



# Bottom-up processes control benthic macroinvertebrate communities and food web structure of fishless artificial wetlands

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**Abstract** In freshwater environments, the relative contributions of top-down and bottom-up effects on invertebrate communities in relation to productivity are largely ecosystem dependent. Artificial wetlands are increasingly developed to compensate for the loss of natural wetlands; however, their trophic processes remain poorly studied. The present study aimed to evaluate the respective contributions of bottom-up and top-down processes in structuring benthic food webs of three artificial wetlands with varying levels of benthic primary productivity. We found that phototrophic-based food webs in our artificial wetlands were controlled from the bottom-up by primary productivity and algal biomass developing at the

water–sediment interface. No significant top-down control of herbivore species by invertebrate predators was detected even in the wetland with the highest productivity. Increased richness of invertebrate grazers and scrapers with benthic primary productivity and algal biomass might have dampened the trophic cascade from predators to primary producers. In contrast with the phototrophic-based food web, analyses performed on the detritus-based food web showed that deposit-feeder invertebrate abundance was not correlated with the quantity of organic matter in sediments, suggesting no bottom-up effect of sedimentary organic matter content on deposit-feeders. More surprisingly, deposit-feeders, especially aquatic oligochaetes, seemed to influence the detritus-based food webs by stimulating organic matter processing and bacterial growth through bioturbation. The present study highlights the occurrence of contrasting trophic processes between phototrophic-based and detritus-based food webs which can have implications on ecosystem functions, such as nutrient cycling and energy fluxes.

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## Introduction

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

In wetlands, a historical view that bottom-up controls have greater relative importance than top-down controls in regulating ecosystem structure and function (e.g., Odum and Smalley 1959) has been reconsidered more recently (Sala et al. 2008; Moore 2018). Indeed, top predators like fish or invertebrates can significantly control the abundance and the assemblage of their prey (Diehl 1992; Magnusson and Williams 2009; Cobbaert et al. 2010; Laske et al. 2017), and top-down control of grazers on primary producers plays a key role on wetland functioning and stability (e.g., limitation of algal blooms; Hillebrand 2009; Bertness et al. 2014). In this context, artificial wetlands, which are increasingly developed to compensate for the loss of natural wetlands (Davidson 2014), could be useful tools for identifying the

respective roles of bottom-up and top-down forces on community structures because they allow for the selection of systems with distinct productivities. Moreover, these artificial systems may be managed to control the water flux of organisms, reducing the heterogeneity in biological colonization among wetlands (De Meester et al. 2005).

We tested the predictions of the EEH in shallow (water depth < 1.5 m) artificial wetlands having area of less than 2 ha and benthic habitat characterized by dense biofilms of phototrophic and heterotrophic microorganisms (Gette-Bouvarot et al. 2014). To test the respective influences of bottom-up and top-down controls on benthic invertebrate communities, we selected three fishless shallow artificial wetlands characterized with contrasting primary productivities (estimated from net photosynthesis of benthic biofilms) associated with differences in sediment composition (proportion of clay and silt) and algal biomass at the water–sediment interface. We expected components of the biofilms to play a key role as food sources for the benthic food web creating a bottom-up effect. However, in accordance with the EEH, we hypothesized that the relative importance of bottom-up and top-down effects would shift from a dominance of bottom-up controls to a dominance of top-down controls with increasing primary productivity. To evaluate the response of food webs, we classified benthic invertebrate communities into trophic functional groups by including both the vertical (linear trophic chain from basal resources to predators through consumers) and horizontal dimensions of food webs (species diversity at each trophic level, following Srivastava and Bell (2009)). Under a bottom-up control scenario, we predicted a positive relationship between the abundance of grazers and scrapers and primary productivity and algal biomass at the water–sediment interface, a positive relationship between deposit-feeders (bacterivores) and bacterial abundance and organic matter (% of total organic carbon and total nitrogen) in sediment, and a positive relationship between macroinvertebrate predator abundance and the abundance of preys at lower trophic levels. Alternatively, under a top-down control scenario, we predicted no positive relationships between consumers and their food sources.

## Materials and methods

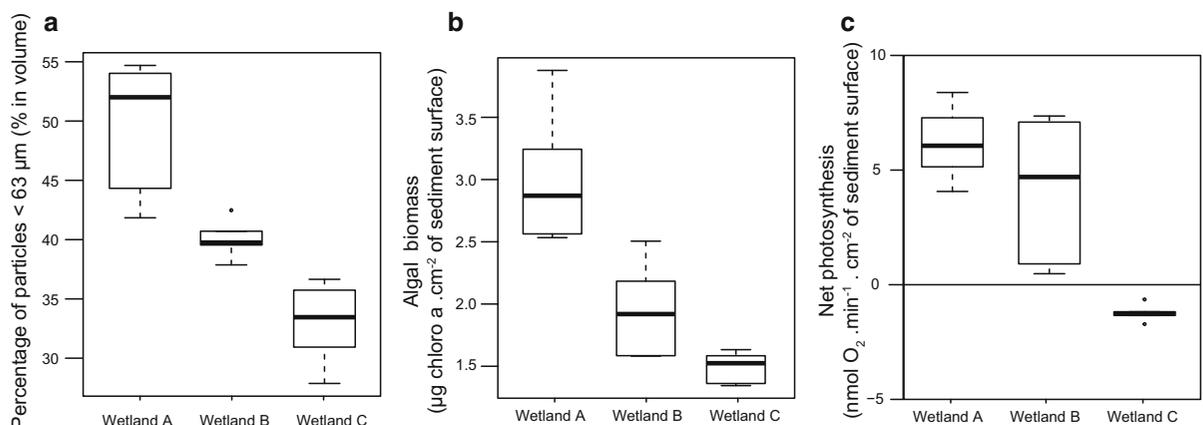
### Study site

Our experiment took place in a pumping well field of «Crépieux-Charmy» (3.75 km<sup>2</sup>) located in the Rhône River floodplain (France), which provides drinking water for the metropolitan area of Lyon (1,280,000 inhabitants supplied). Artificial wetlands (surface area = 0.85–1.5 ha) have been built to recharge the aquifer with river water. All wetlands were built by excavation in natural soils in areas with reduced riparian vegetation and were partially filled with a layer of calibrated sand about 20 cm thick and characterized by a low organic matter content (total organic carbon < 0.1% of sediment dry mass). Their main water supply is pumped in a channel (Vieux Rhône) of the Rhône River using centrifugal pumps (rotation: 1000 rounds per minute) that markedly limit the transport of top-predator fishes from Rhône River to wetlands. Despite similar designs, the wetlands developed differences over time due to the accumulation of fine particles (< 63 µm) at the water–sediment interface, influencing the availability of the benthic habitat for biofilms. Indeed, the presence of fine sediments on a coarse and poorly organic sediment favours the physical attachment and the nutrient availability for benthic biofilms (Sundbäck et al. 2003; van de Koppel et al. 2001; Watermann et al. 1999). For the present study, we selected three wetlands (called A, B, C) that were characterized by varying amounts of fine particles (proportions

determined by laser diffractometry following Estragnat et al. 2018) at the water–sediment interface (Fig. 1a, one-way ANOVAs, comparison of fine sediment proportion among wetlands,  $F_{2,15} = 29.6$ ,  $p < 0.001$ ), leading to contrasted benthic habitats for benthic biofilms. Following the decreasing gradient of fine particle amount from wetland A to wetland C, algal biomass and net photosynthesis activity (see below for details on measurements) of the biofilm decreased from wetland A with a mean chlorophyll a content of 2.85 µg/cm<sup>2</sup> and positive net production to wetland C with a mean chlorophyll a content of 1.55 µg/cm<sup>2</sup> and negative net production as photosynthesis did not compensate for respiration (Fig. 1b, c, one-way ANOVAs, comparisons of algal biomass and net photosynthesis among wetlands,  $F_{2,15} = 26.6$ ,  $p < 0.001$  for algal biomass,  $F_{2,15} = 23.6$ ,  $p < 0.001$  for net photosynthesis). These conditions allowed us to evaluate the trophic relationships between primary productivity, benthic food sources, and invertebrate communities.

### Environmental conditions before sampling date

The three studied wetlands had the same water supply and water column depth during a period of 6 weeks before the sampling date (on 22nd of October 2014), minimizing the potential influence of hydrological conditions on community structure. During this period, we also verified that the three wetlands were characterized by comparable physico-chemical conditions in the water column. In situ monitoring of



**Fig. 1** **a** Percentage of fine particles (< 63 µm), **b** benthic algal biomass and **c** net photosynthetic activity of benthic biofilms measured in the three studied wetlands ( $n = 6$  measures per wetland)

water temperatures showed similar variations (between 14.7 and 24.6 °C) in the three artificial wetlands. Weekly measurements of specific conductivity, pH, and dissolved oxygen (DO) concentrations performed with a HQ40D multiparameter (HACH) also indicated comparable values among artificial wetlands with mean ( $\pm$  standard deviation) values of 337 ( $\pm$  13)  $\mu$ S/cm, 8.3 ( $\pm$  0.3), and 9.4 ( $\pm$  0.5) mg/L for specific conductivity, pH and DO, respectively. Nutrient concentrations were also measured weekly in the water column of the wetlands following Gette-Bouvarot et al. (2014). Comparable dissolved nutrient concentrations and fluctuations were found in the three wetlands with concentrations of N-NO<sub>3</sub><sup>-</sup>, N-NH<sub>4</sub><sup>+</sup> and P-PO<sub>4</sub><sup>3-</sup> of 0.99  $\pm$  0.21 (mean  $\pm$  SD) mg/L, 32.78  $\pm$  20.13  $\mu$ g/L and 12.29  $\pm$  9.27  $\mu$ g/L, respectively.

### Sampling design

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

### Chemical and biological analyses on sediments

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

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

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

Net photosynthetic activity (NP) was determined by measuring oxygen production at 15 °C (close to field temperature at sampling date) on intact biofilms (4 cm<sup>2</sup> collected with a cut syringe, see above) using 4 mL respiration chambers fitted with micro-probes (Microrespiration system, Unisense, see Gette-Bouvarot et al. 2015 for details). Photosynthesis measurements were performed with an irradiance of 150  $\mu$ mol/m<sup>2</sup> s, close to maximal photosynthetically active radiations (PAR) measured at midday with a LI-193 Spherical Quantum Sensor (PAR varying between 20 and 130  $\mu$ mol/m<sup>2</sup> s depending on meteorological conditions). For measurements, total dissolved inorganic carbon concentration was adjusted to 10 mM with KHCO<sub>3</sub> to ensure sufficient supply of inorganic carbon during the incubation and pH was maintained at 6.5 by addition of a citrate buffer. Net photosynthesis rate was expressed as nmol of O<sub>2</sub> min<sup>-1</sup> cm<sup>-2</sup> of sediment surface.

## Analyses on benthic invertebrates

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

## Statistical analyses

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

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

with  $\text{Covv}(X_k, X_l) = \text{Trace}(X_k^T D_n X_l D_p) = \text{Trace}(X_l^T D_n X_k D_p)$  as the vectorial covariance and  $\text{Vav}(X_k) = \text{Trace}(X_k^T D_n X_k D_p)$  and  $\text{Vav}(X_l) = \text{Trace}(X_l^T D_n X_l D_q)$  as the vectorial variance for  $X_k$  and  $X_l$ , respectively; matrix  $D_n$  contains row weights (common to both data sets) and matrices  $D_p$  and  $D_q$  contain the column weights of  $X_k$  and  $X_l$ , respectively (see Blanc et al. 1998). To test the significance of Rv-coefficients, rows were randomly permuted within tables. Permutations were repeated 1000 times to

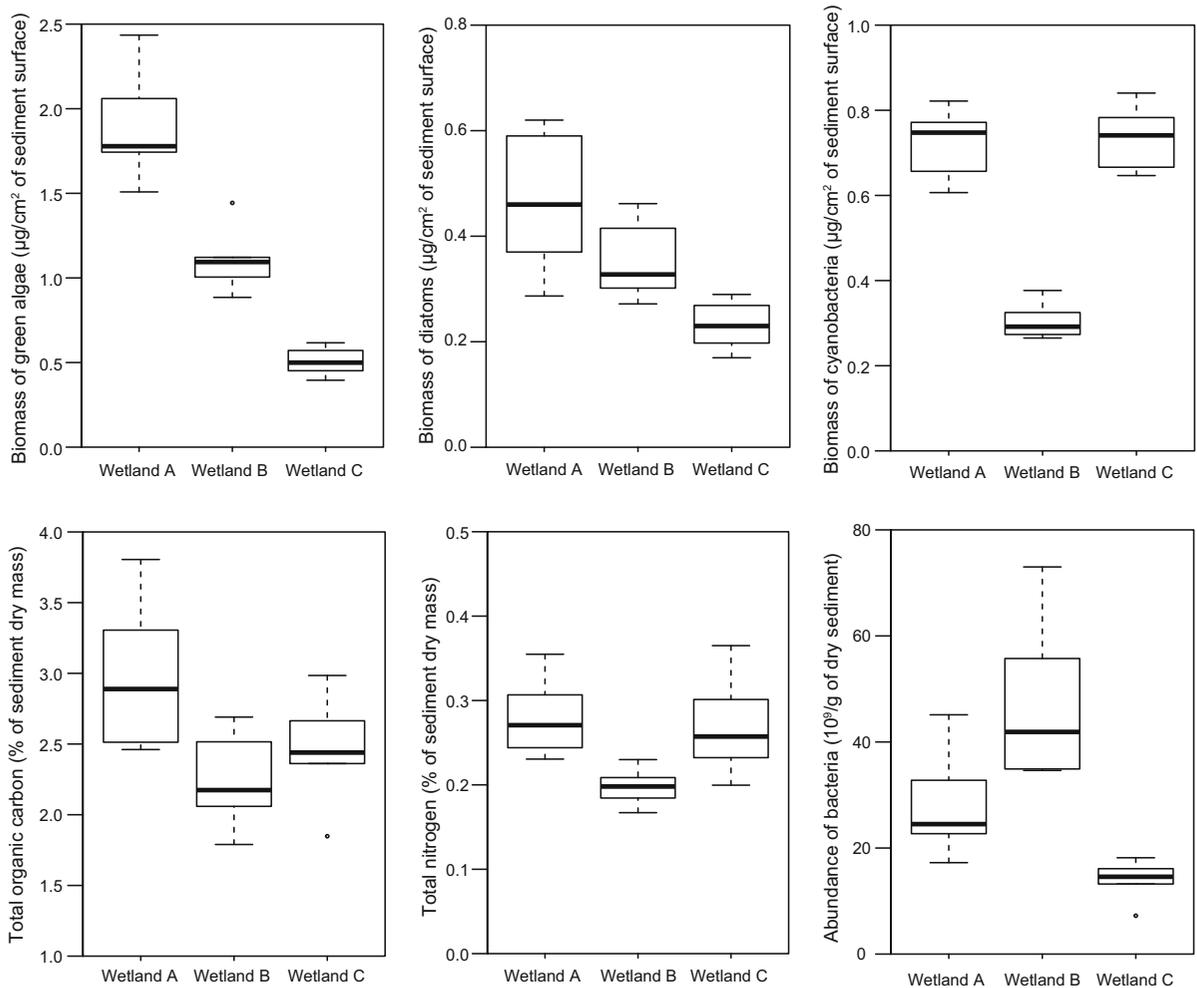
obtain a null distribution of Rv-coefficients. We assessed the statistical significance by determining the proportion of null values that were greater than the observed Rv-coefficients.

Linear regressions were performed to determine the significance of the correlations among biofilm characteristics and the abundance and richness of invertebrate functional groups (e.g., green algae and grazer abundance) by considering all sampled zones (3 wetlands \* 6 replicate zones per wetland = 18 points per regression analysis). For all variables, the normality and the homoscedasticity of the residuals were verified using the Shapiro–Wilk test and the Levene test, respectively. ANOVA analyses, co-inertia analysis, linear regressions and graphical displays were performed using functions in the ade4 package (Chessel et al. 2004; Dray et al. 2007) in R (R Development Core Team 2015). Significance for statistical tests was accepted for a first species risk  $\alpha < 0.05$ .

## Results

### Biofilm characteristics of the three wetlands

Algal colonization of the water–sediment interface was significantly different among wetlands (Fig. 2) and followed the gradient of net productivity measured (Fig. 1): green algae and diatom biomasses were positively correlated (Pearson's  $r = 0.829$ ) and exhibited decreasing values from wetland A to wetland C with intermediate values in wetland B (one-way ANOVAs,  $F_{2,15} = 58.9$ ,  $p < 0.001$  for green algae and  $F_{2,15} = 10.1$ ,  $p < 0.01$  for diatoms). The densities of these two algal groups were positively correlated with the net photosynthetic activity ( $R^2 = 0.65$ ,  $p < 0.001$ ,  $n = 18$  with green algae biomass, and  $R^2 = 0.46$ ,  $p < 0.01$ ,  $n = 18$  with diatom biomass). Cyanobacteria biomass showed a distinct pattern as it was significantly lower in wetland B than in the two other wetlands (Fig. 2, one-way ANOVA,  $F_{2,15} = 79.4$ ,  $p < 0.001$ ). Percentages of total organic carbon and total nitrogen were also the lowest at the sediment interface of wetland B (one-way ANOVAs,  $F_{2,15} = 5.1$ ,  $p < 0.05$  for total organic carbon and  $F_{2,15} = 5.9$ ,  $p < 0.05$  for total nitrogen). Hence, we detected a significant and positive correlation between cyanobacteria biomass and total nitrogen ( $R^2 = 0.37$ ,



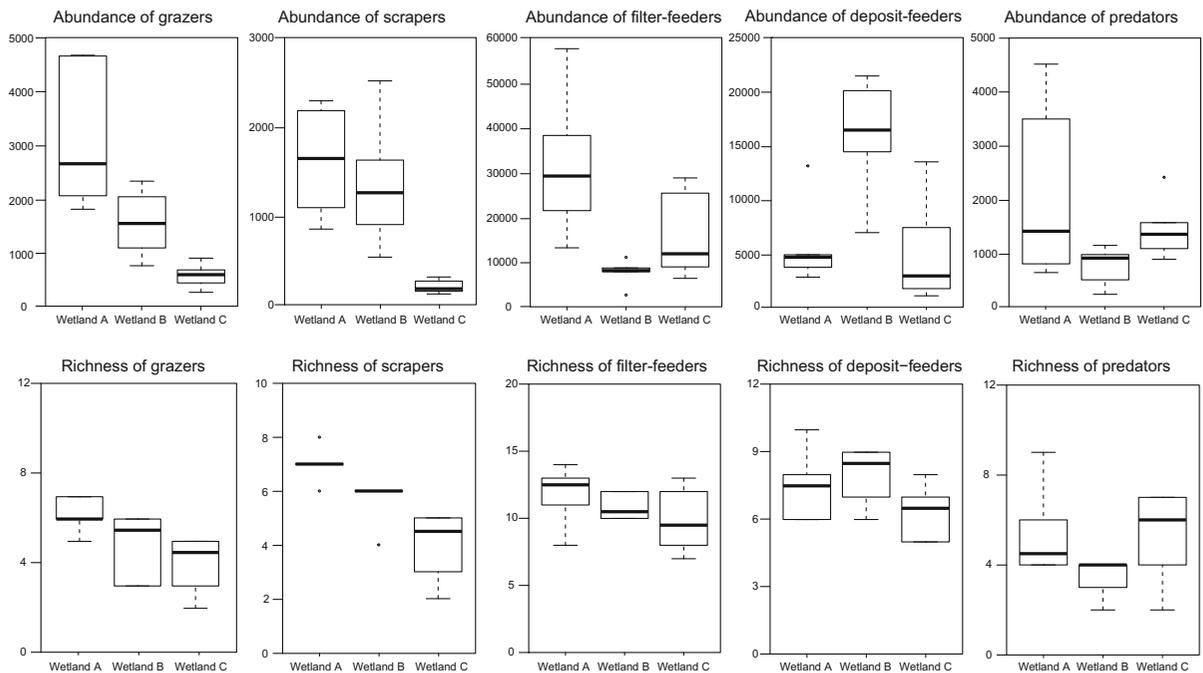
**Fig. 2** Characteristics of the biofilms in the three wetlands ( $n = 6$  measures per wetland for each variable)

$p < 0.01$ ,  $n = 18$ ) but not between cyanobacteria biomass and total organic carbon ( $R^2 = 0.18$ ,  $p > 0.05$ ,  $n = 18$ ). In contrast, bacterial abundances were negatively correlated with cyanobacteria biomasses ( $R^2 = 0.55$ ,  $p < 0.001$ ,  $n = 18$ ) and exhibited higher cell numbers in wetland B than in the other wetlands (one-way ANOVA,  $F_{2,15} = 14.6$ ,  $p < 0.001$ ).

#### Functional composition of benthic invertebrate communities in the three wetlands

Abundances and richness of grazers and scrapers were significantly different among wetlands (one-way ANOVAs,  $F_{2,15} = 14.1$ ,  $p < 0.001$  for grazer abundance,  $F_{2,15} = 11.8$ ,  $p < 0.001$  for scraper abundance,

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



**Fig. 3** Abundance (ind/m<sup>2</sup>) and richness (taxa/sample) of the five major trophic functional groups of benthic invertebrates collected in the three wetlands ( $n = 6$  measures per wetland)

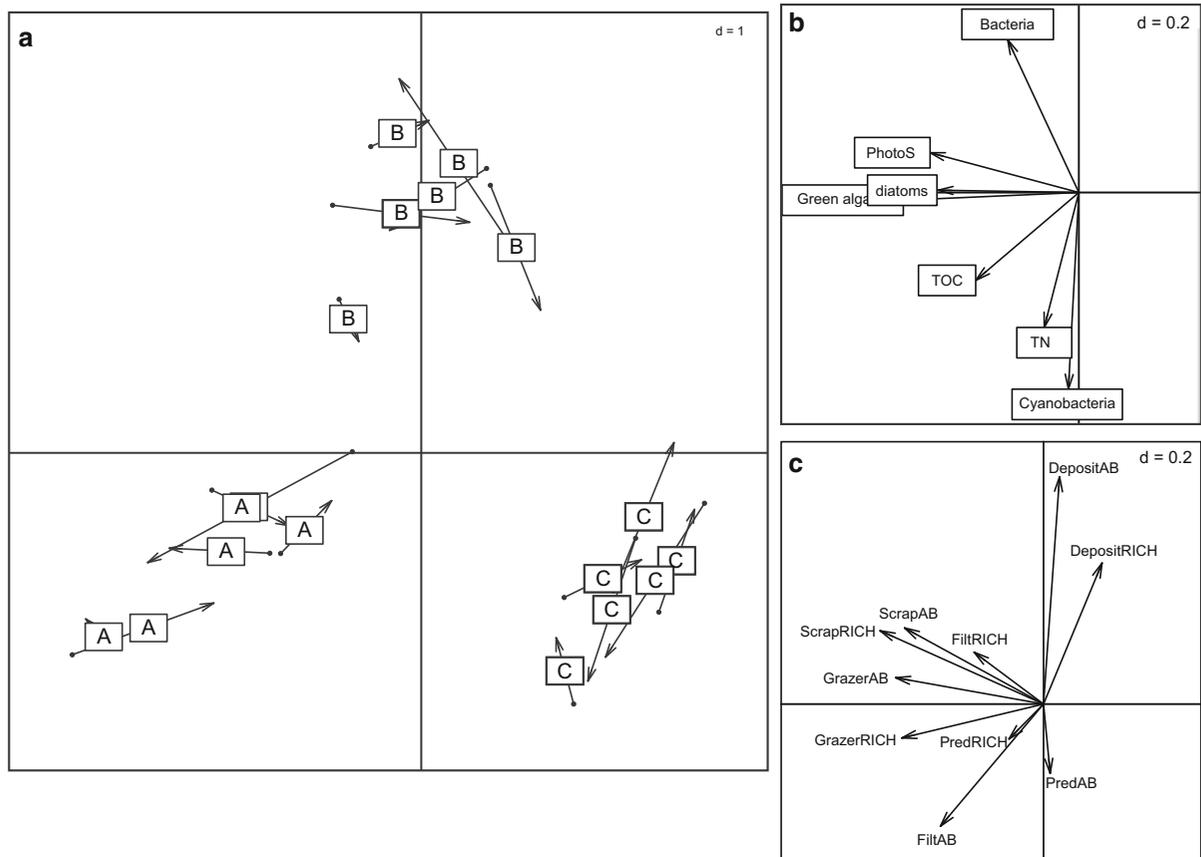
among wetlands (one-way ANOVA,  $F_{2,15} = 2.5$ ,  $p > 0.1$ ). In contrast with the other functional groups, the abundance of predators was not significantly different among wetlands due to the high variability measured among sampled zones of the wetland A (Fig. 3, one-way ANOVA,  $F_{2,15} = 2.4$ ,  $p > 0.1$ ). Similarly, no significant differences in predator richness was measured among wetlands ( $F_{2,15} = 2.3$ ,  $p > 0.15$ ).

#### Relationships between biofilm characteristics and functional composition of benthic invertebrate communities

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

On the factorial map of variables (Fig. 4b, c), the horizontal axis indicated that samples characterized by

high net photosynthetic activity and high diatom and green algae biomasses were also dense and rich in herbivores (grazers and scrapers). There were significant positive linear correlations between these biofilm characteristics (net photosynthetic activity, diatom or green algae biomass) and the densities of herbivores (grazers and scrapers) (Fig. 5). The richness of grazers and scrapers was also linearly and positively correlated with these biofilm characteristics and more especially with the biomass of green algae (relationships illustrated on Fig. 6). The vertical axis of the co-inertia analysis discriminated the samples with high bacterial densities and high abundances of deposit-feeders from those of high cyanobacteria biomass and nitrogen content and low deposit-feeder abundances (Fig. 4b, c). The abundance of deposit-feeders was significantly and positively correlated with bacterial abundance (Fig. 7a) but not with total nitrogen and total organic carbon ( $R^2 < 0.1$ ,  $p > 0.05$ ,  $n = 18$ ). The abundance of deposit-feeders was negatively correlated with cyanobacteria biomass (Fig. 7b). We did not detect clear correlations between biofilm characteristics and the functional groups of filter-feeders and predators. While no significant differences in predator abundance was measured among wetlands, linear



**Fig. 4** Co-inertia analysis showing **a** the shared structure obtained from the biofilm and fauna datasets, **b** the factorial map of biofilm variables and **c** the factorial map of variables associated with invertebrate functional groups. A = Wetland A, B = Wetland B, C = Wetland C, PhotoS = Net Photosynthesis rate, TOC = Total organic carbon, TN = Total nitrogen, DepositAB = Abundances of deposit-feeders, DepositRICH =

Richness of deposit-feeders, ScrapAB = Abundances of scrapers, ScrapRICH = Richness of scrapers, FiltAB = Abundances of filter-feeders, FiltRICH = Richness of filter-feeders, GrazerAB = Abundances of grazers, GrazerRICH = Richness of grazers, PredAB = Abundances of predators, PredRICH = Richness of predators

regression performed on all sampled zones (3 wetlands \* 6 zones = 18 points per regression analysis) showed that the abundance of predators was significantly and positively correlated with the abundance of other invertebrates (Fig. 8). No significant correlations were obtained between predator richness and the abundance and richness of other invertebrates.

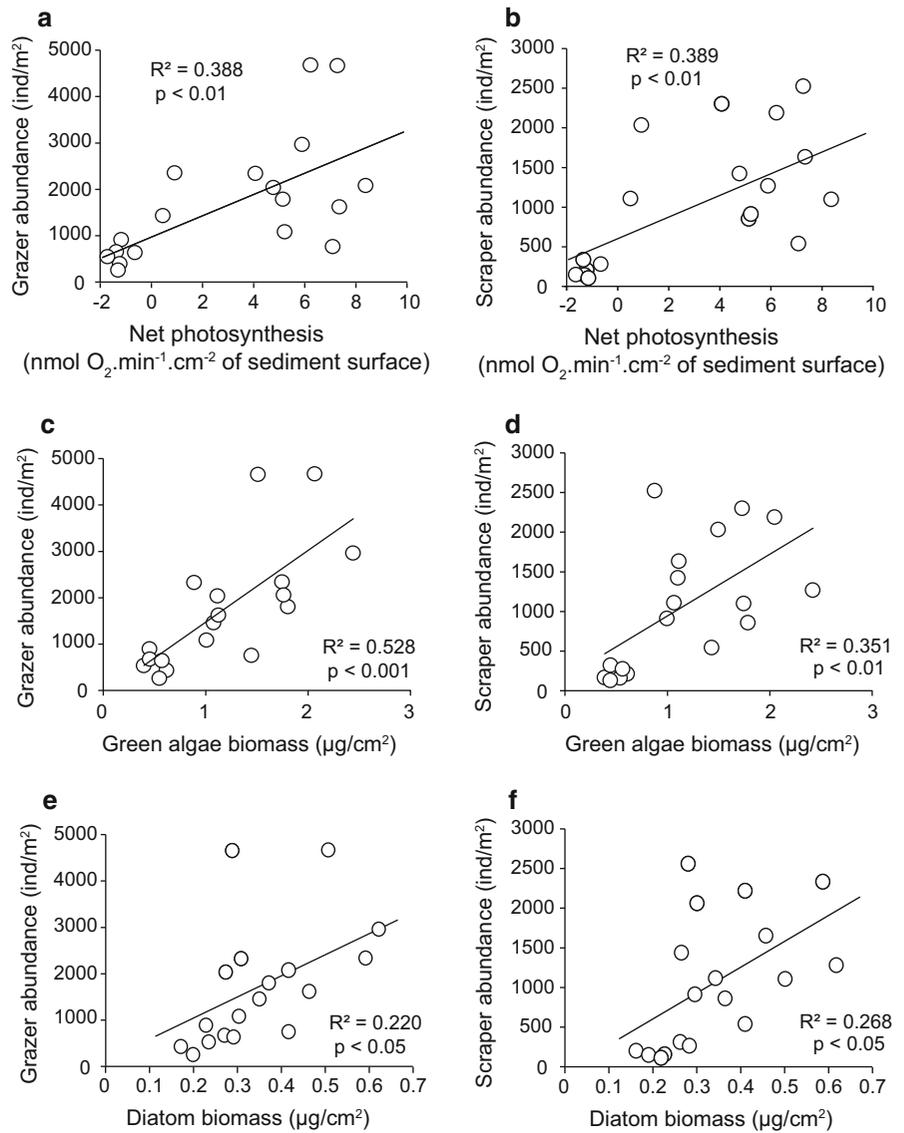
## Discussion

Although the literature highlighted the occurrence of significant top-down control of communities in wetlands (Magnusson and Williams 2009; Hillebrand 2009; Moore 2018), top-down forces were apparently

weak in our systems. Then, our dataset did not corroborate the prediction of EEH (Oksanen et al. 1981) because there was not a significant influence of top-down forces in our most productive wetland. The analysis of the links between biofilms and functional trophic groups of invertebrates clearly showed a dominant bottom-up effect of primary productivity (net photosynthesis) and algal resources on herbivores in artificial wetlands. Indeed, the abundances of both grazers and scrapers were positively and linearly correlated with the biomass of green algae and diatoms in wetlands. These correlations indicate that the bottom-up control of green algae and diatoms was stronger than the top-down influence of herbivores on algal resources. As previous enclosure experiments

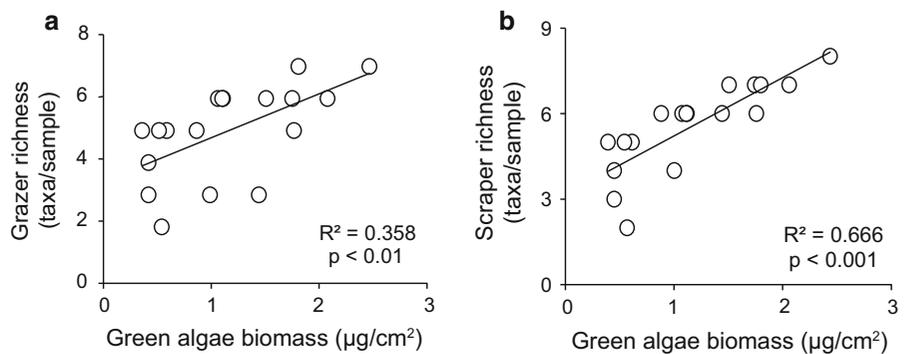
**Fig. 5** Correlations

**a** between net photosynthetic activity and grazer abundance, **b** between net photosynthetic activity and scraper abundance, **c** between green algae biomass and grazer abundance, **d** between green algae biomass and scraper abundance, **e** between diatom biomass and grazer abundance, and **f** between diatom biomass and scraper abundance

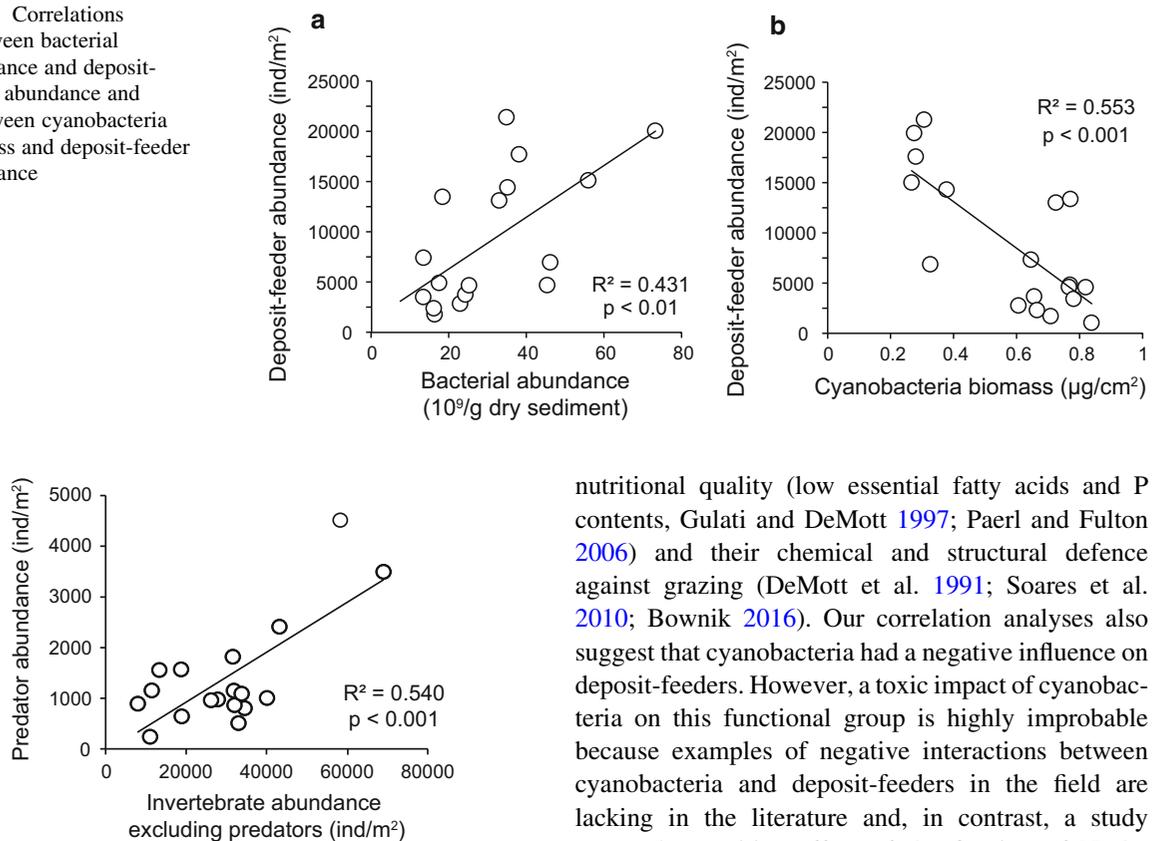


**Fig. 6** Correlations

**a** between green algae biomass and grazer richness and **b** between green algae biomass and scraper richness



**Fig. 7** Correlations  
**a** between bacterial abundance and deposit-feeder abundance and  
**b** between cyanobacteria biomass and deposit-feeder abundance



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

showed that the introduction of a grazer (the gastropod *Viviparus viviparus*, a species which is not naturally present in our artificial wetlands) had a significant top-down effect on algae in these artificial wetlands (Gette-Bouvarot et al. 2015; Estragnat et al. 2018), we can conclude that pressure by grazers and scrapers naturally present in these systems was not sufficient enough to reduce algal biomass.

Positive relationships between herbivore abundance and biomass of green algae and diatoms contrasted with the lack of relationship detected between herbivores and cyanobacteria biomass. This result may suggest that herbivores consumed green algae and diatoms rather than cyanobacteria in wetlands, resulting in no relationship between cyanobacteria biomass and herbivore abundance. This suggestion of a poor trophic transfer from cyanobacteria to herbivores is consistent with several studies indicating that cyanobacteria are generally non-attractive trophic sources for invertebrates due to their poor

nutritional quality (low essential fatty acids and P contents, Gulati and DeMott 1997; Paerl and Fulton 2006) and their chemical and structural defence against grazing (DeMott et al. 1991; Soares et al. 2010; Bownik 2016). Our correlation analyses also suggest that cyanobacteria had a negative influence on deposit-feeders. However, a toxic impact of cyanobacteria on this functional group is highly improbable because examples of negative interactions between cyanobacteria and deposit-feeders in the field are lacking in the literature and, in contrast, a study reported a positive effect of the fixation of N<sub>2</sub> by cyanobacteria on deposit-feeders (Karlson et al. 2014). Moreover, we did not detect any negative influence of cyanobacteria biomass on grazers and scrapers, two trophic functional groups that would be the most affected by toxin produced by cyanobacteria (Bownik 2016). Together, these results suggest that cyanobacteria were probably not toxic for invertebrates in our artificial wetlands. The negative correlation observed between cyanobacteria biomass and deposit-feeder abundance was more likely associated with the feeding preference of deposit-feeders for bacteria than for algae (e.g., Yingst 1976; Lopez and Levinton 1987). Indeed, the abundance of deposit-feeders was significantly and positively correlated with bacterial abundance in our dataset, suggesting a bottom-up effect of bacteria on deposit-feeders. In parallel, a negative correlation between bacterial abundance and cyanobacteria biomass has been detected, explaining the statistical significance of the negative correlation between deposit-feeder abundance and cyanobacteria biomass.

In addition to the positive relationship between algal (green algae and diatoms) biomass and herbivore abundances, we also showed that grazer and scraper richness were positively correlated with the biomasses of green algae, diatoms and photosynthetic activity. These results indicate that basal resources and net primary productivity may positively influence the horizontal diversity of the food web (*sensu* Srivastava and Bell 2009). This positive relationship between primary productivity (and energy associated with trophic resources) and herbivore taxa richness can be related to the “species-energy theory” (Wright 1983; Srivastava and Lawton 1998; Evans et al. 2005). Indeed, several studies support the hypothesis that energy correlates positively with species richness (e.g., Huston 1994; Evans et al. 2005). In our field conditions, we can expect that an increase in benthic primary productivity could have elevated the amount of certain individual resource types (i.e., algal species), enabling specialist herbivore species to feed on them. Consequently, this trophic specialization would have led to reduced niche overlap among herbivores, reducing rates of competitive exclusion and elevating species richness in more productive wetlands. We also suspect that the diversity of individual resource types (i.e., algal species) increased with benthic primary productivity, enabling the highest herbivore diversity in the wetland characterized by the highest algal richness. Nevertheless, we cannot confirm this potential link between the trophic specialization of herbivore taxa and the abundances of individual resource types because green algae and diatom groups contained several species with contrasted trophic preferences for invertebrates (e.g., Tall et al. 2006; Alfaro 2009). More precise analyses such as invertebrate gut analyses using metabarcoding approaches (Pompanon et al. 2012) would be necessary to determine the trophic niche of each herbivore taxa in association with the availability of algal species in artificial wetlands. This perspective is very promising to evaluate whether the trophic specialization of herbivores in the most productive wetlands can explain the positive relationship between net benthic primary productivity (energy) and herbivore taxa richness in our artificial systems.

The positive and significant linear correlation between the abundances of predators and other aquatic invertebrates also suggest that bottom-up control of predators by their preys was stronger than the top-

down control exerted by predators on their preys in our artificial wetlands. The lack of a strong top-down control of invertebrate predators on other invertebrates in the most productive wetland (wetland A) would be associated with the increased horizontal diversity in food web observed for grazers and scrapers in this wetland. Indeed, increased diversity of a trophic level would mitigate top-down control by predators on this trophic level due to differences in predation pressure among the species of this trophic level. More precisely, a resource base with more species is more likely to contain at least one species that is relatively resistant to consumption and can compensate for the decrease of more consumable species in the presence of consumers (Leibold 1989; Duffy et al. 2007). Nevertheless, determining whether the horizontal diversity of preys was responsible of the lack of significant top-down forces in our artificial wetlands is out of the scope of the present study. This further step would require more complete description and quantification of species–species interactions within the food webs.

Within the detritus-based food web, the positive linear relationship between the bacterial abundance and the abundance of deposit-feeders suggests that the functional group of deposit-feeders was also bottom-up controlled by their trophic resources. Nevertheless, the abundance of bacteria was not correlated with the quantity of total organic carbon and total nitrogen in the sediment, suggesting that sedimentary stocks of nitrogen and organic carbon did not control the detritus-based food web (a control largely observed in many sedimentary environments, Danovaro et al. 1995; Lin and Yo 2008; Ramalho et al. 2014). Indeed, bacterial abundance was the highest in the wetland B characterized by the lowest concentrations of total nitrogen and total organic carbon in the sediment. As deposit-feeder abundance was also the highest in wetland B, we can expect that the positive link between bacteria and deposit-feeder abundance was likely due to a positive interaction between deposit-feeding activities and bacteria. The positive effect of deposit-feeders on bacteria has been largely demonstrated in a wide range of freshwater sediments (van de Bund et al. 1994; Griebler 1996; Traunspurger et al. 1997; Wieltschnig et al. 2008; Nogaro et al. 2009; Pignoret et al. 2016). For example, a recent experiment performed in one of the artificial infiltration wetlands studied here demonstrated that aquatic oligochaetes,

which are the main representatives of deposit-feeders in the present study, had a strong positive and significant influence on the abundance (+ 100%) and activity (+ 35%) of bacteria in sediments (Mermillod-Blondin et al. 2018). The stimulation of the bacterial compartment by deposit-feeders also leads to an increased organic matter mineralization in sediments (e.g., Pignieret et al. 2016). Therefore, we can expect that the lower concentrations of total nitrogen and total organic carbon measured in the sediment of wetland B in comparison with the sediments of the two other wetlands were associated with the threefold higher abundances of deposit-feeders in wetland B. Thus, we can argue that the top-down and positive effect of deposit-feeders on microorganisms was a probable mechanism explaining the positive relationship between bacteria and deposit-feeder abundances in the present experiment.

## Conclusions

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

feeder abundance was not linked to the amount of organic matter in sediments. Different feeding rates of invertebrates and contrasted renewal rate of basal resources (more rapid for algae than for detritic organic matter) between the two food webs may explain the different links between invertebrates and basal food sources reported for both food webs. These links are expected to have implications on the whole ecosystem functioning (nutrient cycling, energy fluxes) and need to be considered in future studies. With this aim, development of labelling approaches using stable isotopes  $^{-13}\text{C}$  and  $^{15}\text{N}$  (Christianen et al. 2017) would be very promising to precisely quantify the transfer of energy within the phototrophic-based and detritus-based food webs and their consequences on ecosystem functioning. More research on artificial wetlands is needed because these artificial systems have been increasingly developed to compensate for the loss of natural wetlands, particularly in urbanized landscapes (Davidson 2014). This is a major challenge for the future, considering the dramatic increase of the urbanization and the role played by wetland ecosystems for biodiversity preservation and nutrient retention (Hansson et al. 2005).

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