.d. 0.25 mm, film thickness 0.25 µm) with helium as carrier gas. The GC oven was
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35 260 programmed from 100 to 170°C at 6.5°C min⁻¹, then to 215°C at 2.75°C min⁻¹ and to 230°C at
36
37 261 40°C min⁻¹. 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
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43 264 of individual compounds within the total lipids. Dried zooplankton samples were extracted
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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
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5 268 chloroform/MeOH (2/1, v/v) mixture for 2 h at 80°C. Lipid extracts were analysed as
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7 269 described for seston.
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13 271 Statistical analyses
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19 273 Statistical analyses were performed using R software (www.r-project.org). A linear mixed-
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21 274 effects model (LME) with sediment treatment, time and cross-effect as explanatory variables
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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 (S₀, S₁ and S₂) 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
30
31 279 sediment (May and June), and orthophosphate, ammonium and nitrate concentrations of water
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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
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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
56
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,
4
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 S₂ enclosures was significantly higher
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36 303 than those from S₀ and S₁ 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
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43 306 concentrations)/orthophosphates ratio (IN/P, Table 2). Despite this absence of significant
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45 307 effect, a IN/P ratio from S₂ enclosures (5) much lower than that from both S₀ and S₁ (16 and
46
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 S₂ enclosures was significantly higher than that in S₁ enclosures. In
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3 311 contrast DOC concentration in S₀ and S₁ enclosures did not differ significantly and DOC
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5 312 concentration in S₂ enclosures did not differ significantly from that in S₀ 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
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24 319 average, seston biomass in S₀ and S₁ enclosures did not differ significantly but were lower
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26 320 than those from S₂ 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 S₀ and S₁ enclosures but was lower in S₀
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36 324 enclosures compared to S₂ enclosures, without any time effect (Fig. 2b). The C/N ratio of
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38 325 seston from S₀ treatment was higher than that of seston from S₁ and S₂ 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 S₀ and S₁ enclosures
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7 335 but was higher in S₂ enclosures than in S₀ and S₁ ones, especially in March and April (Fig.
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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
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14 338 treatments since only the concentration of Chydoridae was significantly higher in the S₂
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16 339 enclosures than in S₀ and S₁ ones (Table 4). On average, the number of individuals was lower
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18 340 in February than in May, especially for nauplii of copepods (7.3 ± 3.4 and 180.9 ± 77.7
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20 341 individuals L⁻¹, for February and May, respectively. C and N contents and C/N ratio of
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22 342 zooplankton from S₀, S₁ and S₂ treatments did not differ significantly (Table 2). The C
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24 343 content of zooplankton slightly increased from February to March and then slightly decreased
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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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49 352 Sediment treatments and time did not significantly affect the sedimentation rates (Fig.
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51 353 1c), although sedimentation rates tended to be higher in S₁ and S₂ than in S₀ enclosures.

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54 354 Sediment treatments affected the C, OC and N contents of recent sediments since
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56 355 those from S₁ enclosures were lower than those from S₀ and S₂ ones (Fig. 4a and 4b). The

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3 356 C/N ratio of recent sediment from S₁ treatment was higher than that from S₀ and S₂ 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
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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 S₂ (4.7 ± 1.7 % of total
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33 368 lipids) enclosures than in recent sediments from S₀ (1.8 ± 0.7 % of total lipids, Tukey: $p =$
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35 369 0.033) and S₁ (2.0 ± 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 ≥ 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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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 S₂ 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 S₂ enclosures (direct observations). Moreover, a higher
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29 412 microbial mineralisation of the highly biodegradable S₂ 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 S₀ and S₁ enclosures, and a reduction of such P-limitation, accompanied by a
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37 416 higher primary productivity, in S₂ 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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48 419 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 S₁ and S₀ treatments. This absence of
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52 421 significant difference between S₁ and S₀ 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 S₁ 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 S₂
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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 S₂ 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 S₂ enclosures. The observed increase in the abundance of
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43 442 Chydoridae in the S₂ 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 S₂ 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 S₂ treatment is also supported by the
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10 452 elemental composition of seston. The higher N content of seston observed in S₂ treatment,
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12 453 compared to S₀ and S₁ ones, suggests a release of N from this “labile” sediment. The lower
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14 454 C/N ratio of seston from S₂ 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
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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 S₂ 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 S₂ treatment was similar to that from
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15 503 S₀ treatment. Surprisingly, the elemental composition of recent sediment from S₁ treatment
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17 504 differed from that of recent sediment from S₀ and S₂ 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 S₂ 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
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23 555 effects identified by such manipulations (Spivak & Vanni, 2011). However, it should be kept
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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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46
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48
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 ^a	OC ^a	N ^a	OC/N	Sugars ^a	Proteins ^a	PUFAs ^b
S ₁	5.7	0.9	0.1	9.0	0.1	0.1	4.9
S ₂	23.1	9.7	2.4	4.0	0.7	1.5	12.6

^a % of dry weight

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

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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
Recent sediment											
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	0.0001	2, 21	14.22	< 0.001	0.43	< 0.0001	0.03	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	0.04	0.37	< 0.001	0.17	0.95
OC ^c	23.9 ± 2.6	14.4 ± 5.8	27.3 ± 2.2	0.02	2	8.93	0.05	0.58	0.01	-	-
OC/N ^c	8.9 ± 1.1	9.6 ± 5.8	8.0 ± 0.8	0.94	2	0.06	-	-	-	-	-
Sugars ^c	3.3 ± 0.3	2.7 ± 1.2	3.2 ± 0.8	0.36	2	1.22	-	-	-	-	-
Proteins ^c	2.2 ± 0.3	1.8 ± 0.6	3.2 ± 0.9	0.78	2	0.25	-	-	-	-	-

^a Degrees of Freedom^b Inorganic Nitrogen (sum of ammonium and nitrates)/Phosphates ratio^c 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				OAs	OH-FAs	CHLOs
	Total	SAFA	MUFA	PUFA	BACTFA	Total	C ₂₇ Δ^5	C ₂₉ Δ^5	Stanols	Total	Total	Total
Seston	75.4 \pm 9.3	74.2 \pm 5.4	11.9 \pm 4.4	4.2 \pm 2.8	9.7 \pm 1.5	5.2 \pm 2.0	23.5 \pm 10.8	57.2 \pm 16.0	0.9 \pm 0.6	14.5 \pm 6.9	4.2 \pm 1.2	0.5 \pm 0.1
Zooplankton	87.3 \pm 7.0	52.8 \pm 5.3	21.5 \pm 5.3	19.4 \pm 4.9	6.4 \pm 1.2	6.0 \pm 4.6	68.1 \pm 11.0	21.5 \pm 11.0	1.2 \pm 0.8	3.9 \pm 2.9	1.3 \pm 0.6	1.3 \pm 0.8
Recent sediment	75.0 \pm 7.7	56.2 \pm 3.2	24.0 \pm 2.2	11.1 \pm 2.5	8.7 \pm 1.9	6.8 \pm 4.1	34.1 \pm 7.1	43.9 \pm 9.5	2.3 \pm 0.9	10.5 \pm 3.7	4.6 \pm 1.1	2.8 \pm 1.7

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, OAs: *n*-alkanols, OH-FAs: sum of α -, β - and ω -hydroxy acids, CHLOs: chlorophyll-derived compounds.

Table 4 Mean specific composition of zooplankton communities (Individual L⁻¹) 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 ₀	S ₁	S ₂	P values	DF ^a	F values	S ₀ -S ₁	S ₀ -S ₂	S ₁ -S ₂		
Rotifers	2.8 ± 2.8	1.7 ± 1.2	7.2 ± 15.4	0.86	2, 6	0.15	-	-	-	0.23	0.002
Cladocerans											
<i>Daphnia</i>	23.4 ± 22.2	11.4 ± 13.7	3.4 ± 4.2	0.11	2, 6	3.27	-	-	-	0.066	0.24
<i>Ceriodaphnia</i>	1.1 ± 2.2	0.1 ± 0.3	0.0 ± 0.1	0.18	2, 6	2.33	-	-	-	0.0008	0.0054
<i>Bosminidae</i>	1.3 ± 1.7	2.2 ± 3.9	2.2 ± 4.4	0.95	2, 6	0.05	-	-	-	< 0.0001	0.94
Chydoridae	5.6 ± 6.2	2.8 ± 3.7	16.5 ± 23.3	0.016	2, 6	8.87	0.76	0.02	< 0.005	< 0.0001	< 0.0001
Copepods											
Cyclopids	13.0 ± 14.0	7.5 ± 11.0	12.1 ± 12.5	0.33	2, 6	1.34	-	-	-	< 0.0001	0.67
Calanoids	16.6 ± 10.8	10.3 ± 16.5	15.7 ± 18.6	0.41	2, 6	1.04	-	-	-	0.0001	0.0008
Nauplii	111.9 ± 111.5	61.0 ± 65.1	99.2 ± 124..0	0.11	2, 6	2.22	-	-	-	0.066	0.24

^a Degrees of Freedom

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9 3 Figure 1: Seasonal variations of seston (a) and zooplankton (b) biomass and sedimentation
10 4 rates (c) (mean \pm SE). White, grey and black bars represent the control treatment (S₀), S₁ and
11 5 S₂ treatments respectively. Significant effects of time are represented by different letters.
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19 7 Figure 2: Seasonal variations of carbon (a) and nitrogen (b) contents and C:N ratio (c) of the
20 8 seston (mean \pm SE). White, grey and black bars represent the control treatment (S₀), S₁ and S₂
21 9 treatments respectively. Significant effects of time are represented by different letters.
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29 11 Figure 3: Seasonal variations of carbon (a) and nitrogen (b) contents and C:N ratio (c) of the
30 12 zooplankton (mean \pm SE). White, grey and black bars represent the control treatment (S₀), S₁
31 13 and S₂ treatment respectively. Significant effects of time are represented by different letters.
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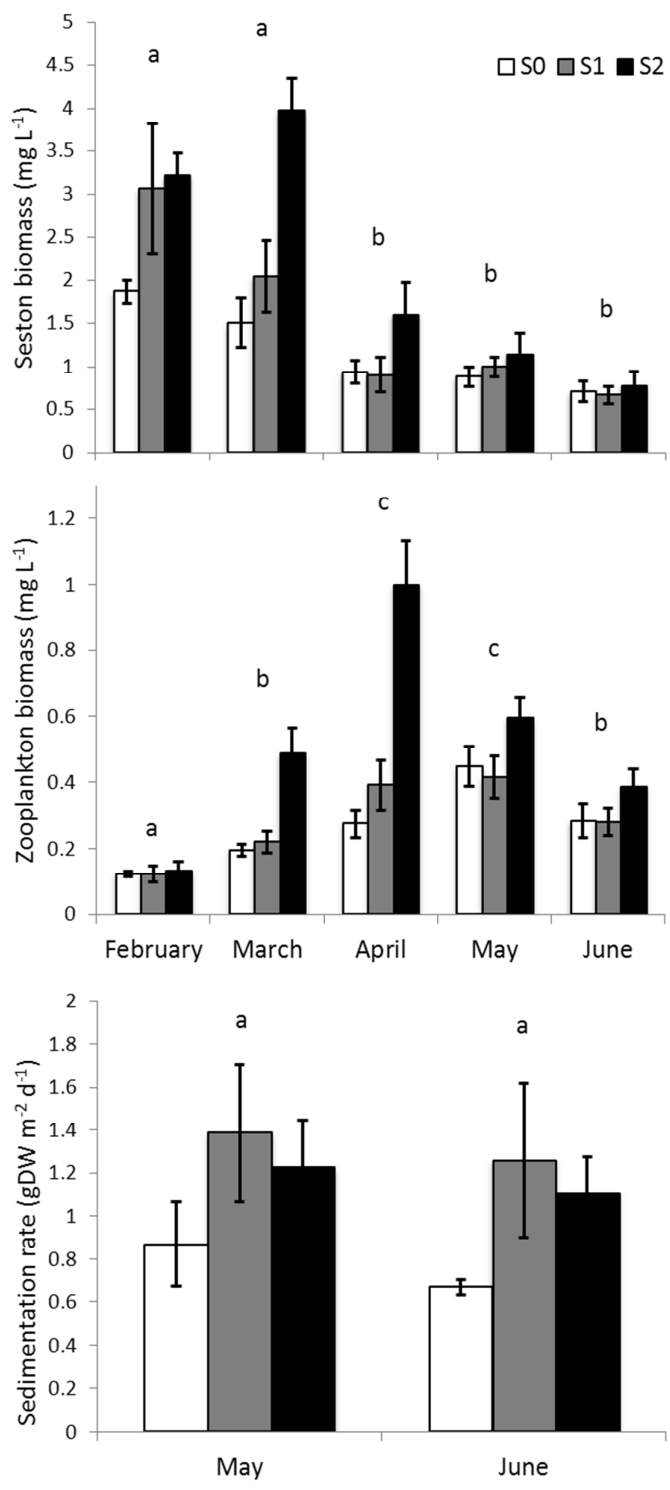
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39 15 Figure 4: Variations of carbon (a) and nitrogen (b) contents and C:N ratio (c) of the short-term
40 16 sediment (mean \pm SE). White, grey and black bars represent the control treatment (S₀), S₁ and
41 17 S₂ treatment respectively. Significant effects of time are represented by different letters.
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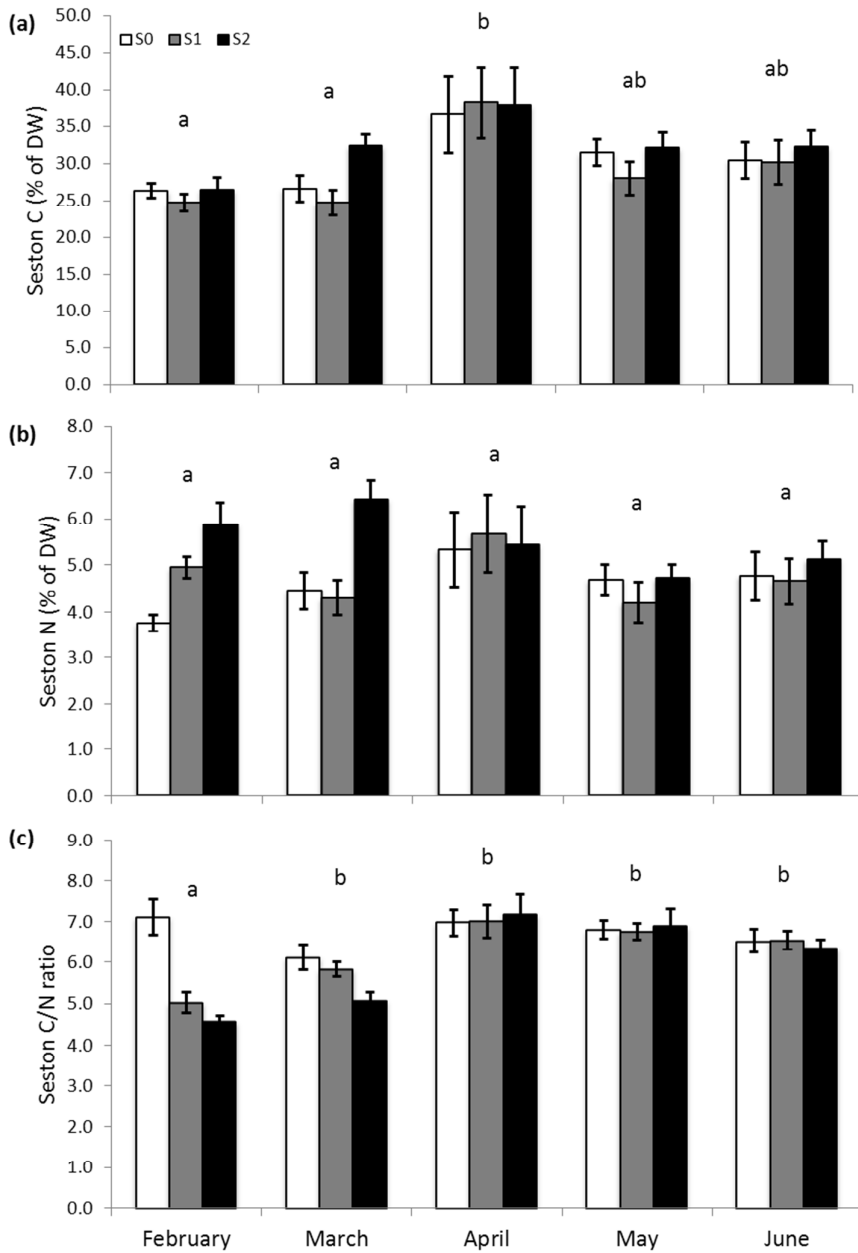
19 Figure 1



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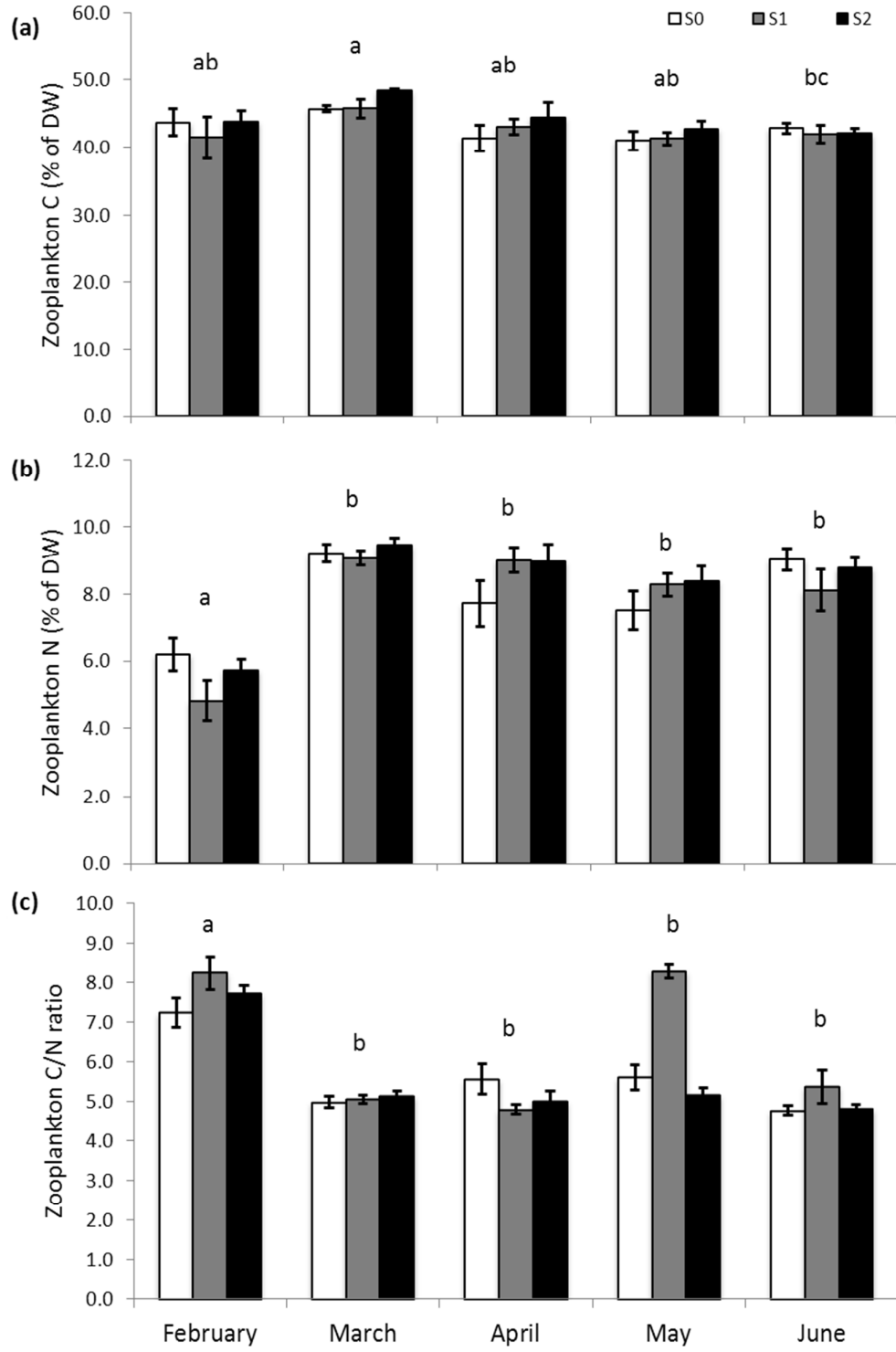


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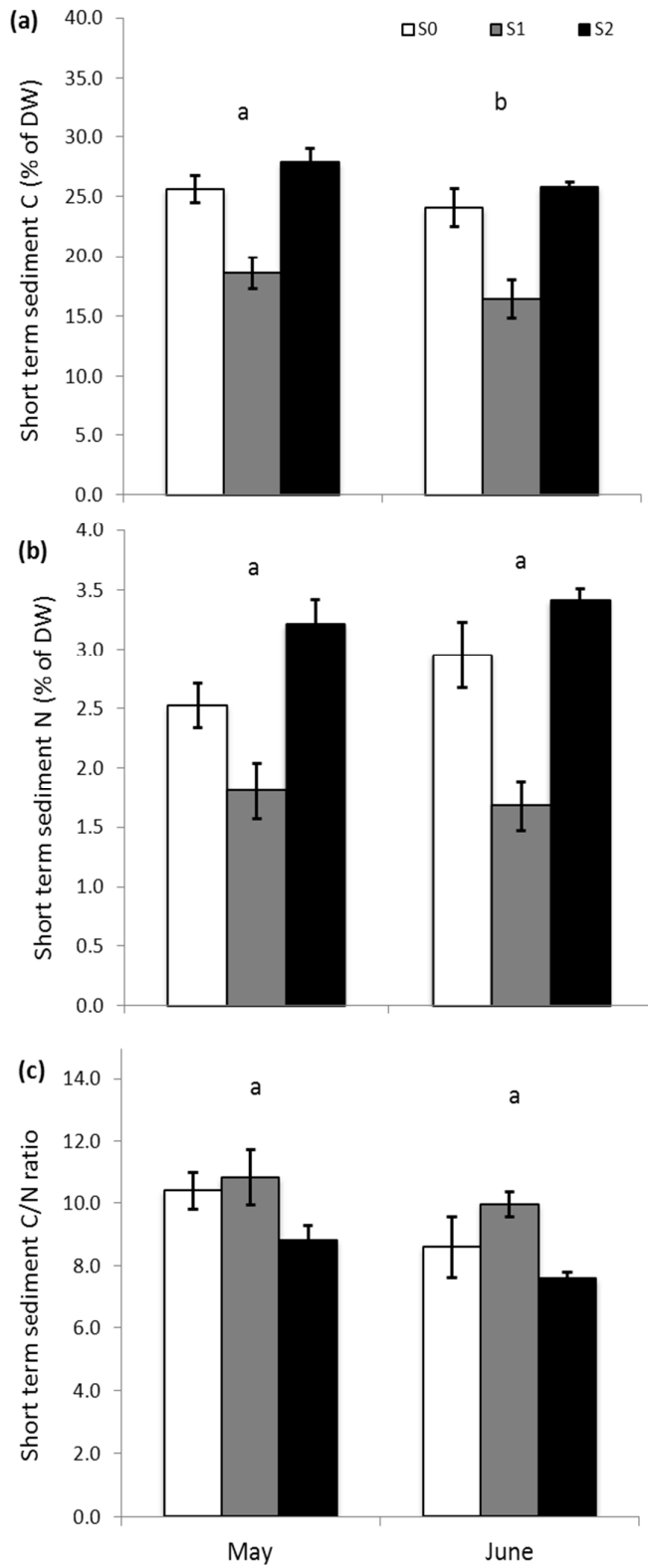
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Supplementary Table 1 Lipid composition of the initial sediments. Total was expressed as % of total lipids. Sub-classes of fatty acids, sterols, alkanols and hydroxy acids were expressed as % of total fatty acids, sterols, alkanols and hydroxy acids,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

	FAs					Sterols				OHs			OH-FAs			CHLOs
	Total	SAFA	MUFA	PUFA	BACTFA	Total	$\Sigma\Delta^5$	$\Sigma\Delta^7$	stanols	Total	SC	LC	Total	$\alpha + \beta$	ω	Total
S ₁	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 ₂	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 Δ^5 -sterols, $\Sigma\Delta^7$: sum of Δ^7 -sterols, OHs: alkanols, SC: short-chain alkanols (carbon number ≤ 18), LC: long-chain alkanols (carbon number ≥ 20), OH-FAs: hydroxy acids, $\alpha + \beta$: sum of α - and β -hydroxy acids, ω : ω -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. α - and β -OH-FAs (Cranwell, 1981), and stanols, the saturated homologues of sterols (Gaskell & Eglinton, 1975).

The high relative abundance of Δ^7 -sterols in S₂ is consistent with the high contribution of Chlorophyceae to S₂ 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, Δ^7 -sterols were not detected in S₁. 24-methyl- and 24-ethyl-cholest-5-enols, present in high amounts in S₁, are abundant in algae and in vascular plants as well. So, the sterol distribution of S₁ cannot allow to discriminate between autochthonous and allochthonous inputs. The higher relative abundances of chlorophyll-derived compounds in S₂ than in S₁ corroborate also a higher phytoplanktonic contribution to S₂. 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 S₁ than in S₂ suggest that S₁ was in a more advanced degradation state than S₂. This is supported by higher amounts of α - and β -OH-FAs and stanols in S₁ than in S₂. Indeed, α - and β -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 S₁ and S₂ (n = 1).

SAFA	S ₁	S ₂	MUFA	S ₁	S ₂	PUFA	S ₁	S ₂	BACT	S ₁	S ₂
14:0	1.3	0.8	16:1 ω x	tr	tr	16:3 ω 3	ND	0.4	14:0 br	0.0	0.2
16:0	12.4	10.7	16:1 ω 7	5.1	1.7	16:2 ω x	ND	0.9	15:0 ^a	2.9	2.0
18:0	8.4	3.2	18:1 ω 9	4.8	9.5	18:3 ω 6	0.0	0.3	16:0 br	0.4	0.4
20:0	3.2	1.0	18:1 ω 7	3.0	2.8	18:4 ω 3	0.0	0.3	17:0 ^a	3.2	1.3
21:0	0.7	0.2	18:1 ω x	0.0	0.7	18:2 ω 6 (LIN)	1.0	1.6			
22:0	5.4	6.1	20:1 ω 9	0.9	1.2	18:3 ω 3 (ALA)	1.6	7.8			
23:0	1.8	0.5	22:1 ω x	0.0	0.2	20:4 ω 6 (ARA)	0.9	0.3			
24:0	12.6	9.7	24:1 ω x	0.0	0.5	20:5 ω 3 (EPA)	1.4	0.9			
25:0	1.6	0.7	26:1 ω x	0.0	0.8	22:5 ω 6	tr	0.1			
26:0	10.7	17.1				22:6 ω 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
Σ short-chain	22.1	14.7				Σ short-chain	2.6	11.2			
Σ long-chain	52.1	50.2				Σ 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: α -linolenic acid, ARA: arachidonic acid, EPA: eicosapentaenoic acid, DHA: docosahexaenoic acid. ^a 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 ₀	S ₁	S ₂	S ₀	S ₁	S ₂	S ₀	S ₁	S ₂
SAFA									
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

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	
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	
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	
MUFA										
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	
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	
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	
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	
18:1ω9	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	
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	
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	
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	
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	
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	
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	
PUFA										
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	
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	
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	
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	

18:2 ω 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 ω 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 ω 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 ω 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 ω 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 ω 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 ω 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 ω 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 ω 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 ω 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 ω 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 ω 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	
Σ 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	
Σ 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	
BACTFA										
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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