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# An evaluation of artificial floating littoral zones to support fish communities in reservoirs

Quentin Salmon<sup>1,2</sup> , Samuel Westrelin<sup>1,2,\*</sup>, Julien Dublon<sup>1,2</sup>, Sebastien Fonbonne<sup>3</sup>  
and Jean-Marc Baudoin<sup>2,4</sup>

<sup>1</sup> INRAE, Aix Marseille Univ, RECOVER, 3275 Route Cézanne, 13100 Aix-en-Provence, France

<sup>2</sup> Pôle R&D Ecosystèmes Lacustres (ECLA), OFB-INRAE-USMB, Aix-en-Provence, France

<sup>3</sup> ECOCEAN, 1342 Avenue de Toulouse, 34070 Montpellier, France

<sup>4</sup> OFB, Service ECOAQUA, DRAS, 3275 Route Cézanne, 13100 Aix-en-Provence, France

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**Abstract** – Artificial water level fluctuations (WLF) in reservoirs impact fish communities by degrading littoral habitats. To mitigate these negative effects, artificial floating islands that mimic natural littoral zones appear as a promising mitigation tool. However, their effectiveness in supporting fish communities remains poorly documented. In this study, three artificial floating littoral zones (FLOLIZ, 70 m<sup>2</sup> surface area) were installed in a French hydropower reservoir subject to extreme WLF. Fish communities were assessed in spring and summer over four years in FLOLIZ and in control littoral stations during daytime and nighttime. Fish, especially juveniles, did not appear more frequently in FLOLIZ than in control littoral stations during daytime. At night, both adult and juvenile fish were more abundant in the littoral zone of the reservoir. During the day, the fish community in FLOLIZ was mainly composed of juvenile *Chondrostoma toxostoma* and adult *Perca fluviatilis*. Differences occurred only for a few species and life stages (juvenile vs adult); however, in general, results indicated greater abundance or richness in control littoral stations. These results do not support the effectiveness of FLOLIZ in mitigating deleterious effects of artificial WLF. The distance of FLOLIZ to the littoral zone could explain these results. Further studies in different environmental conditions, in different ecosystems and with different FLOLIZ designs are needed to provide additional information on the effectiveness of such structures as a mitigation tool.

**Keywords:** Artificial floating island (AFI) / ecological engineering / water level fluctuations (WLF) / mitigation / fish habitat

## 1 Introduction

At the interface between aquatic and terrestrial ecosystems, the littoral zone of lakes offers complex and valuable habitats for biodiversity and plays a major role in their overall functioning (Sala and Güde, 2006; Czarnecka, 2016; Meerhoff and de los Angeles González-Sagrario, 2022). Specifically, it hosts numerous fish species, at least at some life stages, in which they can feed, grow, shelter, and spawn (Winfield, 2004; Říha *et al.*, 2011). Water level fluctuations (WLF), depending on the hydrological regime, control the structure and functioning of littoral zones (Sutela *et al.*, 2013; Zohary and Gasith, 2014; Evtimova and Donohue, 2016). In reservoirs, WLF can be extreme in amplitude and frequency (Coops *et al.*, 2003; Hirsch *et al.*, 2014), leading to an

homogenization and impoverishment of littoral habitats (Furey *et al.*, 2004; Logez *et al.*, 2016). This has cascading negative effects on fish communities (Leira and Cantonati, 2008).

Although fish are often mobile enough to follow WLF, the loss or inaccessibility of littoral habitats can impact their behavior, survival, growth, spawning, and recruitment (Carmignani *et al.*, 2019). For example, artificial WLF reduce the abundance and modify the assemblage of benthic invertebrates, which can decrease insectivorous fish density and diversity or limit the growth of young-of-year (YOY) in some species (Haxton and Findlay, 2009; Sutela *et al.*, 2011; McDowell, 2012). The scarcity of preferred habitats can lead to increased intraspecific competition, which causes smaller individuals to migrate to deeper areas (Fischer and Öhl, 2005). For species that spawn in the littoral zone (*e.g.* phytophilous species), a lack of suitable habitats during the spawning period can lead to poor recruitment and population decline (Wegener and Williams, 1975; Farrell, 2001). A significant drawdown

\*Corresponding author: [samuel.westrelin@inrae.fr](mailto:samuel.westrelin@inrae.fr)

leading to shoreline exposure and egg desiccation after spawning can significantly reduce or even totally suppress recruitment (Grabowski and Isely, 2007; Kahl *et al.*, 2008). In addition, fish populations can decline because of a lack of shelter that exposes YOY to predation (Wolcox and Meeker, 1992). These deleterious effects have led both researchers and managers to look for mitigation solutions to WLF (Trussart *et al.*, 2002; Tundisi and Matsumura-Tundisi, 2003).

The control of WLF when the littoral zone is the most intensively used by fish (*e.g.* spring for spawning) (Westrelin *et al.*, 2022; Maday *et al.*, 2023) often conflicts with the uses of reservoirs and is difficult to implement. Consequently, ecological engineering methods using artificial habitats have been widely studied and their effectiveness to enhance fish habitats has been shown (Zalewski and Frankiewicz, 2002; Pedicillo *et al.*, 2008; Santos *et al.*, 2008). However, the attractiveness of these artificial habitats differs according to various parameters (depth, temperature, diel cycle) (Walters *et al.*, 1991; Moring and Nicholson, 1994). Moreover, most studies were carried out in lakes with low WLF of a few meters. Santos *et al.* (2011) tested littoral artificial habitats in a reservoir with relatively high WLF (around 8 m) and needed to move the habitats several times to keep them immersed. The authors concluded that self-adapting habitats would be much more effective. This is the case of artificial floating islands (AFI), which consist of floating frames covered with plants, available for aquatic fauna no matter the WLF. These one-dimensional floating structures have been widely used in Europe and Asia for aesthetic purposes, for water quality improvement, and for habitat enhancement (Nakamura and Mueller, 2008; Yeh *et al.*, 2015). By providing new and complex substrates, AFI concentrate significant aquatic biodiversity (Prashant and Billore, 2020; Salmon *et al.*, 2022) and were also used as a mitigation tool to sustain fish populations by providing spawning habitats (Nakayama, 1986 in Nakamura and Mueller, 2008; Gillet, 1989). Recently, two studies again highlighted their potential to support juvenile fish (Huang *et al.*, 2017; De Moraes *et al.*, 2023). However, these studies remain few in number and have been carried out over short periods. Additionally, the structures used were mainly designed to support spawning and not to provide refuge and nursery habitats for fish.

In this study, we designed an innovative artificial floating island named Floating Littoral Zones (FLOLIZ) that mimics a natural littoral zone. It is a three-dimensional structure with subaquatic stages, two types of mineral substrate, helophyte and hydrophyte plants. Three FLOLIZ have been installed in a French hydropower reservoir subject to extreme WLF (up to 50m) and studied over four years. We aimed at assessing their effectiveness as new functional habitats to support fish communities. We hypothesized that fish abundance and species richness would be higher in FLOLIZ than in control stations due to the diversity and complexity of that habitats and their availability at any water level. We expected this pattern would be particularly enhanced in spring and summer, compared to low activity seasons. Finally, we expected that the fish assemblage would differ between FLOLIZ and control stations due to significant differences in the habitats. Specifically, we expected a higher abundance of vegetation-dependent species in FLOLIZ.

## 2 Materials and methods

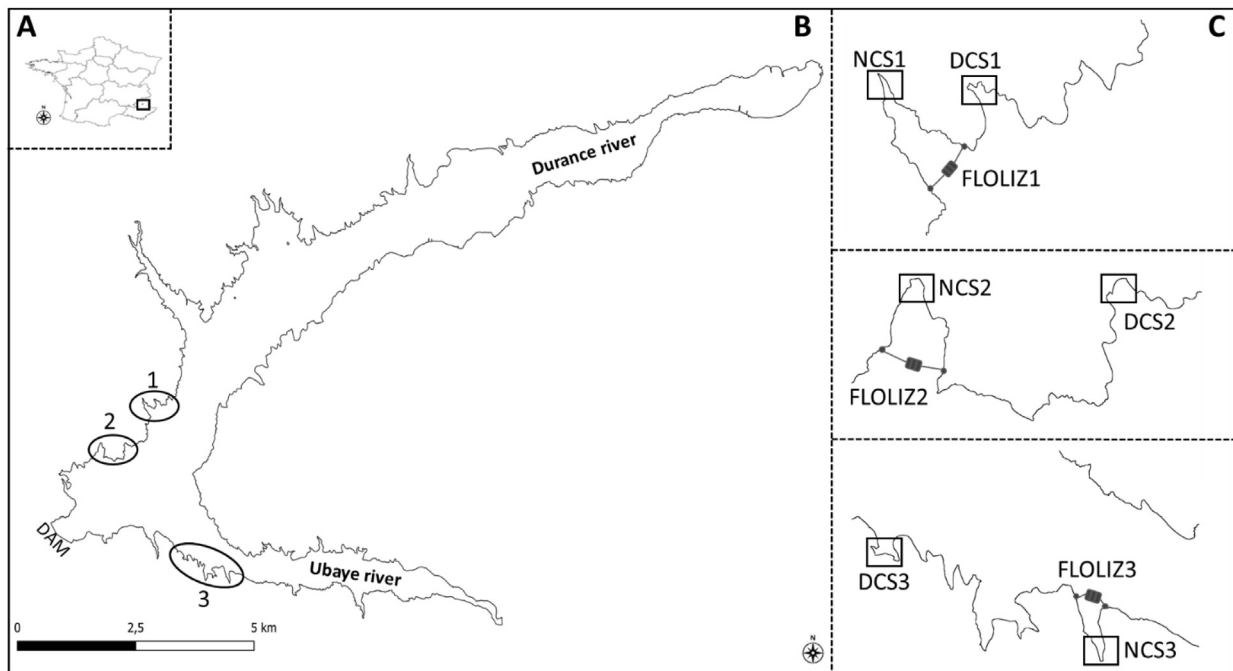
More details on the study site, FLOLIZ design and sampling stations can be found in Salmon *et al.* (2022).

### 2.1 Study site

The study was conducted in Serre-Ponçon reservoir located in South-Eastern France (44.5117°N; 6.3326°E) (Fig. 1A). This is one of the largest reservoirs in Metropolitan France, with a surface area of 28 km<sup>2</sup> (20 km long and 3 km wide at the maximum), a volume of 1272 km<sup>3</sup> at a maximum altitude of 780 m and a maximum depth of about 110 m. The dam was built in 1959 to produce hydropower. The reservoir is also used to control flooding by the two main inflow rivers (Durance and Ubaye) and to supply irrigation and drinking water needs. These uses lead to extreme WLF up to 49 m (27 m in average over 2018–2022) (Data from Electricité de France, French Electrical Company). The fluctuations are seasonal, with a significant decrease in water level between early autumn and late winter, and a significant rise in spring following the snowmelt (Fig. A1 in Appendix). The daily amplitude of WLF can reach 1.6 m (Data from Electricité de France). In summer, the water level is kept stable at a high level for recreational activities (altitude 780 m). These extreme WLF prevent littoral vegetation from growing and lead to morphological alterations on the banks. Serre-Ponçon is a monomictic reservoir, with stratification occurring from March to September. The latest monitoring of Serre-Ponçon's water quality as part of the Water Framework Directive (WFD; 2000/60/EC), concluded that it had good water quality with an oligo-mesotrophic status (Data 2022 from WFD).

### 2.2 FLOLIZ design

FLOLIZ are 14 m long and 5 m wide. The floating part is composed of high-density polyethylene (HDPE) caissons (Fig. 2A). One caisson out of two contains clods of soil with local helophyte plants such as *Phragmites australis*, *Calamagrostis epigeios*, *Salix* sp, and *Carex elaya* (Fig. 2B). The submerged part is made of three extruded aluminium structures (4 m wide × 4 m long); the central one is 1 m deep and the two others are 0.5 m deep. These different underwater levels mimic a natural littoral zone. The aluminium structures are tied to the floating caissons by steel chains. The bottom and two sides of these structures are covered with steel mesh cages (0.5 × 0.8 × 0.25 m) filled with inert, non-pollutant substrates (cellular glass stone, recycled oyster shells) to simulate a mineral soil. The mesh cages on both sides partly protect the inner area from waves and currents. Empty wire mesh cages (2.5 cm mesh) were placed on the lateral sides to create sheltered habitats for fish juveniles (Fig. 2C). Finally, hydrophytes were planted at the bottom of each structure. In the 0.5 m-deep levels, grass-type plants (*Myriophyllum spicatum*, *Stuckenia pectinata* and *Chara* sp) were installed in steel mesh cages containing glass wool (Fig. 2D). At the 1 m-deep level, three species of pondweeds (*Potamogeton coloratus*, *Potamogeton nodosus*, and *Potamogeton lucens*) were planted in plastic boxes



**Fig. 1.** Location of FLOLIZ and control stations in Serre-Ponçon hydropower reservoir. (A) Location of Serre-Ponçon hydropower reservoir in France; (B) Reservoir contour at the highest water level (altitude 780 m) and location of 3 sampling zones (ellipses); (C) Focus on the 3 zones (suffixed 1, 2 and 3) with control stations and FLOLIZ. DCS: Distant Control Station, NCS: Nearby Control Station, FLOLIZ: Floating Littoral Zone.

containing aquatic potting soil (Fig 2E). The vegetated area per FLOLIZ was approximately 14 m<sup>2</sup>. All plants were local to preserve the genetic pool and prevent from introducing exotic species.

### 2.3 Sampling stations

Three FLOLIZ were installed in downstream bays of the reservoir in September 2018 (Fig. 1B). The selected bays met the following criteria: a depth greater than 30 m to avoid the beaching of structures in winter when the water level is lowest, a low exposure to dominant winds to limit wave action, and an area of limited recreational activities. FLOLIZ area (70 m<sup>2</sup>) and depth (1 m maximum) was used to define the size of control stations located in the natural littoral zone (70 m long × 1 m wide and 1 m depth). Two types of control stations were chosen: one at the head of the bays in which FLOLIZ were installed (called NCS for Nearby Control Station) and another at the head of neighbouring bays in the same zone (called DCS for Distant Control Station) (Fig 1C). FLOLIZ could potentially have an influence over a certain area including the NCS; the comparison to DCS, considered far enough from FLOLIZ to be out of this influence radius, could then help to detect potential interactions between FLOLIZ and NCS. Each DCS was selected to be hydro-morphologically similar to the NCS and located in the same zone (see Salmon *et al.*, 2022).

### 2.4 Fish sampling

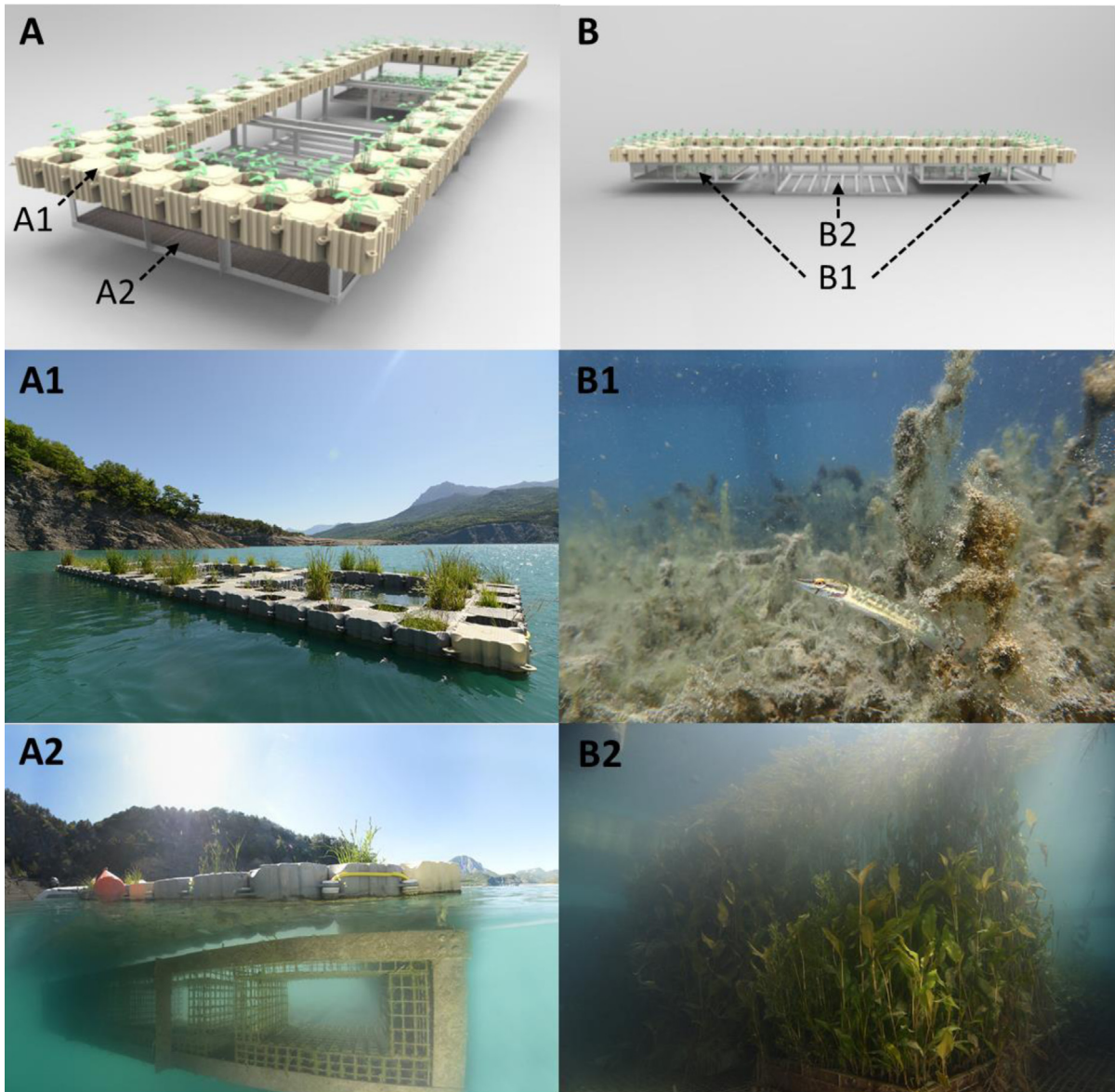
Fish were sampled in FLOLIZ and control stations in spring and summer from 2019 to 2022 using two non-lethal

methods. Fish traps were used at night and visual census performed during daytime to get a complete picture of the fish community accounting for the diversity of daily activity patterns of species (Järvalt *et al.*, 2005; Shoup *et al.*, 2014). Spring and summer correspond to the peak activity period of fish and also give a good picture of the juvenile fish community (Fischer and Quist, 2014). In each season, the two sampling methods were carried out from one to four times (Table A1 in Appendix).

At night, eight unbaited fish traps (45 × 25 × 25 cm, mesh size 4 mm with an opening of 5 cm) were installed in FLOLIZ and control stations (DCS, NCS). In FLOLIZ, four fish traps were randomly placed in the 1 m deep underwater level and two fish traps in each 0.5 m deep underwater level (Fig. 3A). In control stations, fish traps were randomly placed in a 70-m<sup>2</sup> area in the littoral zone. Similarly, in the underwater levels of FLOLIZ, four fish traps were placed at 0.5 m depth and four at 1 m depth in DCS and NCS (Fig. 3A). Fish traps were installed around 6 pm for an approximative duration of 15 h that included a few hours of daylight until dusk and a few hours of daylight after dawn. The next morning, the fish traps were removed and each fish was identified by species and measured (total length). A total of 1272 fish traps were collected (Table A1 in Appendix).

Visual census (snorkelling) was performed during daytime (Turner and Mackay, 1985; Brosse *et al.*, 2001; Plichard *et al.*, 2017). The high water transparency (4.5 m on average) made it possible to count fish and identify their species. Two qualified divers swam along each half of the 70 m-long linear transect in DCS and NCS and recorded all fish seen in the 1 m-wide band from the shoreline (Fig. 3B). The swimming speed was approximately 2 m min<sup>-1</sup>. The two divers took a census





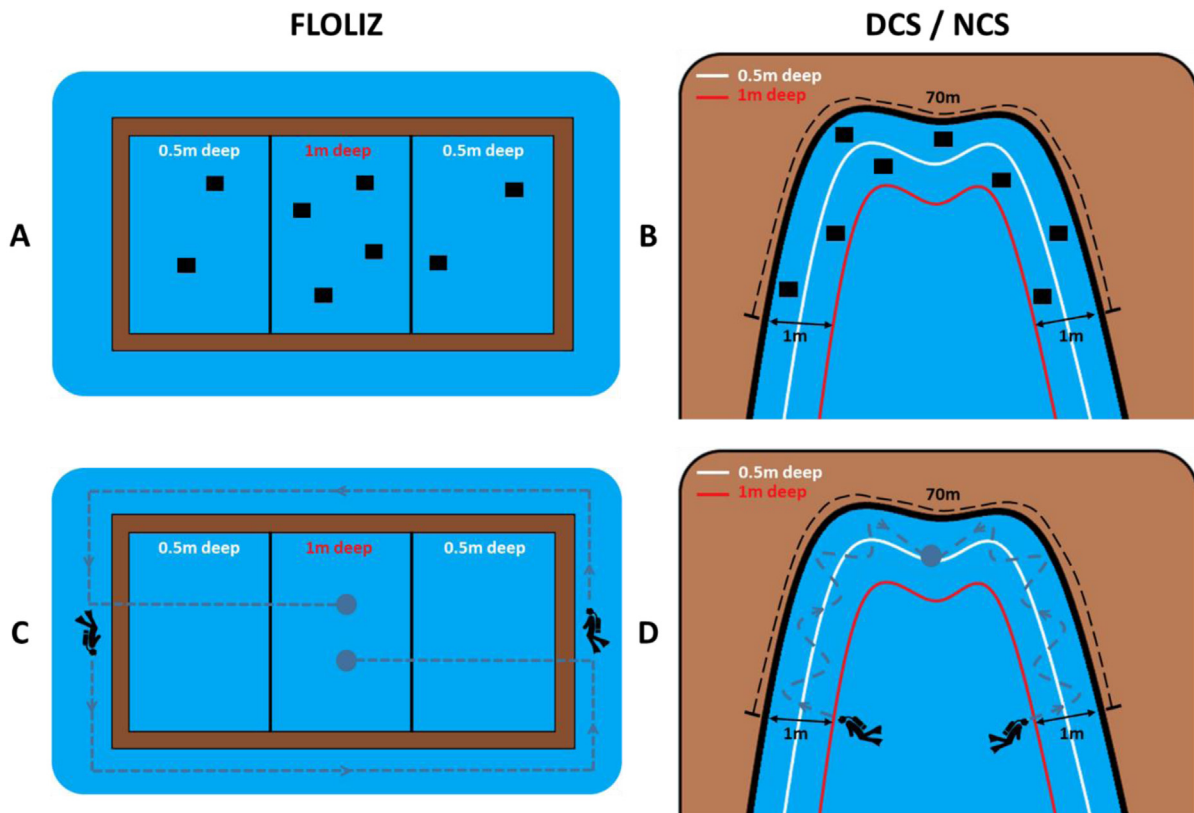
**Fig. 2.** Description of FLOLIZ. (A) & (B) – 3D side and profile design. Letters with a suffix number locate the different parts of the FLOLIZ detailed in each following panel; (A1) Floating part with helophytes; (A2) Underwater view of lateral part with empty wire cages; (B1) Juvenile Pike in 0.5 m-deep vegetation; (B2) Underwater view of 1m deep level with Potamogeton plant bed. ©UROS project (OFB-INRAE-ECOCEAN).

of FLOLIZ by first swimming around the structures and then inside them (Fig. 3B). During visual census, fish abundance was estimated based on a geometric progression factor: 1, 2–5, 6–10, 11–30, 31–50, 51–100, 101–200, 201–500, 500–1000 individuals (Harmelin-Vivien *et al.*, 1985). The total length of individuals was estimated by using size markers. A total of 126 visual censuses were carried out (Table A1 in Appendix).

## 2.5 Statistical analysis

To focus on the functionality of FLOLIZ, analyses have been carried out by separating juvenile and adult fish. The life stage was approximated by the total length. The classification was based on field data and literature data on the growth and maturity of the different species present in the Serre-Ponçon

reservoir or in similar environments (Tab. A2 in Appendix). For each date and station, juvenile and adult fish abundance and species richness were calculated. For visual censuses, the total abundance was estimated by the center of the abundance classes (Harmelin-Vivien *et al.*, 1985). Generalized linear models (GLM) were used to explain variations of abundance and species richness according to station type (FLOLIZ, DCS, NCS), season (Spring, Summer), year (2019, 2020, 2021, 2022) and their interactions (Zuur *et al.*, 2009). For fish abundance, a negative binomial link function (Hardin & Hilbe 2007) was used to take into account over-dispersion and abundant zero values (Lindén and Mäntyniemi, 2011). For species richness, a Conway-Maxwell-Poisson link function, commonly used for count data, was used to take into account data that exhibit over- or under-dispersion (Sellers and Premeaux, 2021).



**Fig. 3.** Schematic drawing of the sampling protocols in FLOLIZ and control stations. (A) Fish trap sampling (during night) in FLOLIZ. Black squares symbolize fish traps; (B) Fish trap sampling in NCS and DCS. The white line marks the 0.5 m-deep littoral zone, the red one corresponds to the 1 m-deep one; (C) Visual census (daytime) in FLOLIZ. The dashed grey line with arrow symbolizes the swimming track of each diver; (D) Visual census (daytime) in NCS and DCS.

GLM were performed with the “*glmmTMB*” R package (Brooks *et al.*, 2017). The goodness of fit of each model was tested by using the `simulateResiduals` function in the “*DHARMa*” package which provided several plots and test functions to check for over/under-dispersion, zero inflation and spatial and temporal autocorrelation of residuals (Hartig and Lohse, 2022). A deviance analysis was run with the “*Anova*” function of the “*car*” package (Fox *et al.*, 2001). For each significant effect, pairwise comparisons using marginal means estimated with a Tukey adjustment were carried out (“*Emmeans*” package ; Lenth, 2017).

To assess the composition of juvenile and adult fish communities and variations between station types over the whole sampling period, a non-metric multidimensional scaling (NMDS) ordination of fish species abundance was performed using the function ‘*metaMDS*’ in the *vegan* R package (Oksanen *et al.*, 2001). Only species with a total abundance greater than 5 were selected. Species abundance was averaged by season for each year, to give each season the same weight in a year. These abundances were transformed into frequencies to get a species composition of 100% in each season of a year. The Bray-Curtis dissimilarity index was used to build a matrix of species frequencies among stations (Bray and Curtis, 1957). The goodness of fit of the NMDS was estimated with a stress function whose value inferior to 0.1 is great, to 0.2 is good, and to 0.3 corresponds to poor representation (Clarke, 1993). In addition, species abundance was compared between station

type by using the Conover-Iman test (“*Conover.test* package” ; Dinno, 2015) with Holm *p*-value adjustment (Holm, 1979) which performs multiple comparisons using rank sums (Iman and Conover, 1979; Conover and Conover, 1999).

All statistical analyses were performed using R software version 4.4.1 (R Core Team, 2024) and RStudio software version 2022.12.0 (RStudio Team, 2022).

### 3 Results

#### 3.1 Fish abundance and diversity

At night, a total of 938 juvenile and 172 adult fish from 10 species were captured by fish traps: 241 juvenile and 19 adults from 7 species in FLOLIZ, 330 juvenile and 101 adults from 9 species in DCS and 367 juvenile and 52 adults from 10 species in NCS.

At night, juvenile fish abundance differed between Season ( $P$ -value=0.002), Year ( $P$ -value=0.031), between Station according to Season ( $P$ -value=0.043) and also according to Year ( $P$ -value=0.007) (Tab. 1A). In the year 2019, mean juvenile abundance was higher in DCS and NCS than in FLOLIZ (Fig. 4A). In spring, in DCS ( $6.10 \pm 15.3$ ;  $P$ -value=0.015) and NCS ( $5.62 \pm 9.54$ ;  $P$ -value=0.020), mean juvenile abundance was higher than in FLOLIZ ( $1.28 \pm 4.62$ ) (Fig 4B). Juvenile species richness differed between Station, Year ( $P$ -value < 0.001 and < 0.001,

**Table 1.** Deviance analysis (ANOVA) for generalised linear models on fish abundance (Negative Binomial link function) and species richness (Conway-Maxwell-Poisson link function). (A) For juvenile and adult stage for fish trap sampling (night) and (B) For juvenile and adult stage for visual census sampling (daytime). Chisq = Wald Chisquare/Df = Degree of freedom/Signification codes: \*\*\* for  $P$ -value < 0.001; \*\* for  $P$ -value < 0.01; \* for  $P$ -value < 0.05.

A	ABUNDANCE	SPECIES RICHNESS	
Factor	Chisq/Df/ $P$ -value	Chisq/Df/ $P$ -value	
Station type	5.88/2/0.053	24.72/2/4.3e-06***	JUVENILES
Season	9.30/1/0.002**	4.15/1/0.042*	
Year	8.85/3/0.031*	20.28/3/1.5e-04***	
Station type × Season	6.31/2/0.043*	1.28/2/0.526	
Station type × Year	17.59/6/0.007**	9.60/6/0.143	
Station type	9.36/2/0.009**	2.99/2/0.224	ADULTS
Season	0.10/1/0.748	2.15/1/0.143	
Year	30.57/3/1.1e-06***	19.75/3/1.9e-04***	
Station type × Season	1.87/2/0.394	0.75/2/0.686	
Station type × Year	11.07/6/0.086	9.51/6/0.147	
B	ABUNDANCE	SPECIES RICHNESS	
Factor	Chisq/Df/ $P$ -value	Chisq/Df/ $P$ -value	
Station type	0.22/2/0.896	1.08/2/0.583	JUVENILES
Season	9.54/1/0.002**	6.53/1/0.011*	
Year	1.81/3/0.612	1.09/3/0.780	
Station type × Season	3.18/2/0.204	4.56/2/0.103	
Station type × Year	6.68/6/0.351	14.37/6/0.026*	
Station type	1.51/2/0.470	0.65/2/0.722	ADULTS
Season	10.07/1/0.002**	34.09/1/5.3e-09***	
Year	11.82/3/0.008**	7.30/3/0.063	
Station type × Season	1.72/2/0.424	0.63/2/0.730	
Station type × Year	45.16/6/4.4e-08***	9.66/6/0.140	

respectively) and Season ( $P$ -value = 0.042) (Tab. 1A). More species were caught in DCS and NCS than in FLOLIZ (Fig. 4C). Adult fish abundance differed between Station ( $P$ -value = 0.009) and Year ( $P$ -value < 0.001) and adult species richness only differed between Year ( $P$ -value < 0.001). Finally, mean adult abundance was higher in DCS and NCS than in FLOLIZ (Fig. 4D).

During daytime, a total abundance of 4820 juveniles and 2119 adults fish from 12 species was estimated by visual census: 1297 juveniles and 1227 adults from 8 species in FLOLIZ; 1873 juveniles and 548 adults from 11 species in DCS; 1650 juveniles and 344 adults from 8 species in NCS. Juvenile fish species richness varied significantly between Season ( $P$ -value = 0.011) and between Station according to Year ( $P$ -value = 0.026). The species richness of juvenile fish was higher in DCS and NCS than in FLOLIZ in 2019 (Fig. 4E). Estimated abundance of juvenile fish differed only between Season ( $P$ -value = 0.002) (Tab. 2). For adult fish, estimated abundance differed significantly between Season ( $P$ -value = 0.002), between Year ( $P$ -value = 0.008) and between Station according to Year ( $P$ -value < 0.001). Adult fish were less abundant in FLOLIZ in 2019 than in NCS (Fig. 4F). They were more abundant in FLOLIZ than in littoral control stations in 2021 and more abundant than in DCS in 2022 (Fig. 4F). Adult species richness only differed between Season ( $P$ -value < 0.001).

### 3.2 Fish community

The composition of fish communities appeared to be slightly different between FLOLIZ and control stations (Figs. 5A and 5B). At night, juvenile gudgeon, chub, perch and also adult blenny were more frequent in littoral communities than in FLOLIZ. During the day, FLOLIZ hosted a higher frequency of juvenile toxostoma (*Chondrostoma toxostoma*) and adult perch (*Perca fluviatilis*) compared to littoral communities. Juvenile gudgeon were also more frequent at daytime in DCS than in FLOLIZ. All the results are shown in Table 2.

## 4 Discussion

Our results showed that abundance and species richness of fish at juvenile and adult stage in FLOLIZ could differ from those of littoral zones at different timescales, and, importantly, that this could coincide with differences in species assemblage.

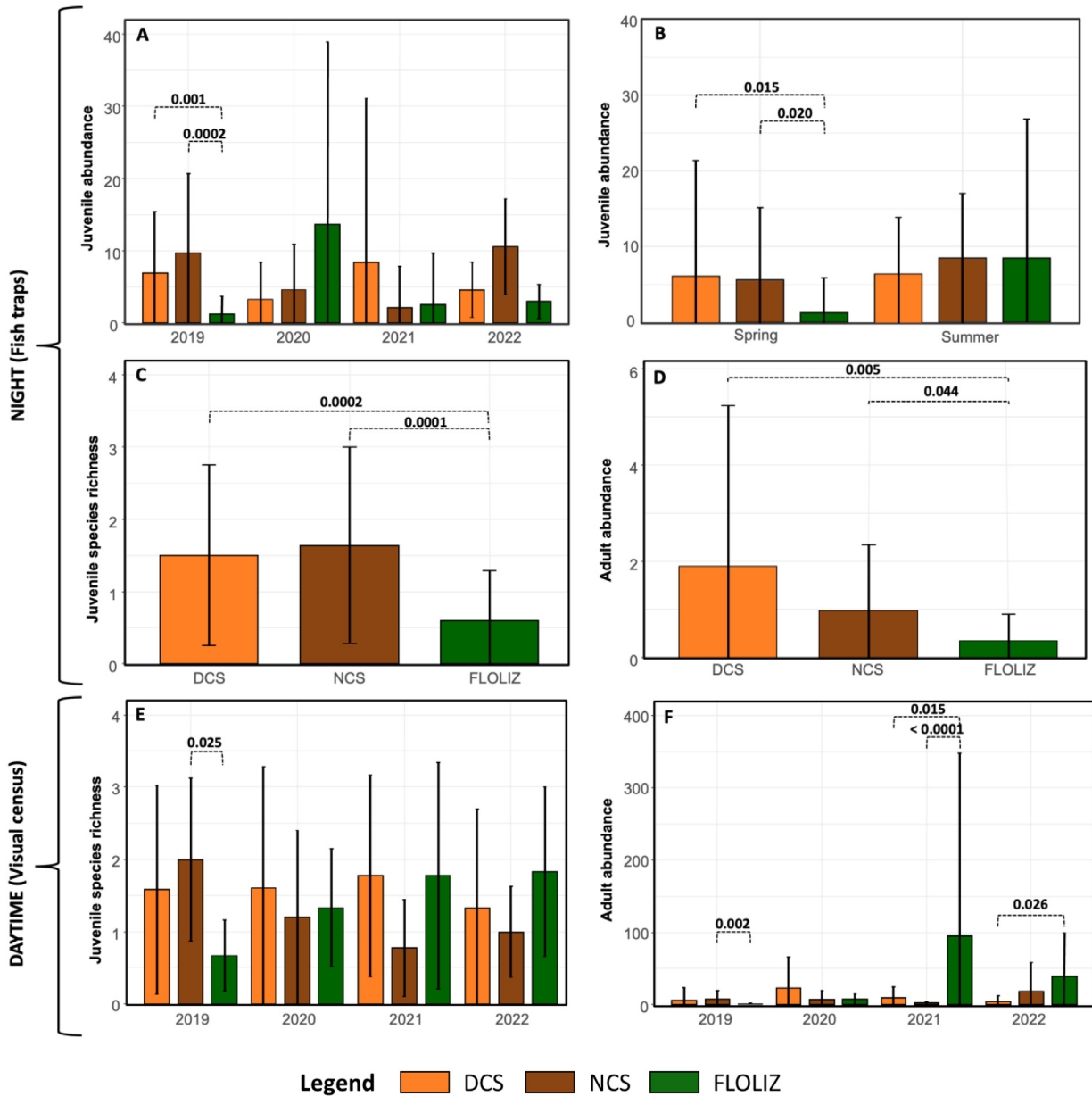
### 4.1 Night use of FLOLIZ

At night, the littoral zone of the reservoir hosted greater fish abundance than FLOLIZ, particularly for juvenile gudgeon, perch, chub, and adult blenny, and higher richness. Gudgeon and blenny are two benthic fish species that preferred

**Table 2.** Mean frequencies  $\pm$  SD of fish species in FLOLIZ and control stations (DCS, NCS) and pairwise comparisons with a Conover-Iman test between station type for night (A) and daytime (B) sampling over the whole sampling period (2019–2022). (NS = No significant/\*\*\* for  $P$ -value  $< 0.001$ / \*\* for  $P$ -value  $< 0.01$ / \* for  $P$ -value  $< 0.05$ ).

A		NIGHT (Fish traps)			
Species (scientific name)	Stage	DCS	NCS	FLOLIZ	$P$ -value
Bleak ( <i>Alburnus alburnus</i> )	Juvenile	0.032 $\pm$ 0.094	0.046 $\pm$ 0.149	0.015 $\pm$ 0.111	NS
	Adult	–	–	–	–
Blenny ( <i>Salaria fluviatilis</i> )	Juvenile	0.15 $\pm$ 0.272	0.222 $\pm$ 0.341	0.352 $\pm$ 0.457	NS
	Adult	0.126 $\pm$ 0.273	0.071 $\pm$ 0.178	0.016 $\pm$ 0.078	NCS/FLOLIZ* DCS/FLOLIZ*
Pike ( <i>Esox lucius</i> )	Juvenile	0.022 $\pm$ 0.113	0.028 $\pm$ 0.152	0.019 $\pm$ 0.137	NS
Chub ( <i>Squalius cephalus</i> )	Juvenile	0.083 $\pm$ 0.223	0.087 $\pm$ 0.234	0 $\pm$ 0	NCS/FLOLIZ** DCS/FLOLIZ**
	Adult	–	–	–	–
Roach ( <i>Rutilus rutilus</i> )	Juvenile	0.054 $\pm$ 0.16	0.017 $\pm$ 0.075	0.018 $\pm$ 0.081	NS
	Adult	0 $\pm$ 0	0.012 $\pm$ 0.086	0 $\pm$ 0	NS
Gudgeon ( <i>Gobio gobio</i> )	Juvenile	0.063 $\pm$ 0.202	0.05 $\pm$ 0.156	0 $\pm$ 0	NCS/FLOLIZ* DCS/FLOLIZ**
	Adult	0.031 $\pm$ 0.113	0.013 $\pm$ 0.092	0.009 $\pm$ 0.069	NS
Perch ( <i>Perca fluviatilis</i> )	Juvenile	0.176 $\pm$ 0.317	0.186 $\pm$ 0.287	0.053 $\pm$ 0.203	NCS/FLOLIZ*** DCS/FLOLIZ**
	Adult	0.091 $\pm$ 0.223	0.055 $\pm$ 0.162	0.136 $\pm$ 0.322	NS
Nase ( <i>Chondrostoma toxostoma</i> )	Juvenile	0.001 $\pm$ 0.009	0.007 $\pm$ 0.033	0.005 $\pm$ 0.034	NS
B		DAYTIME (Visual census)			
Species (scientific name)	Stage	DCS	NCS	FLOLIZ	$P$ -value
Bleak ( <i>Alburnus alburnus</i> )	Juvenile	0.111 $\pm$ 0.251	0.096 $\pm$ 0.217	0.022 $\pm$ 0.089	NS
	Adult	0.035 $\pm$ 0.164	0.012 $\pm$ 0.077	0.043 $\pm$ 0.174	NS
Blenny ( <i>Salaria fluviatilis</i> )	Juvenile	0.199 $\pm$ 0.315	0.254 $\pm$ 0.368	0.363 $\pm$ 0.409	NS
	Adult	0.166 $\pm$ 0.301	0.287 $\pm$ 0.379	0.305 $\pm$ 0.371	NS
Pike ( <i>Esox lucius</i> )	Juvenile	0.026 $\pm$ 0.155	0.034 $\pm$ 0.121	0.083 $\pm$ 0.25	NS
Chub ( <i>Squalius cephalus</i> )	Juvenile	0.006 $\pm$ 0.031	0.014 $\pm$ 0.046	0.003 $\pm$ 0.016	NS
	Adult	0.011 $\pm$ 0.049	0.008 $\pm$ 0.037	0 $\pm$ 0	NS
Roach ( <i>Rutilus rutilus</i> )	Juvenile	0.043 $\pm$ 0.145	0.045 $\pm$ 0.187	0.027 $\pm$ 0.089	NS
	Adult	–	–	–	–
Gudgeon ( <i>Gobio gobio</i> )	Juvenile	0.086 $\pm$ 0.189	0.019 $\pm$ 0.086	0 $\pm$ 0	DCS/NC*** DCS/FLOLIZ***
	Adult	0.028 $\pm$ 0.101	0.026 $\pm$ 0.10	0 $\pm$ 0	NS
Perch ( <i>Perca fluviatilis</i> )	Juvenile	0.103 $\pm$ 0.266	0.095 $\pm$ 0.240	0.024 $\pm$ 0.073	NS
	Adult	0.016 $\pm$ 0.066	0.017 $\pm$ 0.088	0.05 $\pm$ 0.101	NCS/FLOLIZ ** DCS/FLOLIZ **
Nase ( <i>Chondrostoma toxostoma</i> )	Juvenile	0.003 $\pm$ 0.019	0 $\pm$ 0	0.031 $\pm$ 0.099	NCS/FLOLIZ ** DCS/FLOLIZ *

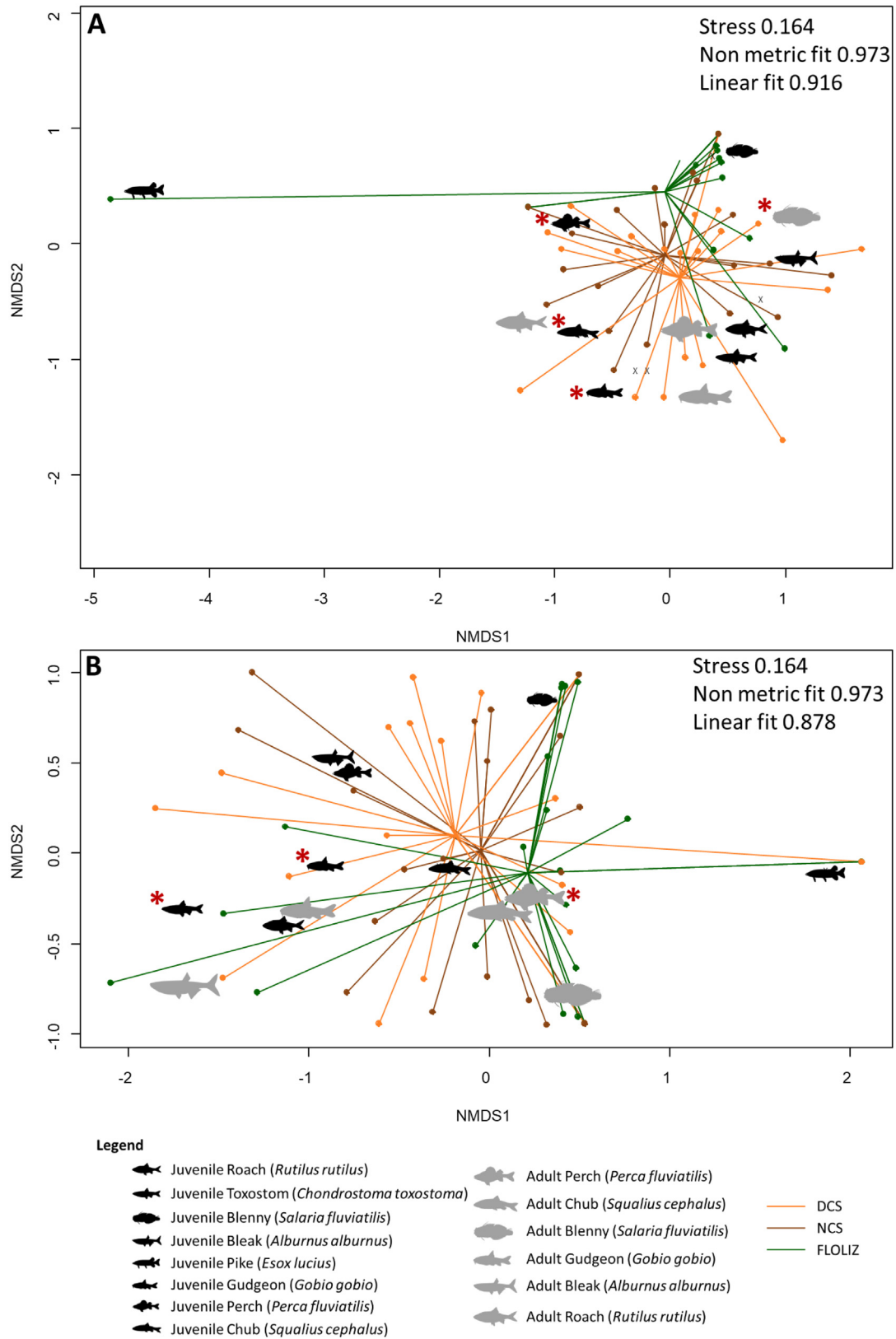




**Fig. 4.** Comparison of fish abundance and species richness at night (fish trap) and daytime (visual census). Only significant effects from the deviance analysis in Table 1 and ones that involve the type of station have been detailed to focus on the station effect. (A) Mean juvenile fish abundance (+ SD) between the different type of stations (DCS, NCS, FLOLIZ) according to year; (B) Mean juvenile fish abundance (+ SD) between the different type of stations (DCS, NCS, FLOLIZ) according to season; (C) Mean juvenile fish richness (+ SD) between the different type of stations; (D) Mean adult fish abundance (+ SD) between the different type of stations; (E) Mean adult fish richness (+ SD) between the different type of stations (DCS, NCS, FLOLIZ) according to year; (F) Mean adult fish abundance (+ SD) between the different type of stations (DCS, NCS, FLOLIZ) according to year.

the fine substrates of debris cones in littoral zone at the head of the bay (Zweimüller, 1995; Mastroillo *et al.*, 1996; Gasith and Goren, 2009) rather than the coarse caged substrates of FLOLIZ. The swimming performance of benthic fish like gudgeon do not allow them to swim long distances in open water to reach the FLOLIZ (Tudorache *et al.*, 2008).

In addition, the riverine origin of gudgeon, chub, and blenny could explain their greater presence in littoral zones compared to FLOLIZ, which mimic small ponds where the flow to which these species are well adapted is dampened (Aarts *et al.*, 2004; Wolter, 2010; Laporte *et al.*, 2016). Finally, many studies have shown that juvenile perch increase their swimming activity at



**Fig. 5.** Non-Metric Multidimensional Scaling ordination of fish species frequencies for FLOLIZ, NCS and DCS over the whole sampling period (2019–2022) at night (A) and during daytime (B). The stress value  $<0.20$  corresponds to a good fit (Clarke, 1993). The non-metric fit  $R^2$  of 0.98 for both and the linear fit  $R^2$  of 0.92 and 0.88 respectively corresponds to a fairly good adjustment. The red stars (\*) show a significant difference in the abundance of the corresponding species between the control stations (DCS, NCS) and the FLOLIZ (refer to Tab. 2).

dusk and migrate in the littoral zone to forage and avoid predators in deep water (e.g. Wang and Eckmann, 1994; Jacobsen *et al.*, 2015). At night, they rest on the bottom in the littoral zone (Imbrock *et al.*, 1996).

#### 4.2 Daytime use of FLOLIZ

During the day, differences of abundance between FLOLIZ and littoral zone could be observed from 2021. We could expect that the structured habitat within FLOLIZ attract fish during the daytime (Lewin *et al.*, 2004; Maciej Gliwicz *et al.*, 2006). In some years, abundance of fish in FLOLIZ could be higher than in littoral zones, FLOLIZ communities globally harboring more juvenile *Toxostoma* and adult perch compared to that littoral areas that hosted more juvenile gudgeon. These results could strengthen the attractiveness of FLOLIZ due to the diversity and complexity of habitats they provide. In particular, aquatic vegetation increases the structural complexity and influences the distribution of fish (Thomaz and Cunha, 2010; Okun and Mehner, 2005). The early life stages of fish represent a critical period in their life cycle, due to high natural mortality and predation (Sifa and Mathias, 1987). The juvenile of *Toxostoma* could take refuge in dense aquatic vegetation and in empty wire mesh cages of FLOLIZ to decrease predation risk (Persson and Eklov, 1995; Bry, 1996; Chick and Mlvor, 1997; Abdel-tawwab, 2005). Additionally, aquatic vegetation and complex structures support high food densities for fish (e.g. biofilm, plankton, macroinvertebrates) (Cazzanelli *et al.*, 2008; Cremona *et al.*, 2008; Jaschinski *et al.*, 2011). This is suitable for *Toxostoma*, which feed upon plankton, perolithon, and macroinvertebrates (Corse *et al.*, 2010). By providing shelter and food, the aquatic vegetation appears to be an essential feature of habitats to support the survival and recruitment of many fish species (Rozas and Odum, 1988; Massicotte *et al.*, 2015). Perch is a very plastic meso-predator which has been stocked since the Serre-Ponçon reservoir was built (Chappaz *et al.*, 1998). The use of FLOLIZ by perch as a feeding ground results from the availability of prey, such as juvenile fish (mainly cyprinids) and the high abundance of macroinvertebrates (Salmon *et al.*, 2022). Indeed, even at the adult stage, the perch diet is very generalist (Dörner *et al.*, 2003). Moreover, the vegetation could provide a suitable spawning habitat for perch (Smith *et al.*, 2001; Čech *et al.*, 2009).

#### 4.3 Attractiveness of FLOLIZ

Shortly after being installed, FLOLIZ became as attractive as littoral zones, at least during daytime. At night, FLOLIZ remained generally less attractive than littoral zones. These results differ significantly from other studies, which found an early and much higher use of AFI (Gillet, 1989; Nakamura *et al.*, 1997; Huang *et al.*, 2017; De Moraes *et al.*, 2023) and other types of artificial structures (Santos *et al.*, 2008, 2011; Feger and Spier, 2010). For example, Nakamura *et al.* (1997) found one hundred times more fish in AFI than in control areas in Lake Kasumigaura, Japan and De Moraes *et al.* (2023) observed densities of fish one to two order of magnitude greater in AFI than in their surroundings in Lipno Reservoir, Czech Republic. All these studies however show variable

results with respect to the distribution of fish size; while De Moraes *et al.* (2023) and Santos *et al.* (2008) found more small fish in AFI, Huang *et al.* (2017) and Feger *et al.* (2010) did not. Some design differences with our study are worth emphasizing. Nakamura *et al.* (1997) tested a much bigger structure (the size of their AFI was 874 m<sup>2</sup>) than ours (70 m<sup>2</sup>), which could have played a role, for example, given the space requirements for pike spawning grounds and home ranges (Chancerel, 2003; Cook and Bergersen, 1988; Sandlund *et al.*, 2016). De Moraes *et al.* (2023) used smaller structures (10 or 14 m<sup>2</sup>), but also a greater number of them distributed in closer proximity, and still observed higher fish densities. Another big difference with our study is the littoral location of artificial structures. In De Moraes *et al.* (2023), structures were located in water at a depth of 1.5 to 1.7 m and very close to the shore; structures were also situated close to the shore in Nakamura *et al.* (1997). This is also the case for artificial reefs, which are often located in the shallow littoral zone (Kelch *et al.*, 1999; Schou *et al.*, 2009; Feger and Spier, 2010; Baumann *et al.*, 2016). This location in the natural littoral area contrasts with our FLOLIZ, which are located about 50 m offshore in waters as deep as 30 m due to constraints linked to extremely high annual WLF (Salmon *et al.*, 2022). This disconnection from the littoral area could have limited the colonization of FLOLIZ; small individuals and benthic species with reduced swimming performance (Ojanguren and Braña, 2003; Tudorache *et al.*, 2008) could fear to swim across a risky pelagic area to reach FLOLIZ (Braband and Faafeng, 1993; Shoup *et al.*, 2014). Gillet (1989) however observed various species such as perch, pike and cyprinids spawning on artificial grounds that could be far from the bank in lakeshore zones of large lakes but without any evaluation of fish densities. The relatively small area of offshore FLOLIZ could be difficult for fish to find and could therefore be a limiting factor in their efficiency. Differences in physico-chemical factors, which have an effect on the attractiveness of artificial structures (Walters *et al.*, 1991; Moring and Nicholson, 1994), could also be involved. Indeed, in these studies showing a positive effect of AFIs on fish, AFIs were installed in sites very different from Serre-Ponçon: much shallower (~5 m), with much lower WLF (up to 3 m), and with eutrophic water.

Studies testing structures comparable to FLOLIZ aiming at providing both spawning substrates and nursery habitats remain scarce and further research into the effectiveness of FLOLIZ in different environmental contexts or with different designs is needed and could offer mitigation solutions against the deleterious effects of WLF, at least for some targeted species. For example, juvenile northern pike seemed to be characteristic of the FLOLIZ community with more frequent observations than in littoral stations during daytime but with a high variability between sampling campaigns. A focus on this species with a slightly different analysis and time period led to some positive effect of FLOLIZ on pike abundance, even if weak (Salmon *et al.*, 2024). This suggests that there may be a positive signal for some species. In Serre-Ponçon reservoir, other phytophilous species are present (*i.e.* tench, carp) but they are less frequent in its downstream section characterized by steep and homogeneous banks and great depths. Studies have shown that there is an upstream/downstream gradient in fish abundance and biomass in reservoirs (Anderson *et al.*, 1983; Swierzowski, 2000; Prchalová *et al.*, 2008, 2009) due to

differences in productivity and littoral habitats. Therefore, it would be interesting to implement new FLOLIZ in the upstream part of the reservoir in order to assess their attractiveness for other species.

Finally, we find it useful to mention that no crayfish were caught or seen in FLOLIZ over these four years even though an exotic species (*Faxonius limosus*) is present in Serre-Ponçon. The disconnection of FLOLIZ from the bank and from the bottom very probably prevented their colonization by crayfish; amphibians (*Bufo bufo*) and their eggs, however, were seen in FLOLIZ.

#### 4.4 Methodological considerations

The use of two different methods with fish traps at night and visual census during daytime did not allow for comparisons between night and day but did allow for the comparison of FLOLIZ with control stations. With passive capture, traps sampled the most mobile fish whereas visual census sampled both mobile and less mobile ones; but visual census probably underestimated the number of individuals in FLOLIZ compared to the littoral zone as fish can hide in numerous cavities, dense vegetation or be hidden by the FLOLIZ structures. Finally, the size of the trap was a limiting factor for the capture of large adult individuals. However, taking into consideration the species sampled during this study, only adult pike and large chub could not be captured by the fish traps.

## 5 Conclusion

The lack of littoral habitats, and particularly refuge and nursery habitats for juvenile fish, can lead to a decline in some populations in reservoirs subject to WLF. By mimicking the habitats of a littoral zone, FLOLIZ could be a potential mitigation solution for such lake ecosystems. This study showed that abundance and richness of both adult and juvenile fish were comparable between FLOLIZ and littoral stations during the day, while at night fish were more abundant in littoral stations, even if this is not generalized to all species. These results show that fish can indeed use FLOLIZ but probably not in a way that could mitigate the deleterious effects of WLF on fish populations. Such studies remain scarce and further ones should be encouraged in other reservoirs (with different sizes and amplitudes of WLF) or other types of artificial lakes (for example, hill reservoirs) and with different FLOLIZ designs in order to obtain robust conclusions on their potential effectiveness.

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#### Supplementary material

**Figure A1.** Daily variations of the elevation of Serre-Ponçon reservoir between 2017 and 2022 (Data from EDF).

**Figure A2.** Fitness of generalised linear models (GLM) by DHARMA package. A – Juvenile abundance for visual census sampling; B – Juvenile species richness for visual census sampling; C – Juvenile abundance for fish trap sampling; D – Juvenile species richness for fish trap sampling; E – Adult abundance for visual census sampling; F – Adult species richness for visual census sampling; G – Adult abundance for fish trap sampling; H – Adult species richness for fish trap sampling.

**Table A1.** Overview of samplings carried out by method and season year.

**Table A2.** Summary of estimated maturity size (total length) for different fishes in Serre-Ponçon reservoir or in similar environments based on literature.

The Supplementary Material is available at <https://www.kmae-journal.org/10.1051/kmae/2024025/olm>.

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