Floating Littoral Zone (FLOLIZ): A solution to sustain macroinvertebrate communities in regulated lakes?

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A B S T R A C T

Artificial water-level fluctuations (WLF) seriously threaten the biodiversity and functioning of littoral zones in lake ecosystems. The use of artificial floating islands (AFI) to compensate for the deleterious effects of WLF on littoral habitats has been of increasing interest to environmental managers. Yet, the ecological efficiency of this solution is still very poorly documented. AFI are usually designed as simple vegetated floating mats. In this study, we designed an artificial Floating Littoral Zone (FLOLIZ), which mimics a natural littoral zone composed of a terrestrial section vegetated with helophytes and several underwater levels containing soil and hydrophytes. Next, we aimed to assess the effectiveness of FLOLIZ in supporting macroinvertebrate communities. Three FLOLIZs were installed in three bays of a French hydroelectric reservoir marked by high WLF. Taxonomic and functional metrics of macroinvertebrate communities in the three FLOLIZs were compared with control littoral stations over four seasons of one year. The cumulated abundance, taxonomic richness and diversity were significantly higher in the FLOLIZs than in the control littoral stations, particularly when water level rose abruptly (i.e., in spring) and during the post-drawdown season (i.e., in summer). Functional profiles of macro-invertebrate communities significantly differed between FLOLIZs and control littoral stations. More specifically, communities in littoral control stations were dominated by highly mobile and resistant taxa (e.g., Beetles, Bugs, Chironomids), while communities in the FLOLIZs were dominated by less mobile species with longer life cycles (e.g., Hydra sp., Oligochaeta). These findings show that FLOLIZs were more successfully colonized by original, diversified, and abundant macroinvertebrate communities with respect to littoral control stations. These preliminary results suggest that FLOLIZs could provide suitable, biogenic habitats for macroinvertebrates in reservoirs exhibiting high WLF. Longer term monitoring, including of other compartments than macroinvertebrates (e.g., fish), could provide additional evidence that FLOLIZs mitigate the deleterious effects of high WLF on aquatic biodiversity.

1. Introduction

Littoral zones of lakes typically support a mosaic of habitats (e.g macrophyte, sediment type, coarse woody debris) (Czarnecka, 2016; Schmieder, 2004) and various abiotic conditions due to interactions between air and water interfaces (Pusey and Arthington, 2003). These heterogeneous conditions favor a great biodiversity of micro- and macro-organisms (Schmieder, 2004) that depend on the littoral zone for their life cycles, whether occasionally (e.g. for breeding, nursery)

(Woodford and Meyer, 2003) or permanently (e.g. feeding, avoiding predation) (Winfield, 2004). For example, macroinvertebrates feed largely on epiphytic algae and decayed macrophytes in the littoral zone (James et al., 2000).

Around the world, littoral zone of lakes are strongly impacted by multiple forms of anthropogenic pressure (Otiang'a-Owiti and Oswe, 2007; Schmieder, 2004; Schnaiberg et al., 2002). In particular, natural water-level fluctuations (WLF) are dominant forces that control the functioning of lacustrine ecosystems (Poff et al., 1997; Wolcox and

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Meeker, 1992). Yet, the use of water for hydropower, agriculture, industry, domestic needs, and flood control leads to high WLF, notably in reservoirs, that are very different (i.e., often much higher and more frequent) than natural fluctuations (Rosenberg et al., 2000). These artificial WLFs increase the erosion of banks (Hellsten, 1997; Hirsch et al., 2017) which results in the degradation of littoral habitats (Evtimova and Donohue, 2016; Furey et al., 2004) and changes lake morphometry (Furey et al., 2004; Hofmann et al., 2008). WLFs also modify abiotic features including the dissolved oxygen, temperature, and nutrients dynamics (Cott et al., 2008; Leira and Cantonati, 2008; Potter et al., 1982) and primary production (Thompson and Ryder, 2008). All littoral communities are impacted, and particularly macroinvertebrates (Baumgärtner, 2008; Brauns et al., 2008; Lemes da Silva and Petrucio, 2018), due to the loss or alteration of habitats (Brauns et al., 2008; Lemes da Silva and Petrucio, 2018). Additionally, macroinvertebrates living in the supra/mediolittoral zone are directly affected by WLF that expose shorelines to desiccation and freezing (Hellsten, 1997).

Macroinvertebrates play a key role in the functioning of aquatic ecosystems (Munn and Brusven, 1991; Solimini et al., 2006). Their population densities are the highest in the littoral zone of lakes and reservoirs (Klimaszyk and Heymann, 2010) and the composition of their communities is closely linked to habitat characteristics (Collier et al., 1998; Tolonen et al., 2001). For this reason, biotic indicators based on macroinvertebrates' taxonomic and functional composition are commonly used to assess the quality of aquatic ecosystems (Mondy et al., 2012; Verneaux et al., 2004) and are implemented into national biomonitoring schemes (Hering et al., 2004; Miler et al., 2013; Rossaro et al., 2007). Many studies have investigated the effects of WLF on macroinvertebrate communities, particularly in reservoirs, and have reported reduced taxa richness, abundance, and biomass with increased WLF (e.g. Aroviita and Hämäläinen, 2008; Haxton and Findlay, 2008; Palomäki, 1994). For example, the study of Valdovinos et al. (2007) reported a taxa richness 6.8 times higher in an unregulated lake compared to a regulated lake in Chile. In addition, WLF affect community composition by selecting the most opportunistic taxa (Munn and Brusven, 1991).

Environmental managers' and scientists' awareness of threats to aquatic biodiversity have enabled restoration ecology to become a major discipline of environmental science over the past four decades (Ormerod, 2003). Several solutions have been proposed to mitigate the deleterious effects of WLF on aquatic biodiversity and to achieve good ecological potential for artificial water bodies as requested by the European Water Framework Directive (WFD 2000/60/EC, 2000). These include the limitation of WLF during the most ecologically sensitive periods (i.e., during spring and summer), the revegetation of banks and shallow littoral areas (Halleraker et al., 2016). Unfortunately, these solutions are often very difficult to reconcile with human interventions that cause strong WLF. Halleraker et al. (2016) also mention the creation of artificial floating islands (AFI) as a mitigation solution. Indeed, AFI are floating structures that provide permanent access to habitats that may mimic those that could be naturally present in lakeshore areas independently of the WLF. Surprisingly, despite the fact that this idea emerged in the 1980s, AFI often only consist of floating mats made of natural or artificial vegetation (Gillet, 1989; Nakamura and Shimatani, 1997) and their effectiveness in supporting aquatic biodiversity, particularly in macroinvertebrates communities, has been overlooked. However, scientific literature is more abundant on the implementation of AFIs as "biological filters" for water quality improvement (see the review of Yeh et al., 2015).

In this study, we designed an artificial Floating Littoral Zone (named herafter, "FLOLIZ") that aimed to mimic the different stages of depth and vegetation of a natural littoral zone, with vegetated substrates of both helophytes and hydrophytes. Next, we evaluated the effectiveness of this newly designed floating structure to support the macroinvertebrate community of a reservoir that exhibits very high WLF (30 m

mean annual amplitude). For this purpose, we compared the macroinvertebrate abundance and taxonomic and functional composition of three FLOLIZs to control littoral stations over one year. We hypothesised that FLOLIZs provide refuge habitats for macroinvertebrates of littoral habitats exposed to WLF and hence, higher abundance and taxonomic richness would be found in FLOLIZs than in control littoral stations after the first event of high WLFs at the end of winter and early spring (april 2019). We also expected different macroinvertebrate taxonomic and functional (by ecological traits) compositions in FLOLIZs and control littoral stations due to the differences in habitats, more diversified, structured, and stable in FLOLIZs compared to littoral control stations. In particular, we expected to find higher abundance of macroinvertebrates organisms exhibiting ecological traits allowing them to maintain in unstable environment (e.g., high mobility, fast breeding) in the control littoral stations than in FLOLIZ habitats. In contrast, we expected to find in FLOLIZs macroinvertebrates that could be found in natural littoral zones, and characterized by traits such as low mobility, low reproduction rate and dependence on plant habitats for example.

2. Materials and methods

2.1. Overview of FLOLIZ design

The FLOLIZ consists of a 70m^2 structure (14 m × 5 m) built with 156 High Density PolyEthylene (HDPE) Caissons (MarineFloor©, Port Leucate city) (Fig. 1A). Slightly less than half of the caissons were opened and holes drilled in bottom to be used as planters. Seventy-two soil clods containing different helophyte species were installed on each FLOLIZ in a uniform way (Fig. 1B). Helophyte roots could grow out of the caissons through the holes, creating habitats for macroinvertebrates (and spawning or nursery habitats for fish). The inside was fabricated with immerged, extruded aluminium structures connected by chains to the floating caissons. Each FLOLIZ was composed of 3 independent aluminium structures (Fig. 1C): two 4 m × 4 m × 0.5 m structures and one 4 m × 4 m × 0.8 m central structure. Both depths of the lower structures provided two underwater levels (Fig. 1A). Stainless steel cages (0,50 m × 0,80 m × 0,25 m) filled with a biogenic component (recycled oyster shells) or inert materials composed of 98% cellular glass stone and 2% minerals (Misapor company, Albula city) were attached to the bottom of the structure to simulate pebble-like soil (Fig. 1C). Both lengthwise sides of the structure were enclosed by cages filled with oyster shells to create a confined environment, preventing the impact of waves and favouring water warming. The width wise sides at the extremities were partially opened with wire mesh cages to allow free movement for aquatic organisms (e.g. invertebrates, fish). Finally, for each FLOLIZ, 21 m^2 were vegetated with various hydrophyte species (Fig. 1D and Fig. 1E) on different types of substrates (horticultural rock wool, aquatic potting soil). More information on vegetalisation is available in the supplementary materials (see Appendix A1a + Fig. S1). The description of the anchoring system, which is an important component of the structure, is also available in the supplementary materials (see Appendix A1b + Fig. S2).

2.2. Study site

Serre-Ponçon is a large French reservoir with a surface area of 28 km^2 (20 km long) and a volume of 1272 km^3 at maximum water elevation. Its mean depth is 72 m and maximum depth 110 m. It is located in South-eastern France (Fig. 2A) at an altitude of 780 m (Fig. 2B). This reservoir was built in 1959 to prevent devastating floods from the two main inflow rivers (Durance and Ubaye) and for hydroelectric power production. It is also used for irrigation, drinking water, and recreational activities. The flow of the Durance and the Ubaye into the lake is respectively between 30–200m^3/s and 10–70m^3/s (excluding floods). These two rivers represent more than 90% of the annual inflow into the reservoir while the remainder comes from many other small
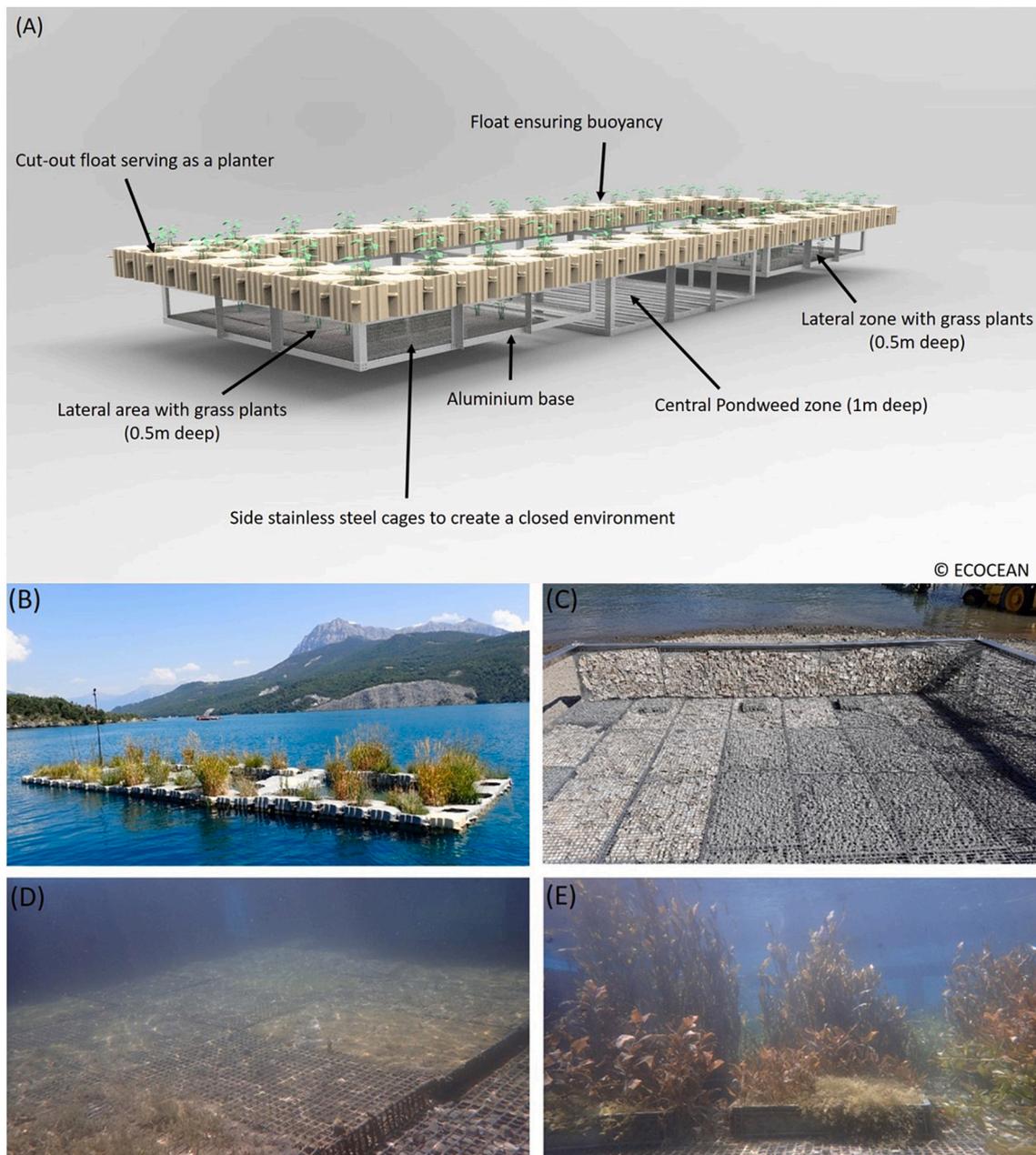
Fig. 1. Design of FLOLIZ structure 14 m long and 5 m wide (© OFB-INRAE-ECOCEAN). (A) 3D design (B) Emerged part with floating caissons and helophyte planters. (C) Submerged aluminium structure with encaged soil. (D) 0.5 m deep stage with grass plants. (E) 1 m deep stage with pondweeds.

tributaries. Serre-Ponçon benefits from a Mediterranean-type climate with many sunshine and moderate winds, but with a mountainous influence. This climatic environment makes this reservoir a monomictic temperate system with stratification from March to September. Water quality in the reservoir has been monitored since 2007 according to the requirements of the European Water Framework Directive (WFD 2000/60/EC, 2000). In 2016, the lake exhibited good water quality (Légifrance: https://www.legifrance.gouv.fr/jorf/id/JORFTEXT0000 37347756) (Table S1). The reservoir exhibits high seasonal WLF (ranging from 20 to 50 m, Fig. S3) between winter and early summer. At the end of spring, the snow melt and reduced hydroelectric production allow the reservoir to refill, but this results in daily water level fluctuations, in the range [−0.2 m; +1.2 m] in the last 4 years. These WLF induce a morphological alteration of the banks by the action of the wind and waves. Therefore, banks present a high degree of homogeneity, with an absence of macrophytes and littoral habitats (Fig. 2C).

2.3. Study stations and experimental design

Three FLOLIZs were anchored on 15 September 2018 in three different bays in the downstream part of the reservoir. These bays were selected to fulfil the following criteria: 1) a depth greater than the average annual WLF (about 30 m) in order to prevent the stranding of the FLOLIZs (Fig. 2C), 2), a limited exposure to recreational activities and wind and 3) the presence of a neighbouring bay sharing similar hydromorphological characteristics where control stations could be chosen. The FLOLIZ area was used to determine the size of the control station; accordingly, each control station was defined by a linear area of about 70 m by 1 m (i.e. 70 m^2). For each FLOLIZ, two control littoral stations were selected: a nearby control station (NCS, Fig. 2C) located at the head of the same bay and a distant control station (DCS, Fig. 2C) in a neighbouring bay. DCS aimed to detect potential impact of the FLOLIZs on macroinvertebrate communities of the nearby littoral zone. Each DCS
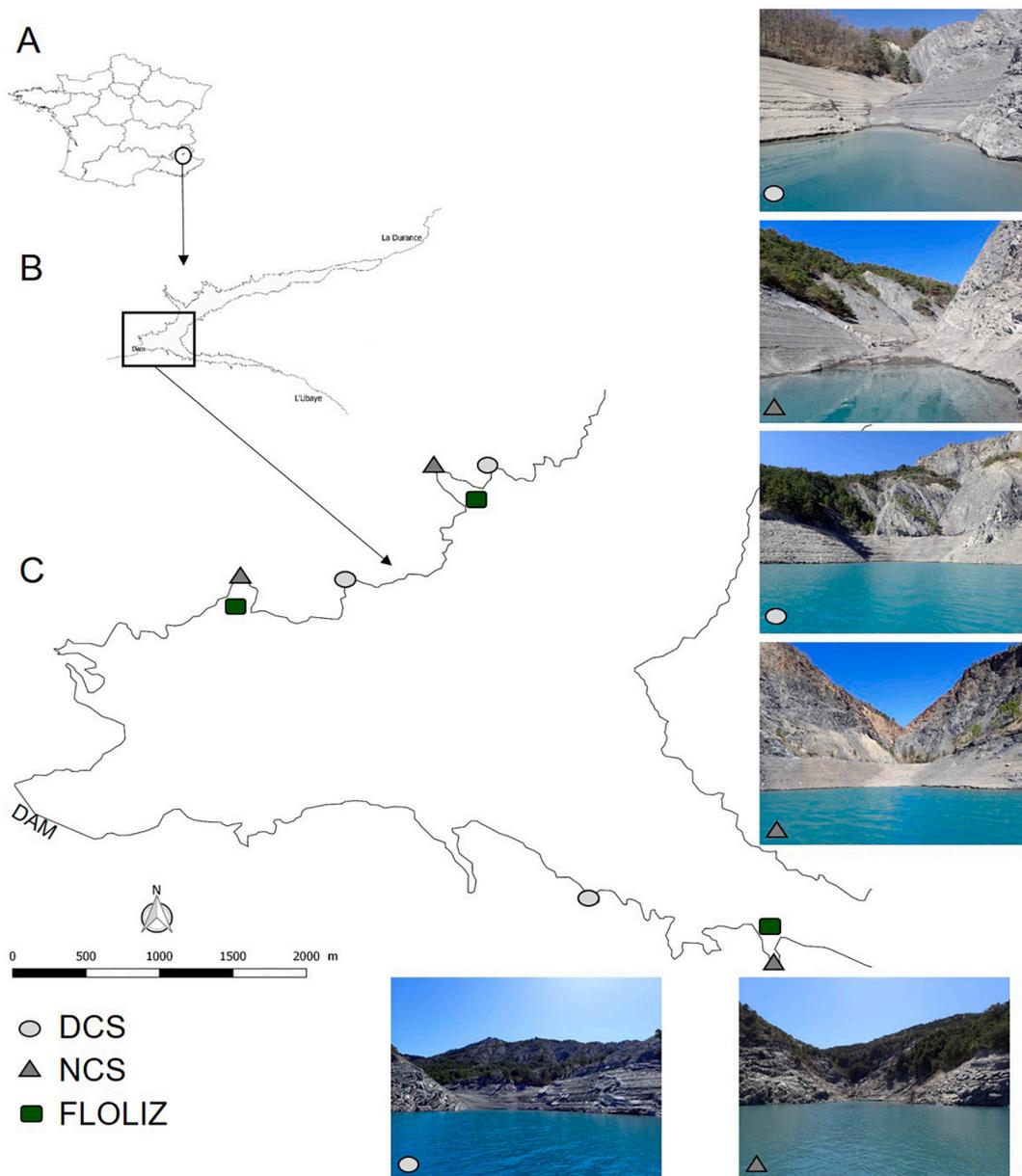
Fig. 2. Location of the FLOLIZ in Serre-Ponçon (WGS84 coordinates X: 44.527287; Y: 6.381121). (A) Location of Serre-Ponçon reservoir in France, (B) Focus on the reservoir (contour at 780 m elevation which is the highest water level) with the both inflow rivers Durance and Ubaye, (C) Focus on the station positions in the downstream part of the reservoir. DCS: Distant Control Station, NCS: Nearby Control Station, FLOLIZ: Floating Littoral Zone.

was selected to be geographically and hydromorphologically similar to the FLOLIZ bay (NCS). For this purpose, a mapping of the different substrates in each bay was carried out using a standardised national protocol (NF 16870, Fig. S4). These maps showed the exclusive presence of mineral substrates in all bays with a predominance of pebbles, slab, or gravel.

In addition, to ensure the absence of environmental variability in stations during each seasonal campaign, the physico-chemical characterisation of the water in each bay was carried out, including temperature and oxygen profiles and various components of the trophic state (see details in Table S2).

2.4. Macroinvertebrate sampling

The monitoring of macroinvertebrates started 2 months after the installation of the FLOLIZs. Macroinvertebrates were sampled seasonally on November 27th, 2018 (corresponding to Autumn 2018), on

February 05th, 2019 (corresponding to Winter 2019), on May 24th, 2019 (corresponding to Spring 2019) and on August 26th, 2019 (corresponding to Summer 2019). Macroinvertebrate communities at DCSs and NCSs were sampled using a surber net (i.e. 250-μm mesh size; sampling area 0.05 m^2). For each control station, two samples were collected at 0.5 m depth and one sample at 1 m depth corresponding to the underwater stages of the FLOLIZs. For macroinvertebrate sampling in the FLOLIZs, the surber net could not be used because the substrate was caged. Thus, 4 removable substrates measuring 20 × 25 × 0.5 cm (i. e. a sampling area of 0.05 m^2) and containing Misapor (98% cellular glass stone and 2% minerals) were previously installed in each aquatic compartment (12 per FLOLIZ). At each seasonal campaign, one removable substrate was collected randomly at each underwater stage (i.e. 2 cages removed at 0.5 m and 1 cage removed at 1 m depth) and placed in 250- μm mesh net. The removable substrate was rinsed and shaken several times in a basin and the Misapor was carefully scrubbed to remove attached organisms. To ensure that all individuals were

collected, an accurate check was performed for each substrate. The sample was then passed over a 250-μm mesh screen to collect the macroinvertebrates. All samples were conserved in pure denatured alcohol (70%) and were rapidly sieved, sorted, and identified in the laboratory under a stereomicroscope (LEICA MZ75, Germany). Organisms were identified at the most precise possible taxonomic level (frequently genus) using several identification keys (Tachet et al., 2010; Perla : http://www.perla.developpement-durable.gouv.fr/index.php).

2.5. Statistical analysis

A total of 108 macroinvertebrates samples were collected corresponding to 3 samples (2 samples at 0.5 m and 1 sample at 1 m depth) by treatment ($n = 3$, i.e. DCS, NCS, FLOLIZ), bay ($n = 3$) and season ($n = 4$). Three metrics of macroinvertebrate assemblages (taxa number, abundance, 1-Hill index that quantifies diversity) were calculated for each sample. The 1-Hill index is a synthetic index that combines the sensitivity of the Shannon index with rare species and the sensitivity of the Simpson index with abundant species (Hill, 1973). Kruskal-Wallis and Wilcoxon post-hoc tests using Holm adjustment (Holm, 1979) were used to evaluate the differences of the three metrics (1) among stations (i.e, FLOLIZ, DCS, and NCS) for each season and (2) among seasons for each type of station. For each Kruskal-Wallis test, the value of the H-statistic, the number of degrees of freedom and the *P*-value were reported. The coefficients of variation were calculated to compare metrics of seasonal variation for each type of station.

A non-metric multidimensional scaling (NMDS) ordination of macroinvertebrate taxa abundance was performed to examine the distribution of assemblages among stations by using the function 'metaMDS' in the vegan R package (Oksanen et al., 2009). Before running the analysis, the samples (2 at 0.5 m depth and 1 at 1 m) were pooled by date and station to avoid null sample size (which would hinder to calculate Bray-Curtis dissimilarity) and the abundance data were transformed using the Hellinger transformation (Rao, 1995; Legendre and Gallagher, 2001). The Bray-Curtis dissimilarity was used to quantify dissimilarity among stations based on macroinvertebrate assemblages (Bray and Curtis, 1957). Goodness-of-fit was estimated with a stress function, which ranges from 0 to 1, with values inferior to 0.15 indicating a good ordination (Clarke, 1993). Permutation tests were used to test the significance of differences in the macroinvertebrate assemblages among stations and between seasons (using the size of ordination hull) using the function 'ordiareatest' in the vegan R package (Oksanen et al., 2009). This function studies the one-sided hypothesis that the area covered by each convex hull (drawed by the function ordihull by groups i.e. stations or seasons) in the two-dimensional ordination space is smaller than expected under the null hypothesis using permutation test (Oksanen et al., 2013).

Mean community trait profiles were calculated from macroinvertebrate abundance data using 16 fuzzy-coded biological and ecological traits described for each taxon (Chevenet et al., 1994) and hereafter called 'functional traits'. The biological traits reflect the life history of taxa (e.g. 'number of cycles per year'), their resistance and resilience abilities (e.g. 'resistance forms') and general morphological ('body form') or physiological (e.g. 'respiration', 'feeding habits') features (Usseglio-Polatera et al., 2000). The ecological traits mainly describe habitat preferences of taxa at different spatial scales (e.g. substratum, current velocity, temperature, pH, saprobity, longitudinal distribution). Each trait is described by a set of modalities (details in Table S4). The mean weighted trait profiles (by log-transformed abundances) of each station assemblage were calculated and expressed as relative abundance distributions of trait modalities within the assemblages (Thioulouse et al., 1997). Then, a Fuzzy Correspondence Analysis (FCA) was used to examine the differences of mean weighted trait profiles among stations using the ADE4 package (Chessel et al., 2004). 'Between-station' comparisons of trait modalities were performed using the Kruskal-Wallis and Wilcoxon posthoc test with the Holm adjustment

after arcsin transformation ($\sqrt{p}$ with p: proportion of each trait modality in the community). The percentage of functional similarity between stations was calculated based on the number of common traits and the total number of traits. Finally, the functional richness (FRic), evenness (FEve) and divergence (Fdiv) were calculated as the three components of functional diversity (Mason et al., 2005) using the FD package (Laliberté et al., 2014).

All statistical analyses were performed using R version 3.5.0 (R Core Team, 2018) and RStudio version 1.2.5033 (RStudio Team, 2019).

3. Results

3.1. Abundance and taxonomic features of macroinvertebrate communities

Total abundance varied from 121.2 ± 50.7 (in winter) to 342.2 ± 148.4 (in spring) in FLOLIZs and from 3.2 ± 2.3 (in spring) to 698.7 ± 751.0 (in winter) and from 6.7 ± 11.3 (in spring) to 391.5 ± 351.4 (in winter), in DCSs and NCSs, respectively (Fig. 3B; Table S4). Abundance was similar among the three types of stations (i.e., FLOLIZ, DCS, NCS) during autumn and winter but significantly differed during spring and summer ($H_{(2)} = 17.5$, *P*-value < 0.001; $H_{(2)} = 15.8$, *P*-value < 0.001 respectively). In particular, abundance was higher in FLOLIZs compared to DCSs and NCSs in spring (*P*-value $= 0.001$ for both) and summer (*P*-value $= 0.002$; *P*-value $= 0.01$, respectively) (Fig. 3B). Invertebrates abundance in NCSs and DCSs only differed in summer (*P*-value $= 0.02$) with highest abundance in NCSs (Fig. 3B).

The mean taxonomic richness were 6.4 ± 1.5, 4.1 ± 2.9 and 4.9 ± 3.0 for FLOLIZs, DCSs and NCSs, respectively. The taxonomic richness was significant different among station types in winter ($H_{(2)} = 10.5$, *P*-value < 0.01) and in spring ($H_{(2)} = 17.8$, *P*-value < 0.001) (Fig. 3C). In particular, the taxonomic richness was significantly higher in DCSs (7.5 ± 1.2) and NCSs (7.4 ± 2.2) than in FLOLIZs (5.4 ± 0.9) during winter (Fig. 3A) but significantly lower in control stations (DCSs: 1.9 ± 1.6; NCSs: 2.1 ± 1.4) than in FLOLIZs (7.8 ± 1.5) during spring. The taxonomic richness was similar between the control stations in both seasons (Fig. 3C). The taxonomic diversity varied from 0.17 ± 0.02 to 0.23 ± 0.06 throughout the sampling year in the FLOLIZs. In control stations, the taxonomic diversity varied from 0.08 ± 0.08 to 0.21 ± 0.06 and from 0.04 ± 0.05 to 0.18 ± 0.06 for DCSs and NCSs, respectively. The taxonomic diversity differed among stations only during spring ($H_{(2)} = 17.4$, *P*-value < 0.001) and summer ($H_{(2)} = 12.1$, *P*-value < 0.01) with higher values in FLOLIZs than in control stations (Fig. 3D) while control stations exhibited similar taxonomic diversity (*P*-value > 0.05)(Fig. 3C).

Macroinvertebrate abundance, richness, and diversity within FLO-LIZs exhibited lower seasonal variation (CV $= 23.4\%$, 70.1% and 29.6% respectively) compared to control stations (CV: 71.2%, 231.6%, 97.3%, respectively for DCSs and 60.5%, 173.9%, 79.0%, respectively, for NCSs). In particular, the mean abundance of macroinvertebrates in DCSs and NCSs decreased significantly by 99.5% and 98.3% between winter and spring, respectively, while it increased significantly by 182.3% in FLOLIZs (Table 1; Table S4). The mean taxonomic richness decreased significantly in control stations between winter and spring (by 74.7% and 71.6% for DCSs and NCSs, respectively) (Table 1; Table S4). In contrast, it increased by 44.4% in FLOLIZs (Table 1; Table S4). The mean diversity decreased significantly in control stations (by 87.6% and 79.6% for DCSs and NCSs, respectively) while it was constant in FLOLIZs between winter and spring (Table 1; Table S4).

3.2. Macroinvertebrate assemblages

The Fig. 4 shows the NMDS analysis performed on taxa abundance sampled in FLOLIZs, NCSs and DCSs over all sampling campaigns. The NMDS clearly discriminates the macroinvertebrate assemblages in FLOLIZs from those in control stations (permutation test, *P*-value < 0.005). Both control station types exhibited similar assemblages as
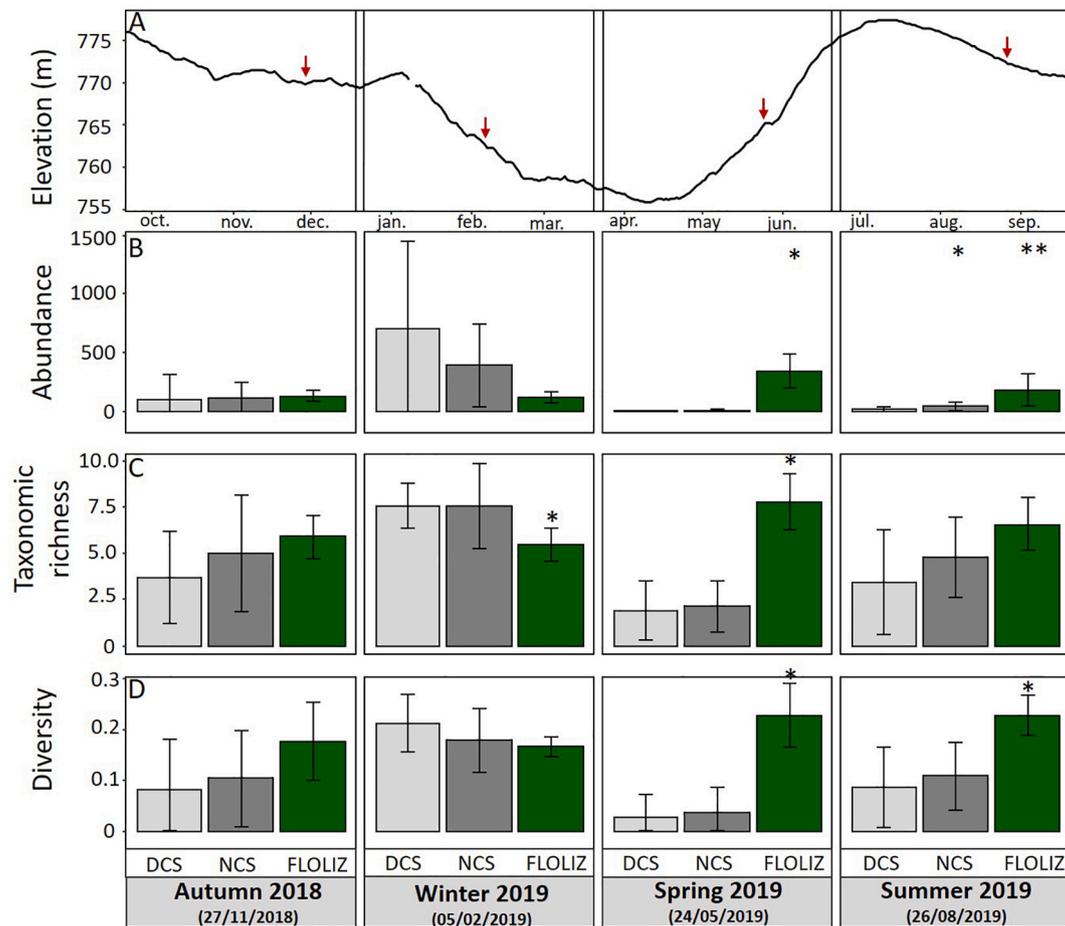
Fig. 3. Seasonal comparison of macroinvertebrates abundance, taxonomic richness and diversity between FLOLIZs and control stations. Daily variations of elevation between September 2018 and September 2019 (red arrows indicate the sampling date for macroinvertebrates). Daily data from Electricité de France (EDF) (A) and barplot (mean ± SD) of Abundance (B), Taxonomic richness (C) and Diversity (1-Hill index) (D) by season for each type of station. For each season and each metric, different labels (* for P-value < 0.05 and ** for P-value < 0.01) between stations indicate significant differences. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

shown by the strong overlap of their polygons. More specifically, while all stations shared some common taxa (e.g., Chironomids, Oligochaeta, Hydracarina), some other taxa were only reported in FLOLIZs such as Gyraulus sp. (Gastropoda) Stagnicola sp. (Gastropoda), Kempia sp (Diptera), Wiedemannia sp. (Diptera), Caenis sp. (Ephemeroptera) and Ecnomus sp. (Trichoptera). Additionally, some common taxa were more abundant in FLOLIZs than in control stations such as Hydra sp. (Cnidaria) and *Dreissena polymorpha* (Bivalvia) (a table with taxa occurrence in each station is provided in Table S4). DCSs and NCSs assemblages exhibited larger polygon surfaces (NMDS polygon surfaces of 1.98 and 1.86 respectively) than FLOLIZs assemblages (NMDS polygon surface of 0.27), suggesting a strong variability among seasons and stations for both control station types.

Table 2 reports pairwise-comparisons of the three components of functional diversity (i.e., functional richness, evenness, and divergence) among stations over the sampled year. The functional richness was higher in FLOLIZs (mean ± SD: 40.6 ± 18.1) than in control stations (16.8 ± 21.1 and 15.5 ± 16.6 in DCSs and NCSs, respectively). The functional divergence differed significantly between FLOLIZs and DCSs, with higher values in FLOLIZs (0.79 ± 0.1) than DCSs (0.6 ± 0.3). In contrast, the functional evenness was similar among the three type of stations.

The two first axes of the FCA performed on the mean functional profiles of the macroinvertebrate communities accounted for 34.04% and 21.75% of the functional variability (Fig. 5). The first axis separates

the trait profiles of FLOLIZs from those of the control stations while the second axis discriminates the trait profiles of FLOLIZs and NCSs from those of the DCSs. More specifically, the assemblages in FLOLIZs exhibited an average functional similarity of 54.5% ± 0.9% with the assemblages in control stations, while assemblages of both control station types (i.e., NCS, DCS) exhibited high functional similarity (98.7%) (Table 3). Compared to control stations, the macroinvertebrate community in FLOLIZs showed a higher proportion of large-sized organisms commonly reported in small water bodies with warm water and vegetal environments (roots, vegetation) such as ponds (e.g. Ecnomus sp). These organisms were not very mobile (attached or interstitial) and exhibited a passive aquatic dispersal (e.g. Hydra sp., *Dreissena polymorpha*). They were mainly absorbers or deposit feeders (e.g. Oligochaeta, Caenis sp), filters or predators (e.g. Ecnomus sp., Hydra sp). They had long life spans (more than one year), a low reproduction rate (one cycle per year) and mostly asexual mode of reproduction (e.g Oligochaeta, Planariidae). They were pollutant-sensitive (oligosaprobic, oligotrophic) with no resistant forms or cocoon-housing against desiccation (e.g. Hydra sp., Planariidae, Hydroptila sp). In contrast, assemblages in control stations presented a higher abundance of small, mobile organisms (crawlers, swimmers) (e.g. Chironomidae, Micronecta sp., Hydracarina) with aerial active dispersal (e.g. Bidessus sp., Ephemera sp.), commonly found in river channels. Their feeding habits were dominated by shredding activities (e.g. Bidessus sp., Ephemera sp., Micronecta sp.). Assemblages in these control stations were dominated by eurythermic

Table 1
Kruskal-Wallis and pairwise Wilcox test of abundance, taxonomic richness and diversity between seasons among station types.[a]

	Abundance			Taxonomic richness			Diversity		
	DCSs ($H_{(3)}$ = 17.8, P-value = 5^{e-04} ***)	NCSs ($H_{(3)}$ = 18.9, P-value = 3^{e-04} ***)	FLOLIZs ($H_{(3)}$ = 12.3, P-value = 6^{e-03} **)	DCSs ($H_{(3)}$ = 16.5, P-value = 9^{e-04} ***)	NCSs ($H_{(3)}$ = 16.4, P-value = 9^{e-04} ***)	FLOLIZs ($H_{(3)}$ = 11.9, P-value = 8^{e-03} **)	DCSs ($H_{(3)}$ = 16.0, P-value = 1^{e-03} **)	NCSs ($H_{(3)}$ = 12.7, P-value = 5^{e-03} **)	FLOLIZs ($H_{(3)}$ = 10.3, P-value = 0.02 *)
Autumn vs Winter	0.03 *	NS	NS	0.02 *	NS	NS	NS	NS	NS
Autumn vs Spring	NS	NS	0.009 **	NS	NS	NS	NS	NS	NS
Autumn vs Summer	NS	NS	NS	NS	NS	NS	NS	NS	NS
Winter vs Spring	0.002 **	0.003 **	0.005 **	0.002 **	0.005 **	0.01 *	0.002 **	0.006 **	NS
Winter vs Summer	0.004 **	0.02 *	NS	0,046 *	NS	NS	0.01 *	NS	0.003 **
Spring vs Summer	NS	0.01 *	NS	NS	NS	NS	NS	NS	NS

NS means no significant difference.
[a] Means significant difference with *** for P-value <0.001, ** for P-value <0.01 and * for P-value <0.05.

organisms resistant to organic pollution (mesotrophic, b-mesosaprobic organisms) (e.g. Erpobdella sp., Chironomidae, *Dreissena polymorpha*).

4. Discussion

Hydropower reservoirs are ecosystems that have fragmented rivers and damaged natural aquatic and terrestrial ecosystems in their creation. For these artificial ecosystems, there are environmental directives (such as the Water Framework Directive in Europe, 2000/60/CE) that aim to achieve biodiversity and ecological functioning as close as possible to that of similar natural ecosystems. However, the problem in fluctuating ecosystems is the poor condition of the littoral zones, which are normally very biogenic zones and host many essential ecological functions. The objective is therefore to find solutions to mitigate the effects of WLFs and to maintain biodiversity and functions close to those of natural ecosystems. To do this, we need technical solutions to support or increase biodiversity in these degraded artificial ecosystems to compensate for the initial loss of biodiversity, to allow the development of biodiversity and functions close to those of nearby natural ecosystems, and to limit the impacts on upstream and downstream ecosystems. The use of artificial floating islands (AFIs) has been proposed in a European technical report (Halleraker et al., 2016), however their effectiveness to support aquatic biodiversity and thus mitigate the impacts of WLFs in reservoirs remains poorly documented. Here, we reported that complexified structures that mimic natural littoral zones were successfully colonized by diversified and original macroinvertebrate communities exhibiting low seasonal variation despite high WLF compared to control stations. This finding exemplifies for the first time the effectiveness of FLOLIZ to mitigate impacts of artificial WLF on macroinvertebrate biodiversity and provide initial insights before a broader implementation of such structures in reservoirs affected by WLF.

4.1. Macroinvertebrates successfully colonized the FLOLIZs

In this study, we reported that the substrates offered by the FLOLIZs were suitable for macroinvertebrates as they were successfully colonized. These results confirm that artificial complex substrates can support a great diversity and abundance of macroinvertebrates (Schmude et al., 1998) by providing more interstitial space favourable to macroinvertebrates (Erman and Erman, 1984). Moreover, the FLOLIZs provide more heterogeneous habitats than control littoral stations thanks to several types of substrates (Misapor, oyster shells, plants, and roots) and various water depths, which promote macroinvertebrate diversity and density. In contrast, control stations exhibit homogeneous and mineral habitats (i.e. pebbles, slab, or gravel) with frequent dry periods leading to low abundance and richness of invertebrates (Aroviita and Hämäläinen, 2008; Haxton and Findlay, 2008; Palomäki, 1994). Additionally, the vegetation covering FLOLIZs provides a habitat that can be abundantly colonized by diverse macroinvertebrates (Beckett et al., 1992; Schramm and Jirka, 1989; Takamura et al., 2009) and may reduce predation pressure from fish (Diehl, 1992; Eklöv, 1997; Kornijów et al., 2016), while WLF do not allow the development of such habitats in natural littoral areas (Casanova and Brock, 2000).

Additionally, macroinvertebrate communities exhibited low seasonal variation in the FLOLIZs compared to control stations. FLOLIZs provide stable and permanently accessible habitats for macroinvertebrates regardless of water level since they are floating structures. Indeed, we reported a significant increase in abundance and taxon richness during periods of high WLFs in FLOLIZs. Conversely, a drastic decrease in abundance (−98%) and taxonomic richness (−70%) in control littoral stations was observed during periods of high WLFs (i.e., between winter and spring), as already reported in previous studies (see review of Carmignani and Roy, 2017). In particular, Richardson et al. (2002) reported that successive drawdown events could lead to the total elimination of insects and molluscs from the littoral zone. Indeed, the high amplitude and frequency of WLFs have a direct impact on
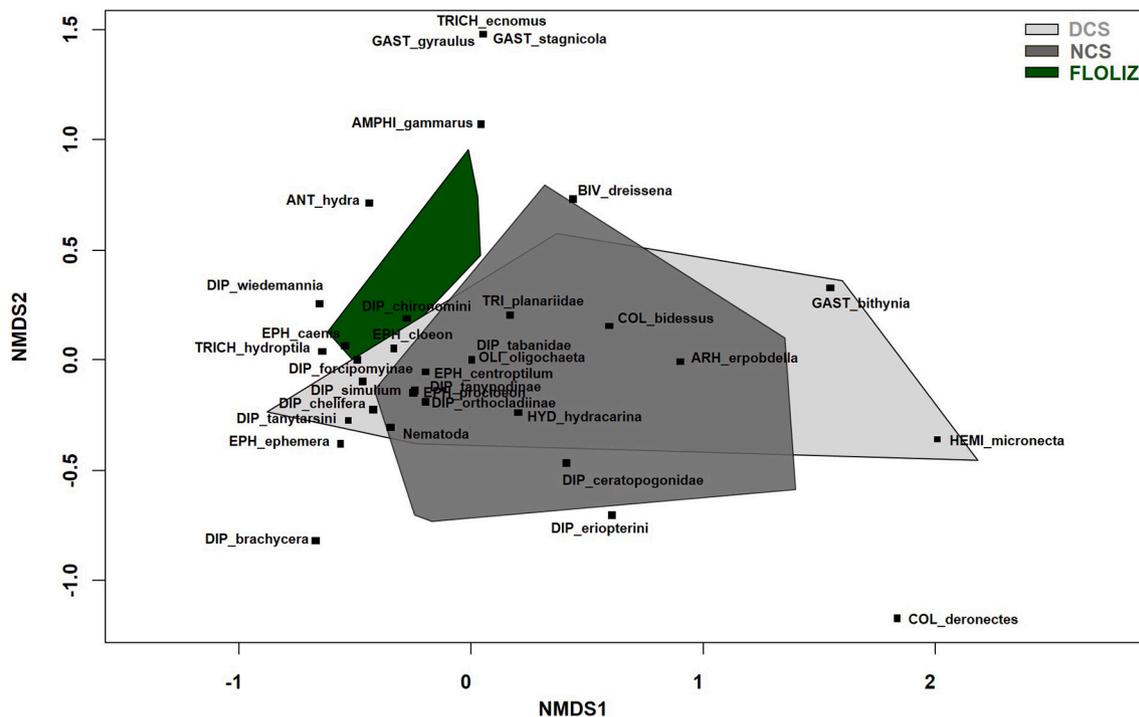
Fig. 4. Non-Metric Multidimensional Scaling ordination of taxa abundance for FLOLIZ, NCS and DCS over all sampling campaigns (27/11/2018; 26/02/2019; 25/05/2019; 26/08/2019). The results are represented in the two first components space. The stress value of 0.137 corresponds to a good fit (Clarke, 1993) and $R^2 = 0.92$ corresponds to a good adjustment. Permutation test showed significant difference for FLOLIZ ($p = 0.003$). The plot shows the taxa (black square) and the convex hulls corresponding to assemblages sampled for each type of station (DCS, NCS and FLOLIZ) on the plot.

macroinvertebrates and create unstable and homogeneous environments incompatible with the resistance capacities of macroinvertebrate communities (Friberg et al., 1994). In addition, hydraulic disturbances reduce the accessibility of some habitats and hence the diversity of macroinvertebrates (Dewson et al., 2007).

4.2. An original macroinvertebrate assemblage in FLOLIZs

FLOLIZs shelter original macroinvertebrate communities in terms of taxonomic and functional composition with only 54.5% similarity with the control littoral stations. This low functional similarity was due to the greater stability of the habitats but also to their heterogeneity and complexity in the FLOLIZs. Effectively, some additional taxa found in the FLOLIZs (e.g. Hydroptila sp, Caenis sp) are littoral taxa that were also found upstream and downstream of the reservoir during sampling under the Water Framework Directive (WFD 2000/60/EC, 2000) (https://hydrobiologie-paca.fr/). This observation clearly indicated that FLOLIZs were spontaneously colonized by taxa that require stable and complex habitats. Moreover, numerous taxa with low mobility (e.g.

Bivalve, Cnidaria) settled within the FLOLIZs. By exposing these low-mobility taxa to desiccation and/or colder temperatures, WLFs hinder their establishment in the littoral zone (Hellsten, 1997; Werner and Rothhaupt, 2008). This is why we found a higher abundance of highly mobile taxa with aerial dispersal (e.g. chironomids, beetles, heteroptera) in littoral stations; this result was expected as shown by White et al. (2011) in lakes with a drawdown >3 m. The mobile or non-substrate-

Table 2
Kruskal-Wallis and pairwise Wilcox test of the three components of functional diversity (i.e., functional richness (Fric), evenness (FEve) and diversity (Fdiv)) among station types over the sampled year.[a]

	Functional richness (Fric) ($H_{(2)} = 31.5$, P-value = 1.4^{e-07} ***)	Functional evenness (FEve) ($H_{(2)} = 2.4$, P-value = 0.3)	Functional diversity (Fdiv) ($H_{(2)} = 11.0$, P-value = 0.4^{e-02} ***)
FLOLIZ vs DCS	1.1^{e-05} ***	0.39	0.003 **
FLOLIZ vs NCS	9.1^{e-07} ***	0.77	0.09
DCS vs NCS	0.61	0.77	0.17

[a] Means significant difference with *** for P-value <0.001, ** for P-value <0.01 and * for P-value <0.05.
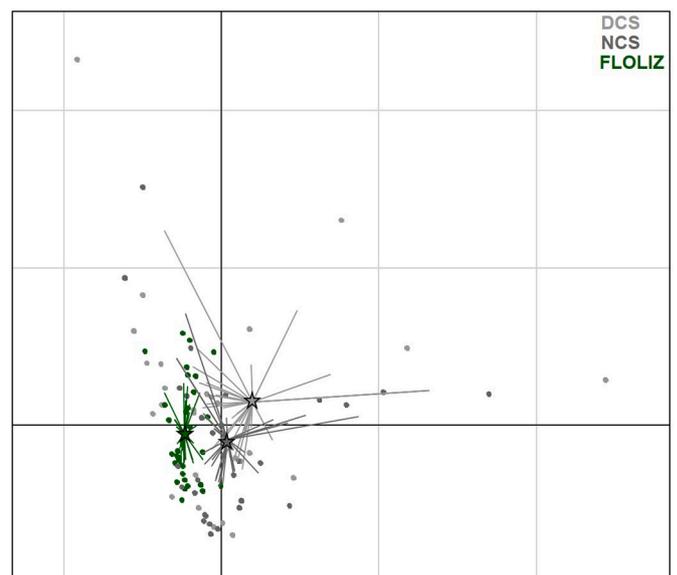

Fig. 5. Fuzzy Coding Analysis of functional trait profiles of each type of stations over all sampling campaigns (27/11/2018; 26/02/2019; 25/05/2019; 26/08/2019). Two first axes accounted for 55.79% of the functional variability. Stars indicates the centroid of all functional trait profiles for the corresponding station.

Table 3

Mean frequencies of traits modalities (with standard deviation) identified as significantly different by Kruskal-Wallis test between all three types of stations and pairwise Wilcox test performed on stations trait profiles.

	FLOLIZs	DCSs	NCSs	FLOLIZs vs DCSs	FLOLIZs vs NCSs	DCSs vs NCSs
Biomass						
[0–0.5]mg MS	0,35 (0,13)	0,41 (0,3)	0,37 (0,2)	↘	↘	NS
[0.5–2]mg MS	0,25 (0,07)	0,16 (0,14)	0,23 (0,13)	↗	NS	NS
[8–32]mg MS	0,11 (0,06)	0,07 (0,09)	0,07 (0,07)	↗	↗	NS
>128 mg MS	0,13 (0,08)	0,08 (0,14)	0,07 (0,08)	↗	↗	NS
Maximal size						
>0.5–0.1 cm	0,35 (0,07)	0,25 (0,17)	0,31 (0,17)	↗	NS	NS
>1–2 cm	0,23 (0,07)	0,13 (0,11)	0,18 (0,12)	↗	↗	↘
>2–4 cm	0,16 (0,06)	0,20 (0,17)	0,14 (0,14)	NS	↗	NS
>4 cm	0,11 (0,06)	0,08 (0,14)	0,07 (0,08)	↗	↗	NS
Life span (year)						
≤1 year	0,65 (0,13)	0,68 (0,29)	0,73 (0,29)	NS	↘	NS
>1 year	0,35 (0,13)	0,26 (0,25)	0,19 (0,2)	↗	↗	NS
Number of reproductive cycles per year						
<1	0 (0)	0,03 (0,05)	0,01 (0,03)	↘	↘	NS
1	0,52 (0,09)	0,42 (0,23)	0,43 (0,19)	↗	↗	NS
Reproduction						
Asexual reproduction	0,12 (0,06)	0,02 (0,05)	0,02 (0,03)	↗	↗	NS
Dispersal						
Aquatic passive	0,48 (0,09)	0,45 (0,22)	0,40 (0,17)	NS	↗	NS
Aerial active	0,11 (0,04)	0,11 (0,08)	0,14 (0,07)	NS	↘	NS
Resistance forms						
Cocoons / housings against desiccation	0,07 (0,05)	0,03 (0,09)	0,03 (0,05)	↗	↗	NS
Diapause or dormancy	0,11 (0,05)	0,25 (0,3)	0,15 (0,11)	↘	↘	NS
None	0,81 (0,06)	0,63 (0,32)	0,70 (0,24)	↗	NS	NS
Respiration						
Tegument	0,76 (0,07)	0,55 (0,22)	0,55 (0,21)	↗	↗	NS
Plastron	0 (0)	0,05 (0,11)	0,01 (0,04)	↘	↘	NS
Spiracle	0,03 (0,04)	0,09 (0,12)	0,10 (0,13)	↘	↘	NS
Locomotion						
Surface and full water swimmer	0,19 (0,03)	0,24 (0,15)	0,22 (0,1)	NS	↘	NS
Crawler	0,27 (0,06)	0,31 (0,12)	0,30 (0,12)	↘	↘	NS
Interstitial	0,17 (0,05)	0,11 (0,11)	0,13 (0,08)	↗	↗	NS
Temporarily or permanently attached	0,25 (0,08)	0,16 (0,13)	0,13 (0,1)	↗	↗	NS
Food						
Microorganisms	0,04 (0,02)	0,03 (0,04)	0,03 (0,03)	↗	NS	NS
Dead animal (≥ 1 mm)	0,01 (0,01)	0,02 (0,02)	0,03 (0,02)	NS	↘	NS
Feeding habits						
Absorber	0,02 (0,01)	0,01 (0,03)	0,01 (0,02)	↗	↗	NS

Table 3 (*continued*)

	FLOLIZs	DCSs	NCSs	FLOLIZs vs DCSs	FLOLIZs vs NCSs	DCSs vs NCSs
Deposit feeder	0,26 (0,07)	0,17 (0,16)	0,2 (0,11)	↗	NS	NS
Shredder	0,10 (0,03)	0,15 (0,11)	0,12 (0,08)	↘	↘	NS
Filter-feeder	0,18 (0,07)	0,21 (0,2)	0,15 (0,18)	NS	↗	NS
Predator	0,24 (0,08)	0,13 (0,12)	0,19 (0,13)	↗	NS	NS
Transversal distribution						
River channel	0,07 (0,03)	0,10 (0,06)	0,07 (0,06)	↘	NS	NS
Ponds, pools, marshes, peat bogs	0,26 (0,04)	0,21 (0,08)	0,23 (0,08)	↗	NS	NS
Groundwaters	0,02 (0,01)	0,01 (0,02)	0,01 (0,01)	↗	NS	NS
Substrate preferences						
Flags/boulders/cobbles/pebbles	0,22 (0,05)	0,23 (0,13)	0,19 (0,1)	NS	↗	NS
Microphytes or macrophytes	0,25 (0,03)	0,19 (0,07)	0,19 (0,07)	↗	↗	NS
Twigs/roots	0,12 (0,03)	0,08 (0,06)	0,08 (0,05)	↗	↗	NS
Organic detritus/litter	0,07 (0,01)	0,08 (0,04)	0,08 (0,04)	NS	↘	NS
Trophic status						
Oligotrophic	0,32 (0,09)	0,23 (0,13)	0,21 (0,11)	↗	↗	NS
Mesotrophic	0,37 (0,05)	0,42 (0,12)	0,41 (0,14)	↘	↘	NS
Temperature						
Warm (>15 °C)	0,23 (0,07)	0,12 (0,1)	0,13 (0,07)	↗	↗	NS
Eurythermic	0,57 (0,07)	0,67 (0,23)	0,60 (0,23)	↘	↘	NS
Saprobity						
Oligosaprobic	0,36 (0,09)	0,26 (0,1)	0,25 (0,1)	↗	↗	NS
b-mesosaprobic	0,31 (0,06)	0,37 (0,11)	0,34 (0,12)	↘	NS	NS
Number of similar modalities (Total: 78)				42	43	71
Percentage of similarity (%)				53,8%	55,1%	98,7%

Only modalities with significance between stations were listed. Results of pairwise comparisons between the three types of stations are exposed for each trait modality. For example, when FLOLIZ vs DCS is considered, ↗, respectively ↘, means that the trait modality is significantly more, respectively less, represented in FLOLIZ than in DCS. NS stands for non-significant.

dependent taxa are less severely affected by WLF because, to some extent, they are able to move with the water level (Gasith and Gafny, 1990; Whittemore Jr et al., 2016). Moreover, the presence of more species with a longer lifespans, slower reproduction strategies and no resistant forms in FLOLIZs enhanced the steadiness of the environment that these structures can offer. Various studies on WLFs (Furey et al., 2006; Valdovinos et al., 2007) or flooding (Gallardo et al., 2009) impacts have shown that these pressures tend to favor organisms with fast-breeding and short life cycles, which would allow fast recolonisation of the environment after the impact. While we expected to find a higher abundance of fast-breeding organisms such as Chironomidae and Oligochaeta in littoral communities but this did not prove to be significant. Conversely, they had a slow reproduction rate (less than 1 reproductive cycle per year). The presence of rather pollutant-sensitive taxa in FLO-LIZs (e.g Hydra sp., Planariidae, Hydroptila sp.) and pollutant-resistant ones in littoral stations (e.g Erpobdella sp., Chironomidae) also probably resulted from the WLFs, which select in a general way more resistant and tolerant taxa (Munn and Brusven, 1991; Valdovinos et al., 2007). Several studies have shown that heterogeneous littoral habitats (Heino, 2008; Jurca et al., 2012), particularly vegetation, are a determining factor in the structure of littoral macroinvertebrate communities (Chilton, 1990; Krull, 1970) and support significant diversity (Friberg et al.,

1994; Iversen et al., 1985; Milner and Gloyne-Phillips, 2005; O'Connor, 1991). For example, certain species are more likely to be found on some species of plants (Kouamé et al., 2011). Helophyte roots also showed a strong attraction for macroinvertebrates (Prashant and Billore, 2020). Finally, vegetation cover in FLOLIZs could contribute positively to the attraction of organisms dependent on small, vegetated water bodies such as ponds (Ecnomus sp., Planariidae).

4.3. Limitations and perspectives

The findings of this study suggest that the FLOLIZs may provide a promising solution to mitigate the impacts of WLF on macroinvertebrate communities. Yet, such findings must be confirmed by long-term studies covering several lakes. In addition, such studies would allow us to know the lifetime of these structures under variable conditions. Finally, all this information would produce knowledge about the efficiency of FLOLIZs in their support of aquatic biodiversity of reservoirs in light of the surface area of the structures and the surface area of the water body. The control site close to the FLOLIZ (i.e., NCS) exhibited higher macroinvertebrate abundances than assemblages in distant control sites (i.e. DCS) during the post-drawdown season. Additionally, we reported a slightly higher similarity in functional profiles between

macroinvertebrate assemblages in NCSs and FLOLIZs. These results may suggest a positive effect of FLOLIZ on macroinvertebrate assemblages in close natural littoral areas. More research will be needed to check this assumption and in particular, to test whether the FLOLIZs may constitute a recolonization pool for littoral habitats exhibiting WLF.

5. Conclusion

High WLFs due to human activities are an increasing threat to aquatic ecosystems that managers try to mitigate using Artificial Floating Islands. FLOLIZs, as newly designed AFIs that mimic littoral habitats, provide promising solution to sustain the biodiversity of reservoirs exhibiting high WLF. Indeed, this study showed that macroinvertebrates were more abundant and diversified in FLOLIZs than in littoral stations during periods of high water-level rise (i.e. spring) and during the post-drawdown period (i.e. summer). In addition, macroinvertebrate communities exhibited less variability in FLOLIZs than in control littoral stations over the year, suggesting that habitats in the FLOLIZs were unimpacted by WLF. Additionally, the FLOLIZs exhibited original macroinvertebrate assemblages in terms of functional and taxonomic composition compared to control stations, suggesting a colonization by taxa from the lakeshore that could not survive in an environment with high WLFs. In particular, assemblages colonizing the FLOLIZs, suggest that they can mimic a natural littoral zone by providing complex and diverse habitats available for the different stages of macroinvertebrate lifecycles.

Declaration of Competing Interest

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoleng.2021.106509.

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