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Florian Mermillod-Blondin, Pierre Marmonier, Mélissa Tenaille, Damien Lemoine, Michel Lafont, Ross Vander Vorste, Laurent Simon, Laurence Volatier

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1 TITLE: Bottom-up processes control benthic macro-invertebrate communities and food web
2 structure of fishless artificial wetlands

3
4 Authors: Florian Mermillod-Blondin F.^{1*}, Pierre Marmonier¹, Mélissa Tenaille¹, Damien G.
5 Lemoine¹, Michel Lafont¹, Ross Vander Vorste², Laurent Simon¹, Laurence Volatier¹

6
7 ¹ UMR 5023 LEHNA, Université de Lyon, CNRS, Université Claude Bernard Lyon 1, ENTPE, 6
8 rue Raphaël Dubois, 69622 Villeurbanne, France.

9 ² Department of Biology, University of Wisconsin, WI 54601, La Crosse, USA.

10 * Corresponding author: Florian Mermillod-Blondin

11 UMR 5023 LEHNA, Université de Lyon, CNRS, Université Claude Bernard Lyon 1, ENTPE, 6
12 rue Raphaël Dubois, 69622 Villeurbanne.

13 E-mail: florian.mermillod-blondin@univ-lyon1.fr

14 Phone number: (33) 4 72 43 13 64

15 Fax number: (33) 4 72 43 11 41

16

17 Abstract

18 In freshwater environments, the relative contributions of top-down and bottom-up effects on
19 invertebrate communities in relation to productivity are largely ecosystem dependent. Artificial
20 wetlands are increasingly developed to compensate for the loss of natural wetlands however their
21 trophic processes remain poorly studied. The present study aimed to evaluate the respective
22 contributions of bottom-up and top-down processes in structuring benthic food webs of three
23 artificial wetlands with varying levels of benthic primary productivity. We found that phototrophic-
24 based food webs in our artificial wetlands were controlled from the bottom-up by primary
25 productivity and algal biomass developing at the water-sediment interface. No significant top-
26 down-control of herbivore species by invertebrate predators was detected even in the wetland with
27 the highest productivity. Increased richness of invertebrate grazers and scrapers with benthic
28 primary productivity and algal biomass might have dampened the trophic cascade from predators
29 to primary producers. In contrast with the phototrophic-based food web, analyses performed on the
30 detritus-based food web showed that deposit-feeder invertebrate abundance was not correlated with
31 the quantity of organic matter in sediments, suggesting a weak bottom-up effect of sedimentary
32 organic matter content on deposit-feeders. More surprisingly, deposit-feeders, especially aquatic
33 oligochaetes, seemed to influence the detritus-based food webs by stimulating organic matter
34 processing and bacterial growth through bioturbation. The present study highlighted the occurrence
35 of contrasting trophic processes between phototrophic-based and detritus-based food webs which
36 can have implications on ecosystem functions, such as nutrient cycling and energy fluxes.

37
38 Keywords: functional feeding groups, benthic food webs, invertebrates, benthic biofilm, algae, bacteria,
39 trophic relationships

40 Introduction

41 The relative importance of bottom-up and top-down controls on the structure of communities has
42 long been an intense debate (Oksanen et al. 1981; Hunter and Price 1992; Polis and Strong 1996;
43 Gruner et al. 2008). The exploitation ecosystem hypothesis (EEH) predicts that resource
44 availability and predation control densities within adjacent trophic levels (Oksanen et al. 1981).
45 Accordingly, increasing primary productivity lengthens food webs by boosting the establishment
46 of predators, that will, in turn, have a greater impact on lower trophic levels. In nutrient-poor
47 ecosystems, biomass of basal species is severely constrained by resource availability and is too low
48 to support a significant consumer biomass (Menge 2000). In more nutrient-rich ecosystems,
49 productivity of basal species increases with elevated resources but their biomass is kept constant
50 by predation as consumers become more abundant (Steiner 2001). Although it has been shown that
51 the predictions of EEH are modulated by biotic (e.g., diversity of the food webs) and abiotic (e.g.,
52 habitat heterogeneity, disturbance) factors (Hunter and Price 1992; Leibold et al. 1997; Menge et
53 al. 2002; Foulquier et al. 2011), it provides a robust theoretical framework to evaluate the roles of
54 bottom-up and top-down controls on ecosystem structure (e.g., Shurin et al. 2002; Aunapuu et al.
55 2008; Lezama et al. 2014; Du et al. 2015; Hoset et al. 2017).

56 In wetlands, a historical view that bottom-up controls have greater relative importance than top-
57 down controls in regulating ecosystem structure and function (e.g., Odum and Smalley 1959) has
58 been reconsidered more recently (Sala et al. 2008; Moore 2018). Indeed, top predators like fish or
59 invertebrates can significantly control the abundance and the assemblage of their prey (Diehl 1992;
60 Magnusson and Williams 2009; Cobbaert et al. 2010; Laske et al. 2017) and top-down control of
61 grazers on primary producers play a key role on wetland functioning and stability (e.g., limitation
62 of algal blooms; Hillebrand 2009; Bertness et al. 2014). In this context, artificial wetlands, which

63 are increasingly developed to compensate for the loss of natural wetlands (Davidson 2014), could
64 be useful tools for determining the respective roles of bottom-up and top-down forces on
65 community structures because they allow for the selection of systems with distinct productivities.
66 Moreover, these artificial systems may be managed for controlling the water flux of organisms,
67 reducing the heterogeneity in biological colonization among wetlands (De Meester et al. 2005).
68 We tested the predictions of EEH in shallow (water depth < 1.5 m) artificial wetlands having area
69 of less than 2 ha and benthic habitat characterized by dense biofilms of phototrophic and
70 heterotrophic micro-organisms (Gette-Bouvarot et al. 2014). To test the respective influences of
71 bottom-up and top-down controls on benthic invertebrate communities, we selected three fishless
72 shallow artificial wetlands characterized with contrasting primary productivities (estimated from
73 net photosynthesis of benthic biofilms) associated with differences in sediment composition
74 (proportion of clay and silt) and algal biomass at the water-sediment interface. We expected
75 components of the biofilms to play a key role as food sources for the benthic food web creating a
76 bottom-up effect. However, in accordance with the EEH we hypothesized the relative importance
77 of bottom-up and top-down effects to shift from a dominance of bottom-up controls to a dominance
78 of top-down controls with increasing primary productivity. To evaluate the response of food webs,
79 we classified benthic invertebrate communities into trophic functional groups by including both
80 the vertical (linear trophic chain from basal resources to predators through consumers) and
81 horizontal dimensions of food webs (species diversity at each trophic level, following Srivastava
82 and Bell (2009)). Under a bottom-up control scenario, we predicted a positive relationship between
83 the abundance of grazers and scrapers and primary productivity and algal biomass at the water-
84 sediment interface, a positive relationship between deposit-feeders (bacterivores) and bacterial
85 abundance and organic matter (% of total organic carbon and total nitrogen) in sediment, and a
86 positive relationship between macroinvertebrate predator abundance and the abundance of preys at

87 lower trophic levels. Alternatively, under a top-down control scenario, we predicted no positive
88 relationships between consumers and their food sources.

89

90 Material and Methods

91 *Study site*

92 Our experiment took place in a pumping well field of « Crépieux-Charmy » (3.75 km²) located in
93 the Rhône River floodplain (France), which provides drinking water for the metropolitan area of
94 Lyon (1,280,000 inhabitants supplied). Artificial wetlands (surface area = 0.85-1.5 ha) have been
95 built to recharge aquifer with river water. All wetlands were built by excavation in natural soils in
96 areas with reduced riparian vegetation and were partially filled with a layer of calibrated sand about
97 20 cm thick and characterized by a low organic matter content (total organic carbon < 0.1% of
98 sediment dry mass). Their main water supply is pumped in a channel (Vieux Rhône) of the Rhône
99 River using centrifugal pumps (rotation: 1000 rounds per minute) that markedly limit the transport
100 of top-predator fishes from Rhône River to wetlands. Despite similar designs, wetlands evolved
101 over time due to the accumulation of fine particles (< 63 µm) at the water-sediment interface,
102 influencing the availability of the benthic habitat for biofilms. Indeed, presence of fine sediments
103 on a coarse and poorly organic sediment ameliorate the physical attachment and the nutrient
104 availability for benthic biofilms (Sundbäck et al. 2003; van de Koppel et al. 2001; Watermann et
105 al. 1999). For the present study, we selected three wetlands (called A, B, C) that were characterized
106 by varying amounts of fine particles (proportions determined by laser diffractometry following
107 Estragnat et al. 2018) at the water-sediment interface (Fig. 1A, one-way ANOVAs, comparison of
108 fine sediment proportion among wetlands, $F_{2,15} = 29.6$, $p < 0.001$), leading to contrasted benthic

109 habitats for benthic biofilms. Following the decreasing gradient of fine particle amount from
110 wetland A to wetland C, algal biomass and net photosynthesis activity (see below for details on
111 measurements) of the biofilm decreased from wetland A with a mean chlorophyll a content of 2.85
112 $\mu\text{g per cm}^2$ and positive net production to wetland C with a mean chlorophyll a content of 1.55 μg
113 per cm^2 and negative net production as photosynthesis did not compensate for respiration (Fig.
114 1BC, one-way ANOVAs, comparisons of algal biomass and net photosynthesis among wetlands,
115 $F_{2,15} = 26.6$, $p < 0.001$ for algal biomass, $F_{2,15} = 23.6$, $p < 0.001$ for net photosynthesis). These
116 conditions allowed us to evaluate the trophic relationships between primary productivity, benthic
117 food sources, and invertebrate communities.

118 *Environmental conditions before sampling date*

119 The three studied wetlands had the same water supply and water column depth during a period of
120 6 weeks before sampling date (on 22nd of October 2014), minimizing the potential influence of
121 hydrological conditions on community structure. During this period, we also verified that the three
122 wetlands were characterized by comparable physico-chemical conditions in the water column. *In*
123 *situ* monitoring of water temperatures showed similar variations (between 14.7 and 24.6 °C) in the
124 three artificial wetlands. Weekly measurements of specific conductivity, pH, and dissolved oxygen
125 (DO) concentrations performed with a HQ40D multiparameter (HACH) also indicated comparable
126 values among artificial wetlands with mean (\pm standard deviation) values of 337 (\pm 13) $\mu\text{S/cm}$, 8.3
127 (\pm 0.3), and 9.4 (\pm 0.5) mg/L for specific conductivity, pH and DO, respectively. Nutrient
128 concentrations were also measured weekly in the water column of the wetlands following Gette-
129 Bouvarot et al. (2014). Comparable dissolved nutrient concentrations and fluctuations were found
130 in the three wetlands with concentrations of N-NO_3^- , N-NH_4^+ and P-PO_4^{3-} of 0.99 ± 0.21 (mean \pm
131 SD) mg/L, 32.78 ± 20.13 $\mu\text{g/L}$ and 12.29 ± 9.27 $\mu\text{g/L}$, respectively.

132

133 *Sampling design*

134 Biofilm and invertebrate samples were collected on the same day (October 22, 2014) to obtain a
135 data set linking benthic fauna with characteristics of the sedimentary biofilm. Analyses on benthic
136 samples were performed to determine biofilm characteristics (fluorescence measurements of
137 benthic algal biomass and composition, bacterial abundance, total organic carbon and total nitrogen
138 of the biofilm) and benthic communities of invertebrates. To facilitate the collection of benthic
139 samples, the water pumping into the study wetlands was stopped 2 days before the sampling date
140 to have between 30 and 40 cm of water level in all wetlands. In each wetland, we randomly selected
141 6 replicate zones. For biofilm analyses, the top layer (0-1 cm) of sediments was cored in each zone
142 using cut syringes (internal diameter = 15 mm). Fifteen samples were collected, mixed and
143 homogenized per zone to obtain representative sediment samples. For net photosynthetic activity
144 of the biofilm, analyses were performed on one intact core collected per zone. Benthic invertebrates
145 were sampled in each zone using a 200- μm -mesh surber net following core collections for sediment
146 and biofilm analyses. The top sediment layer was collected on a surface of 150 cm^2 per zone and
147 preserved with 96% ethanol. All samples were then stored at $\sim 10^\circ\text{C}$ during transport to the
148 laboratory within 4 hours.

149

150 *Chemical and biological analyses on sediments*

151 The biomass of green algae, diatoms and cyanobacteria at the water-sediment interface were
152 estimated by *in situ* measurements of chlorophyll-*a* concentration and were expressed as
153 chlorophyll-*a* equivalent per unit of surface. These measurements were performed with a benthic
154 fluorimetric probe (BenthoTorch, bbe Moldaenke GmbH) (see Harris and Graham 2015 for
155 details).

156 The bacterial cell numbers were evaluated on sediment previously fixed with formaldehyde (final
157 concentration 2 % v/v) by direct microscopy counts after incubation of the sediment with the Syto9
158 green fluorescent nucleic acid stain (Invitrogen). Details of the protocol were given in Gette-
159 Bouvarot et al. (2014). The total bacterial abundance (cells/g of dry sediment) was then determined.

160
161 Total organic carbon (TOC) and total nitrogen (TN) were measured as estimators of the
162 sedimentary biofilm biomass. Following Mermillod-Blondin et al. (2015), TOC and TN were
163 determined by high-temperature combustion of *in situ* pre-acidified (HCl 2N, to remove inorganic
164 carbon) dry samples (60°C, 48h) and subsequent measurements of CO₂ and N₂ by thermal
165 conductometry using an elemental analyzer (FlashEA 1112, Thermo Electron Corporation).

166 Net photosynthetic activity (NP) was determined by measuring oxygen production at 15 °C (close
167 to field temperature at sampling date) on intact biofilms (4 cm² collected with a cut syringe, see
168 above) using 4 mL respiration chambers fitted with micro-probes (Microrespiration system,
169 Unisense, see Gette-Bouvarot et al. 2015 for details). Photosynthesis measurements were
170 performed with an irradiance of 150 μmol.m⁻².s⁻¹, close to maximal photosynthetically active
171 radiations (PAR) measured at midday with a LI-193 Spherical Quantum Sensor (PAR varying
172 between 20 and 130 μmol m⁻² s⁻¹ depending on meteorological conditions). For measurements,
173 total dissolved inorganic carbon concentration was adjusted to 10 mM with KHCO₃ to ensure
174 sufficient supply of inorganic carbon during the incubation and pH was maintained at 6.5 by
175 addition of a citrate buffer. Net photosynthesis rate was expressed as nmol of O₂.min⁻¹.cm⁻² of
176 sediment surface.

177

178 *Analyses on benthic invertebrates*

179 Benthic invertebrates were collected by scraping a surface area of 150 cm² with a surber net in each
 180 sampled zone. Invertebrates were sorted and identified using Tachet et al. (2000) in the laboratory
 181 using a stereomicroscope. All taxa were classified into seven trophic functional groups (grazers,
 182 scrapers, deposit-feeders, filter-feeders, predators-parasites, detritivores and shredders) according
 183 to their trophic affinities (Tachet et al. 2000). When one taxon was affiliated to 2 or more functional
 184 groups, we applied a percentage of functional affinity in the abundance table for the given taxon
 185 (i.e., 50 % and 50 % for one taxon affiliated to 2 functional groups).

186
 187 *Statistical analyses*

188 One-way ANOVAs were performed to compare biofilm variables and the abundances and richness
 189 (numbers of taxa) of each functional group of benthic invertebrates among wetlands. The
 190 relationship between the biofilm table and the fauna table was evaluated by a co-inertia analysis
 191 (see Dolédec and Chessel 1994; Dray et al. 2003). This multi-table analysis was performed to
 192 examine the links between the two tables, each table using the same 18 samples as rows. The
 193 relationship between each pair of data sets was measured using the Rv-coefficient (vectorial
 194 correlation coefficient; Robert and Escoufier 1976). The Rv-coefficient between two tables ranges
 195 between 0 and 1 and is a multidimensional equivalent of the ordinary correlation coefficient
 196 between two variables. For two given data sets X_k and X_l, the Rv-coefficient writes as follows:

197
$$Rv(X_k, X_l) = \frac{Covv(X_k, X_l)}{\sqrt{Vav(X_k)} \sqrt{Vav(X_l)}}$$

198 with $Covv(X_k, X_l) = \text{Trace} (X_k^t D_n X_l D_p)$ as the vectorial covariance and $Vav (X_k) = \text{Trace}$
 199 $(X_k^t D_n X_k D_p)$ and $Vav (X_l) = \text{Trace} (X_l^t D_n X_l D_q)$ as the vectorial variance for X_k and X_l,

200 respectively; Matrix D_n contains row weights (common to both data sets) and matrices D_p and D_q
201 contain the column weights of X_k and X_l , respectively (see Blanc et al. 1998). To test the
202 significance of R_v -coefficients, rows were randomly permuted within tables. Permutations were
203 repeated 1,000 times to obtain a null distribution of R_v -coefficients. We assessed the statistical
204 significance by determining the proportion of null values that were greater than the observed R_v -
205 coefficients.

206 Linear regressions were performed to determine the significance of the correlations among biofilm
207 characteristics and the abundance and richness of invertebrate functional groups (e.g., green algae
208 and grazer abundance). For all variables, the normality and the homoscedasticity of the residuals
209 were verified using the Shapiro-Wilk's test and the Levene's test, respectively. ANOVA analyses,
210 co-inertia analysis, linear regressions and graphical displays were performed using functions in the
211 ade4 package (Chessel et al. 2004; Dray et al. 2007) in R (R Development Core team 2015).
212 Significance for statistical tests was accepted for a first species risk $\alpha < 0.05$.

213

214 Results

215 *Biofilm characteristics of the three wetlands*

216 Algal colonization of the water-sediment interface was significantly different among wetlands (Fig.
217 2) and followed the gradient of net productivity measured (Fig. 1): green algae and diatom
218 biomasses were positively correlated (Pearson's $r = 0.829$) and exhibited decreasing values from
219 wetland A to wetland C with intermediate values in wetland B (one-way ANOVAs, $F_{2,15} = 58.9$, p
220 < 0.001 for green algae and $F_{2,15} = 10.1$, $p < 0.01$ for diatoms). The densities of these two algal
221 groups were positively correlated with the net photosynthetic activity ($R^2 = 0.65$, $p < 0.001$, $n = 18$

222 with green algae biomass, and $R^2 = 0.46$, $p < 0.01$, $n = 18$ with diatom biomass). Cyanobacteria
223 biomass showed a distinct pattern as it was significantly lower in wetland B than in the two other
224 wetlands (Fig. 2, one-way ANOVA, $F_{2,15} = 79.4$, $p < 0.001$). Percentages of total organic carbon
225 and total nitrogen were also the lowest at the sediment interface of wetland B (one-way ANOVAs,
226 $F_{2,15} = 5.1$, $p < 0.05$ for total organic carbon and $F_{2,15} = 5.9$, $p < 0.05$ for total nitrogen). Hence, we
227 detected a significant and positive correlation between cyanobacteria biomass and total nitrogen
228 ($R^2 = 0.37$, $p < 0.01$, $n = 18$) but not between cyanobacteria biomass and total organic carbon (R^2
229 $= 0.18$, $p > 0.05$, $n = 18$). In contrast, bacterial abundances were negatively correlated with
230 cyanobacteria biomasses ($R^2 = 0.55$, $p < 0.001$, $n = 18$) and exhibited higher cell numbers in
231 wetland B than in the other wetlands (one-way ANOVA, $F_{2,15} = 14.6$, $p < 0.001$).

232

233 *Functional composition of benthic invertebrate communities in the three wetlands*

234 Abundances and richness of grazers and scrapers were significantly different among wetlands (one-
235 way ANOVAs, $F_{2,15} = 14.1$, $p < 0.001$ for grazer abundance, $F_{2,15} = 11.8$, $p < 0.001$ for scraper
236 abundance, $F_{2,15} = 5.0$, $p < 0.05$ for grazer richness, and $F_{2,15} = 15.3$, $p < 0.001$ for scraper richness).
237 Following the decreasing gradient of net productivity, they were the highest in wetland A and the
238 lowest in wetland C with intermediate values in wetland B (Fig. 3). The abundance of filter-feeders
239 tended to follow the same pattern with highest values in wetland A (Fig. 3, one-way ANOVA, $F_{2,15}$
240 $= 7.8$, $p < 0.01$) although filter-feeder richness did not vary significantly among wetlands (one-way
241 ANOVA, $F_{2,15} = 1.7$, $p > 0.22$). Deposit-feeders exhibited a particular distribution compared with
242 grazers, scrapers and filter-feeders (Fig. 3). They were the most numerous in wetland B (one-way
243 ANOVA, $F_{2,15} = 10.8$, $p < 0.01$) but their richness was low (between 1 and 2 taxa) and not

244 significantly different among wetlands (one-way ANOVA, $F_{2,15} = 2.5$, $p > 0.1$). In contrast with
245 the other functional groups, the abundance and richness of predators were not significantly different
246 among wetlands (Fig. 3, one-way ANOVA, $F_{2,15} = 2.4$, $p > 0.1$ for predator abundance and $F_{2,15} =$
247 2.3 , $p > 0.15$ for predator richness).

248 *Relationships between biofilm characteristics and functional composition of benthic invertebrate*
249 *communities*

250 The first two axis of co-inertia analysis explained more than 95% of the co-variation between
251 biofilm and fauna datasets and the structure shared by the two datasets was significantly different
252 from a structure expected from random association ($Rv = 0.60$, $p < 0.001$). Samples were
253 discriminated among wetlands (Fig. 4A) and the short arrows displayed on Fig. 4A underlined the
254 good fit between biofilm and fauna datasets in the shared structure.

255 On the factorial map of variables (Fig. 4BC), the horizontal axis indicated that samples
256 characterized by high net photosynthetic activity and high diatom and green algae biomasses were
257 also dense and rich in herbivores (grazers and scrapers). There were significant positive linear
258 correlations between these biofilm characteristics (net photosynthetic activity, diatom or green
259 algae biomass) and the densities of herbivores (grazers and scrapers) (Fig. 5). The richness of
260 grazers and scrapers were also linearly and positively correlated with these biofilm characteristics
261 and more especially with the biomass of green algae (relationships illustrated on Fig. 6). The
262 vertical axis of the co-inertia analysis discriminated the samples with high bacterial densities and
263 high abundances of deposit feeders from those of high cyanobacteria biomass and nitrogen content
264 and low deposit-feeder abundances (Fig. 4BC). The abundance of deposit feeders was significantly
265 and positively correlated with bacterial abundance (Fig. 7A) but not with total nitrogen and total

266 organic carbon ($R^2 < 0.1$, $p > 0.05$, $n = 18$). The abundance of deposit feeders was negatively
267 correlated with cyanobacteria biomass (Fig. 7B). We did not detect clear correlations between
268 biofilm characteristics and the functional groups of filter feeders and predators. The abundance of
269 predators was significantly and positively correlated with the abundance of other invertebrates (Fig.
270 8). No significant correlations were obtained between predator richness and the abundance and
271 richness of other invertebrates.

272

273 Discussion

274 Although the literature highlighted the occurrence of significant top-down control of communities
275 in wetlands (Magnusson and Williams 2009; Hillebrand 2009; Moore 2018), top-down forces were
276 apparently weak in our systems. Then, our dataset did not corroborate the prediction of EEH
277 (Oksanen et al. 1981) suggesting a significant influence of top-down forces in our most productive
278 wetland. The analysis of the links between biofilms and functional trophic groups of invertebrates
279 clearly showed a dominant bottom-up effect of primary productivity (net photosynthesis) and algal
280 resources on herbivores in artificial wetlands. Indeed, the abundances of both grazers and scrapers
281 were positively and linearly correlated with the biomass of green algae and diatoms in wetlands.
282 These correlations indicate that the bottom-up control of green algae and diatoms swamped out the
283 top-down influence of herbivores on algal resources. As previous enclosure experiments showed
284 that the introduction of a grazer (the gastropod *Viviparus viviparus*, a species which is not naturally
285 present in our artificial wetlands) had a significant top-down effect on algae in these artificial
286 wetlands (Gette-Bouvarot et al. 2015; Estragnat et al. 2018), we can conclude that pressure by

287 grazers and scrapers naturally present in these systems was not sufficient enough to reduce algal
288 biomass.

289 Positive relationships between herbivore abundance and biomass of green algae and diatoms
290 contrasted with the lack of relationship detected between herbivores and cyanobacteria biomass.

291 This result may suggest that herbivores consumed green algae and diatoms rather than
292 cyanobacteria in wetlands, resulting in no relationship between cyanobacteria biomass and
293 herbivore abundance. This suggestion of a poor trophic transfer from cyanobacteria to herbivores
294 is consistent with several studies indicating that cyanobacteria are generally non-attractive trophic
295 sources for invertebrates due to their poor nutritional quality (low essential fatty acids and P
296 contents, Gulati and DeMott 1997; Paerl and Fulton 2006) and their chemical and structural defense
297 against grazing (DeMott et al. 1991; Soares et al. 2010; Bownik 2016). Our correlation analyses
298 also suggest that cyanobacteria had a negative influence on deposit-feeders. However, a toxic
299 impact of cyanobacteria on this functional group is highly improbable because examples of
300 negative interactions between cyanobacteria and deposit feeders in the field are lacking in the
301 literature and, in contrast, a study reported a positive effect of the fixation of N₂ by cyanobacteria
302 on deposit feeders (Karlson et al. 2014). Moreover, we did not detect any negative influence of
303 cyanobacteria biomass on grazers and scrapers, two trophic functional groups that would be the
304 most affected by toxin produced by cyanobacteria (Bownik 2016). Together, these results suggest
305 that cyanobacteria were probably not toxic for invertebrates in our artificial wetlands.

306 In addition to the positive relationship between algal (green algae and diatoms) biomass and
307 herbivore abundances, we also showed that grazer and scraper richness were positively correlated
308 with the biomasses of green algae, diatoms and photosynthetic activity. These results indicate that
309 basal resources and net primary productivity may positively influence the horizontal diversity of
310 the food web (*sensu* Srivastava and Bell 2009). This positive relationship between primary

311 productivity (and energy associated with trophic resources) and herbivore taxa richness can be
312 related to the “species-energy theory” (Wright 1983; Srivastava and Lawton 1998; Evans et al.
313 2005). Indeed, several studies support the hypothesis that energy correlates positively with species
314 richness (e.g, Huston 1994; Evans et al. 2005). In our field conditions, we can expect that an
315 increase in benthic primary productivity could have elevated the amount of certain individual
316 resource types (i.e., algal species), enabling specialist herbivore species to feed on them.
317 Consequently, this trophic specialization would have led to reduced niche overlap among
318 herbivores, reducing rates of competitive exclusion and elevating species richness in more
319 productive wetlands. We also suspect that the diversity of individual resource types (i.e., algal
320 species) increased with benthic primary productivity, enabling the highest herbivore diversity in
321 the wetland characterized by the highest algal richness. Nevertheless, we cannot confirm this
322 potential link between the trophic specialization of herbivore taxa and the abundances of individual
323 resource types because green algae and diatom groups contained several species with contrasted
324 trophic preferences for invertebrates (e.g., Tall et al. 2006; Alfaro 2009). More precise analyses
325 such as invertebrate gut analyses using metabarcoding approaches (Pompanon et al. 2012) would
326 be necessary to determine the trophic niche of each herbivore taxa in association with the
327 availability of algal species in artificial wetlands. This perspective is very promising to evaluate
328 whether the trophic specialization of herbivores in the most productive wetlands can explain the
329 positive relationship between net benthic primary productivity (energy) and herbivore taxa richness
330 in our artificial systems.

331 The positive and significant linear correlation between the abundances of predators and other
332 aquatic invertebrates also suggest that bottom-up control of predators by their prey blurred the top-
333 down control exerted by predators on their prey in our artificial wetlands. The lack of a strong top-
334 down control of invertebrate predators on other invertebrates in the most productive wetland

335 (wetland A) would be associated with the increased horizontal diversity in food web observed for
336 grazers and scrapers in this wetland. Indeed, increased diversity of a trophic level would mitigate
337 top-down control by predators on this trophic level due to differences in predation pressure among
338 the species of this trophic level. More precisely, a resource base with more species is more likely
339 to contain at least one species that is relatively resistant to consumption and can compensate for
340 the decrease of more consumable species in the presence of consumers (Leibold 1989, Duffy et al.
341 2007). However, the mechanism responsible of the lack of top-down cascade in our artificial
342 wetlands is out of the scope of the present study. This further step would require more complete
343 description and quantification of species-species interactions within the food webs.

344 Considering the detritus-based food web, the positive linear relationship between the bacterial
345 abundance and the abundance of deposit-feeders suggests that the functional group of deposit-
346 feeders was also bottom-up controlled by their trophic resources. Nevertheless, the abundances of
347 bacteria and deposit-feeders were not correlated with the quantity of total organic carbon and total
348 nitrogen in the sediment. These results are not consistent with the positive relationship between
349 organic matter quantity and decomposer (micro- and macro-organisms) abundance classically
350 supporting the bottom-up theory in sedimentary environments (Dannovaro et al. 1995; Lin and Yo
351 2008; Ramalho et al. 2014). The positive link between bacteria and deposit-feeder abundance
352 observed in the present study was likely due to a positive influence of deposit-feeding activities on
353 bacteria, a process largely demonstrated in a wide range of freshwater sediments (van de Bund et
354 al. 1994; Griebler 1996; Traunspurger et al. 1997; Wieltschnig et al. 2008; Nogaro et al. 2009;
355 Pigneret et al. 2016). A recent experiment performed in one of the artificial infiltration wetlands
356 studied here demonstrated that aquatic oligochaetes, which are the main representatives of deposit-
357 feeders in the present study, had a strongly positive and significant influence on the abundance and
358 activity of bacteria in sediments (Mermillod-Blondin et al. 2018). More precisely, the bioturbation

359 associated with the addition of the tubificid worm *Limnodrilus hoffmeisteri* increased the bacterial
360 abundance by 2-fold and the microbial hydrolytic activity by 35% without influencing the quantity
361 of total nitrogen and organic carbon in sediments (Table 1). Thus, the top-down and positive effect
362 of deposit-feeders on micro-organisms was the most probable mechanism explaining the positive
363 relationship between bacteria and deposit-feeder abundances in the present experiment.

364

365 *Conclusions*

366 Our results did not corroborate the predictions of EEH suggesting that top-down controls would
367 have a significant influence on community structure in the most productive ecosystems. Indeed, a
368 dominance of bottom-up processes in the phototroph-based food web occurred in our artificial
369 wetlands whatever their productivity. Our strong linear correlations between the biomasses and
370 productivity of the algal component of the biofilm (especially green algae and diatoms) and the
371 abundances of grazers and scrapers suggest that algal biomass and benthic primary productivity
372 supported the herbivore trophic level. In contrast with the phototroph-based food web, results
373 obtained for the detritus-based food web illustrate a positive effect of deposit-feeding invertebrates
374 on bacteria. As observed in sedimentary environments with oligochaetes (Brinkhurst and Chua
375 1969; Wavre and Brinkhurst 1971; Fukuhara et al. 1980) and polychaetes (gardening effect,
376 Hylleberg 1975), the feeding activities of deposit-feeder such as aquatic oligochaetes might have
377 stimulated organic matter decomposition and bacterial growth in sediments. Thus, the present
378 experiment showed that phototroph-based and detritus-based food webs were not dominated by the
379 same processes in our artificial wetlands as herbivore abundance was likely controlled by the
380 biomass of basal resources (algae) whereas deposit-feeder abundance was not linked to the amount
381 of organic matter in sediments. Different feeding rates of invertebrates and contrasted renewal rate

382 of basal resources (more rapid for algae than for detritic organic matter) between the two food webs
383 may explain the different links between invertebrates and basal food sources reported for both food
384 webs. These links are expected to have implications on the whole ecosystem functioning (nutrient
385 cycling, energy fluxes) and need to be considered in future studies. With this aim, development of
386 labelling approaches using stable isotopes ^{13}C and ^{15}N - (Christianen et al. 2017) would be very
387 promising to precisely quantify the transfer of energy within the phototrophic-based and detritus-
388 based food webs and their consequences on ecosystem functioning. More research on artificial
389 wetlands is needed because these artificial systems have been increasingly developed to
390 compensate for the loss of natural wetlands, particularly in urbanized landscapes (Davidson 2014).
391 This is a major challenge for the future, considering the dramatic increase of the urbanization and
392 the role played by wetland ecosystems for biodiversity preservation and nutrient retention (Hanson
393 et al. 2005).

394

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404

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585

586 Figure legends:

587 Fig 1: Percentage of fine particles ($< 63 \mu\text{m}$), benthic algal biomass and net photosynthetic activity
588 of benthic biofilms measured in the three studied wetlands ($n = 6$ measures per wetland).

589 Fig 2: Characteristics of the biofilms in the three wetlands ($n = 6$ measures per wetland for each
590 variable).

591 Fig 3: Abundances (ind/m^2) and richness (taxa/sample) of the five major trophic functional groups
592 of benthic invertebrates collected in the three wetlands ($n = 6$ measures per wetland).

593 Fig 4: Co-inertia analysis showing a) the shared structure obtained from the biofilm and fauna
594 datasets, b) the factorial map of biofilm variables and c) the factorial map of variables associated
595 with invertebrate functional groups. A = Wetland A, B = Wetland B, C = Wetland C, PhotoS = Net
596 Photosynthesis rate, TOC = Total organic carbon, TN = Total nitrogen, DepositAB = Abundances
597 of deposit feeders, DepositRICH = Richness of deposit feeders, ScrapAB = Abundances of
598 scrapers, ScrapRICH = Richness of scrapers, FiltAB = Abundances of filter-feeders, FiltRICH =
599 Richness of filter-feeders, GrazerAB = Abundances of grazers, GrazerRICH = Richness of grazers,
600 PredAB = Abundances of predators, PredRICH = Richness of predators.

601 Fig 5: Correlations a) between net photosynthetic activity and grazer abundance, b) between net
602 photosynthetic activity and scraper abundance, c) between green algae biomass and grazer
603 abundance, d) between green algae biomass and scraper abundance, e) between diatom biomass
604 and grazer abundance, and f) between diatom biomass and scraper abundance.

605 Fig 6: Correlations a) between green algae biomass and grazer richness and b) between green algae
606 biomass and scraper richness.

607 Fig 7: Correlations a) between bacterial abundance and deposit-feeder abundance, and b) between
608 cyanobacteria biomass and deposit-feeder abundance.

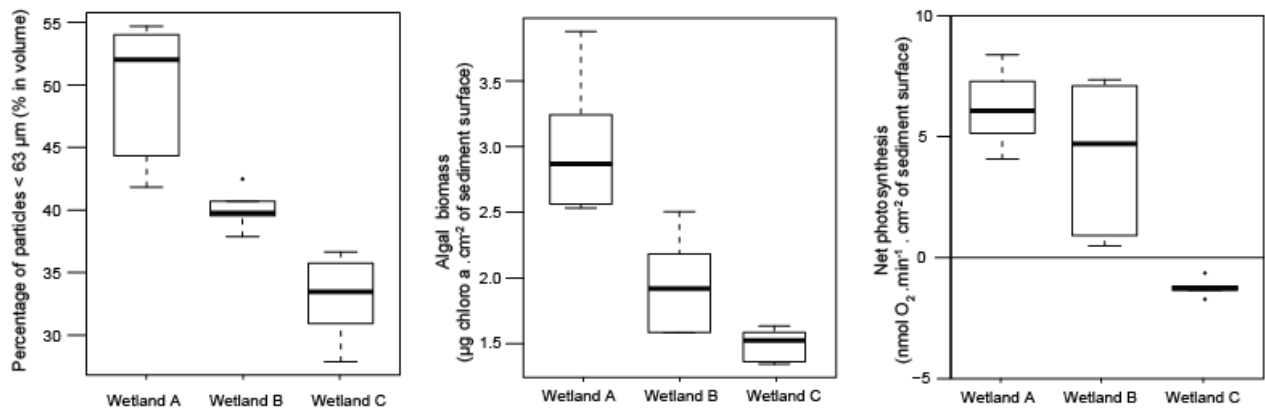
609 Fig 8: Correlation between predator abundance and the abundance of other invertebrates.

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Fig 1

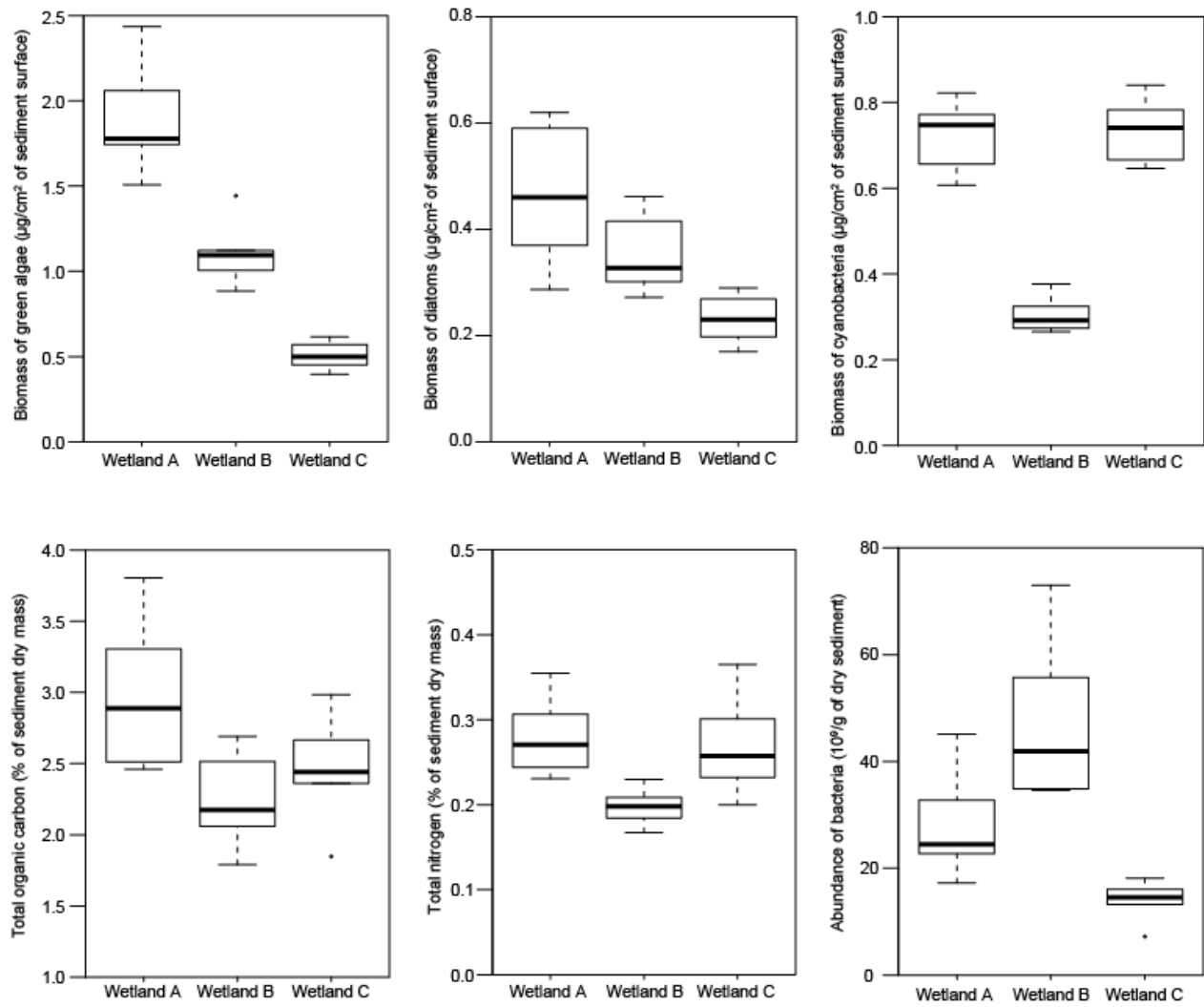
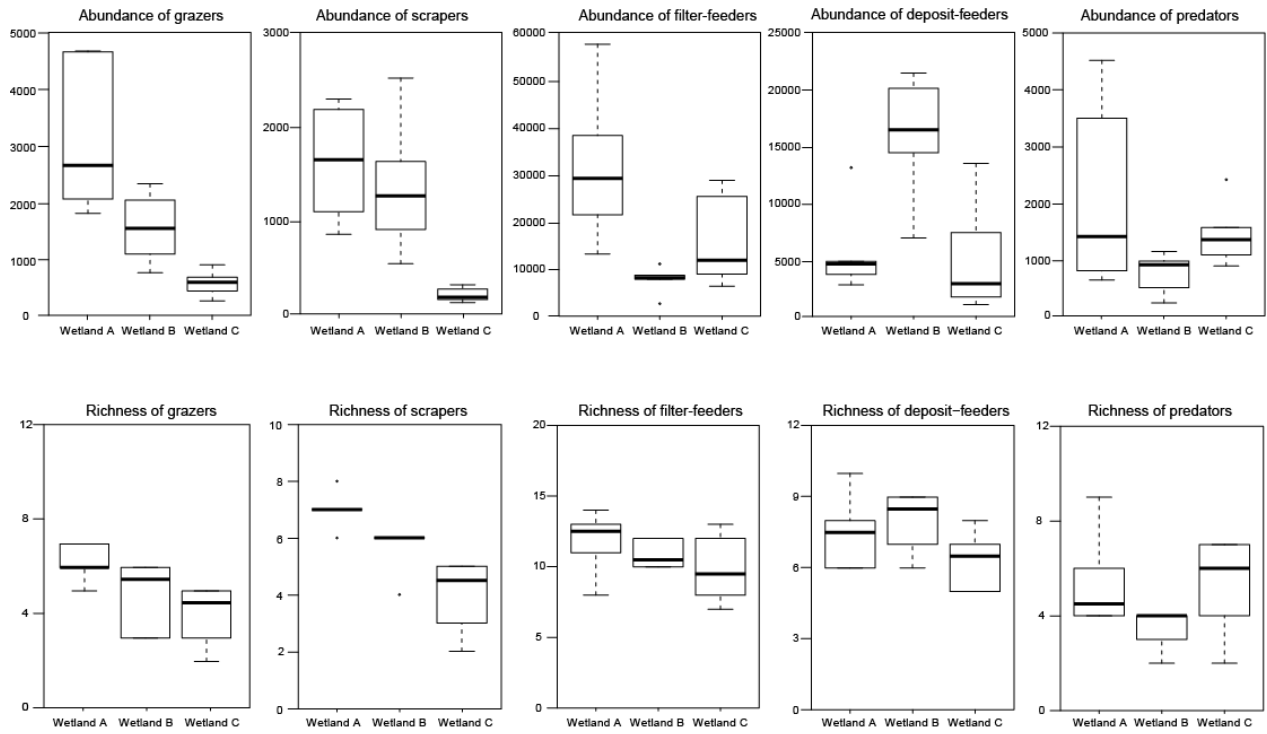


Fig 2

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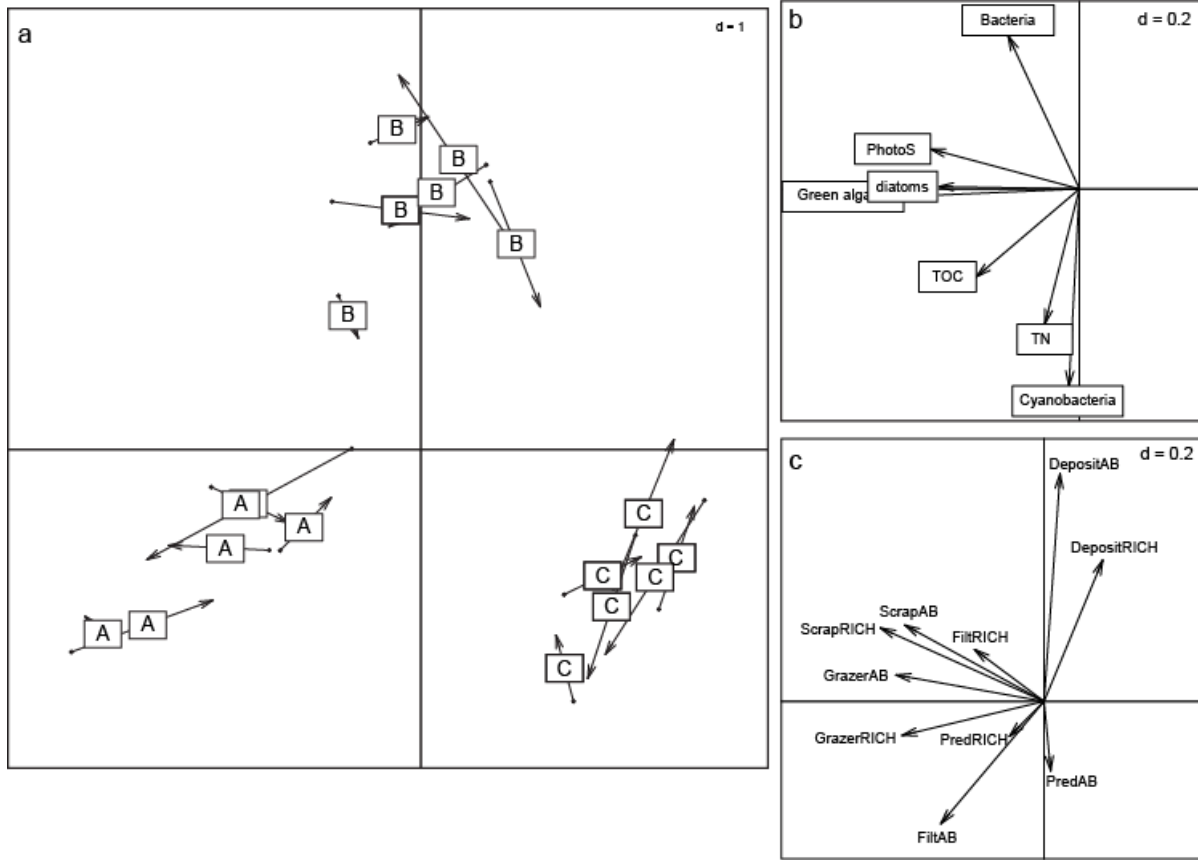
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Fig 3

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Fig 4

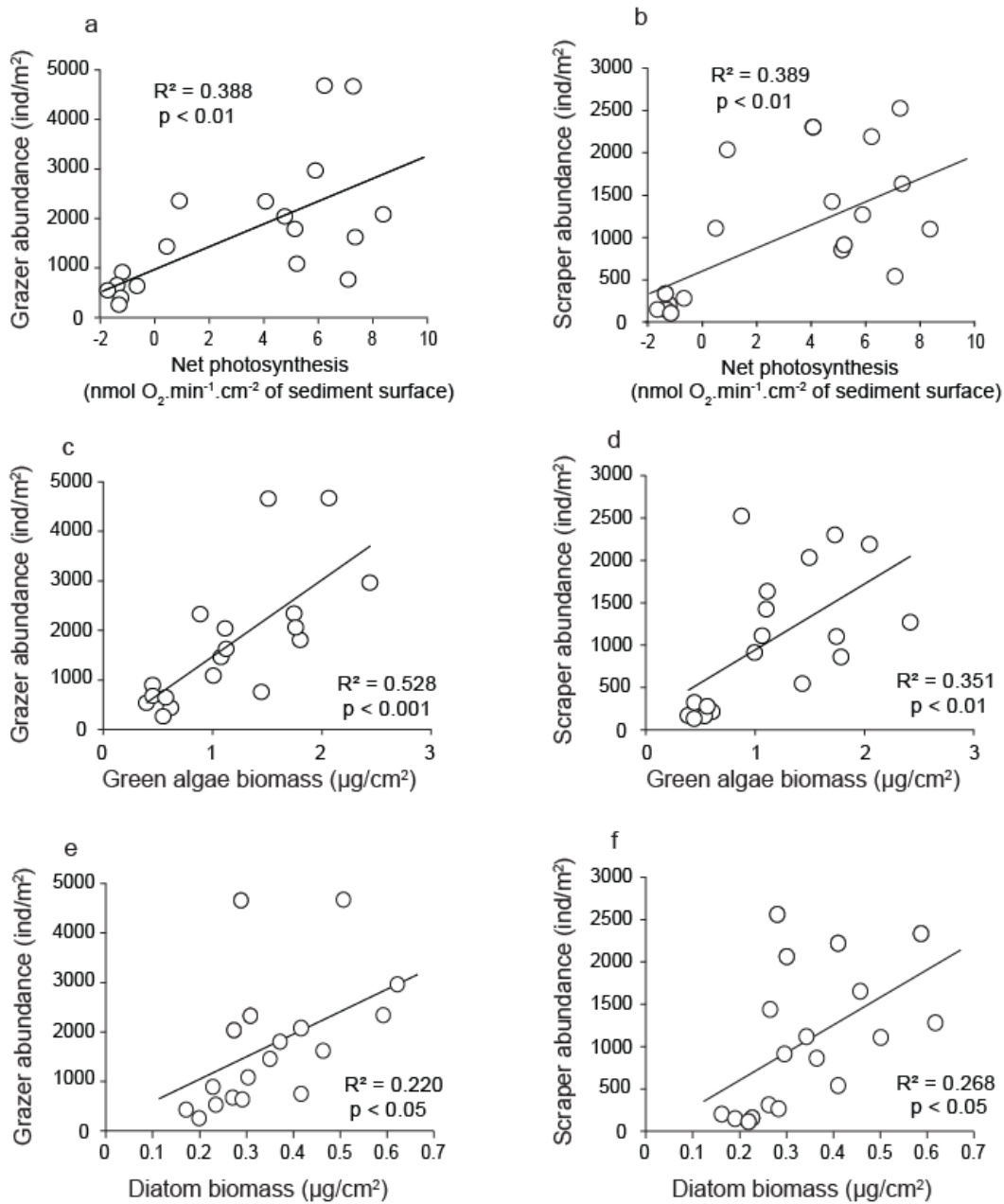


Fig 5

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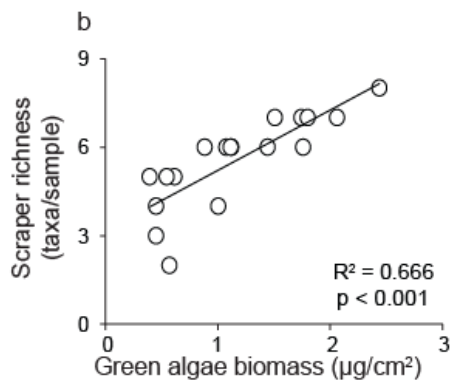
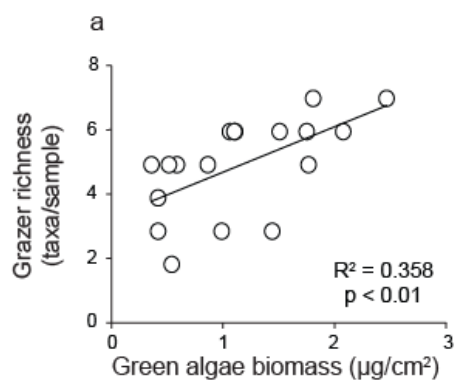


Fig 6

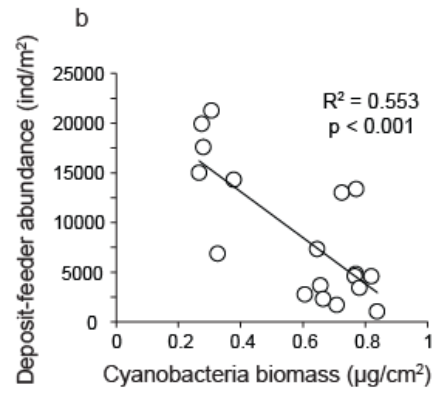
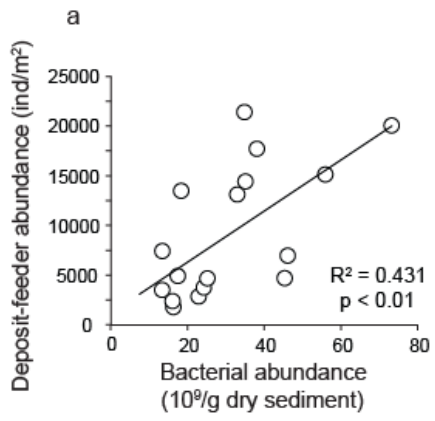
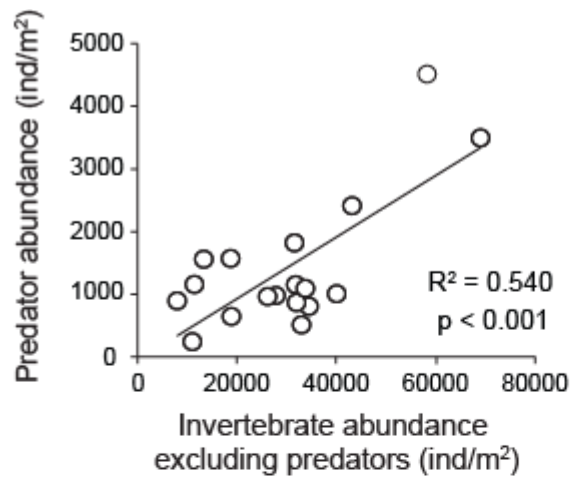


Fig 7



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Fig 8

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630 Table 1. Mean values (\pm SD) of the biofilm variables measured in 6 enclosures without worms and
 631 6 enclosures in which a density of 20,000 individuals.m⁻² of the tubificid worm *L. hoffmeisteri* has
 632 been added. Student-t tests were run to evaluate the influence of tubificid worm addition on biofilm
 633 variables. Modified from Mermillod-Blondin et al. (2018)
 634
 635

Measured variables	Control enclosures averaged values \pm standard deviation	Worm enclosures averaged values \pm standard deviation	t _(10, 0.05)	p-values
Bacterial cells (10 ⁹ /g of dry sediment)	3.20 \pm 1.05	6.48 \pm 1.90	4.04	0.002
Total organic carbon (% of dry sediment)	0.788 \pm 0.424	0.704 \pm 0.268	0.41	0.689
Total nitrogen (% of dry sediment)	0.117 \pm 0.056	0.112 \pm 0.034	0.19	0.857
Hydrolytic activity (10 ⁻² μ mol of hydrolyzed FDA .h ⁻¹ .g ⁻¹ of dry sediment)	4.57 \pm 1.00	6.16 \pm 0.84	2.99	0.013

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637

638 Supplementary Material 1: Table of taxa abundances for each sample (sampled surface: 150 cm²).
 639 The last column indicates the affiliation of taxa to functional groups. G: Grazers, S: Scrapers, DF:
 640 Deposit-feeders, F: filter-feeders, P: predators and parasites, D: Detritivores, and Shr: Shredders.

641

Taxa	Sampled basin						Feeding groups
	A	A	A	A	A	A	
<i>Naidinae sp.</i>	35	32	47	57	56	104	G/S
other oligochaetes	30	13	7	8	8	8	G/S
Enchytraeidae	116	82	127	235	464	104	DF
<i>Hydra sp.</i>	54	6	32	27	24	152	P
<i>Dugesia spp.</i>	4	0	0	1	8	0	P
Nematoda	98	63	58	36	568	168	P/DF
<i>Erpobdella sp.</i>	0	0	0	0	0	0	P
<i>Physa acuta + Physa fontinalis</i>	7	5	2	4	8	0	G/S
<i>Galba truncatula</i>	161	45	44	40	168	88	G/S
<i>Gyraulus sp.</i>	0	0	0	2	0	8	G/S
Hydracarina	0	0	0	1	0	0	P
Cyclopoida	721	277	740	524	1048	1624	F
Calanoida	0	0	0	0	0	0	F
Harpacticoida	0	2	0	0	0	0	B
<i>Chidorus sphaericus + Chidorus sp.</i>	14	0	120	0	145	94	F
<i>Eurycercus lamellatus</i>	95	40	150	137	181	188	F
<i>Sida crystallina</i>	27	26	180	0	0	141	F
<i>Simocephalus vetulus</i>	191	40	120	0	36	423	F
<i>Simocephalus expinosus</i>	109	92	209	137	508	470	F
<i>Simocephalus sp.</i>	0	13	60	55	36	0	F
<i>Alona quadrangularis</i>	82	0	30	0	109	141	F
<i>Pleuroxus sp.</i>	14	0	0	0	36	0	F
<i>Acroperus harpae</i>	0	13	0	0	36	0	F
<i>Daphnia pulex</i>	123	357	568	906	290	800	F
Non identified cladocera + other Daphnia	14	0	60	0	109	94	F
<i>Pseudocandona albicans</i>	0	0	0	1	0	0	DF
<i>Ilyocypris bradyi</i>	0	0	0	1	0	0	DF
<i>Heterocypris salina</i>	4	2	0	4	0	0	DF

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645 Suppl Material 1 (continued)

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Taxa	Sampled basin						Feeding groups
	A	A	A	A	A	A	
<i>Cypridopsis vidua</i>	20	1	0	9	0	8	DF
<i>Bradleystrandesia obliqua</i>	22	6	8	7	16	0	F
<i>Limmocythere inopinata</i>	0	0	0	0	0	0	DF
<i>Gammarus sp.</i>	1	0	0	0	0	0	Shr/P
<i>Cloeon sp.</i>	43	76	95	152	208	224	B
<i>Caenis sp.</i>	0	0	0	0	0	0	Shr/D
<i>Hydroptilidae agrayla</i>	11	3	0	3	2	4	G/S
<i>Haliplidae haliplus</i>	6	6	0	4	1	0	Shr
<i>Gyrinidae gyrinus + Hydrophilidae berosus + Elmidae esolus</i>	1	1	0	0	0	0	P
Chironomidae Tanytarsini	145	108	116	48	264	112	F/DF
Chironomidae Chironominae	85	31	41	6	48	56	F/DF
Chironomidae Orthocladinae	58	18	33	50	32	88	R/DF
Chironomidae Tanypodinae	11	7	9	0	0	8	P
Nymphs of chironomidae	44	8	43	29	24	16	P/F/DF/S
<i>Chaoborus sp.</i>	1	0	0	0	0	0	P
Ceratopogoninae	2	0	0	3	0	0	D
Dasyhelinae	0	0	0	3	1	3	D
Other diptera	3	0	0	6	1	3	P
Libellulidae + Sympetrinae + Plactycnemididae	5	0	1	4	2	0	P

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651 Suppl Material 1 (continued)

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Taxa	Sampled basin						Feeding groups
	B	B	B	B	B	B	
<i>Naidinae sp.</i>	64	40	87	53	60	23	G/S
other oligochaetes	32	0	1	0	10	3	G/S
Enchytraeidae	640	1000	1289	699	1191	415	DF
<i>Hydra sp.</i>	0	0	1	0	4	0	P
<i>Dugesia spp.</i>	0	0	4	0	0	0	P
Nematoda	128	128	50	102	104	18	P/DF
<i>Erpobdella sp.</i>	0	0	0	0	0	0	P
<i>Physa acuta</i> + <i>Physa fontinalis</i>	8	0	2	1	2	0	G/S
<i>Galba truncatula</i>	160	64	43	131	104	40	G/S
<i>Gyraulus sp.</i>	0	0	0	0	0	0	G/S
Hydracarina	0	0	0	0	0	1	P
Cyclopoida	312	248	238	219	200	68	F
Calanoida	0	0	0	0	0	0	F
Harpacticoida	0	0	2	2	0	0	B
<i>Chidorus sphaericus</i> + <i>Chidorus sp.</i>	38	25	0	14	48	7	F
<i>Eurycerus lamellatus</i>	19	0	39	12	12	3	F
<i>Sida crystallina</i>	19	25	65	16	83	13	F
<i>Simocephalus vetulus</i>	0	0	45	16	24	6	F
<i>Simocephalus expinosus</i>	29	62	39	0	12	14	F
<i>Simocephalus sp.</i>	0	0	0	0	0	1	F
<i>Alona quadrangularis</i>	19	25	0	21	24	10	F
<i>Pleuroxus sp.</i>	0	0	0	0	0	2	F
<i>Acroperus harpae</i>	29	0	0	5	0	0	F
<i>Daphnia pulex</i>	0	12	13	21	0	0	F
Non identified cladocera + other Daphnia	0	12	0	11	12	0	F
<i>Pseudocandona albicans</i>	0	0	11	2	1	0	DF
<i>Ilyocypris bradyi</i>	0	8	0	3	2	0	DF
<i>Heterocypris salina</i>	0	0	0	0	0	0	DF

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657 Suppl Material 1 (continued)

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Taxa	Sampled basin						Feeding groups
	B	B	B	B	B	B	
<i>Cypridopsis vidua</i>	0	24	6	11	5	0	DF
<i>Bradleystrandesia obliqua</i>	37	16	9	14	9	0	F
<i>Limmocythere inopinata</i>	19	0	2	0	0	0	DF
<i>Gammarus sp.</i>	0	0	0	0	0	0	Shr/P
<i>Cloeon sp.</i>	32	24	34	18	55	19	B
<i>Caenis sp.</i>	0	0	3	1	0	0	Shr/D
<i>Hydroptilidae agrayla</i>	0	0	0	3	1	1	G/S
<i>Haliplidae haliplus</i>	4	0	4	7	9	1	Shr
<i>Gyrinidae gyrinus + Hydrophilidae berosus + Elmidae esol</i>	1	0	0	0	0	0	P
Chironomidae Tanytarsini	464	243	210	292	177	65	F/DF
Chironomidae Chironominae	137	46	131	171	135	56	F/DF
Chironomidae Orthocladinae	61	21	15	35	15	7	R/DF
Chironomidae Tanypodinae	15	5	3	14	4	7	P
Nymphs of chironomidae	61	5	15	13	16	3	P/F/DF/S
<i>Chaoborus sp.</i>	0	0	0	0	0	0	P
Ceratopogoninae	0	0	0	1	0	0	D
Dasyhelinae	0	0	0	0	0	0	D
Other diptera	1	0	0	1	0	0	P
Libellulidae + Sympetrinae + Plactycnemididae	0	0	3	2	1	0	P

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663 Suppl Material 1 (continued)

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Taxa	Sampled basin						Feeding groups
	C	C	C	C	C	C	
<i>Naidinae sp.</i>	4	1	1	0	0	0	G/S
other oligochaetes	0	3	0	0	8	0	G/S
Enchytraeidae	16	13	101	28	432	724	DF
<i>Hydra sp.</i>	1	0	0	2	0	0	P
<i>Dugesia spp.</i>	0	0	0	0	0	0	P
Nematoda	149	115	198	202	152	331	P/DF
<i>Erpobdella sp.</i>	0	1	0	1	0	0	P
<i>Physa acuta</i> + <i>Physa fontinalis</i>	4	3	1	8	0	0	G/S
<i>Galba truncatula</i>	19	14	17	7	32	37	G/S
<i>Gyraulus sp.</i>	1	0	0	0	0	0	G/S
Hydracarina	0	1	1	0	0	1	P
Cyclopoida	115	42	48	168	96	266	F
Calanoida	28	15	71	76	272	208	F
Harpacticoida	0	0	0	1	0	0	B
<i>Chidorus sphaericus</i> + <i>Chidorus sp.</i>	19	0	0	16	0	100	F
<i>Eurycerus lamellatus</i>	0	0	19	62	56	166	F
<i>Sida crystallina</i>	9	0	19	31	0	66	F
<i>Simocephalus vetulus</i>	0	0	10	0	0	33	F
<i>Simocephalus expinosus</i>	19	0	38	47	0	166	F
<i>Simocephalus sp.</i>	0	0	0	0	0	0	F
<i>Alona quadrangularis</i>	9	0	0	0	0	33	F
<i>Pleuroxus sp.</i>	37	0	0	0	0	0	F
<i>Acroperus harpae</i>	0	0	0	0	0	0	F
<i>Daphnia pulex</i>	346	372	392	622	1324	763	F
Non identified cladocera + other Daphnia	19	16	0	0	28	166	F
<i>Pseudocandona albicans</i>	1	0	8	8	0	0	DF
<i>Ilyocypris bradyi</i>	0	0	0	0	0	0	DF
<i>Heterocypris salina</i>	0	0	0	0	0	0	DF

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669 Suppl Material 1 (continued)

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Taxa	Sampled basin						Feeding groups
	C	C	C	C	C	C	
<i>Cypridopsis vidua</i>	2	0	4	8	0	1	DF
<i>Bradleystrandesia obliqua</i>	3	3	12	40	0	2	F
<i>Limmocythere inopinata</i>	0	0	0	0	0	0	DF
<i>Gammarus sp.</i>	0	1	0	0	0	0	Shr/P
<i>Cloeon sp.</i>	16	7	27	54	27	26	B
<i>Caenis sp.</i>	0	0	0	0	0	0	Shr/D
<i>Hydroptilidae agrayla</i>	0	0	1	0	0	0	G/S
<i>Haliplidae haliplus</i>	0	0	0	0	0	0	Shr
<i>Gyrinidae gyrinus + Hydrophilidae berosus + Elmidae esol</i>	0	0	2	0	1	1	P
Chironomidae Tanytarsini	40	6	51	31	16	121	F/DF
Chironomidae Chironominae	16	2	13	7	8	2	F/DF
Chironomidae Orthocladinae	0	0	2	1	0	0	R/DF
Chironomidae Tanypodinae	5	1	3	2	0	1	P
Nymphs of chironomidae	2	1	0	2	8	1	P/F/DF/S
<i>Chaoborus sp.</i>	0	0	2	1	0	1	P
Ceratopogoninae	0	0	0	1	0	0	D
Dasyhelinae	0	0	0	0	0	0	D
Other diptera	0	0	2	2	0	1	P
Libellulidae + Sympetrinae + Plactycnemididae	1	2	1	2	0	0	P

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