

School of Doctoral Studies in Biological Sciences

University of South Bohemia in České Budějovice

Faculty of Science

**Enhancement of fish communities,  
improvement of sampling and stock  
assessment in lakes and reservoirs.**

**Ph.D. Thesis**

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## **Annotation**

This Ph.D. thesis focuses on fish habitats, how we can improve their natural complexity, and how we can improve techniques to survey these habitats. With increasing human activities affecting freshwater ecosystems due to human population growth and industrial expansion, it is crucial to study environmental changes, their impacts, and ways to mitigate damage. As many biotic and abiotic factors can influence the health and diversity of the community, for our study, we focused on habitat definition and complexity, and the effect of fishery management.

Paper (I) focuses on the transition between littoral (shallow areas) and pelagic (open water) habitats and their impact on fish communities. The littoral zone, typically the most intricate segment of a water body, serves as the primary habitat for a significant portion of the fish community and species diversity. However, its spatial extent is very limited. Littoral delimitation is important for obtaining a true picture of the fish community composition and for its sustainable management decisions.

Paper (II) investigated the impact of protected areas on fish populations in the Lipno reservoir in the Czech Republic, specifically focusing on the abundance, biomass, standard length, and diversity indices. Protected areas have legislation that reduces or stops certain anthropological impacts to help recover the ecosystem. These areas are normally linked to spawning areas, feeding grounds, or rare species and are vital for the restoration and proliferation of specific environments. In our case we revealed more and larger predatory fish in protected and low anthropological impact areas.

Paper (III) tests the introduction of artificial habitats, which are man-made structures or environments created to provide additional habitats and support for various organisms. Despite efforts to restore habitats to their natural states, there are instances where complete restoration is challenging. In particular, water bodies are subjected to significant anthropogenic alterations, such as reservoirs. In such instances, the introduction of artificial habitats has emerged as a solution to rapidly enhance the complexity of these environments. In Lipno reservoir, artificial floating islands attracted young-of-the-year of common species.

## **Declaration**

I hereby declare that I am the author of this dissertation and that I have used only those sources and literature detailed in the list of references.

Karlos Ribeiro de Moraes

České Budějovice

Date

This thesis originated from a partnership of Faculty of Science, University of South Bohemia, and Institute of Hydrobiology, Academy of Sciences of the Czech Republic, supporting doctoral studies in the Hydrobiology study programme.



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## List of papers and author's contribution

The thesis is based on the following papers (listed chronologically):

- I. **Moraes K.**, Souza A., Vašek M., Bartoň D., Blabolil P., Čech M., Dos Santos R.A., Draštík V., Holubová M., Jůza T., Kočvara L., Kolářová K., Matěna J., Peterka J., Říha M., Sajdlová Z., Tsering L., Šmejkal M., Kubečka J. (2021) Openness of fish habitat matters: Lake pelagic fish community starts very close to the shore. *Water* 13: 3291. DOI: 10.3390/w13223291. (IF = 3.4)  
KM helped with the designing of the field sampling, took part at the field work, did the statistical analyses of the data and wrote the manuscript with the help of the co-authors. His contribution was 65%.
  
- II. **de Moraes K. R.**, Souza A., Bartoň D., Blabolil P., Muška M., Prchalová M., Randák T., Říha M., Vašek M., Turek J., Tušer M., Žlábek V., Kubečka J. (2023) Can a protected area help improve fish populations under heavy recreation fishing? *Water* 15: 632. DOI: 10.3390/w15040632 (IF = 3.4)  
KM did the statistical analyses of the data and wrote the manuscript with the help of the co-authors. His contribution was 60%.
  
- III. **de Moraes K. R.**, Souza A., Muška M., Hladík M., Čtvrtlíková M., Draštík V., Kučerová A., Krolová M., Sajdlová Z., Šmejkal M., Kubečka J. (2023) Artificial floating islands: a promising tool to support juvenile fish in lacustrine systems. *Hydrobiologia* 850: 1969–1984. DOI: 10.1007/s10750-023-05204-8 (IF = 2.6)  
KM helped with the designing of the field sampling, took part at the field work, did the statistical analyses of the data and wrote the manuscript with the help of the co-authors. His contribution was 55%.

## Co-author agreement

Jan Kubečka, the supervisor of this Ph.D. thesis and co-author of PAPER I, II and III, fully acknowledges the stated contribution of Student's Name to these manuscripts.

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RNDr. Jan Kubečka, Ph.D.

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# **1. Introduction**



Freshwater ecosystems, such as reservoirs, lakes, ponds, rivers, streams, and wetlands are crucial to human life because of the ecosystem services provided by these systems, including sources of drinking water, food production, and recreation (Daily, 1997). Freshwater ecosystems are exposed to dire pressures coming from agricultural, industrial and urban activities, such as pollutants, sedimentation, changes in water body, dams and others factors (Anh et al., 2023). Freshwater ecosystems are one of the most threatened in the world, as there are being constantly overused and polluted, have not been often protected by managing actions, despite the fact of housing the highest portion of endangered and threatened species among all ecosystems on Earth (Dudgeon et al., 2006; Strayer & Dudgeon, 2010; Collen et al., 2014). With the increased demand for food by humans due to an increase in population and dietary shifts (higher protein demand), food production systems have evolved to try to meet new requirements; as a result, many fish stocks are being over-exploited (United Nations, 2015). Over-exploitation of fish stocks can lead to declines in fish populations and alter the structural and functional properties of the aquatic community and the ecosystem services provided by them (Caddy & Seijo, 2005; Hauge et al., 2009; Dugan et al., 2010).

Overexploitation of fish stocks has been studied since the 90's, and it has been shown that the capture fisheries has stagnated since in recent decades (David Allan et al., 2005; Mota et al., 2014; Palomares et al., 2020). Freshwater fish have been exploited by human society mainly in three areas: food, recreation (angling) and ornamental fish keeping. Eventual stock collapse has great economic and social consequence (David Allan et al., 2005). Inland stocks have been boosted by aquacultures and hatchery stocking, but even with the increase of the individuals numbers in the waterbodies, it still shows a decline in many stocks (Agostinho et al., 2010). There are several reasons for the decline or collapse of freshwater fisheries, typically when they are affected by external drivers (pollution, habitat loss, barriers, siltation, invasive species and altered river flow), and it is much rarer for them to collapse from overfishing alone (Mims & Olden, 2013; Kjelland et al., 2015; Hamilton et al., 2016; Nöges et al., 2017; Volta et al., 2018; Volta & Jeppesen, 2021).

One of the causes of habitat loss in Europe is water impoundment, the creation of dams or reservoirs that change the configuration and dynamics of rivers around Europe (Belletti et al., 2020). In Europe more than 1.2 million impoundment barriers exist, which is calculated to be 0.74 barriers per kilometre of rivers (Belletti et al., 2020; Parasiewicz et al., 2023). This changes the type of environment upstream, making it a pond like, favouring more generalist and limnophilous species, and causing great alterations in the littoral zone (Wang et al., 2019; Parasiewicz et al., 2023; Šmejkal et al., 2023). Hydrodynamic changes are not the only impact; changes in temperature, chemicals, and turbidity have a negative impact on benthic producers and littoral habitats and affect the downstream environment (Dudgeon et al., 2006; Wang et al., 2019; Belletti et al., 2020; Parasiewicz et al., 2023; Šmejkal et al., 2023). Other negative effect of impoundment is the habitat fragmentation, the separation of the natural habitat has considerable impact on the genetics, migration behaviour and reproduction cycles of the local fish population (Wang et al., 2019; Brauer & Beheregaray, 2020; Parasiewicz et al., 2023; Šmejkal et al., 2023; Sun et al., 2023).

However, impoundment creates new artificial lakes which provide valuable ecosystem services for the society, such as hydropower, water retention, flood protection, navigation and recreation (Daily, 1997; Dai et al., 2010). Water reservoirs play roles similar to lakes in the landscapes where the lakes are

scarce. With the expansion or creation of new habitats, both pelagic and benthic, and the reorganization of biotic and abiotic factor, the fish community will be heavily impacted (Sánchez-Botero et al., 2008; Trigal & Degerman, 2015; Wong & Candolin, 2015; Cottet et al., 2016; Bartoň et al., 2022; Šmejkal et al., 2023). During a span of few years, the fish community will pass by a great increase in abundance and diversity, followed by a decline and then stabilize in to a steady-state (Kubečka, 1993; Cottet et al., 2016).

With the fish stocks of newly created reservoirs comes inevitably the question of sustainable fishery and fishery management (Bernacsek, 2001). Human impacts on fish are usually more pronounced in the reservoirs than in lakes, as the reservoir use would determine the changes in the environment. For example, water retention would increase the water level fluctuation, thus preventing the full development of littoral vegetation (Hellsten & Riihimäki, 1996; Krolová et al., 2012; Krolová & Hejzlar, 2013; Zhang et al., 2015; Cummings et al., 2017; Zamora et al., 2020). This can negatively affect the fish as they need littoral vegetation as a habitat for reproduction and early life history (Winfield, 2004; Logez et al., 2016; Hinz et al., 2023; Sajdlová et al., 2023). Many reservoirs are also subject to high recreation pressure including recreation fishing, eutrophication, water level fluctuation and other anthropogenic impacts which complicate fish life and underline the need for sound fishery management.

For sound fishery management to be precise and successful, representative research is needed to gain a good understanding of the state of the fish community and its problems (Kubečka et al., 2009; Cooke et al., 2023). In assessing large lakes as a whole, one of the crucial questions is proportional representation of different habitats which differ by the fish composition. To this end, the most important has been the definition the relation between benthic and pelagic habitats. The fact that benthic and pelagic habitats harbour different fish communities has been known for decades (Prchalová et al., 2008, 2009a; Alexander et al., 2015a, 2015b). However, we are not aware of any study showing exactly where the benthic/littoral community transitions to the pelagic community and how gradual or abrupt this transition is. Identifying the boundaries between the benthic and pelagic zones is important for estimating fish catch per unit effort, or other characteristics of fish from across the lake such as size or age distribution (Kubečka et al., 2013; Alexander et al., 2015a, 2015b). To date, only arbitrarily assumed values such as distance depth 1.5 m (Mehner et al., 2005; Kubečka et al., 2013) or 3 m (Alexander et al., 2015a), or even 1.5–3 m depending on the thickness of the layer (Lauridsen et al., 2008), have been used without verification to draw the boundary between the two habitats.

Standard Nordic multimesh gillnets has become the main sampling tool in Europe (Mehner et al., 2005; Prchalová et al., 2009b; Argillier et al., 2013; Brucet et al., 2013; Fjälling et al., 2015; Ritterbusch et al., 2022). However, the first version of the CEN standard (CEN, 2005) was heavily dedicated to benthic habitats and paid little attention to pelagic habitats. This has been inevitably causing distortion of the overall picture of fish community (Lauridsen et al., 2008). So many researchers felt that the boundary between the benthic and pelagic habitats needs to be evaluated but no one knew how to do this. Pelagial and littoral can have many definitions (Schindler & Scheuerell, 2002; Peters & Lodge, 2009; Reynolds, 2012; Alexander et al., 2015a; Seekell et al., 2021) but we decided to address the problem from the perspective of the gillnet catch itself. We took the littoral as the most important representative of benthic habitat and installed the gillnets here. In the same night we installed the

gillnets in the pelagial in different distances from the littoral starting at the point where there was just enough depth to install pelagic gillnet (3,5 m). In such an experiment, the catch of gillnets can indicate what part can be considered as littoral and what areas are pelagic.

**PAPER I** was about the delimitation of the littoral zone in two differently shaped waterbodies. Littoral and pelagic species have distinct preferences, but the main goal was to check whether the fish population would be able to demonstrate this separation in space. There are two main scenarios, where the first one would be a sharp decrease or increase in habitat-associated species, as we go further away from the coast. The second scenario would be the opposite, a mild gradual decrease, which would make it difficult to notice the division of habitats.

Water bodies around the world have been severely altered or damaged, all linked with human activities, during the last decades (Dudgeon et al., 2006; Angeler et al., 2014; Grantham et al., 2019). Therefore, major efforts in terms of ecological rehabilitation of water bodies are required in order for fish diversity to persist and prosper. However, the implementation of management and conservation measures is difficult and need new know how. Some of the options for increasing fish populations are: the reduction of the fishing pressure, to improve the catchment and habitat management and restocking effort. Those methodologies have proven successful in various systems, but not all of them can be the solution for every aquatic systems (Dudgeon et al., 2006; Dugan et al., 2010; Uusi-Heikkilä et al., 2018).

One possibility to minimize human influence on fish by creating protected areas. In poor habitat structure situation, creation of fish friendly habitats could be a good way to mitigate negative anthropogenic impacts (Nakamura & Mueller, 2008; Paiva et al., 2015). The IUCN definition for protected areas is a clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values (Dudley, 2008). Historically, protected areas have been designed for protection of endangered species, expecting that the community would have an increase in biomass, abundance and species diversity (Fox et al., 2012). The benefits freshwater protected areas for the fish community often have showed positive results, like the increase in the diversity, abundance and/or biomass of the community (Sarkar et al., 2013; Bower et al., 2015; Campos-Silva & Peres, 2016; Sweke et al., 2016). The results can also be neutral with no difference in abundance, biomass or diversity have been found (Chessman, 2013;, Srinoparatwatana and Hyndes, 2011).

On the topic of protected areas and fish, marine protected areas have much more research done in the last decades than the freshwater (Figure 1). Given that freshwater environments are more vulnerable than marine ones and the scientific knowledge accumulated in the freshwater ecosystems is currently much smaller than in the marine ecosystems, consequently it is of utterly relevance to study the effects of protected area in freshwater systems. Some studies can be used for the comparison, as an example Nelson (2018), where this research have similar species as **PAPER II** and can be analysed how the protection can influence the individual growth in different environments.

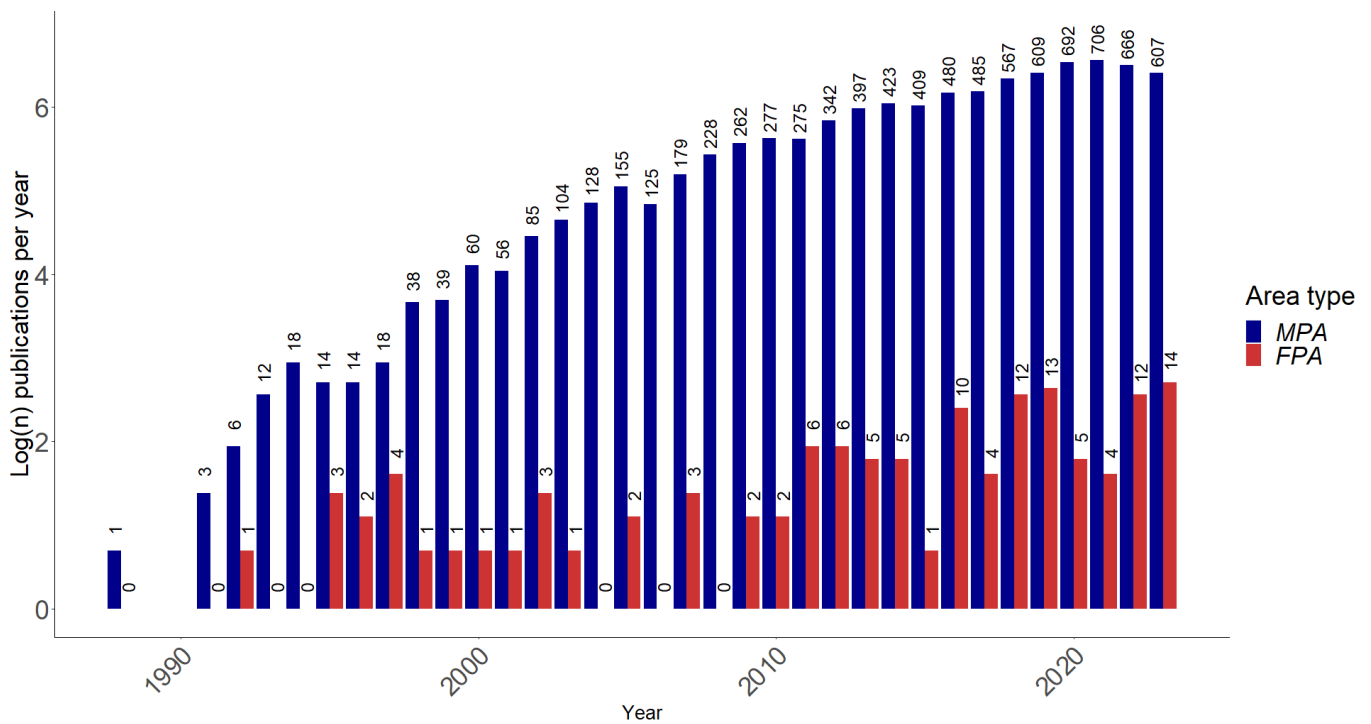


Figure 1: The Log number of published papers per year focusing on the topic of fish and marine protected areas (MPA) or freshwater protected areas (FPA). The number on top of each bar represents to total number of publications per year. Source: Web of Science (February of 2024).

**PAPER II** discusses the protection area in the Lipno reservoir and puts its efficiency in question about helping to increase the fish population in the reservoir. The general role of the protected area is that the fish population would experience less anthropogenic impact and that, in theory, it would help increase the population. We tested this theory with the gillnet catch and compared fish abundance biomass and diversity with other areas in the reservoir.

Studies in lentic environments were found in Canada (Zolderdo et al., 2023) and Tanzania (Sweke et al., 2016) where gillnets were also utilised for the sampling. Sweke experiment shown that the protected area had higher abundance, biomass and diversity than the unprotected areas. Zolderdo research focused in the abundance and metabolism of largemouth bass (*Micropterus salmoides*), and both factors shown better results for the protected area. Other studies on freshwater protected areas concentrated on rivers; in Europe, they focused on Natura 2000 sites (Trochet & Schmeller, 2013; Valavidis et al., 2021; Gavioli et al., 2023; Kail et al., 2023), but they would focus more on the coverage of Natura 2000 sites in relation to the global range of the fish distribution.

In cases where the environment suffers from intense habitat alterations in the water body, the implementation of artificial habitats can be a solution. Artificial habitats to support aquatic organisms have been studied since the 1930s. These studies have focused in creating new habitats to help restore or recolonize underwater communities in impacted areas (Santos et al., 2008). Successful introduction of artificial habitats has been reported in different ecosystems, including artificial reefs in marine environments and artificial floating islands in freshwater lakes, rivers, and reservoirs (Figure 2) (Nakamura et al., 1997; Gatz, 2008; Nakamura & Mueller, 2008; Taquet, 2013; Campbell et al., 2016; Moreno et al., 2016). The fish communities can use artificial or natural structures as new habitats, and are likely to benefit from them (Madhavan & Neethiselvan, 2002; Dempster & Taquet, 2004; Santos

et al., 2008; Feger & Spier, 2010; Wolter, 2010; Campbell et al., 2016). The depth, complexity, and size of the artificial habitat were found to be the factors affecting different fish communities to a different extent (Santos et al., 2008). Artificial habitats can provide benefits to communities, such as shelter, shade, and food (Nakamura et al., 1997; Gatz, 2008; Santos et al., 2008), or even become successful spawning habitats for some species (Roseman et al., 2011).

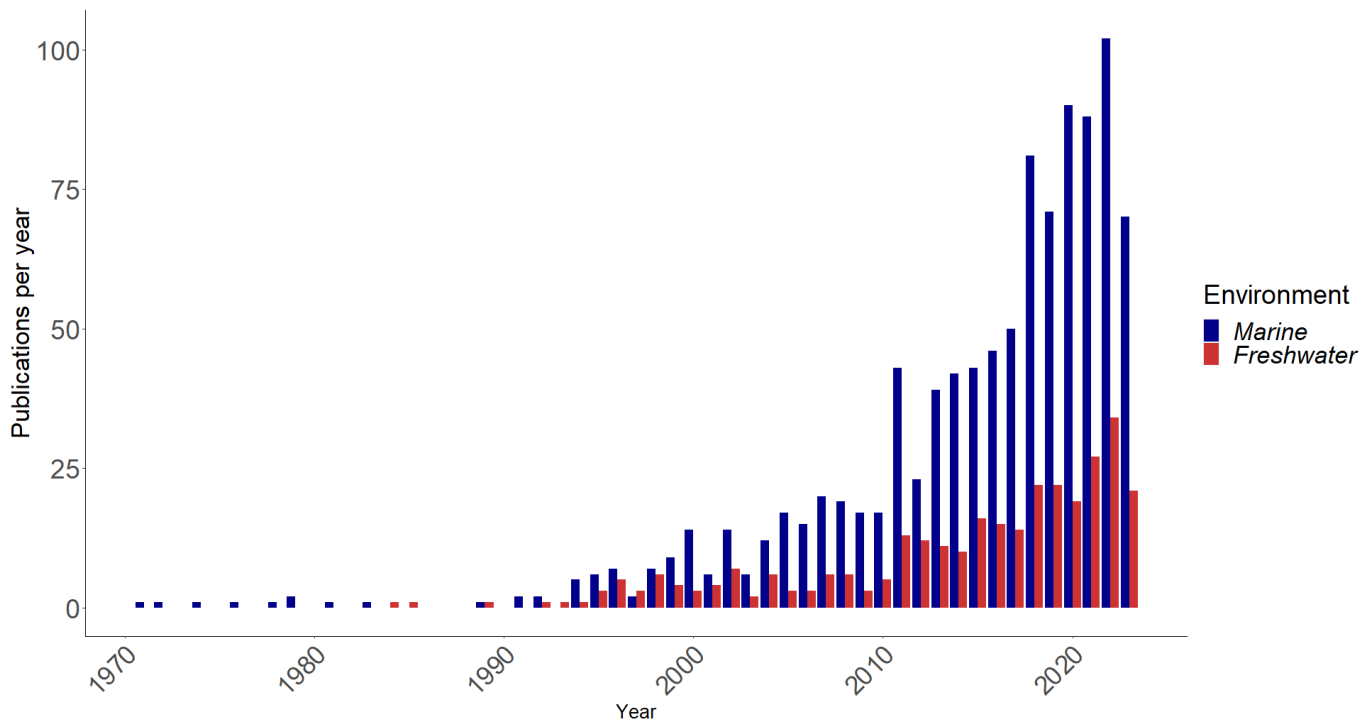


Figure 2: The number of published papers per year focuses on the study of artificial habitats in Marine or Freshwater environments. Source: Web of Science (February of 2024)

Freshwater artificial habitats are mainly represented by artificial floating islands. Artificial floating islands can provide environmental and societal applications such as increased aesthetic of the waterbody, erosion prevention, and most notably in nutrient removal and cycling, of the water, depending on what species of plants are incorporated on the island (Nakamura & Mueller, 2008; Weragoda et al., 2012; Winston et al., 2013; de Freitas et al., 2015). Floating islands have been used for treatment of wastewater like stormwater-sewer, sewage, livestock effluent, and water supply reservoirs, also the ability to help clean up streams and rivers (Nakamura & Mueller, 2008; Weragoda et al., 2012; Winston et al., 2013; Yeh et al., 2015). Floating islands can function in a similar way to macrophytes, as fish are normally attracted to these structures seeking shelter, food or spawning grounds (Dempster & Taquet, 2004; Orue et al., 2019).

Comparable studies to our methodologies was done by Nakamura et al., 1997 and Santos et al., 2008. Nakamura had a set of floating islands in Kasumigaura lake, Japan, surveyed it using set-nets and dip-net, and found an increase of diversity and abundance of the fish community. Santos placed artificial fish habitat, with 2 different depths, 1.5 m midwater floating and bottom, with three different concentrations of artificial vegetation density; with bare, average or dense coverage. The fish surveys were conducted by divers using an underwater visual census of five minutes per week per structure for 11 months. The results showed that the bare habitats of both depths had zero fish observations,

and both bottom habitats with different coverages showed higher abundance and diversity of fish species, but the midwater with dense coverage was the one with the highest abundance.

In our PAPER III we had an experimental design for artificial floating islands in Lipno reservoir. Artificial habitats helped creating complexity in the littoral areas of the water body and provide safe space for the fish community. During the experiment we sampled areas with and without the islands, and compared them in relation of abundance and diversity which developed during several months.



## 2. Results



## **Paper I**

### **Openness of Fish Habitat Matters: Lake Pelagic Fish Community Starts Very Close to the Shore.**

Karlos Moraes, Allan T. Souza, Mojmír Vašek, Daniel Bartoň,  
Petr Blabolil, Martin Čech, Romulo A. dos Santos, Vladislav  
Draštík, Michaela Holubová, Tomáš Jůza, Luboš Kočvara,  
Kateřina Kolářová, Josef Matěna, Jiří Peterka, Milan Říha,  
Zuzana Sajdlová, Marek Šmejkal, Lobsang Tsering and Jan  
Kubečka (2021)

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(IF = 3.4)



## Article

# Openness of Fish Habitat Matters: Lake Pelagic Fish Community Starts Very Close to the Shore

Karlos Moraes <sup>1,2,†</sup>, Allan T. Souza <sup>1,†</sup>, Mojmír Vašek <sup>1,†</sup> , Daniel Bartoň <sup>1</sup>, Petr Blabolil <sup>1</sup>, Martin Čech <sup>1</sup> , Romulo A. dos Santos <sup>1</sup>, Vladislav Draštkík <sup>1</sup>, Michaela Holubová <sup>1</sup> , Tomáš Jůza <sup>1</sup>, Luboš Kočvara <sup>1</sup>, Kateřina Kolářová <sup>1,3</sup>, Josef Matěna <sup>1,‡</sup>, Jiří Peterka <sup>1</sup> , Milan Říha <sup>1</sup>, Zuzana Sajdlová <sup>1</sup>, Marek Šmejkal <sup>1</sup>, Lobsang Tsering <sup>1</sup> and Jan Kubečka <sup>1,2,\*</sup> 

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† These three authors contributed equally to this work.

‡ This paper is dedicated to the living memory of Josef Matěna who deceased during preparation of this paper in September 2021.



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**Abstract:** Fish communities differ significantly between the littoral and the pelagic habitats. This paper attempts to define the shift in communities between the two habitats based on the European standard gillnet catch. We sampled the benthic and pelagic habitats from shore to shore in Lake Most and Římov Reservoir (Czech Republic). The 3 m deep pelagic nets were spanned across the water body at equal distances from two boundary points, where the depth was 3.5 m. The benthic community contained more fish, more species, and smaller individuals. The mild sloped littoral with a soft bottom attracted more fish than the sloping bank with a hard bottom and less benthos and large *Daphnia*. The catch of the pelagic nets was dominated by eurytopic fish—rudd (*Scardinius erythrophthalmus*) and roach (*Rutilus rutilus*) in Most and bleak (*Alburnus alburnus*) in Římov. With the exception of one case where overgrown macrophytes extended the structured habitat, the largest shift from the benthic to the pelagic community was observed only in the first pelagic gillnet above the bottom depth of 3.5 m. Open water catches were relatively constant with small signs of decline towards the middle of the lake. The results indicate that the benthic gillnet catch is representative of a very limited area and volume, while most of the volume is dominated by the pelagic community. This has important consequences for the assessment of the community parameters of the whole lake following the European standards for gillnet sampling design.

**Keywords:** habitat use; spatial distribution; ecotone; open water *Scardinius*; *Rutilus*; *Alburnus*; *Perca*

## 1. Introduction

In any environment, species composition changes gradually or abruptly between habitats. These ecological gradients have been the subject of a number of studies in ecology and usually reflect the abundance and richness of species [1–4]. Rapid changes in species ecological gradients, termed ecotones, have been observed in a variety of ecosystems [1]. Ecotones can affect the abundance and distribution of organisms.

The distribution of fish species is not random and their distribution in different habitats depends on several factors, including substrate composition [5–7], depth [8–10], habitat

complexity [5,9,11,12], temperature [13–15], oxygen concentration [13,16], distribution of planktonic and benthic organisms [14,17,18], and other factors. Biotic and abiotic factors both influence fish distribution, but the contribution of each variable is difficult to separate, especially because of seasonal variance [19]. We can assume that the spatial distribution of fish is optimized by strategies to maximize habitat and resource use with the aim of increasing individual fitness [20]. Predation risk must also be considered. In a dynamic environment, defining habitat boundaries for highly vagrant species is a challenging task. In lentic ecosystems, the boundary between the littoral (shallow areas) and pelagic zones is poorly understood [21].

The definition of the pelagic and littoral zones is based on the physical or biological characteristics of lentic ecosystems. Pelagic zones, also referred to as open water, are usually assumed to be the deeper areas of water bodies characterized by the absence of bottom or habitat structure [8]. Primary production in the pelagic zone is highly dependent on phytoplankton and is therefore often lower than in the littoral zones [22]. On the other hand, littoral zones are usually defined as nearshore areas where light intensity is sufficient to reach the bottom sediment and allow the primary producers (macrophytes and algae) to thrive [23].

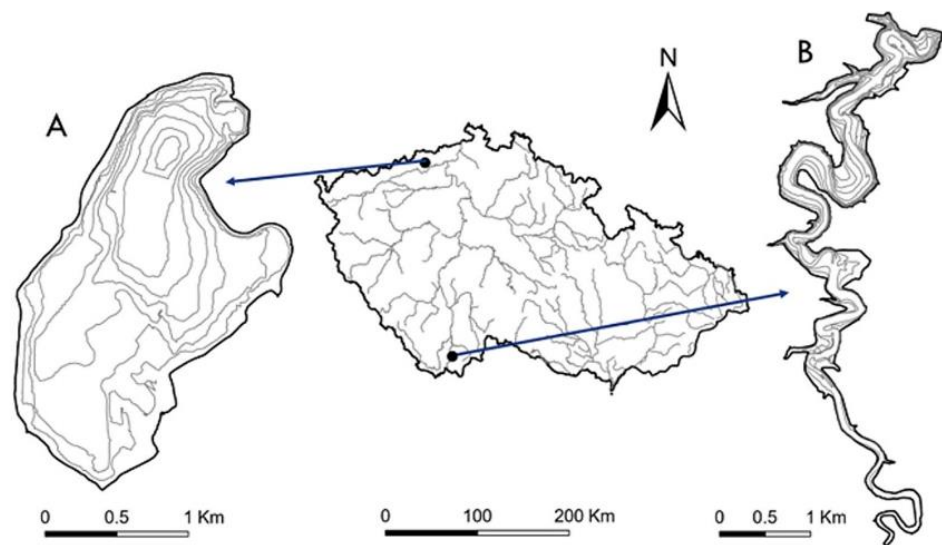
For prey fish, open water is far less safe than the structured littoral. Fernando and Holčík [24] proposed a theory that fishes in evolutionarily young Palearctic systems are mostly of riverine origin and are not sufficiently specialized to take advantage of the pelagic production. Consequently, they expected far fewer fish in the pelagic regions. This is especially true for small fish during the day. Dense schools of species such as juvenile perch, *Perca fluviatilis*; bleak, *Alburnus alburnus*; roach, *Rutilus rutilus*; asp, *Leuciscus aspius*; and dace, *Leuciscus leuciscus*, reside in the littoral during the day [25]. The productivity of the spatially restricted littoral is often insufficient to maintain such high fish densities, forcing even small fish to migrate to offshore during the dusk to feed and return to the littoral before dawn [25–27]. Larger fish, which are less threatened by predators, stay in open water during the day and partially migrate ashore in the evening [28–30]. These patterns have been formulated based on active sampling techniques and hydroacoustics. With the tremendous expansion of the European Standard gillnets (ESG), which are currently the most common sampling tool on the continent, sampling thousands of lakes [31,32], the reflection of the above patterns in gillnet catches becomes relevant. The ESG catches include evening, night, and morning events, and particularly reflect fish abundance and activity. It is well known that the benthic fish community in ESG catches differs from the pelagic one [33–35]. This is true even in smaller waters [8,11]. However, we are not aware of any study showing exactly where the benthic/littoral community transitions to the pelagic and how gradual or abrupt this transition is. Identifying the boundaries between the benthic and pelagic zones is important for estimating fish catch per unit effort [33], or other characteristics of fish from across the lake such as size or age distribution [36]. To date, only arbitrarily assumed values such as distance from the bottom 1.5 m [31,36] or 3 m [33], or even 1.5–3 m depending on the thickness of the layer [35], have been used without verification to draw the boundary between the two habitats.

The aim of this study is to investigate the proportions of the littoral and the pelagic communities in two water bodies with different environmental conditions (Most Lake and Římov Reservoir). With regard to the preference of the littoral over the pelagic, we can divide the fish community into three possible groups: the most diverse benthic fishes, which are strongly bound to the bottom and the littoral zone, the eurytopic fishes, which can use both the littoral and the pelagic habitat, and the open-water fishes, which prefer the pelagic habitat in open waters. Our hypothesis is that during the transition from the littoral to the pelagic, the benthic-bound species will greatly decrease, while the open-water species will greatly increase, and the eurytopic species will show little variation.

## 2. Materials and Methods

### 2.1. Sampling Sites

Two water bodies in the Czech Republic, Lake Most and the Římov Reservoir, were chosen for the experiment (Figure 1). Most is a post-coal mining lake (Ústí nad Labem region, 50.54 N, 13.65 E, see Figure 1) with an area of 310 ha, a maximum depth of 75 m, and a mean depth of 22 m. The lake was formed after the termination of coal mining in the summer of 1999 due to the filling of the open pit from autumn 2008 to autumn 2012. Most is an oligotrophic lake with a high abundance of macrophytes in its littoral area and a high water transparency [37].



**Figure 1.** Map of Czech Republic with major rivers and the location and shape of Most Lake (A) and Římov Reservoir (B) with their respective bathymetries.

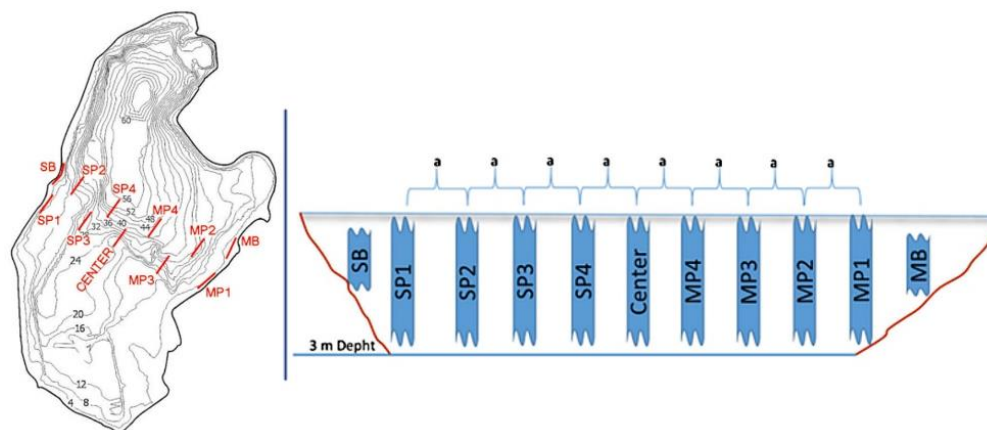
The Římov Reservoir (South Bohemia Region, 48.848 N, 14.487 E) is a canyon-shaped reservoir with a narrow (max. width 600 m) and elongated shape (length 10 km). The reservoir was built during the 1970s (from 1971 to 1978) and covers an area of about 200 ha with a volume of  $34.3 \times 10^6 \text{ m}^3$ , a maximum depth of 40 m, and an average depth of 12 m. Compared to the Most Lake, the Římov Reservoir has a gently to steeply sloping shore without submerged vegetation, which is missing due to significant water level fluctuations and low water transparency due to the eutrophic status of the water [38].

### 2.2. Gillnet Sampling in General

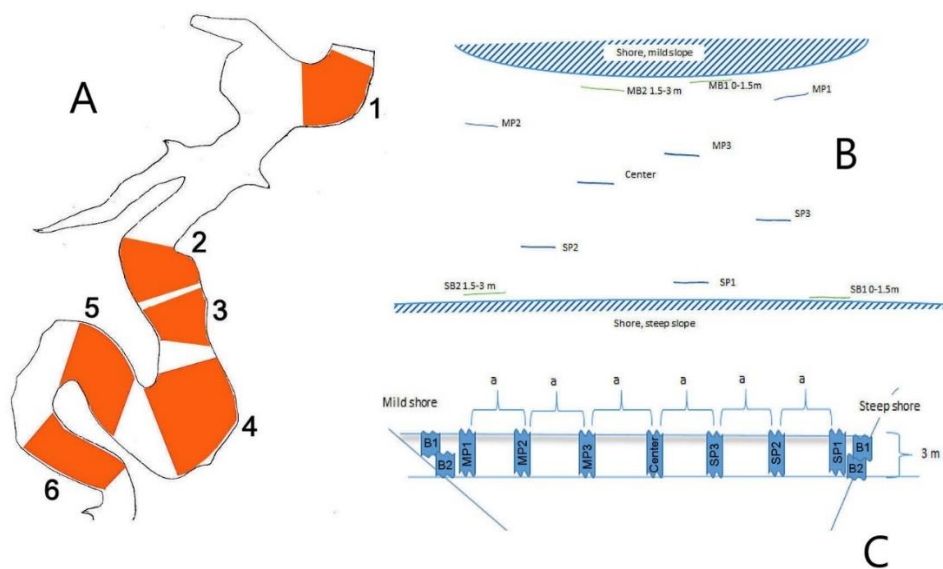
The European Standard gillnets (ESG) [39] were used to estimate the association of fish with littoral and pelagic habitats. The benthic ESG gillnet with 1.5 m height  $\times$  30 m length and 2.5 m mesh panels for each of the 12 mesh sizes was deployed in the littoral, while the pelagic gillnet with 3 m height  $\times$  30 m length and 2.5 m mesh panels for each of the 12 mesh sizes was deployed in the open water. The mesh sizes of the ESG followed a geometric series with a ratio of approximately 1.25 (5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43, and 55 mm) in random order. The first pelagic gill net from the shore was deployed above the bottom depth of 3.5 m (bottom line of the gillnet 0.5 m above the bottom). Depth was measured using a Humminbird Piranha echo sounder operating at 200 kHz.

Gillnet deployment was from bank to bank (Figures 2 and 3). The opposite banks differed in bottom slope, as is common in riverine waterbodies, and the fish community is influenced by the slope [40]. The mild sites had a bank slope of less than  $8^\circ$ , while the steep sites had a slope of more than  $15^\circ$ . The pelagic nets were laid out equidistantly, from the first pelagic net of the mild side to the first pelagic net of the steep side (Figures 2 and 3). The gillnets were named according to the slope of the bank on which they were deployed.

The benthic gillnets were named MB (mild benthic—benthic net on the mild slope) and SB (steep benthic), while the pelagic gillnets were named MP (mild pelagic—pelagic net on the side, adjacent to the mild slope) and SP (steep pelagic), with one pelagic gillnet deployed in the center of the lake (mid distance between the two 3.5 m isobaths in the sampled area) referred to as the center net. Given that the pelagic area had more nets, the number immediately following the acronym indicates the number of gillnets deployed from the shore, e.g., SP1 is the first pelagic gillnet from the steep shore, while SP2 is the following pelagic gillnet, and so on (Figures 2 and 3).



**Figure 2.** Sampling sites in the shape of Most Lake, on the left, and gillnet deployment scheme, on the right. SB—benthic gillnet at steep slope; SP1—center—MP1—pelagic gillnets; MB—benthic gillnet at mild slope. See Material and Methods for detailed explanations.



**Figure 3.** Sampling sites (orange markings in the shape of Římov Reservoir, (A)), gillnet deployment scheme for each area (B) and net scheme from shore to shore (C). B1—benthic gillnet at depth 0–1.5 m; B2—benthic gillnet at depth 1.5–3 m; SP1—center—MP1—pelagic gillnets. See Material and Methods for detailed explanations.

Sampling was done in accordance with CEN standards [39], with the gillnets being deployed 2 h before the sunset and lifted 2 h after the sunrise [41]. Standard fish length and weight of all the captured individuals were measured to the nearest mm and g, respectively. The catch per unit of effort (CPUE) was defined as the number of individuals per 1000 m<sup>2</sup> of net per night, analogically the sampled biomass per unit of effort (BPUE) was defined as number of grams per 1000 m<sup>2</sup> of a net per night.



### 2.3. Most Lake Sampling Design

Sampling in Lake Most was conducted from 3–6 September 2018. The transect area in Lake Most was in the form of a ribbon that extended from shore to shore across the lake. We sampled two benthic and nine pelagic sites in the lake (Figure 2). The east mild shore had a slope of 7° of declination and the west steep shore had a slope of 15°. At each littoral or pelagic location shown in Figure 2, we set up three ESG nets connected by a 40 m rope to ensure adequate spacing between them. The distance between gillnet sampling locations was 150 m. The benthic gillnets were deployed at a depth of 1.5–2.5 m, and the first pelagic gillnet was deployed at a depth greater than 3.5 m from each bank. The remaining pelagic gillnets were deployed at the same spacing. The gillnets were deployed parallel to the shore. Altogether 6 benthic and 27 pelagic gillnets were deployed.

### 2.4. Římov Reservoir Sampling Design

Sampling of the Římov Reservoir was conducted from 30 July to 2 August 2019. Six locations in the reservoir were sampled, each with both a mild slope shore (2° to 8° slope) and a steeply sloping bank (20° to 35° slope). We selected sites only in the true lacustrine zone (Figure 3) to avoid the change in productivity that increases further upstream [42]. A single ESG device was deployed at each net location of each site. The nets were scattered to ensure that no net interfered with the others (Figure 3B). The minimum distance between nets was 60 m, but usually it was more than 100 m. For this experiment, we also deployed two sets of benthic gillnets on either side of the reservoir (one in the 0–1.5 m depth range and the second in 1.5–3 m). For this article, the CPUE and BPUE values from these two nets were combined so that they well represent the littoral range of 0–3 m. Altogether, 24 benthic and 42 pelagic gillnets were deployed.

Zooplankton samples were collected 30–60 min after each gillnet deployment. Vertical hauls with a plankton net (diameter 20 cm, mesh size 0.2 mm) were made at both ends of each pelagic net. Hauls were made from 3 m depth to the surface and two hauls were combined in each zooplankton sample. Samples of littoral zooplankton were collected using a Schindler sampler (volume 30 L, mesh size 0.2 mm). Each sample of littoral zooplankton was collected by combining two samples (one from the upper, 0–1.5 m, and one from the lower, 1.5–3 m, portion of the sampled layer up to 3 m) in one bottle. Samples of littoral zooplankton were collected from both ends of the benthic gillnets deployed in the littoral zones. The zooplankton was divided into 3 groups: *Daphnia galeata*, other Cladocera (*Acroperus harpae*, *Bosmina coregoni*, *Bosmina longirostris*, *Ceriodaphnia quadrangula*, *Diaphanosoma brachyurum*, *Chydorus sphaericus*, *Leptodora kindti*, and *Leydigia leydigi*), and Copepoda (*Cyclops vicinus*, *Eudiaptomus gracilis*, *Mesocyclops leuckarti*, *Thermocyclops crassus*, *Thermocyclops oithonoides*, Cyclopoida–copepodites, and Diaptomidae–copepodites). In addition, 100 individuals of *D. galeata* were measured for body size in each zooplankton sample. The body size of the *Daphnia* was measured from the top of the head to the base of the caudal spine. An amount of 1 mm of the body length of the *Daphnia* was chosen as the threshold between the small and the large individuals.

Benthic samples were collected from the same six locations where benthic gillnets were set. We conducted kick sampling [43] at two depths, 0.3 m and 1 m, for 2 min using a bar net with a mesh size of 0.4 mm. We also attempted to sample the 2 m depth with a 20 cm × 20 cm Eckmann grab, but sampling was often unsuccessful due to the hard substrate, especially on steep banks. The benthic macroinvertebrates were divided into 4 groups: Permanent fauna (*Hydra*, *Planaria*, *Stylaria*, *Nais*, *Dero*, Tubificidae, Nematoda, *Helobdella*, *Lymnaea*, and *Asellus*), Ephemeropteran larvae (*Caenis*, *Cloeon*, and *Ephemera*), Chironomid larvae (*Ablabesmyia*, *Corynoneura*, *Cricotopus*, *Cryptochironomus*, *Dicrotendipes*, *Polypedilum*, *Glyptotendipes*, *Endochironomus*, and *Tanytarsus*); and the other temporal fauna (*Zygoptera*, *Leptoceridae*, *Ecnomus*, *Limnephilidae*, *Tabanidae*, *Sialis*, *Hydrophilidae*, and *Micronecta*).

## 2.5. Data Analyses

Catch per unit effort (CPUE) was calculated as the mean of the total number of individuals divided by the total sampling effort (net surface area), while biomass per unit effort (BPUE) was calculated as the total weight of catch per 1000 m<sup>2</sup> of net area. CPUE and BPUE were calculated for individual species as well as for the entire fish assemblage.

Negative binomial generalized linear models (GLM) were applied to describe the differences in fish CPUE and BPUE values (CPUE and BPUE) with distance from shore in Most. The negative binomial generalized linear model was chosen because it can cope with a large number of zeros and over-dispersed data [44]. The MASS package was used to compute all GLMs [45].

For the analyses in the Římov Reservoir, a generalized linear mixed effects model (GLMM) fitted for the negative binomial family was used, with localities included in the model as a random effect. The model was applied to describe differences in fish CPUE and BPUE and zooplankton density as a function of distance from shore, as well as benthic macroinvertebrate numbers on gentle and steep slopes and at different depths. All data analyses were performed using R software [46].

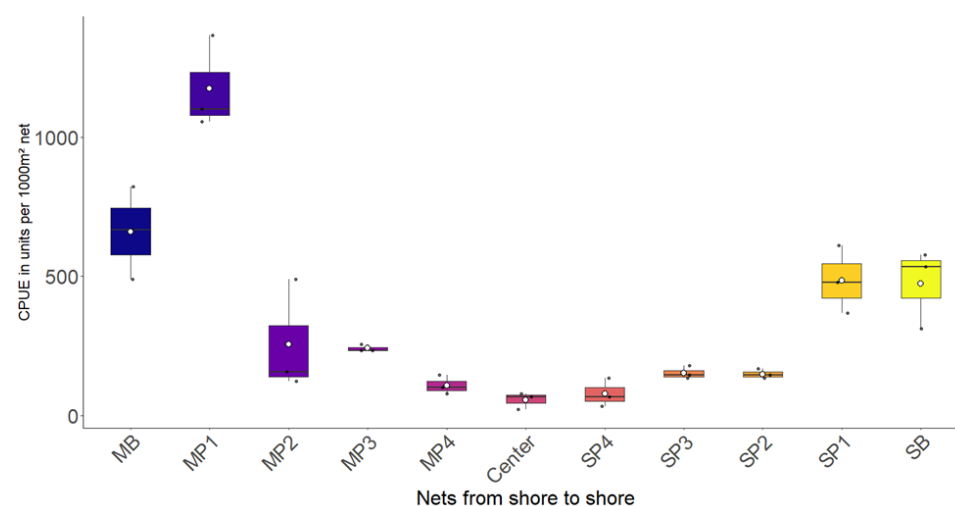
Diversity indices (Shannon–Weaver, Simpson, Pielou’s evenness, and richness) of fish communities were also calculated using the Vegan package of the R software [47].

## 3. Results

### 3.1. Most

A total of 881 fishes belonging to five different species were captured. The most abundant species were the roach (*Rutilus rutilus*)—62.43%; rudd (*Scardinius erythrophthalmus*)—29.63%; European perch (*Perca fluviatilis*)—7.72%; northern pike (*Esox lucius*) and ruffe (*Gymnocephalus cernua*), both with 0.11% of the total fish captured.

CPUE values for the entire fish community decreased sharply from the shore to the center of the lake, on both mild ( $p < 0.001$ , deviance = 18.6) and steep ( $p < 0.001$ , deviance = 15.5) shores (Figure 4). This pattern is particularly striking from the first pelagic gill net SP1 to the middle gill net, which had the lowest CPUE values among all gill nets used (Table 1).



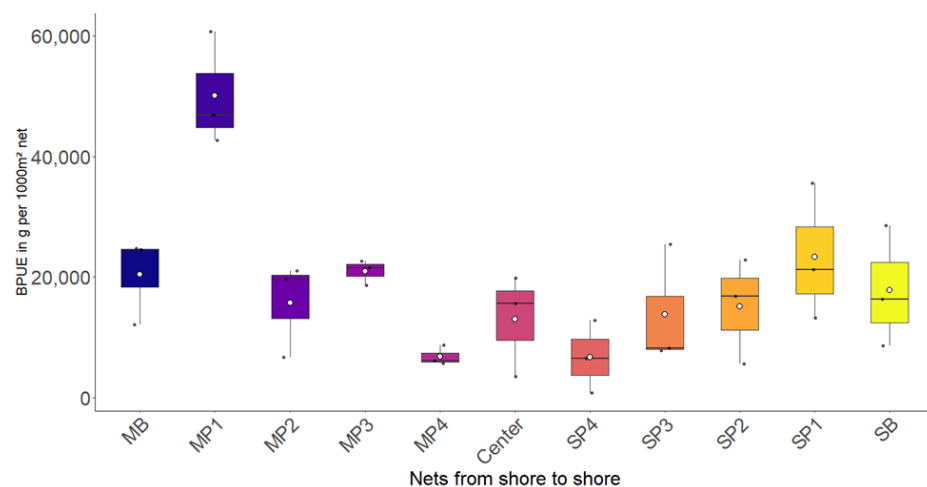
**Figure 4.** Total catch per unit effort (CPUE; individuals per 1000 m<sup>2</sup> of net) from 11 gillnets fished in Most Lake. The boxplot represents the quartile value of the CPUE, the grey dots represent the CPUE of three individual nets deployed at the same distance from shore, the thick middle line represents the median, and the white dot represents the arithmetic mean. The site MP1 was surrounded by overgrown macrophytes.

**Table 1.** Catch per unit of effort (inds. 1000 m<sup>-2</sup> of gillnets), standard errors (se), and the significance level (p) at various benthic and pelagic sites of Most Lake. See Section 2 for detailed explanations of gillnet locations.

Species	MB	se	MP1	se	MP2	se	MP3	se	MP4	se	Center	se	p_Value
<i>Esox lucius</i>	0	0	0	0	0	0	0	0	3.70	3.70	0	0	ns
<i>Gymnocephalus cernua</i>	0	0	0	0	0	0	0	0	0	0	0	0	ns
<i>Perca fluviatilis</i>	177.78	22.22	29.63	9.80	7.41	0	0	0	0	0	0	0	ns
<i>Rutilus rutilus</i>	400.1	111.1	859.26	53.9	181.5	94.57	137.04	9.80	55.56	12.80	18.52	13.35	0.00
<i>Scardinius erythrophthalmus</i>	81.48	45.07	285.19	53.4	66.67	27.96	103.7	3.70	48.15	9.80	37.04	9.80	0.00
Species	SB	se	SP1	se	SP2	se	SP3	se	SP4	se	Center	se	p_Value
<i>Esox lucius</i>	0	0	0	0	0	0	0	0	0	0	0	0	ns
<i>Gymnocephalus cernua</i>	7.41	0	0	0	0	0	0	0	0	0	0	0	ns
<i>Perca fluviatilis</i>	222.22	102.64	11.11	0	0	0	0	0	3.70	0	0	0	ns
<i>Rutilus rutilus</i>	162.96	51.85	325.93	45.1	51.85	9.80	111.1	0	14.81	7.41	18.52	13.4	0.00
<i>Scardinius erythrophthalmus</i>	81.48	60.63	148.15	16.14	96.3	18.52	40.74	13.35	59.26	20.62	37.04	9.80	ns

At the site of MP1 (bottom depth = 3.5 m), many high macrophyte stands were still present, so the habitat cannot be considered truly pelagic. This may have been the cause of the higher CPUE values at this site (Figure 4). When analyzing each species independently, two of the five species showed significant non-random distribution from bank to bank, namely roach (mild:  $p < 0.001$ , deviance = 21.9; steep:  $p < 0.001$ , deviance = 18.3) and rudd (mild:  $p = 0.003$ , deviance = 21.5).

The BPUE values differed significantly for both the mild slope ( $p < 0.001$ , deviance = 18.9) and the steep shores ( $p < 0.023$ , deviance = 16, Figure 5, Table 2). The influence of the macrophyte beds at the site of MP1 was again very evident, with BPUE more than twice that of the other gillnets (Table 2). When analyzing the distribution of the individual species on both slopes, the results followed a similar pattern to the CPUE in the case of roach (mild:  $p < 0.001$ , deviance = 21.1; steep:  $p < 0.002$ , deviance = 18.2), with a significant response to distance from both shores, and also perch, but only for the mild slope side (mild:  $p < 0.001$ , deviance = 12.6).

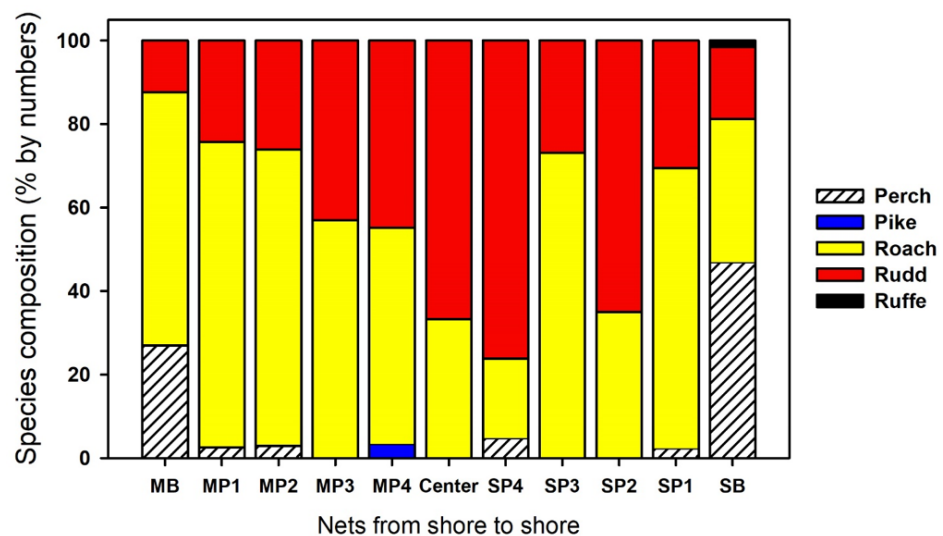


**Figure 5.** Total biomass per unit effort (BPUE; kg per 1000 m<sup>2</sup> of net) from 11 gillnets fished in Most Lake. The boxplot represents the quartile value of the BPUE, the grey dots represent the mean of the individual net, the thick middle line represents the median, and the white dot represents the arithmetic mean. The site MP1 was surrounded by overgrown macrophytes.

**Table 2.** Biomass catch per unit of effort (BPUE, g.1000 m<sup>-2</sup> of gillnets), standard errors (se), and the significance level (p) at various benthic and pelagic sites of Most Lake. See Section 2 for detailed explanations of gillnet locations.

Species	MB	se	MP1	se	MP2	se	MP3	se	MP4	se	Center	se	p_Value
<i>Esox lucius</i>	0	0	0	0	0	0	0	0	607.41	0	0	0	ns
<i>Gymnocephalus cernua</i>	0	0	0	0	0	0	0	0	0	0	0	0	-
<i>Perca fluviatilis</i>	11,422	1824	6526	3593	700	0	0	0	0	0	0	0	0.0001
<i>Rutilus rutilus</i>	7387	3283	1611	2290	8170	2073	5770	763	2044	742	1151	1089	0.0001
<i>Scardinius erythrophthalmus</i>	1659	830	27,444	8510	6911	2269	15,193	1817	4207	2120	11,874	4166	ns
Species	SB	SP1	SP2	SP3	SP4	Center	p_Value						
<i>Esox lucius</i>	0	0	0	0	0	0	-						
<i>Gymnocephalus cernua</i>	281	0	0	0	0	0	ns						
<i>Perca fluviatilis</i>	12,385	4375	1233	0	0	0	ns						
<i>Rutilus rutilus</i>	3911	2410	6091	1774	2733	1389	2503	633.28	229.63	114.99	1150	1089	0.002
<i>Scardinius erythrophthalmus</i>	1259	1004	16,025	3609	12,381	4658	11,348	6231	5577	2549	11,874	4165	ns

Rudd and roach clearly dominated the fish community of Most Lake (Figure 6). They had absolute dominance in the open water habitats, while inshore at the benthic habitat, the dominance was shared with perch (and rarely with ruffe). The dominance of rudd was even more evident in the biomass (Figure 7). This means that, on average, rudd were larger than roach in open waters (see also Table 3). Analysis of the overall size distribution also showed that the lowest mean sizes were found in the first nets on each shore, and the highest mean size would be in the center ( $p < 0.001$ , deviance = 903.44). Rarely, larger individuals of pike and perch were also caught in the pelagic area (Figure 7). Perch dominated the benthic habitats in terms of biomass, which was significantly different from all pelagic habitats. The diversity indices of the fish community of Lake Most were generally low and showed a weak tendency to decrease towards the center of the lake (Figure 8). The low values correspond to a low number of species present. The presence of littoral elements such as perch and ruffe and the lower dominance of rudd resulted in a slightly higher diversity in the littoral. However, none of the diversity indices showed a significant trend between the littoral and the pelagic.



**Figure 6.** Fish species numerical percental composition at different distances from the shore of Most Lake.

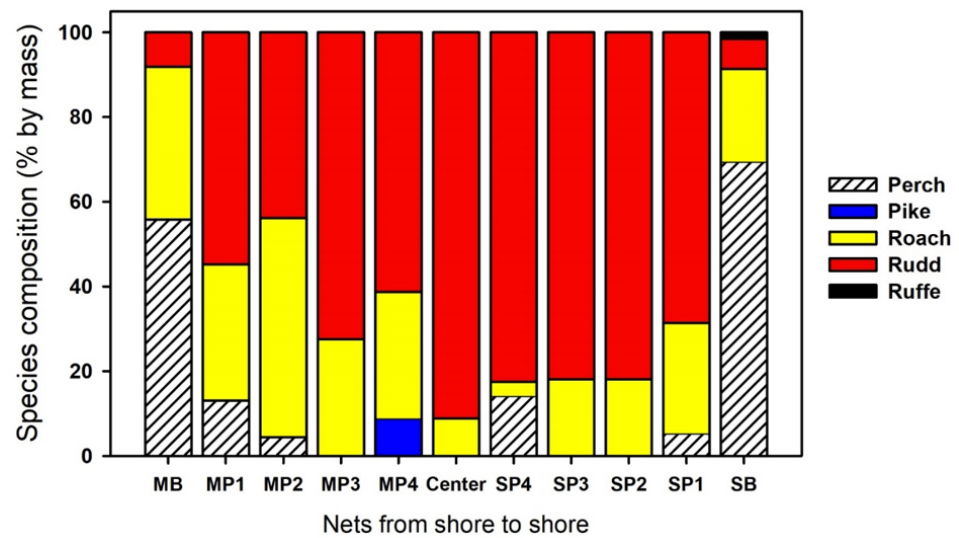


Figure 7. Fish species biomass composition at different distances from the shore of Most Lake.

Table 3. Average standard length (mm) and standard errors (se) of individual species at various benthic and pelagic sites of Most Lake. See Section 2 for detailed explanations of gillnet locations.

Species	MB	se	MP1	se	MP2	se	MP3	se	MP4	se	Center	se
<i>Esox lucius</i>	0	0	0	0	0	0	0	0	260	0	0	0
<i>Gymnocephalus cernua</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Perca fluviatilis</i>	138.33	6.87	196.25	28.53	167.5	22.5	0	0	0	0	0	0
<i>Rutilus rutilus</i>	85.61	2.46	89.16	1.6	109.49	6.82	108.24	7.11	110.67	9.18	126	21.35
<i>Scardinius erythrophthalmus</i>	96.91	4.79	138.25	5.81	137.22	13.64	155	11.26	128.85	14.73	198.5	23.52
Species	SB	se	SP1	se	SP2	se	SP3	se	SP4	se	Center	se
<i>Esox lucius</i>	0	0	0	0	0	0	0	0	0	0	0	0
<i>Gymnocephalus cernua</i>	125	0	0	0	0	0	0	0	0	0	0	0
<i>Perca fluviatilis</i>	131.5	6.96	161.67	32.19	0	0	0	0	220	0	0	0
<i>Rutilus rutilus</i>	85.14	7.63	91.89	2.41	106.07	15.35	94.5	4.39	90	9.13	126	21.35
<i>Scardinius erythrophthalmus</i>	86.55	4.03	145.4	8.36	136.35	13.63	195	20.83	134.69	13.58	198.5	23.52

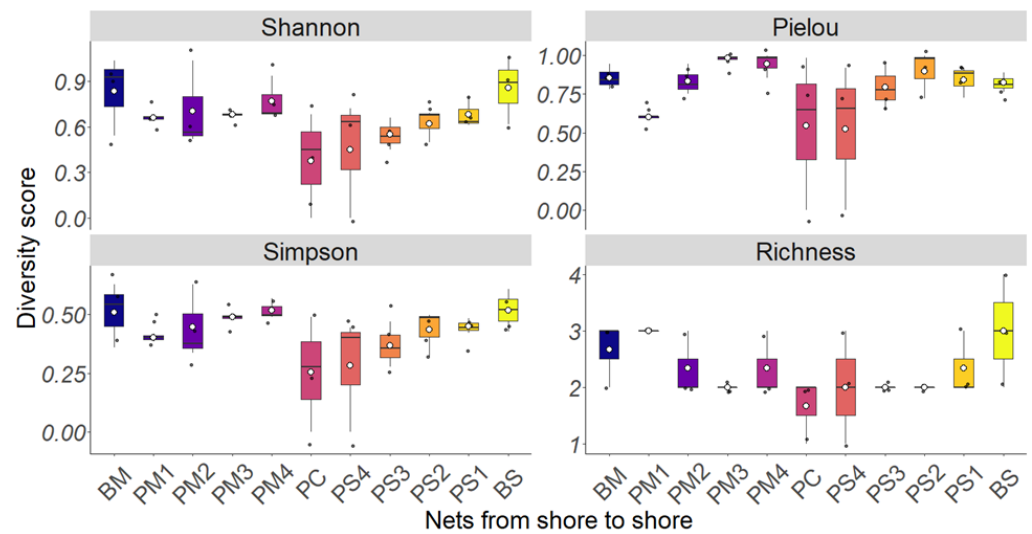


Figure 8. Fish diversity indices at different distances from the shore of Most Lake.

3.2. Římov

A total of 5791 fish were caught from nine different species: 76.19% bleak (*Alburnus alburnus*); 13.78% roach; 5.13% perch; 2.19% ruffe; 0.98% asp (*Leuciscus aspius*); 0.98% bream (*Abramis brama*); 0.5% pikeperch (*Sander lucioperca*); 0.14% rudd; and 0.10% wels catfish (*Silurus glanis*).

The CPUE values gradually decreased from the shore to the center of the reservoir, both the mild slope ( $p < 0.001$ , deviance = 543.8, variance = 0.05) and the steep slope ( $p < 0.01$ , deviance = 554.7, variance = < 0.001), with little variance between the sites according to the model for both mild and steep slopes (Figure 9). When we compared the CPUE at the species level (Table 4), the perch (mild:  $p < 0.001$ , deviance = 296.6, variance < 0.001; and steep:  $p < 0.001$ , deviance = 257.5, variance < 0.001) and roach (mild:  $p < 0.001$ , deviance = 430.4, variance < 0.001; and steep:  $p < 0.001$ , deviance = 367.4, variance < 0.001) showed significant differences in both banks. Asp ( $p = 0.013$ , deviance = 156.6, variance < 0.001) and bream ( $p < 0.015$ , deviance = 179.9, variance = 9.215) showed a significant difference in the CPUE for the mild bank.

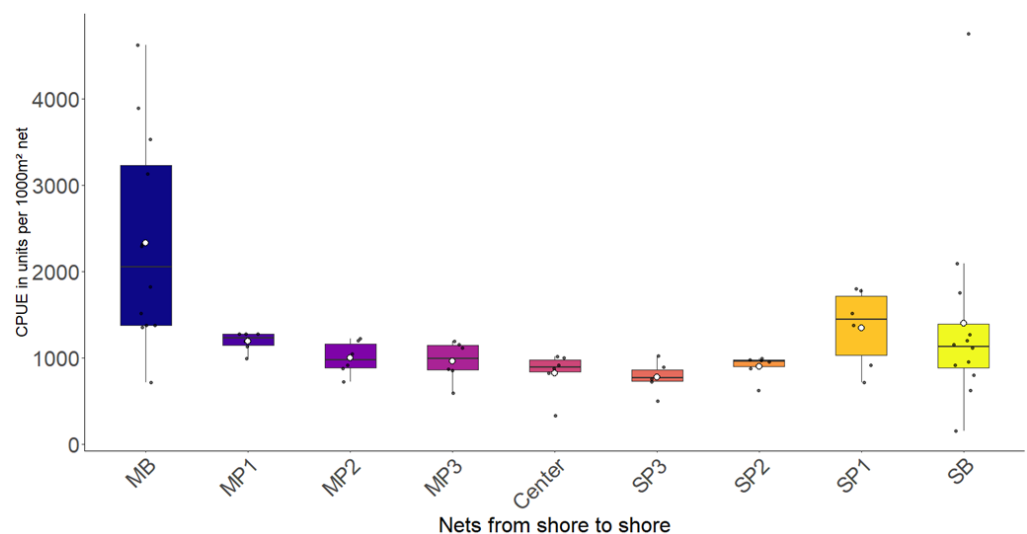
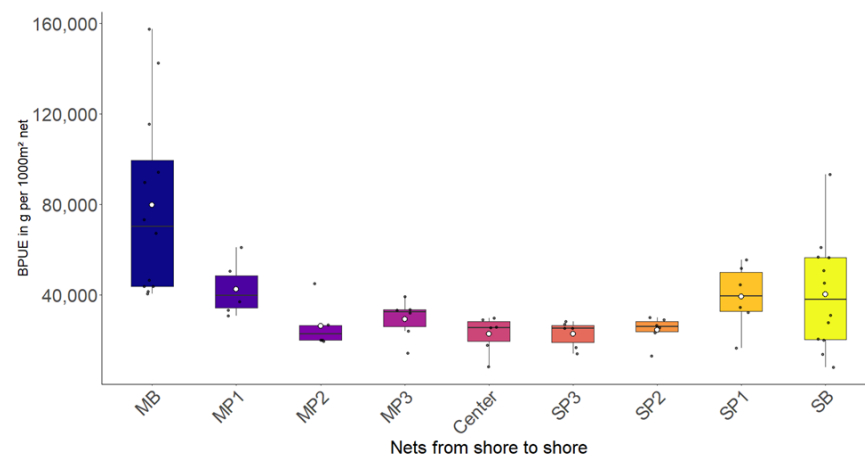


Figure 9. Total catch per unit effort (CPUE; individuals per 1000 m<sup>2</sup> of net) from 9 gillnet sites at different distances from the shore across the Římov Reservoir. The boxplot represents the quartile value of the CPUE, the grey dots represent the mean of the individual locality, the thick middle line represents the median, and the white dot represents the arithmetic mean.

**Table 4.** Catch per unit of effort (inds. 1000 m<sup>-2</sup> of gillnets), standard errors (*se*), and the significance level (*p*) at various benthic and pelagic sites of Římov Reservoir. See Section 2 for detailed explanations of gillnet locations.

Species	MB	<i>se</i>	MP1	<i>se</i>	MP2	<i>se</i>	MP3	<i>se</i>	Center	<i>se</i>	<i>p</i> _Value
<i>Abramis brama</i>	42.59	16.74	12.96	4.46	3.7	0	1.85	0	3.7	0	0.015
<i>Alburnus alburnus</i>	1220	312.11	1083	50.25	924.07	77.8	903.7	89.57	775.93	91.06	ns
<i>Gymnocephalus cernua</i>	112.96	25.87	0	0	0	0	0	0	0	0	ns
<i>Leuciscus aspius</i>	37.04	16.26	7.41	4.68	5.56	3.8	0	0	1.85	0	0.013
<i>Perca fluviatilis</i>	327.78	59.37	18.52	5.49	3.7	2.34	1.85	1.85	1.85	0	0.0001
<i>Rutilus rutilus</i>	561.11	68.45	62.96	19.6	55.56	10.34	48.15	9.37	38.89	11.74	0.0001
<i>Sander lucioperca</i>	24.07	6.95	3.7	2.34	3.7	2.34	3.7	2.34	3.7	0	ns
<i>Scardinius erythrophthalmus</i>	0	0	0	0	0	0	1.85	0	0	0	ns
<i>Silurus glanis</i>	1.85	1.85	1.85	0	0	0	0	0	0	0	ns
Species	SB	<i>se</i>	SP1	<i>se</i>	SP2	<i>se</i>	SP3	<i>se</i>	Center	<i>se</i>	<i>p</i> _Value
<i>Abramis brama</i>	18.52	9	1.85	0	3.7	2.34	16.6	12.75	3.7	0	ns
<i>Alburnus alburnus</i>	520.37	262.7	1200	166.27	837.04	64.26	705.56	58.36	775.93	91.06	ns
<i>Gymnocephalus cernua</i>	122.22	28.23	0	0	0	0	0	0	0	0	ns
<i>Leuciscus aspius</i>	22.22	7.74	18.52	6.2	7.41	4.68	5.56	3.8	1.85	0	ns
<i>Perca fluviatilis</i>	166.67	21.1	22.22	14.05	3.7	2.34	3.7	2.34	1.85	0	0.0001
<i>Rutilus rutilus</i>	529.63	107.93	96.3	24.29	44.44	11.83	40.74	6.83	38.89	11.74	0.0001
<i>Sander lucioperca</i>	7.41	4.18	1.85	0	1.85	0	3.7	0	3.7	3.7	ns
<i>Scardinius erythrophthalmus</i>	3.7	2.5	7.41	2.34	0	0	1.85	0	0	0	ns
<i>Silurus glanis</i>	7.41	3.16	0	0	0	0	0	0	0	0	ns

As for the BPUE, the values gradually decreased from the shore to the center of the reservoir, both on the mild slopes ( $p < 0.001$ , deviance = 312.0, variance = < 0.001) and on the steep slopes ( $p < 0.001$ , deviance = 285.3, variance = 0.05), with low variance among the localities according to the model for both mild and steep slopes (Figure 10). The perch (mild:  $p < 0.001$ , deviance = 158.5, variance < 0.001; and steep:  $p < 0.001$ , deviance = 143.9, variance < 0.01) and roach (mild:  $p < 0.001$ , deviance = 223.4, variance < 0.001; and steep:  $p < 0.05$ , deviance = 155.7, variance = 0.479) showed differences in distance for both banks, while bream ( $p = 0.0026$ , deviance = 97.0, variance = 2.557) showed differences just for the mild shore, and asp ( $p = 0.043$ , deviance = 117.1, variance = 0.28) for the steep shore (Table 5). Ruffe was caught only in the benthic gillnets.



**Figure 10.** Total biomass per unit effort (BPUE; kg per 1000 m<sup>2</sup> of net) from nine gillnet sites at different distances from the shore across the Řimov Reservoir. The boxplot represents the quartile value of the BPUE, the grey dots represent the mean of the individual locality, the thick middle line represents the median, and the white dot represents the arithmetic mean.

**Table 5.** Biomass catch per unit of effort (BPUE, g.1000 m<sup>-2</sup> of gillnets), standard errors (*se*), and the significance level (*p*) at various benthic and pelagic sites of Řimov Reservoir. See Section 2 for detailed explanations of gillnet locations.

Species	MB	<i>se</i>	MP1	<i>se</i>	MP2	<i>se</i>	MP3	<i>se</i>	Center	<i>se</i>	<i>p_value</i>
<i>Abramis brama</i>	6050	3132	3118	2085	37	0	70.44	0	133	0	0.0026
<i>Alburnus alburnus</i>	24,742	5686	24,826	1582	19,927	11,885	21,618	2746	17,156	2029	ns
<i>Gymnocephalus cernua</i>	645	145	0	0	0	0	0	0	0	0	ns
<i>Leuciscus aspius</i>	5986	2811	840	589	803	618	0	0	1065	0	ns
<i>Perca fluviatilis</i>	16,799	2945	3702	1119	608	420	230	0	249	0	0.0001
<i>Rutilus rutilus</i>	19,992	2805	7441	3326	4307	3116	4236	1831	2391	970.4	0.0001
<i>Sander lucioperca</i>	5084	1656	1235	784	574	571	2348	2068	1749	0	ns
<i>Scardinius erythrophthalmus</i>	0	0	0	0	0	0	972	0	0	0	ns
<i>Silurus glanis</i>	459	0	1435	0	0	0	0	0	0	0	ns
Species	SB	<i>se</i>	SP1	<i>se</i>	SP2	<i>se</i>	SP3	<i>se</i>	Center	<i>se</i>	<i>p_value</i>
<i>Abramis brama</i>	297	140	1653	0	143	98	568	364	132	0	ns
<i>Alburnus alburnus</i>	9610	4590	24,794	2798	19,455	1948	15,913	1347	17,156	2029	ns
<i>Gymnocephalus cernua</i>	774	138	0	0	0	0	0	0	0	0	ns
<i>Leuciscus aspius</i>	3598	2065	4690	2324	1475	976	787	690	1065	0	0.043
<i>Perca fluviatilis</i>	9545	2346	4199	2069	682	524	891	613	249	0	0.0001
<i>Rutilus rutilus</i>	11,999	3441	1928	737	1972	822	1692	1185	2391	970	0.05
<i>Sander lucioperca</i>	2816	2228	287	0	916	0	2093	0	1748	0	ns
<i>Scardinius erythrophthalmus</i>	1332	921	1733	937	0	0	913	0	0	0	ns
<i>Silurus glanis</i>	496	301	0	0	0	0	0	0	0	0	ns



Bleak superdominance was evident in all the pelagic samples (Figure 11). Only in the benthic samples on both sides of the lake did other species make up a larger proportion. When the biomass was expressed, the dominance of bleak persisted but was less evident (Figure 12). The species composition shows a gradual change from the shore to the open water, where the first pelagic net showed a species composition between the benthic and the pelagic habitat (still a conspicuous presence of roach, perch, bream, and asp). Ruffe is the best indicator of the benthic habitat, followed by the perch. Pikeperch, asp, catfish, and bream were caught in the open water, but their proportion was often lower than near shore. Rudd was not abundant, but also behaved like a eurytopic species, showing a homogeneous horizontal distribution. The distinct pattern of species distribution is reflected in a clear pattern of diversity indices (Figure 13). Species richness and diversity were always highest in the nearshore habitat and decreased towards the center of the reservoir. The Shannon index ( $p = 0.0316$ ) and the number of species ( $p = 0.0040$ ) showed a significant negative trend from the littoral to the pelagic. The size distribution also showed that the lowest mean lengths were found in the first nets on each side of the reservoir and the highest mean length was found in the center ( $p < 0.001$ , deviance = 56,291.8, variance = 0.0004, Table 6).

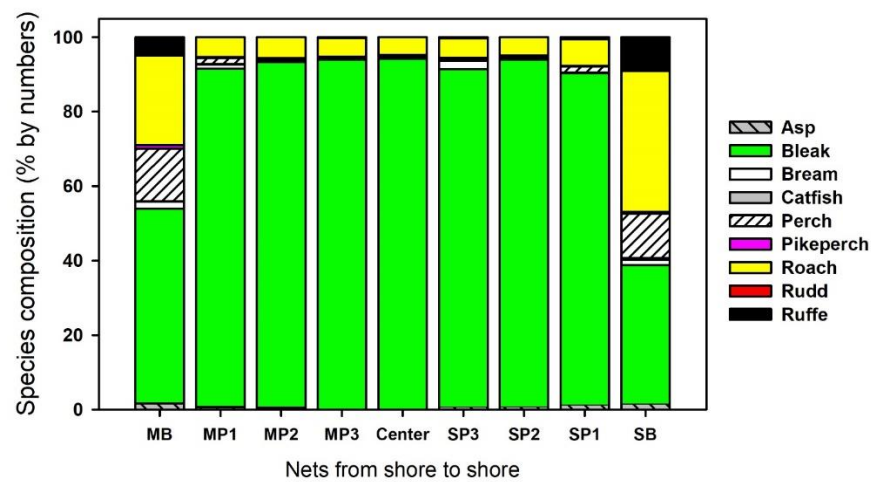


Figure 11. Fish species percentual numerical composition at different distances from the shore of Římov Reservoir.

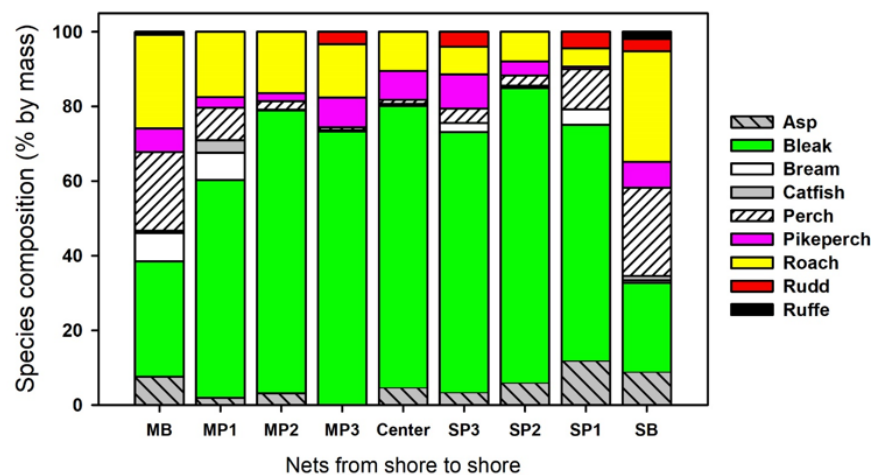


Figure 12. Fish species biomass composition at different distances from the shore of Římov Reservoir.

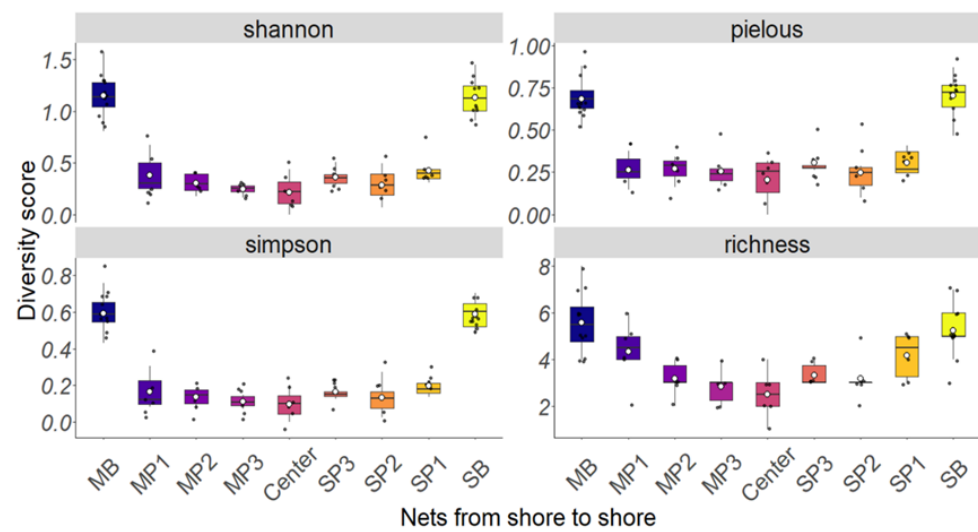


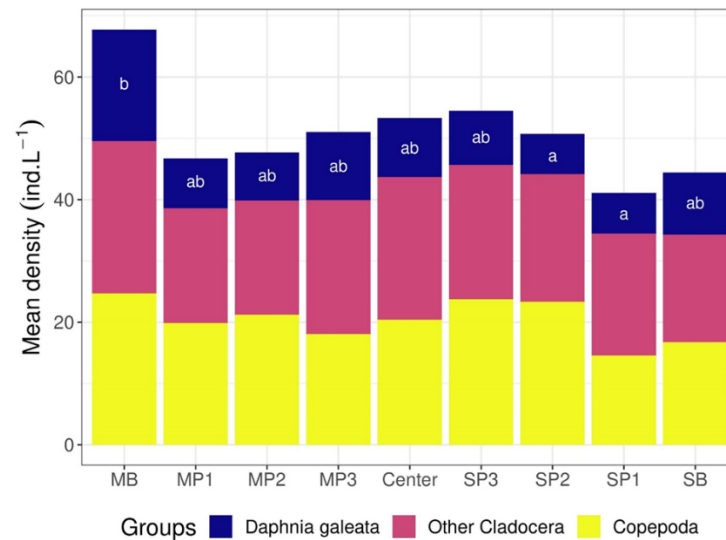
Figure 13. Fish diversity indices at different distances from the shore of Římov Reservoir.

Table 6. Average standard length (mm) and standard errors (se) of individual species at various benthic and pelagic sites of Římov Reservoir. See Section 2 for detailed explanations of gillnet locations.

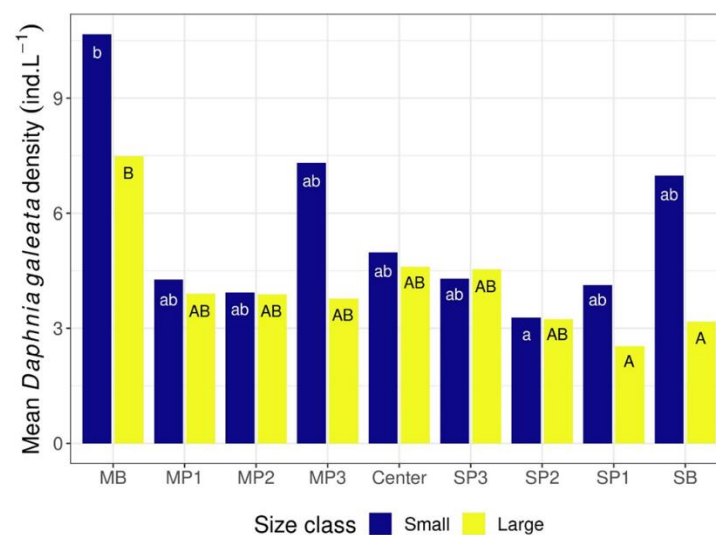
Species	MB	se	MP1	se	MP2	se	MP3	se	Center	se
<i>Abramis brama</i>	150.13	15.24	165.14	41.07	67.5	27.5	120	0	116	14
<i>Alburnus alburnus</i>	111.64	0.65	116.69	0.63	114.27	0.71	118.1	0.73	115.05	0.8
<i>Gymnocephalus cernua</i>	60.02	1.93	-	-	-	-	-	-	-	-
<i>Leuciscus aspius</i>	193.8	16.6	187.5	24.19	206.67	26.82	-	-	340	0
<i>Perca fluviatilis</i>	96	5.17	214.5	7.65	200	25	185	0	190	0
<i>Rutilus rutilus</i>	104.15	2.17	136.5	13.04	113.63	12.53	121.19	13.69	99.62	14.24
<i>Sander lucioperca</i>	241.08	17.53	297.5	7.5	168	122	334	116	332.5	27.5
<i>Scardinius erythrophthalmus</i>	-	-	-	-	-	-	265	0	-	-
<i>Silurus glanis</i>	340	0	480	0	-	-	-	-	-	-
Species	SB	se	SP1	se	SP2	se	SP3	se	Center	se
<i>Abramis brama</i>	88.8	3.75	340	0	119	14	110	8.85	116	14
<i>Alburnus alburnus</i>	108.79	0.89	112.24	0.67	116.79	0.79	115.07	0.93	115.05	0.8
<i>Gymnocephalus cernua</i>	63.85	1.35	-	-	-	-	-	-	-	-
<i>Leuciscus aspius</i>	187.83	23.18	228.1	28.02	221.25	36.08	193.33	43.43	340	0
<i>Perca fluviatilis</i>	108.23	6.85	196.58	18.77	202.5	42.5	227.5	27.5	190	0
<i>Rutilus rutilus</i>	88.93	1.92	85.98	4.16	95.58	10.94	98.73	10.73	99.62	14.24
<i>Sander lucioperca</i>	260	69.13	230	0	340	0	341.5	71.5	332.5	27.5
<i>Scardinius erythrophthalmus</i>	235	15	188.75	33.44	-	-	260	0	-	-
<i>Silurus glanis</i>	206.25	39.34	-	-	-	-	-	-	-	-

The mean densities of *Daphnia galeata* (the main food of non-predatory fish) were slightly higher at the littoral of the mild slope but were not significantly different from the other sampling stations along the transverse profile, with the exception of sites SP2 and SP1 (Figure 14). We also divided *D. galeata* into two size classes (small: body size  $\leq 1$  mm;

large: body size > 1 mm) and tested whether the densities of these size classes differed along the cross-section. Densities of small and large *Daphnia* were higher on average at the littoral of the mild slope littoral but were generally not significantly different from the other sampling stations, except for SP2 (small *Daphnia*), SP1, and SB (large *Daphnia*; Figure 15). The other two groups of zooplankton, other Cladocera, and Copepoda, were evenly distributed across the transverse profile (Figure 14).



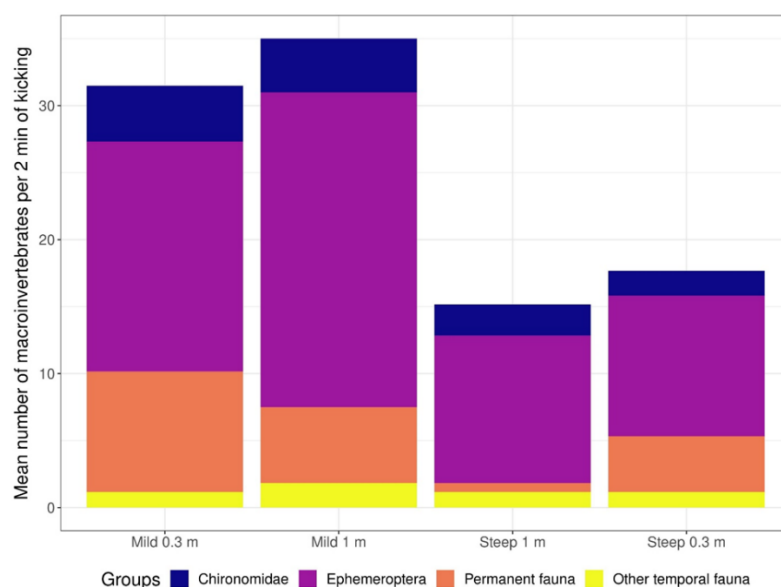
**Figure 14.** Mean density of three zooplankton groups (*Daphnia galeata*, other Cladocera, and Copepoda) at different distances from the shore of Řimov Reservoir. Different letters indicate significant differences ( $p < 0.05$ ) in *D. galeata* density between different distances from shore to shore. The densities of other Cladocera and Copepoda did not differ across the transverse profile ( $p > 0.05$ ). Letters a and b denominate significant differences in *D. galeata* densities.



**Figure 15.** Mean density of small ( $\leq 1$  mm) and large ( $> 1$  mm) *Daphnia galeata* at different distances from the shore of Řimov Reservoir. Significant differences ( $p < 0.05$ ) in the density of small *D. galeata* between different distances from shore to shore are indicated by different lowercase letters. Significant differences ( $p < 0.05$ ) in the density of large *D. galeata* between different distances from shore to shore are indicated by different uppercase letters.

Benthic macroinvertebrates were generally more abundant on the gentle slopes (Figure 16). A significant difference between the mild and steep sites was found for the

Chironomidae ( $p = 0.02$ , deviance = 101.6, variance < 0.001), Ephemeroptera ( $p < 0.001$ , deviance = 161.7, variance = 0.060), and permanent fauna ( $p < 0.001$ , deviance = 116.7, variance < 0.001) groups. For the difference in depth, only the permanent fauna was significantly less abundant in deeper water ( $p < 0.001$ , deviance = 123.2, variance < 0.001).



**Figure 16.** Mean number of benthic macroinvertebrates collected by kick-sampling at two depths on mild and steep slopes of Řimov Reservoir.

#### 4. Discussion

Our experiments have shown that the fish community changes very abruptly from the littoral to the pelagic in two different systems just near the benthic habitat. At the first pelagic point only 0.5 m above the bottom, the proportion of littoral species abruptly decreased. The pelagic habitat showed a homogeneous fish community composition, with a slight gradient corresponding to the distance from the littoral. This result supports previous assumptions that the definition of the benthic habitat only applies within a few meters of the bottom, and that the assumed height of the benthic habitat of 1.5 m above the bottom [31,36] may be accurate. The exception was the mild slope of Lake Most (site MP1), where the presence of abundant macrophytes created conditions that were very different from the pelagic habitat. The results also support previous assumptions that the pelagic habitat is the main volume even in medium-sized lakes, and that large volumes of open water must be considered if representative fish community values are to be obtained for the entire lake. Our results provide reassurance that the volume of the pelagic habitat is as large as estimated in previous studies [33,35] and that it is by far the most important habitat, even in relatively small waters [36].

The majority of species showed that they were benthic-bound, such as perch, ruffe, bream, pikeperch, asp, and roach (in some BPUE, also catfish). Bleak and rudd were determined to be typical eurytopic species. No exclusively pelagic species was found, which is consistent with the theory of Fernando and Holčík [24] about the scarcity of truly pelagic fish in young ecosystems. Consequently, the transition from the littoral to the pelagic community is mainly characterised by a sharp decline in the abundance and proportion of benthic species. This reflects the fact that the pelagic community is much simpler and less diverse, with fewer fish species willing to leave the safety of the littoral [24,26]. The results of this study showed that the fish community changes very quickly on the way from the bottom to the open water, and what we may call the pelagic community shapes most of the volume of lakes and reservoirs. This supports previous studies indicating that volume-weighted estimates provide much more realistic estimates for entire lakes than the global CEN CPUE [33].

The gradual decrease in fish abundance from the littoral to the pelagic zone in the middle of the lake was more evident in Most than in Římov. One reason for this difference could be the higher complexity of the habitat in the littoral of Most, due to the lower steepness and the high macrophyte density in the littoral zone, or the higher steepness in Římov. Littoral aquatic macrophytes are important components of habitat complexity and heterogeneity, as they dominate the nearshore zones of lakes and support diverse fish communities [48,49]. Macrophytes can influence fish habitat selection and ecological relationships such as predation and competition, which in turn affect the fish community structure. For example, predators may induce their prey to seek shelter in roots, leaves, and stems, which act as visual and physical barriers and provide protection from predators [27,50], while competition may induce fish individuals to seek new feeding grounds and reproduce [51]. Macrophyte habitats are considered nursery grounds for juvenile fish because they provide numerous sheltering opportunities, as smaller fish are more vulnerable to predators than larger fish [52,53]. The high macrophyte stems most likely caused very high fish catches at the first pelagic net at the mild slope of Most Lake.

However, even in the habitat without true aquatic macrophytes (Římov Reservoir), the CPUE, BPUE, and species diversity were mostly higher in the benthic habitats. This indicates that for many species at least the presence of some substrate is also important. The comparison between the benthic net catches shows that the mild slope “beach-type” habitats contained more fish than the steep slopes. Although the steep slopes may be more structured by rocks and tree remains [30,54], they are more open and clearly less safe for prey fish (see also [40]). The soft bottom substrate of mild slope shores is more favorable for benthic macroinvertebrates, and habitats with gentle slopes have also been found to have slightly higher densities of cladoceran *D. galeata*. According to previous studies carried out in the Římov Reservoir, cladoceran *D. galeata* is the main prey of the dominant non-predatory fish species [18,55,56]. Therefore, the reason for fish staying in the mild slope littoral of the Římov Reservoir could be both the protection from predators and feeding on *D. galeata* and the available benthic resources [30]. Other Cladocera (mostly represented by small species such as *Diaphanosoma brachyurum* and *Eubosmina coregoni*) and Copepoda were evenly distributed across the transverse profile of this reservoir and therefore did not appear to affect fish distribution. In general, the lowest average fish lengths were found in the littoral habitats, suggesting that juvenile fish feel more secure in the nearshore zone. This is in general agreement with the results of previous studies from other limnetic ecosystems [27]. While fish densities in the littoral mild slope habitats were considerably higher than in the open water, the CPUE and BPUE in the littoral habitats with the steep slopes were similar to those in the pelagic area. This may also be because in the steep slope habitats, the first pelagic net above the 3.5 m isobath was necessarily very close to the shore.

Our study only has a horizontal dimension. It deals with a layer of 0–3 m, which is normally the most populated by fish [8,11]. It was beyond our capabilities to extend the study to deeper habitats. However, the results from the 3 m depth are quite convincing, and we cannot expect the situation to change significantly in further layers. Fishes that require the substrate tend to stay close to it [57], while eurytopic fishes disperse without much regard to the benthic habitat.

## 5. Conclusions

Our experiment showed that the littoral zone was characterized by high numbers of fish, especially perch, and by the presence of smaller individuals. The catch of the pelagic nets was dominated by eurytopic fish—rudd and roach in Most and bleak in Římov. With the exception of one case where abundant macrophytes extended the structured habitat, the largest shift from the benthic to the pelagic community was observed only at the first pelagic gillnet at a bottom depth of 3.5 m. Open water catches were relatively consistent with small signs of a gradient towards the middle of the lake. The results indicate that the benthic gillnet catch is representative of a very limited area and volume, while most of

the volume is dominated by the pelagic community, the most important habitat even in relatively small waters. This has important consequences for the assessment of community parameters of the whole lake.

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**Data Availability Statement:** The data are available in the database of the Biology Centre CAS and can be provided upon request.

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## **Paper II**

### **Can a protected area help improve fish populations under heavy recreation fishing?**

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## Article

# Can a Protected Area Help Improve Fish Populations under Heavy Recreation Fishing?

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**Abstract:** Freshwater protected areas are designated parts of the inland waters that restrict human activities. They were created as a mechanism to combat the decline of fauna and flora of the world. Some authors have questioned their actual effectiveness in terms of the purpose of protecting endangered fauna and flora. We conducted an experiment in Lipno reservoir in the Czech Republic to evaluate the impact of protection against angling pressure on the fish community. We selected data from two years of gill netting and analyzed the difference between areas of low anthropogenic impact (LAI) and those of high anthropogenic impact (HAI) in terms of abundance, biomass, standard length, and diversity indices. Three groups of fish were found to prefer protected areas with low anthropogenic pressure: 1. YOY (Young-of-the-year) perch (*Perca fluviatilis*), the dominant of the young-of-the-year fish community. 2. Pike (*Esox lucius*), wels catfish (*Silurus glanis*) and rudd (*Scardinius erythrophthalmus*), which were not found in HAI areas at all. 3. Larger individuals of pikeperch (*Stizostedion lucioperca*), which survived better in LAI areas. Some factors may affect LAI, such as illegal poaching or setting out food bait to attract the fish outside. Another factor that can be considered is the migration of fish, either to forage or to reproduce, since the LAI areas are open to the reservoir. The areas of LAI act as protective habitats for heavily exploited predatory fish species and increase fish diversity indexes. The example of the protected and low-impact areas of Lipno should be followed in other water bodies with high fishing pressure and anthropogenic impact.

**Keywords:** protected areas; anthropogenic impact; angling; recreation pressure; exploitation; CEN gillnets; recreation fishing



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## 1. Introduction

Humans are intimately linked to freshwater ecosystems, and both humans and nature benefit when the risks to the health of these habitats are managed [1–3]. Among all ecosystems, inland waters are one of the most affected, and freshwater fishes have been one of the most threatened vertebrate groups in the world in recent decades [4–7]. Moreover, they are unique, and their loss could have irreparable consequences for global biodiversity [3,8]. Despite the economic and cultural value of freshwater fishes, the threat from anthropogenic impacts is still quite high [9]. Habitat degradation and loss, hydrological modifications, construction of instream barriers, excessive water abstraction, overexploitation and intensification of agricultural activities, introduction and spread of alien species and pollution have been identified as the main threats to freshwater ecosystems and their

biodiversity [10–15]. Due to these multiple impacts and threats, increasing attention is being paid to freshwater ecosystems worldwide to find effective ways to restore lost habitats and important sites for endangered species [3,15–17].

Habitat overexploitation may be associated with declining populations. These declines have been linked to several factors, including overfishing and littoral habitat destruction [10,18]. Some studies have shown a widespread recruitment deficit in species that use the shallows as spawning grounds for reproduction, and increased mortality during the early stages due to loss of protective habitats has been suggested as one of the causes of declines of adult fish populations [15,19–22]. For example, Ljunggren [23] showed that populations of top predators (such as pike (*Esox lucius*) and Eurasian perch (*Perca fluviatilis*)) had a continuous decline in density and abundance of coastal areas in parts of the Baltic Sea; Kubečka [24] showed that the populations of pike-perch (*Stizostedion lucioperca*) in the Lipno reservoir, Czech Republic had been declining sharply since 2004, recovering partly only after 2017. The relationships between the size of adult fish populations and the availability and quality of recruitment habitats, along with the other types of pressures facing littoral areas, may be the cause of declines in fish recruitment in diverse types of freshwater habitats [18,25]. Moreover, changes in the abundance and diversity of large piscivorous fishes can trigger community-wide trophic cascades that have far-reaching, detrimental consequences for ecosystem functioning and stability, as well as human livelihoods [26–28].

According to the IUCN definition, a protected area (hereafter PA) is a defined geographical space recognized, dedicated and managed by legal or other effective means to achieve the long-term conservation of nature with associated ecosystem services and cultural values [26]. In the past, protected areas were established to protect endangered species with the expectation that the community would have an increase in biomass, abundance, and species diversity [27]. The study of PAs in freshwater systems is far less developed than in marine environments. Research on marine PAs began to be studied nearly a decade before freshwater PAs and currently includes nine times more scientific papers than freshwater PAs. Given that freshwater environments are more vulnerable than marine environments and that scientific knowledge of freshwater ecosystems is much less than that of marine ecosystems, it is of great importance to study the effects of PAs in freshwater systems. The benefits of freshwater PAs to the fish community have shown positive results [28–31] or neutral effects [32,33].

Although there are a large number of protected areas in many regions of the world, their effectiveness in protecting freshwater systems and their biodiversity has been questioned in recent years [9,34,35]. This is because the designation of protected areas in the past was largely based on the need to protect terrestrial diversity [8,17]. Although freshwater systems are among the most highly threatened ecosystems globally, they have been overlooked in the designation of PAs, and often, their inclusion in existing protected areas has mainly been incidental rather than intentional [35–37]. The lack of inclusion of freshwater systems in the designation and establishment of the protected areas has been identified as a limiting factor in the effectiveness of freshwater fish conservation. Bastin [38] shows in his work that 15% of inland waters worldwide are at PA, but in some continents such as Asia and Africa, only 5% of inland waters are; Azevedo-Santos [17] showed that large migratory fish lack the necessary habitat to complete their life cycles; Chessman [32] reported that PAs in Murray–Darling Basin of Australia, had no effect on protecting native fish populations because they were ineffective in curbing the threat of non-native fish and altering the water regime; Lawrence [39] reported that less than 20% of the highly endangered fish species are protected under the PA territories. Therefore, broad-based research is needed to verify the effectiveness of each PA.

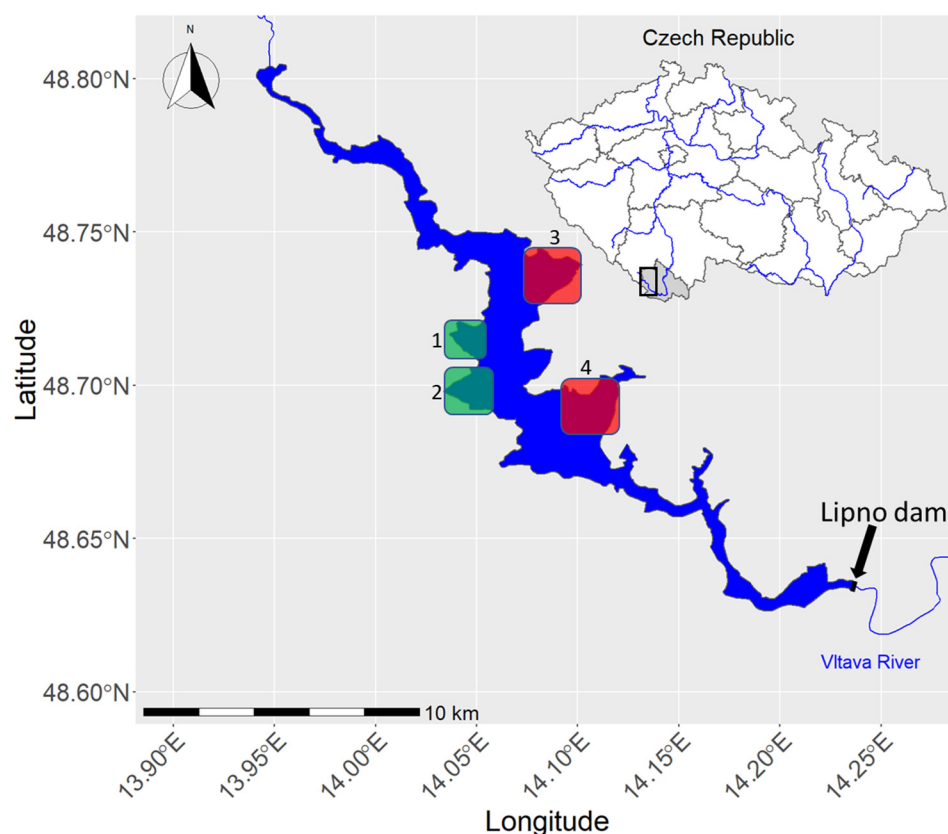
The protected areas in the studied area (Lipno reservoir, the largest water body in the Czech Republic) were created with the aim of increasing the abundance and biomass of target species (especially predatory species) by recreational anglers. Therefore, a better understanding of the effects of lowering anthropogenic activities on these habitats and the dependence of fish on these habitats is essential for guiding management actions aimed

at maintaining, enhancing or restoring ecosystem services. In this study, we examine the effectiveness of Lipno PAs and nearby areas of low anthropogenic impact in protecting highly valued wildlife species and associated fish diversity. We sampled and analyzed fish assemblage abundance, biomass, size structure, species richness and composition of four different regions, two with high and direct anthropogenic and angling impact and two with lower and indirect impact.

## 2. Materials and Methods

### 2.1. Study Area

Lipno reservoir (Figure 1) is a dam impoundment, near the border with Austria, on the Vltava River in the foothills of the Šumava Mountains (Bohemian Forest); in Southern Bohemia, Czech Republic. The reservoir was built in 1960 as a hydropower reservoir; nowadays, it also serves as flood control, flow augmentation, drinking water supply and recreation. The reservoir has a volume of 306 million m<sup>3</sup>, a surface area of 46.5 km<sup>2</sup>, a maximum depth of 22 m and a mean depth of 6.6 m [40].



**Figure 1.** Outline map of Lipno reservoir, with its location in the Czech Republic (black rectangle) and the detailed location of the low anthropogenic impact areas (Green squares, 1. Racinska zatoka; and 2. Kyselovska zatoka) and the control high anthropogenic impact sites (Red squares, 3. Hurka; and 4. Dolni Vltavice).

The sites for this study are located in the middle section of the reservoir. The study areas with low anthropogenic impact (hereafter LAI) are located on the south-west side of the reservoir, the protected area (Kyselovská bay, max. 8 m depth) and in an adjacent bay (Račinská bay, max. 6 m depth). In Kyselovská Bay (2.15 km<sup>2</sup>), angling has been prohibited all year round since 2009, while Račinská bay (0.82 km<sup>2</sup>) is protected by its remoteness and difficult access for the public. These two bays are located on a forested, wind-protected shore without recreational facilities or cottage districts. During the “iron curtain” period (1948–1989), this area at the border with Austria was strictly closed to the public so that no one could approach the border. The high anthropogenic impact (hereinafter HAI, see

Figure 1) areas are located in two nearby areas, Hůrka area (max. 8 m depth). and Dolní Vltavice basin (max. 10 m depth). HAI areas are located near local settlements with recreational facilities and cottage districts. These areas are among the most visited areas for recreational fishing. Angling is generally allowed throughout all year; predatory fish are protected between 1 January till 16 June.

## 2.2. Fishing Gear and Field Work Dates

European Standard gillnets (ESG) [41] and Large Mesh Gillnet (LMG) [42] methodologies were used in this experiment. ESG following the European Standard Document (benthic gillnet: 1.5 m height  $\times$  30 m length, 2.5 m panels for each 12 mesh sizes; pelagic gillnet: 3 m height  $\times$  30 m length, 2.5 m panels for each 12 mesh sizes) were used for sampling from 2016 and 2017 in Lipno reservoir. ESG mesh sizes follow a geometric series with a ratio of about 1.25 (5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm).

LMG consists of four mesh sizes extending the ESG geometric series (70, 90, 110 and 135 mm; knot to knot; pelagic net size 3 m height  $\times$  40 m length, 10 m panels for each of 4 mesh sizes and benthic net size 1.5 m height  $\times$  40 m length, 10 m panels for each of 4 mesh sizes) were deployed in the same habitats and localities along with the ESG. Three nets of ESG and three nets of LMG were deployed in every habitat of each area. The large mesh nets ( $\geq 70$  mm) had four times higher effort (net area) than the CEN standard nets ( $< 70$  mm) to catch sufficient numbers of larger fish. Therefore, the catches and net areas of the large mesh gillnets were divided by four to standardize the length of each panel to 2.5 m for all meshes. When all 16 meshes were the same length (2.5 m), catch data were standardized to 1000 m<sup>2</sup> of net area. Gillnets were set at depths of 0–3 m and 3–6 m for benthic habitats; and 0–3 m for pelagic habitats, respectively.

Gillnet deployment occurred on 28–29 August and 1 September 2016, and 27–30 August 2017. To cover both sunset and sunrise peaks of fish activity, gillnets were deployed two hours before sunset and lifted two hours after sunrise. The catch was sorted by species, and standard length and weight were measured for each fish (accuracy of 1 mm and 0.1 g, respectively). Catch per unit of effort (CPUE) was defined as the number of individuals per standardized 1000 m<sup>2</sup> of net area per night; similarly, sampled biomass per unit of effort (BPUE) was defined as kilograms per 1000 m<sup>2</sup>. CPUE and BPUE were reported separately for young of the year (YOY) and older year classes (older fish, estimates based on size structure verified by the scale and otolith reading). The CPUE and BPUE were calculated for individual species as well as for the entire fish assemblage.

## 2.3. Data Analysis

Negative binomial generalized linear models (NBGLM) were applied to describe the differences in fish standard lengths, CPUE and BPUE values with the difference between LAI and HAI areas and the different habitats (benthic and pelagic), as shown in Equation (1).

$$\text{Model} = \text{Value} \sim \text{Impact} + \text{Habitat} \quad (1)$$

The negative binomial generalized linear model was chosen because it can handle large numbers of zeros and over-dispersed data [43]. The MASS package was used for the calculation of all NBGLMs [44].

Shannon–Wiener diversity, Simpson’s diversity, Pielou’s evenness, and Richness indices were calculated by treatments, time periods, and years of sampling using the Vegan package [45]. The generalized linear negative binomial model was also used to compare the diversity index values using the same structure as the previous models, Equation (1).

Three significance levels were considered, \*  $p < 0.05$ , \*\*  $p < 0.01$  and \*\*\*  $p < 0.001$ . All data analyzes were performed in R software [46].

## 3. Results

In total, 102 nets 12 species from 4 orders. The Cypriniformes were represented by common bream (*Abramis brama*), bleak (*Alburnus alburnus*), silver bream (*Blicca bjoerkna*),

carp (*Cyprinus carpio*), asp (*Leuciscus aspius*) and roach (*Rutilus rutilus*) and rudd (*Scardinius erythrophthalmus*); the Perciformes were represented by ruffe (*Gymnocephalus cernua*) perch (*Perca fluviatilis*) and pikeperch (*Stizostedion lucioperca*); the Esociformes by pike (*Esox lucius*) and the Siluriformes by wels catfish (*Silurus glanis*). The Cypriniformes (56,39%) were the most abundant group of the older fish community, followed by Perciformes (43,47%), Esociformes and Siluriformes (0.07% each) (Table 1).

**Table 1.** Species of fish older than young-of-the-year from gillnetting at high-impact sites (HAI) and low-impact (LAI) areas of the Lipno reservoir captured in the study, with their individual catch and proportion of the total catch.

	HAI		LAI	
	Individuals	Proportion	Individuals	Proportion
<i>Abramis brama</i>	128	3.41	60	1.72
<i>Alburnus alburnus</i>	1029	27.39	568	16.29
<i>Blicca bjoerkna</i>	274	7.29	317	9.09
<i>Cyprinus carpio</i>	21	0.56	33	0.95
<i>Esox lucius</i>	0	0.00	5	0.14
<i>Gymnocephalus cernua</i>	1436	38.22	1187	34.05
<i>Leuciscus aspius</i>	9	0.24	7	0.20
<i>Perca fluviatilis</i>	124	3.30	441	12.65
<i>Rutilus rutilus</i>	683	18.18	795	22.81
<i>Sander lucioperca</i>	53	1.41	56	1.61
<i>Scardinius erythrophthalmus</i>	0	0.00	13	0.37
<i>Silurus glanis</i>	0	0.00	4	0.11
Total	3757	100.00	3486	100.00

In the YOY fish group, Perciformes (75, 62%) was the most abundant group, followed by Cypriniformes (24, 38%) (Table 2).

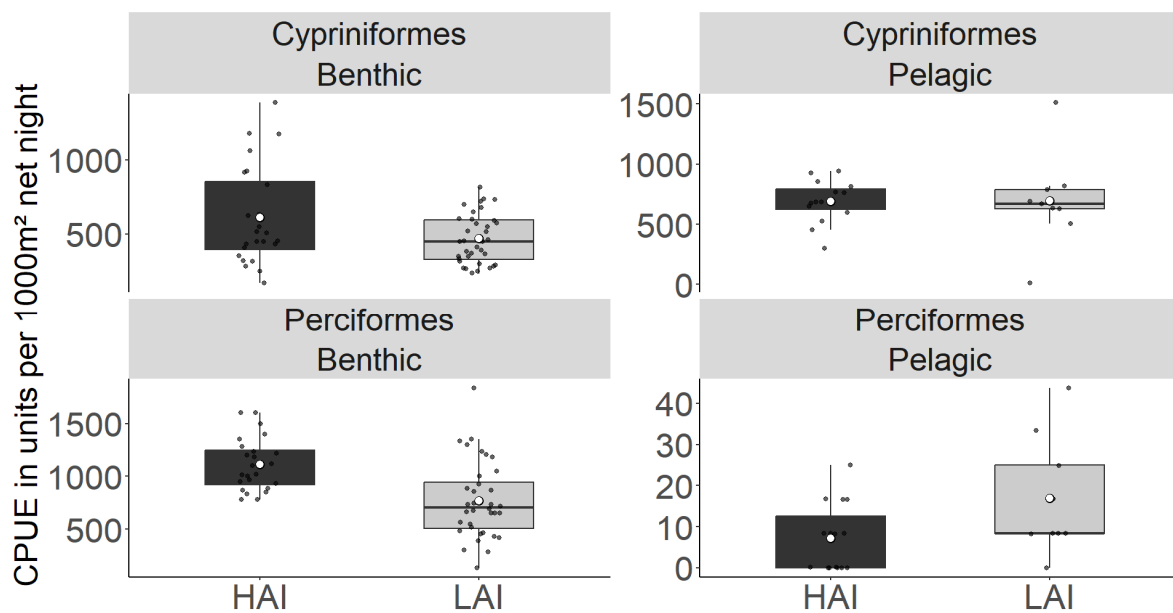
**Table 2.** Species of fish young-of-the-year from gillnetting at high-impact sites (HAI) and low-impact (LAI) areas of the Lipno reservoir captured in the study with their individual catch and proportion of the total catch.

	HAI		LAI	
	Individuals	Proportion	Individuals	Proportion
<i>Abramis brama</i>	10	0.51	20	0.29
<i>Alburnus alburnus</i>	1	0.05	54	0.79
<i>Blicca bjoerkna</i>	10	0.51	20	0.29
<i>Gymnocephalus cernua</i>	523	26.45	311	4.54
<i>Perca fluviatilis</i>	1256	63.53	6171	90.04
<i>Rutilus rutilus</i>	29	1.47	155	2.26
<i>Sander lucioperca</i>	148	7.49	123	1.79
Total	1977	100.00	6854	100.00

Average abundance of Cypriniformes older than YOY did not differ significantly between areas HAI and LAI. Common bream showed a preference for the HAI ( $p$ -value = \*), especially in the benthic areas (Table 3). Pike, wels catfish and rudd were caught only in the LAI areas. The mean abundance of Perciformes showed no preference between LAI or HAI, but perch showed a strong preference for benthic habitat in both areas ( $p$ -value = \*\*\*). Ruffe and pikeperch showed a preference for HAI, and this was also true for all species taken together (total catch,  $p$ -value = \*\*). When comparing habitat preferences, Cypriniformes ( $p$ -value = \*) and Perciformes ( $p$ -value = \*\*\*) showed a preference for benthic areas (Figure 2, Table 3). Most species showed a clear preference for benthic habitats, opposite preference was found for bleak, rudd and asp.

**Table 3.** Mean and standard error (SE) of the fish older than young-of-the-year CPUE (catch per unit of effort) of gillnets from Lipno reservoir, in individual units per 1000 m<sup>2</sup> of nets. \*\*\* =  $p < 0.001$ , \*\* =  $p < 0.01$ , \* =  $p < 0.05$  and ns =  $p \geq 0.05$ . Families and total catch are given in bold.

Species	Benthic		Pelagic		p_Treatment	p_Habitat
	HAI	LAI	HAI	LAI		
<i>Abramis brama</i>	54.7 ± 16.4	21.2 ± 3.3	23.6 ± 8.1	11.1 ± 8.1	*	ns
<i>Alburnus alburnus</i>	37.5 ± 19.8	37.5 ± 13.0	541.7 ± 38.4	450.9 ± 86.1	ns	***
<i>Blicca bjoerkna</i>	159.9 ± 33.1	106.1 ± 10.0	23.9 ± 6.8	80.6 ± 16.8	ns	***
<i>Cyprinus carpio</i>	2.4 ± 0.7	2.8 ± 0.7	0.97 ± 0.5	2.1 ± 0.7	***	*
<i>Leuciscus aspius</i>	0.35 ± 0.2	0.23 ± 0.16	2.2 ± 1.8	1.2 ± 0.5	ns	ns
<i>Rutilus rutilus</i>	354.9 ± 41.1	298.2 ± 25.0	95.6 ± 10.5	139.8 ± 33.2	ns	***
<i>Scardinius erythrophthalmus</i>	0	1.4 ± 0.78	0	9.3 ± 2.9	ns	***
<b>Cypriniformes</b>	<b>609.7 ± 68.2</b>	<b>467.4 ± 27.7</b>	<b>687.9 ± 44.5</b>	<b>694.9 ± 129.2</b>	<b>ns</b>	<b>*</b>
<i>Esox lucius</i>	0	1.39 ± 0.78	0	1.85 ± 1.22	ns	ns
<b>Esociformes</b>	<b>0</b>	<b>1.39 ± 0.78</b>	<b>0</b>	<b>1.85 ± 1.22</b>	<b>ns</b>	<b>ns</b>
<i>Gymnocephalus cernua</i>	997.2 ± 57.1	549.1 ± 56.0	0	0.93 ± 0.93	**	***
<i>Perca fluviatilis</i>	83.3 ± 19.6	198.7 ± 23.3	2.2 ± 1.3	11.1 ± 4.2	***	***
<i>Sander lucioperca</i>	30.6 ± 6.2	22.1 ± 4.2	5 ± 1.8	4.9 ± 2.8	***	***
<b>Perciformes</b>	<b>1111.1 ± 50.7</b>	<b>769.9 ± 60.3</b>	<b>7.2 ± 2.1</b>	<b>16.9 ± 4.8</b>	<b>ns</b>	<b>***</b>
<i>Silurus glanis</i>	0	0.58 ± 0.47	0	0.46 ± 0.46	ns	ns
<b>Siluriformes</b>	<b>0</b>	<b>0.58 ± 0.47</b>	<b>0</b>	<b>0.46 ± 0.46</b>	<b>ns</b>	<b>ns</b>
Total catch	1720.8 ± 77.3	1239.2 ± 67.8	695.1 ± 45.3	714.1 ± 129.6	**	***



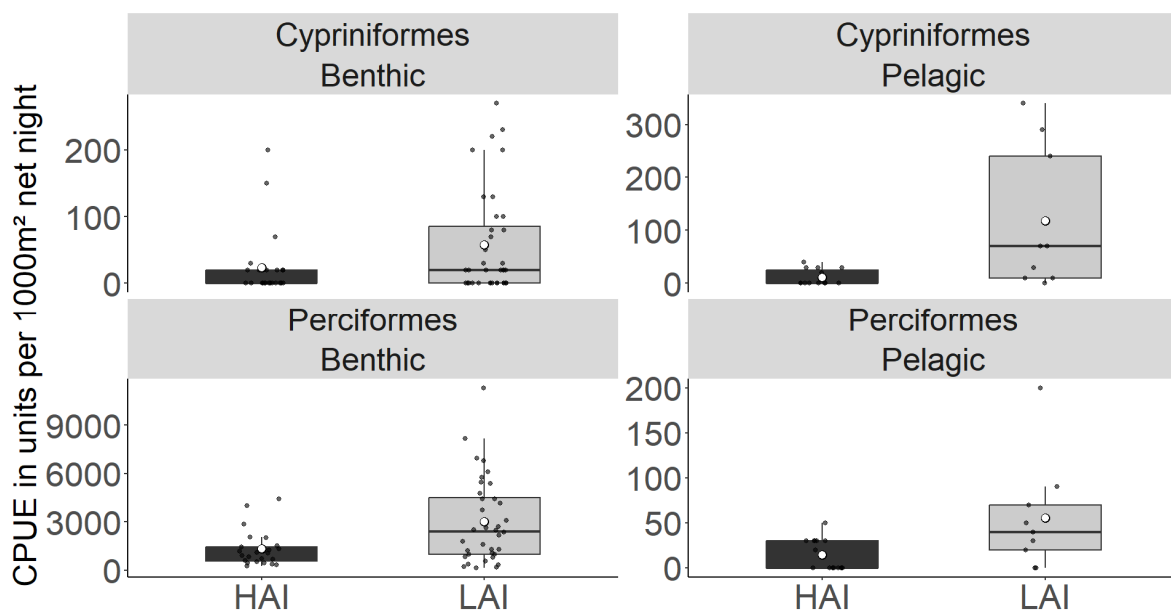
**Figure 2.** A Total catch-per-unit effort (CPUE; individuals per point) of fish older than young-of-the-year from gillnetting at high-impact sites (HAI) and low-impact (LAI) areas of the Lipno reservoir. The boxplot represents the quartile value of CPUE, the black dots represent the means of individual nets, the thick middle line represents the median, the white dot represents the overall mean of all measurements, and the whiskers represent the lowest and highest actual value of the quartile.

With YOY fish, LAI showed a higher preference for roach, which dominated amongst cyprinids (Table 4). Roach was the most important cyprinid YOY species and thus also caused the overall YOY cyprinid preference for LAI areas (Figure 3). Amongst percid species, perch was the most abundant, with a strong affinity to LAI areas ( $p$ -value = \*\*\*). Ruffe ( $p$ -value = \*\*\*) and pikeperch (not significant) preferred HAI areas. Overall, perch dominated YOY catch, so total percid CPUE (Figure 3) and total catch of YOY (Table 4) was significantly higher in LAI areas ( $p$ -value = \*\*\*).



**Table 4.** Mean and standard error (SE) of the young of the year class fish CPUE (catch per unit of effort) of gillnets from Lipno reservoir, in individual units per 1000 m<sup>2</sup> of nets. \*\*\* =  $p < 0.001$ , \* =  $p < 0.05$  and ns =  $p \geq 0.05$ .

Species	Benthic		Pelagic		p_Treatment	p_Habitat
	HAI	LAI	HAI	LAI		
<i>Abramis brama</i>	6.94 ± 3.74	2.78 ± 1.94	0	12.96 ± 4.19	ns	ns
<i>Alburnus alburnus</i>	0.69 ± 0.69	0.46 ± 0.46	0	49.07 ± 24.86	ns	ns
<i>Blicca bjoerkna</i>	2.08 ± 1.15	3.24 ± 1.11	3.89 ± 2.68	12.04 ± 5.03	ns	ns
<i>Rutilus rutilus</i>	13.19 ± 6.88	50.46 ± 12.69	5.56 ± 2.25	42.59 ± 16.4	*	ns
<b>Cypriniformes</b>	<b>22.92 ± 10.17</b>	<b>56.94 ± 13.1</b>	<b>10 ± 3.47</b>	<b>116.67 ± 45.24</b>	<b>*</b>	<b>ns</b>
<i>Gymnocephalus cernua</i>	361.81 ± 42.49	143.52 ± 17.82	1.11 ± 1.11	0.93 ± 0.93	***	***
<i>Perca fluviatilis</i>	862.5 ± 200.61	2829.98 ± 445.8	7.78 ± 3.4	53.7 ± 19.79	***	***
<i>Sander lucioperca</i>	96.53 ± 21.59	56.48 ± 10.14	5 ± 2.27	0.93 ± 0.93	ns	***
<b>Perciformes</b>	<b>1320.83 ± 222.11</b>	<b>3029.98 ± 438.72</b>	<b>13.89 ± 4.35</b>	<b>55.56 ± 20.65</b>	<b>***</b>	<b>***</b>
<b>Total catch</b>	<b>1343.75 ± 228.79</b>	<b>3086.92 ± 447.58</b>	<b>23.888 ± 6.99</b>	<b>172.22 ± 59.56</b>	<b>***</b>	<b>***</b>

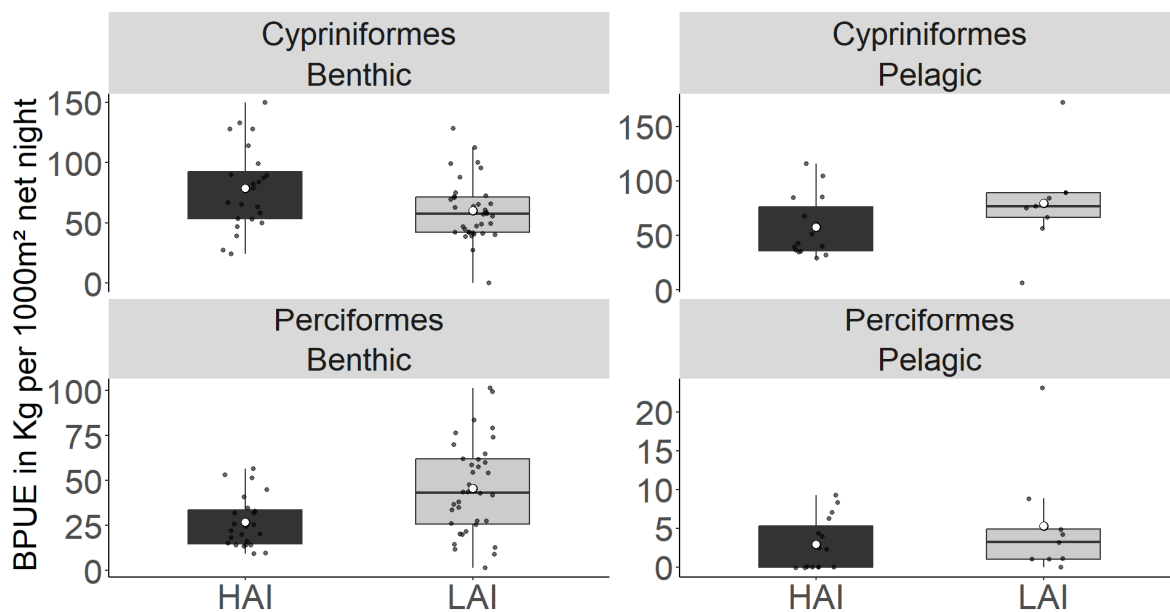


**Figure 3.** A Total catch-per-unit effort (CPUE; individuals per point) of young-of-the-year fish from gillnetting at high-impact (HAI) sites and low-impact (LAI) areas of the Lipno reservoir. The boxplot represents the quartile value of CPUE, the black dots represent the means of individual nets, the thick middle line represents the median, the white dot represents the overall mean of all measurements, and the whiskers represent the lowest and highest actual value of the quartile.

Biomass of older cyprinids showed no significant differences between LAI and HAI areas. (Table 5). Perciformes ( $p$ -value = \*\*\*) showed a significant preference for the LAI (Figure 4, Table 5), especially due to the strong dominance of perch in benthic habitats ( $p$ -value = \*\*\*). Ruffe showed a trend toward HAI ( $p$ -value = \*), and perch showed a trend towards LAI ( $p$ -value = \*\*\*), both for the benthic area. Esociformes and Siluriformes were represented only in the LAI areas. Total fish biomass was not significantly different between LAI and HAI areas. Habitat preferences of different species are generally similar to CPUE, mainly toward benthic habitats (Figures 2 and 4, Tables 3 and 5).

**Table 5.** Mean and standard error (SE) of the fish older than YOY BPUE (biomass per unit of effort) of gillnets from Lipno reservoir, in kilograms per 1000 m<sup>2</sup> of nets. \*\*\* =  $p < 0.001$ , \*\* =  $p < 0.01$ , \* =  $p < 0.05$  and ns =  $p \geq 0.05$ .

Species	Benthic		Pelagic		p_Treatment	p_Habitat
	HAI	LAI	HAI	LAI		
<i>Abramis brama</i>	8.51 ± 2.15	6.28 ± 1.07	8.3 ± 3.08	3.86 ± 2.98	ns	ns
<i>Alburnus alburnus</i>	1.02 ± 0.45	0.91 ± 0.3	13.49 ± 1.57	10.47 ± 2.25	ns	***
<i>Blicca bjoerkna</i>	26.28 ± 4.07	20.35 ± 2.06	6.22 ± 1.9	17.75 ± 3.94	ns	***
<i>Cyprinus carpio</i>	4.79 ± 1.31	5.7 ± 1.73	1.86 ± 0.9	4.67 ± 1.37	ns	ns
<i>Leuciscus aspius</i>	0.98 ± 0.69	0.58 ± 0.4	3.28 ± 2.15	2.61 ± 1.09	ns	ns
<i>Rutilus rutilus</i>	37.14 ± 4.4	26.43 ± 2.68	24.02 ± 2.28	36.27 ± 9.31	ns	ns
<i>Scardinius erythrophthalmus</i>	0	0.48 ± 0.3	0	3.7 ± 1.28	ns	ns
<b>Cypriniformes</b>	<b>78.72 ± 6.88</b>	<b>60.13 ± 4.2</b>	<b>57.17 ± 7.25</b>	<b>79.33 ± 14.36</b>	<b>ns</b>	<b>ns</b>
<i>Esox lucius</i>	0	1.24 ± 0.71	0	3.6 ± 2.39	ns	ns
<b>Esociformes</b>	<b>0</b>	<b>1.24 ± 0.71</b>	<b>0</b>	<b>3.6 ± 2.39</b>	<b>ns</b>	<b>ns</b>
<i>Gymnocephalus cernua</i>	8.3 ± 0.51	4.91 ± 0.54	0	0.01 ± 0.01	*	*
<i>Perca fluviatilis</i>	9.27 ± 2.12	29.09 ± 3.4	0.39 ± 0.22	1.82 ± 0.62	***	***
<i>Sander lucioperca</i>	9.12 ± 2.32	11.52 ± 1.93	2.53 ± 0.88	3.44 ± 2.37	ns	**
<b>Perciformes</b>	<b>26.69 ± 2.88</b>	<b>45.51 ± 4.25</b>	<b>2.92 ± 0.88</b>	<b>5.27 ± 2.4</b>	<b>***</b>	<b>***</b>
<i>Silurus glanis</i>	0	0.45 ± 0.33	0	1.16 ± 1.16	ns	ns
<b>Siluriformes</b>	<b>0</b>	<b>0.45 ± 0.33</b>	<b>0</b>	<b>1.16 ± 1.16</b>	<b>ns</b>	<b>ns</b>
<b>Total catch</b>	<b>105.41 ± 6.619</b>	<b>107.94 ± 7.05</b>	<b>60.087 ± 7.726</b>	<b>89.367 ± 14.96</b>	<b>ns</b>	<b>**</b>

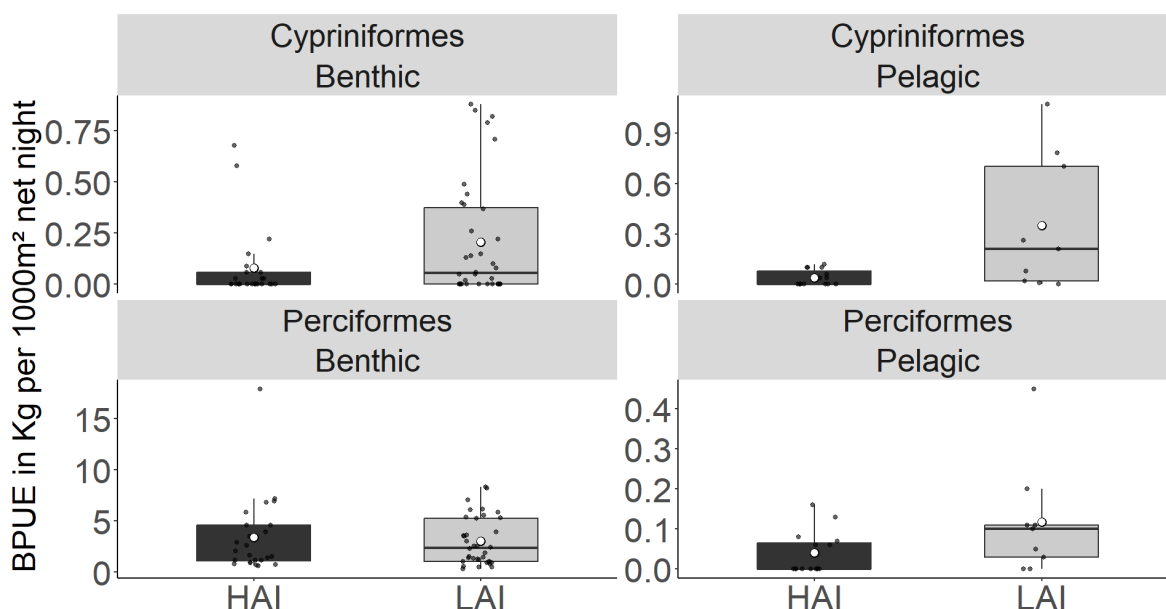


**Figure 4.** A Total biomass-per-unit effort (BPUE; kg per point) of fish older than YOY from gillnetting at high-impact (HAI) sites and low-impact (LAI) areas of the Lipno reservoir. The boxplot represents the quartile value of BPUE, the black dots represent the means of individual nets, the thick middle line represents the median, the white dot represents the overall mean of all measurements, and the whiskers represent the lowest and highest actual value of the quartile.

YOY BPUE of cyprinid fish was very low and without significant differences between LAI and HAI areas. The same is true for YOY percids with the exception of ruffe with the preference for benthic HAI areas ( $p$ -value = \*\*). Habitat preferences of cyprinids YOY were not significant, while percids YOY showed a clear preference for benthic habitats (Table 6, Figure 5).

**Table 6.** Mean and standard error (SE) of the young of the year class fish BPUE (biomass per unit of effort) of gillnets from Lipno reservoir, in kilograms per 1000 m<sup>2</sup> of nets. \*\*\* =  $p < 0.001$ , \*\* =  $p < 0.01$ , \* =  $p < 0.05$  and ns =  $p \geq 0.05$ .

Species	Benthic		Pelagic		p_Treatment	p_Habitat
	HAI	LAI	HAI	LAI		
<i>Abramis brama</i>	0.03 ± 0.02	0.01 ± 0.01	0	0.04 ± 0.02	ns	ns
<i>Alburnus alburnus</i>	0	0	0	0.11 ± 0.06	ns	ns
<i>Blicca bjoerkna</i>	0.01 ± 0.001	0.01 ± 0.001	0.01 ± 0.01	0.04 ± 0.02	ns	ns
<i>Rutilus rutilus</i>	0.05 ± 0.02	0.18 ± 0.05	0.02 ± 0.01	0.15 ± 0.06	ns	ns
<b>Cypriniformes</b>	<b>0.08 ± 0.04</b>	<b>0.21 ± 0.05</b>	<b>0.04 ± 0.01</b>	<b>0.35 ± 0.13</b>	<b>ns</b>	<b>ns</b>
<i>Gymnocephalus cernua</i>	0.85 ± 0.12	0.3 ± 0.04	0	0	**	ns
<i>Perca fluviatilis</i>	1.17 ± 0.48	1.75 ± 0.3	0.02 ± 0.01	0.11 ± 0.04	ns	***
<i>Sander lucioperca</i>	1.39 ± 0.34	0.96 ± 0.23	0.02 ± 0.01	0	ns	*
<b>Perciformes</b>	<b>3.4 ± 0.77</b>	<b>3.01 ± 0.39</b>	<b>0.04 ± 0.01</b>	<b>0.11 ± 0.05</b>	<b>ns</b>	<b>***</b>
<b>Total catch</b>	<b>3.48 ± 0.786</b>	<b>3.219 ± 0.4</b>	<b>0.077 ± 0.02</b>	<b>0.46 ± 0.16</b>	<b>ns</b>	<b>ns</b>



**Figure 5.** A Total biomass-per-unit effort (BPUE; kg per point) of YOY fish from gillnetting at high-impact (HAI) sites and low-impact (LAI) areas of the Lipno reservoir. The boxplot represents the quartile value of BPUE, the black dots represent the means of individual nets, the thick middle line represents the median, the white dot represents the overall mean of all measurements, and the whiskers represent the lowest and highest actual value of the quartile.

The size spectrum of fishes showed that the peak abundance of larger fishes for most species was found in LAI rather than HAI, mainly in the pelagic habitat (Table 7).

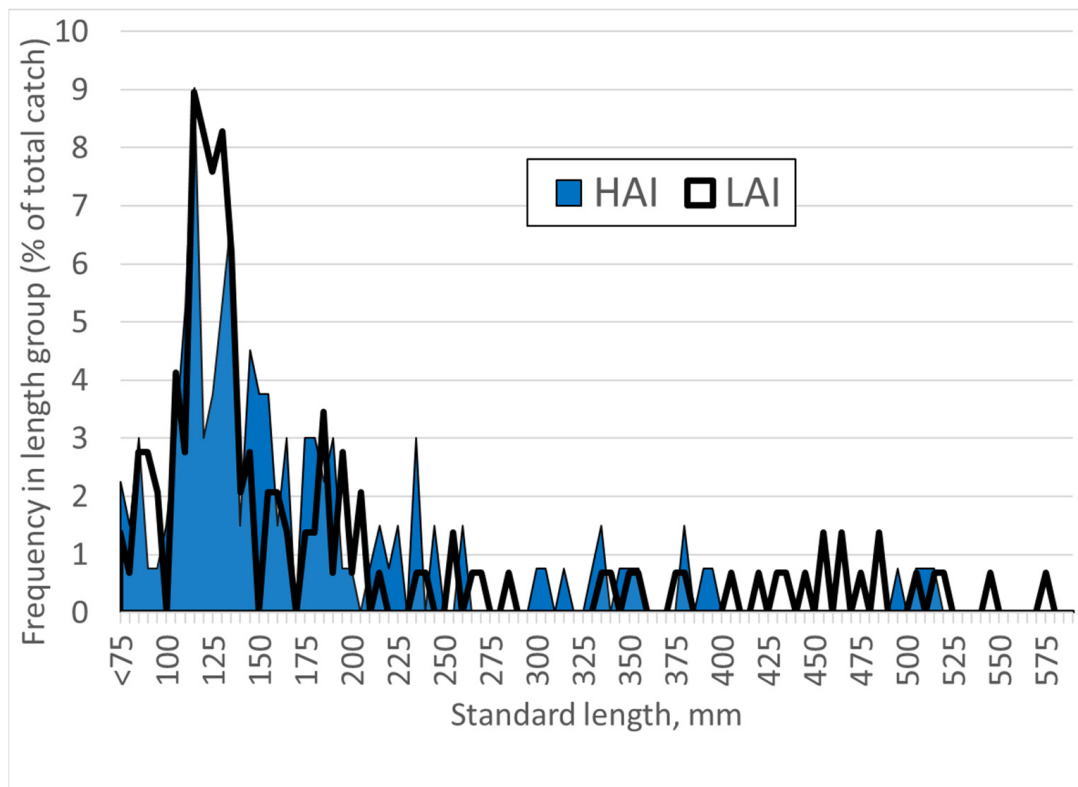
This trend was confirmed for common bream ( $p$ -value = \*\*), carp ( $p$ -value = \*\*\*), ruffe ( $p$ -value = \*\*), pikeperch ( $p$ -value = \*\*\*) and perch ( $p$ -value = \*\*). Pikeperch is probably the most important species highly valued by anglers, and Figure 6 shows how the protection at LAI areas is reflected in the length frequency distribution. The legal size of the pikeperch was 450 mm in total length, which is approximately 395 mm in standard length. It can be seen that individuals of this size and larger are much more common in the areas of LAI. Asp ( $p$ -value = \*\*\*) and roach ( $p$ -value = \*\*) had larger sizes in HAI areas. Of the YOY fish, larger individuals were found in HAI areas for common bream ( $p$ -value = \*\*\*) and roach ( $p$ -value = \*\*), while larger white bream ( $p$ -value = \*\*\*) and pikeperch ( $p$ -value = \*\*\*) were found in LAI areas (Table 8).

**Table 7.** Mean, standard error (SE), maximum (Max) and minimum (Min) standard length of fish older than YOY, in millimeters, from gillnets of Lipno reservoir. \*\*\* =  $p < 0.001$ , \*\* =  $p < 0.01$ , and ns =  $p \geq 0.05$ . For complete species names, check Table 1 or Table 3.

Species	Benthic				Pelagic				p_Treatment	p_Habitat
	HAI		LAI		HAI		LAI			
	Mean ± SE	Max-Min	Mean ± SE	Max-Min	Mean ± SE	Max-Min	Mean ± SE	Max-Min		
<i>A. brama</i>	172.48 ± 8.09	320-69	222.46 ± 11.14	320-85	255.11 ± 6.24	400-170	240.83 ± 16.37	310-105	**	ns
<i>A. alburnus</i>	121.94 ± 2.36	150-75	116.35 ± 2.01	145-75	124.13 ± 0.6	180-70	125.47 ± 0.84	155-70	***	***
<i>B. bjoerkna</i>	160.61 ± 4.37	305-66	173.93 ± 4.31	295-66	204.98 ± 6.83	275-85	194.26 ± 5	320-86	ns	***
<i>C. carpio</i>	399.29 ± 13.3	455-280	413.96 ± 9.39	490-310	403.57 ± 13.39	445-350	423.33 ± 20.16	580-390	***	***
<i>E. lucius</i>	-	-	466.67 ± 24.55	510-425	-	-	585 ± 15	600-570	ns	***
<i>G. cernua</i>	73.62 ± 0.24	113-55	75.17 ± 0.32	130-55	-	-	85	85	**	***
<i>L. aspius</i>	525 ± 30	555-495	505 ± 5	510-500	457.86 ± 38.51	560-315	512 ± 4.06	520-500	***	***
<i>P. fluviatilis</i>	157.82 ± 4.96	310-83	172.53 ± 3.02	320-70	202.5 ± 13.15	240-180	193.33 ± 9.5	255-150	***	***
<i>R. rutilus</i>	155.06 ± 2.08	290-75	145.09 ± 1.91	280-75	221.87 ± 2.45	310-75	221.79 ± 2.78	285-80	**	***
<i>S. lucioperca</i>	241.84 ± 15.53	520-156	305.54 ± 18.52	580-158	326.11 ± 20.98	395-230	380 ± 46.94	525-235	***	***
<i>S. erythrophthalmus</i>	-	-	228.33 ± 18.78	260-195	-	-	243 ± 4.84	275-220	ns	***
<i>S. glanis</i>	-	-	502.5 ± 162.5	665-340	-	-	672.5 ± 47.5	720-625	ns	***

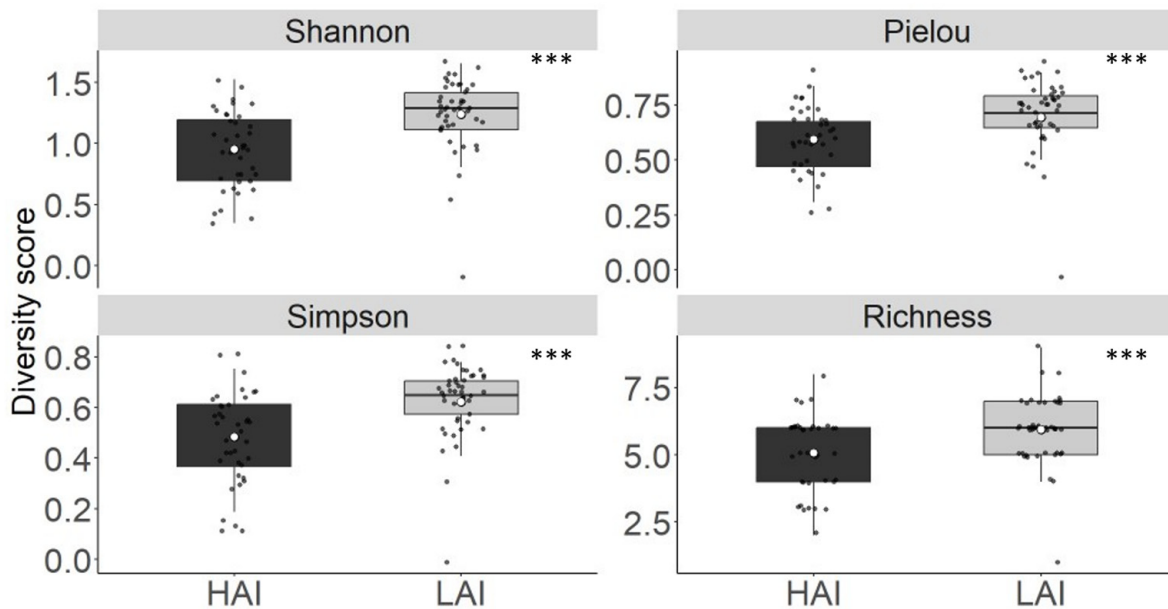
**Table 8.** Mean, standard error (SE), maximum (Max) and minimum (Min) standard length of the young of the year class fish, in millimeters, from gillnets of Lipno reservoir. \*\*\* =  $p < 0.001$ , \* =  $p < 0.05$  and ns =  $p \geq 0.05$ . For complete species names, check Table 2 or Table 4.

Species	Benthic				Pelagic				p_Treatment	p_Habitat
	HAI		LAI		HAI		LAI			
	Mean ± SE	Max-Min	Mean ± SE	Max-Min	Mean ± SE	Max-Min	Mean ± SE	Max-Min		
<i>A. brama</i>	55.8 ± 2.32	62-40	54.17 ± 2.34	65 ± 49	-	-	54.07 ± 1.61	63-40	***	***
<i>A. alburnus</i>	56	56	65	65	-	-	56.74 ± 0.56	65-49	ns	ns
<i>B. bjoerkna</i>	55.67 ± 5.9	63-44	58.14 ± 2.01	65-53	53.86 ± 1.39	59-51	54.46 ± 1.57	65-46	***	***
<i>G. cernua</i>	47.64 ± 0.18	55-33	45.88 ± 0.26	55-30	48 ± 2	50-46	43	43	ns	***
<i>P. fluviatilis</i>	52.55 ± 0.22	72-37	48.23 ± 0.12	73-33	52 ± 1.57	60-42	48.52 ± 0.52	56-39	ns	*
<i>R. rutilus</i>	55.53 ± 1.02	65-43	56.38 ± 0.42	66-42	58.4 ± 1.16	64-51	55.76 ± 0.56	65-49	***	***
<i>S. lucioperca</i>	90.88 ± 2.96	155-41	100.58 ± 2.8	155-42	55.78 ± 7.28	95-29	43	43	***	***



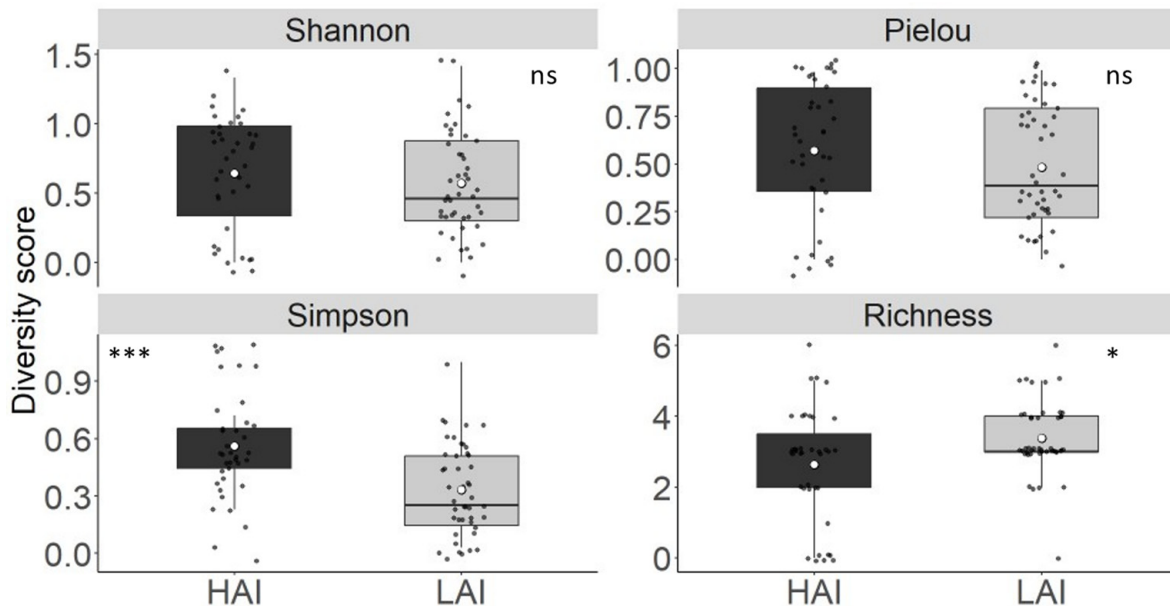
**Figure 6.** Length frequency distribution of pikeperch at high impact (HAI) and low impact (LAI) areas of the Lipno reservoir.

The values of the Shannon, Simpson, Pielou’s and Richness diversity indices showed significantly higher values for the older fish in LAI ( $p$ -value = \*\*\*) (Figure 7).



**Figure 7.** Diversity score of the fish older than YOY in the Lipno experiment from Shannon, Pielou’s, Simpson and Richness indices. The boxplot represents the quartile value of the diversity score, the black dots represent the means of individual nets, the thick middle line represents the median, the white dot represents the overall mean of all measurements, and the whiskers represent the lowest and highest actual value of the quartile. \*\*\* =  $p < 0.001$ .

Differences in the diversity indices of YOY fish were largely nonsignificant, except for species richness, which was higher at LAI ( $p$ -value = \*) and Simpson for HAI ( $p$ -value = \*\*\*, Figure 8).



**Figure 8.** Diversity score of the YOY fish in the Lipno experiment from Shannon, Pielou's, Simpson and Richness indices. The boxplot represents the quartile value of the diversity score, the black dots represent the mean of the individual net, the thick middle line represents the median, the white dot represents the overall mean of all measurements, and the whiskers represent the lowest and highest actual value of the quartile. \*\*\* =  $p < 0.001$ , \* =  $p < 0.05$  and ns =  $p \geq 0.05$ .

#### 4. Discussion

The most fished species in Czech reservoirs are carp and predatory fish such as pikeperch and pike [47,48]. Our results showed that the main predatory fish species targeted by the angler's pikeperch, perch, wels catfish and pike, have to some extent either more CPUE/BPUE or larger average size inside the LAI than in the control areas. Pike and wels catfish densities in the HAI areas were so low that no individuals were captured during the current survey. The lower exploitation in the LAI areas allows fish to reach larger sizes or densities, as shown in Figure 6. Smaller percid fish may be more abundant in HAI areas, while larger ones are more abundant in LAI areas. With the exception of pike and wels catfish, there is not much difference in densities, possibly due to fish migration from LAI and limited fishing pressure, including illegal poaching. It is also interesting to note that the two bays on the southwest coast of Lipno had very similar fish compositions, even though only one of them is designated as a no-fishing zone. The results suggest that the remote location of Račinská Bay may also serve as a protection, as it is difficult for anglers to reach.

Protection in the Lipno LAI areas consists mainly of the angling ban and isolation from tourism and local anglers. While in other parts of the reservoir, fishing pressure is quite strong, in these areas, there is theoretically little or no fishing. However, the two areas of LAI are not closed off from the lake so that fish can migrate, but they are large enough (several tens to hundreds of hectares) to develop stronger subpopulations of some species [49–51]. The differences between the LAI and HAI areas' fish communities may also be caused by some inherent differences between the west and east side of the lake, which are not related to anthropogenic pressure. In order to limit recreational fishery as little as possible, all the protected areas were declared at the western shore of the reservoir. However, the differences in predatory species abundance and size structure (Figure 6) show that the life expectancy of these highly valued fish species is much higher in the LAI

areas. Recreational angling can be as or even more impactful than commercial fishery in different environments and habitats, even though commercial fishery is completely banned in Czech reservoirs [52–54].

Total fish densities were actually lower in LAI. Some fish are highly attracted to feeding anglers at their favorite sites; this tactic is quite effective for cyprinids such as carp and roach [55–57], so anglers attract these cyprinid fishes to HAI areas that are more frequented by anglers. HAI areas also receive more nutrients and are likely to be more productive. It was interesting to observe that rudd were more abundant in LAI areas. This species, which is not common in reservoirs, seems to prefer sheltered bays. In the late stages of its life, it changes to a more herbivorous diet [58]. In Czech reservoirs, it is considered an indicator of the presence of macrophytes and good ecological potential [59], and it is more abundant in bays protected from prevailing westerly winds [40].

Protected areas are essential for biodiversity conservation and are essentially the cornerstones of all national and international conservation strategies [17,60,61] that aim to maintain functioning natural ecosystems, act as refugia for species, and preserve ecological processes in all types of environments [10,62]. Intact freshwater systems are becoming increasingly rare worldwide and require administrative, ecological, and social action before they fall victim to a range of threats to maintain their natural state or unique biodiversity [13,63]. Protected areas are often the most important measure we have to save many threatened or endemic species from extinction [10,15,64].

Due to the global decline in freshwater biodiversity [3], the literature on PA has mainly focused on the diversity benefits of PA [65]. Freshwater fish have received the most attention in the analysis of the effectiveness and success of PA, although there is some evidence that aquatic invertebrates and freshwater-dependent mammals are also underrepresented in existing PA networks [66–68]. For a PA to be truly successful, all elements should be included in the management strategy, such as water flow, water quality, surrounding vegetation, and control of potential invasion by alien species [65]. Considering the ecosystem as a whole brings the next level of PA, as it focuses more on restoring the entire environment as close as possible to its original state and helping the entire species community to recover [8]. LAI areas in Lipno are more exposed to mammalian predators, such as otters (*Lutra lutra*) and avians (heron, *Ardea cinerea*, sea eagle, *Haliaeetus albicilla*, cormorant, *Phalacrocorax carbo*). Increased predation and low nutrient and fish bait input likely negatively affect fish abundance and biomass in LAI areas.

Fish migration is one of the most controversial drawbacks of PA [28,69,70]. Because the PA of Lipno is a bay open to the rest of the reservoir, migration to new habitats or new food sources may cause populations to leave the PA [69,70]. Larval dispersal from the PA may also be included in this equation, with juvenile perch, and YOY pikeperch being more abundant outside of the LAI areas. As our results indicate, perch are one of the most abundant fish in the PA, and their population may exert pressure on the YOY and juveniles to seek habitat and refuge outside the protected area [71–74].

The European standard gillnets have proven effective in the sampling of the study areas. Of course, it should be noted that the CEN gillnets underestimate the YOY fish, especially the cyprinids of some small-bodied fish species [75]. However, this bias should affect the results of LAI and HAI in the same way. The same is true for some other selectivity characteristics of the gillnets. The fish community in Lipno reservoir is monitored by several other methods (fry seining, fry trawling, electrofishing and hydroacoustics [24]). However, none of these methods revealed any important species that were not recorded in the gillnet catches. In other words, the CEN multimers gillnets performed very reasonably in assessing the fish community in the LAI and HAI areas. The loss or destruction of nets and habitat complexity created by submerged trees in some areas was another complication encountered, especially at LAI. The beneficial effects of the LAI areas may be underestimated or overestimated in this study because fish migrate between the LAI areas and the HAI areas. For some fish species, the home range may be larger than the actual LAI areas, and they spend only part of the diurnal cycle in the area [32]. One solution to this type of

problem is to use telemetry to monitor movement behavior and obtain a more accurate estimate of home range for the community in the LAI areas.

## 5. Conclusions

Our study represents an attempt to assess the impact of protected areas in the largest water body in the Czech Republic, the Lipno reservoir, on fish abundance, biomass, and species composition. Three groups of fish were found to prefer protected areas with low anthropogenic pressures:

1. YOY perch, as the superdominant of the young-of-the-year fish community.
2. Pike, wels catfish and rudd, which were not found at high anthropogenic impact areas during this survey.
3. Larger individuals of pikeperch, which apparently survive better in low anthropogenic impact areas.

The latter two groups benefit from protection from angling, which is otherwise a fairly strong mortality factor in the reservoir. The abundance of all fish older than YOY was higher in the high anthropogenic impact areas, likely due to higher nutrient inputs and extensive use of fish bait. The fish community in the protected areas had greater values of estimated diversity indices due to both the promotion and protection of less common species (pike, perch, rudd) and limited attractiveness to superdominant cyprinids. It can be concluded that the areas of LAI serve as protective habitats for heavily fished species and increase the diversity of the fish community in the reservoir. The example of the protected and low impact areas of Lipno should be followed in other water bodies with high fishing pressure and anthropogenic impact.

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## **Paper III**

### **Artificial floating islands: a promising tool to support juvenile fish in lacustrine systems.**

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(IF = 2.6)





# Artificial floating islands: a promising tool to support juvenile fish in lacustrine systems

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**Abstract** Habitat complexity of freshwater ecosystems has been decreasing due to human impacts. Therefore, conservation and environmental management actions have intensified in the recent years. Artificial floating islands (AFIs) are one environmental management action intended to promote the populations of aquatic organisms. In this study, we installed eight AFIs in the littoral area of Lipno Reservoir, Czech Republic and covered them with local wetland vegetation to study the impact of this mitigation action on the fish community. The AFIs were sampled by Point Abundance Sampling Electrofishing (PASE). The AFIs were mainly inhabited by juvenile roach (*Rutilus rutilus*) and

perch (*Perca fluviatilis*), with densities one to two orders of magnitude higher than in the surrounding control sites. Juvenile catfish (*Silurus glanis*) and adult northern pike (*Esox lucius*) were apex predators that were recorded exclusively at AFIs. More fish were captured in AFIs than in control areas (up to 29.2 times more). Even AFIs of simple construction harboured significantly more age 0+ and juvenile fish than control areas, confirming their potential to serve as nursery ground for age 0+ fish in lentic systems. Artificial floating islands can be used to support juvenile fish in the conditions of impoverished littoral structured habitat.

**Keywords** Artificial habitat · FAD (fish aggregation device) · Stock enhancement · Fish management · Habitat restoration

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## Introduction

Alteration of hydrological cycles at local to global scales due to reservoir construction (Xiong et al., 2020; Zamora et al., 2020), water withdrawals (Kumar & Carolin, 2019; Murphy et al., 2021), and climate change (Middelkoop et al., 2001; Zhao et al., 2021) are some of the impacts that humans have on freshwater habitats (Haddeland et al., 2014). In water accumulation reservoirs, structural habitat complexity in the littoral zone is typically low due to high water-level fluctuations (Zohary & Ostrovsky, 2011;

Krolová et al., 2012). This usually favours eurytopic species that are tolerant to a wide range of spawning substrates (Persson & Greenberg, 1990; Kubečka, 1993; Hladík & Kubečka, 2004; Lima et al., 2017). Incubation of eggs on less favourable substrates and early life history in bare, unstructured littoral zones leads to higher fry mortality, low recruitment, and consequently, the fish fauna is impoverished in both in terms of quality and quantity (Duncan & Kubečka, 1995; Kahl et al., 2008; Čech et al., 2009; Cantonati et al., 2020).

Water-level fluctuations in still waterbodies have great influence on the littoral zones, in relation of sedimentation, vegetation, and also play an important role in influencing the lake's animal biota (Zohary & Ostrovsky, 2011). This can directly affect substrates (which can improve or restrict colonization by vegetation, which part depends on silt accumulation for rooting), and alteration of habitats suitable for aquatic flora and fauna (Gownaris et al., 2018; Khanal et al., 2021; Zhao et al., 2021). Any significant change to the water level of a lake will affect the biological productivity, so when water levels fluctuate persistently, such as in accumulation reservoirs, it is notoriously difficult to support the natural structural diversity of the littoral zone (Krolová & Hejzlar, 2013). One alternative for improving the impacted littoral zones is to create artificial habitats that are not dependent on water levels (Yeh et al., 2015).

Artificial habitats have been studied since the 1930s to create new habitats for underwater communities (Santos et al., 2008). Some factors like the depth of deployment, structural complexity, and size of the artificial habitat have been found to affect fish communities (Santos et al., 2008), so many of them have been used as fish aggregation devices (FADs), like artificial reefs, sunken vessels or artificial structures associated with the bottoms of aquatic ecosystems (Bergström et al., 2013; Riera et al., 2014; Consoli et al., 2015; Smith et al., 2015; Hylkema et al., 2020), with a small proportion of FADs being Artificial floating islands (AFIs). AFIs are man-made floating structures capable of supporting aquatic vegetation and creating new habitats for aquatic fauna (Oliver & McKaye, 1982; Winston et al., 2013). AFIs provide benefits such as shelter, shade, and food (Nakamura et al., 1997; Gatz, 2008) to the aquatic community or even become successful spawning habitats for some

species (Byeon, 2014), which has led many Asian and some European countries, like England and Germany, to recognize AFIs as a successful habitat restoration tool (Nakamura & Mueller, 2008), with many environmental applications. These include improved stream aesthetics, erosion control, and most importantly, nutrient removal and reduced water mixing (Nakamura & Mueller, 2008; Winston et al., 2013; de Freitas et al., 2015). They can be used in the treatment of wastewater (Weragoda et al., 2012; Winston et al., 2013; Yeh et al., 2015), they can create new nearshore habitats without taking up shoreline space and also act as FADs (Oliver & McKaye, 1982; Nakamura & Mueller, 2008). Of studies focussing on fish aggregating devices and AFIs, the majority took place in marine systems (Morrisey et al., 2006; Eighani et al., 2019), so knowledge of the effects of AFIs on freshwater fish is remarkably understudied.

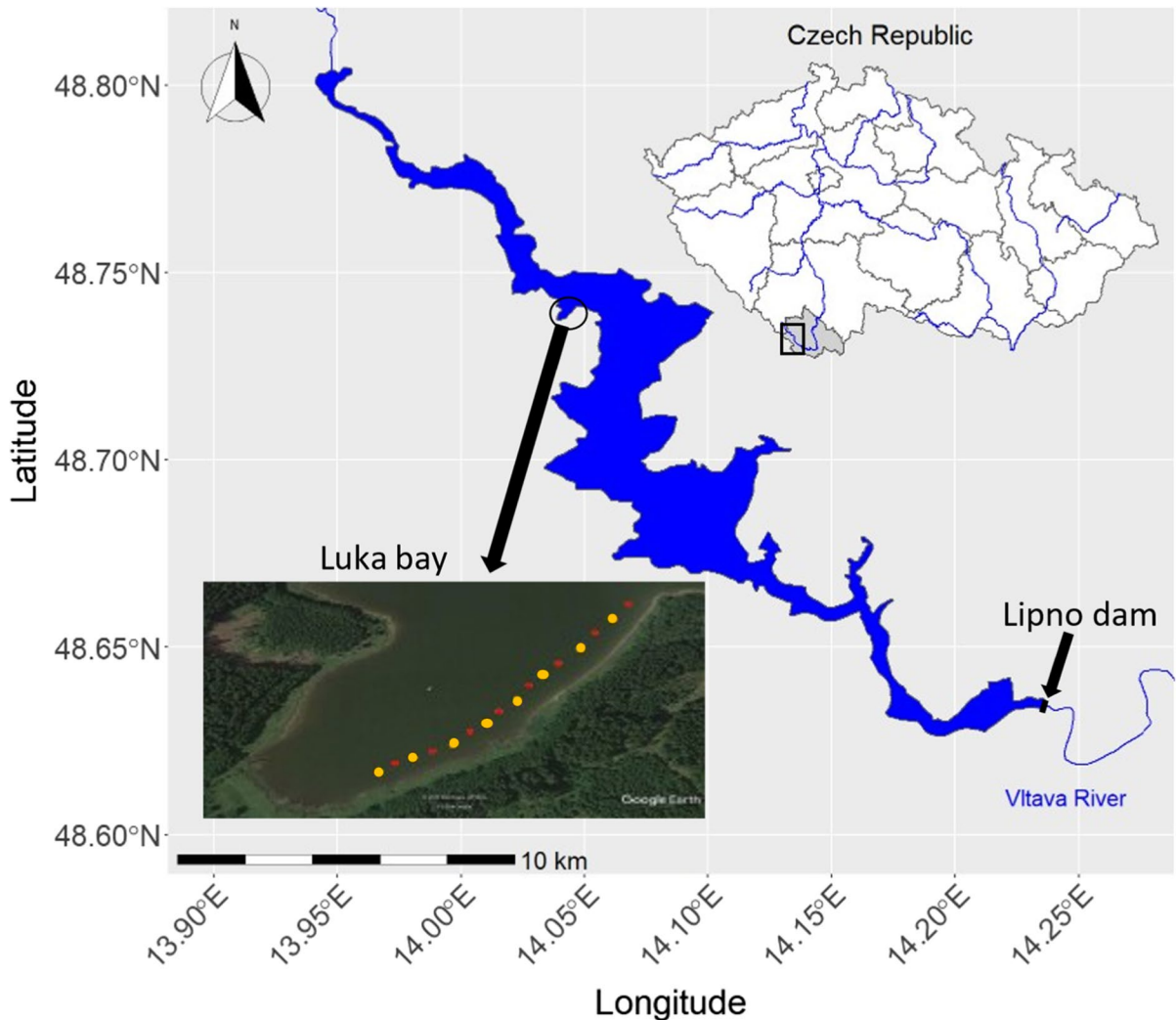
Our study site, Lipno Reservoir, Czech Republic, is a typical water storage reservoir with very impoverished littoral habitat (Krolová et al., 2013). Poor littoral habitat complexity was suspected as one of the reason for fish population decline in this important angling site (De Moraes et al., 2023; Vehanen et al., 2020). The aim of this study was to investigate whether AFIs can affect fish fauna in a eutrophic system. For this purpose, AFIs in Lipno Reservoir were used to compare fish abundance, biomass, and diversity in areas with and without AFIs. As AFIs created visually suitable habitat for fish, we predicted that fish abundance would be higher in AFIs compared to control areas and that AFIs would attract predominantly juvenile fish needing shelter.

## Material and methods

### Study area

Lipno Reservoir (Fig. 1) is a reservoir located at Vltava River in the foothills of the Bohemian Forest (Czech Republic). The reservoir was built in 1960 as a hydroelectric reservoir. Nowadays, it has more uses, such as flood control, flow control, drinking water supply, and recreation (Krolová et al., 2012). The reservoir has a volume of 306 million m<sup>3</sup>, a surface area of 46.5 km<sup>2</sup>, an average depth of 6.6 m, and a maximum depth of 22 m. The reservoir's storage



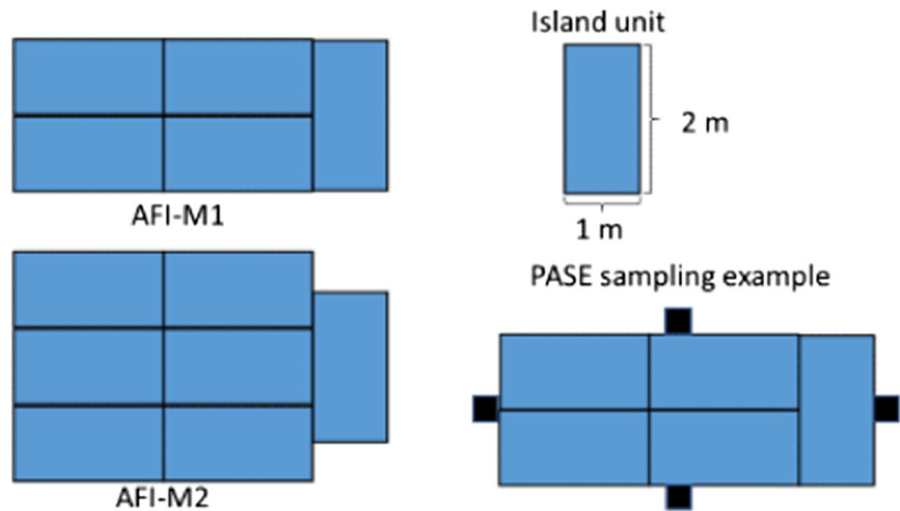


**Fig. 1** Outline map of Lipno Reservoir, with its location in Czechia (black rectangle) and the detailed location of this experiment (Luka Bay, black circle). In the satellite image, the AFIs are represented by red dots and the control by yellow dots

capacity varies in an annual cycle due to the different demands on it, typically with a maximum volume in spring and then a gradual decrease until winter. The decrease depends on flow conditions, i.e. with a decrease in water level of up to 3 m in dry years, but with little or no decrease in wet years. The reservoir is moderately eutrophic with phosphorus as the limiting nutrient (mean total P:  $25 \mu\text{g l}^{-1}$ ; mean/max chlorophyll-a:  $14/25 \mu\text{g l}^{-1}$ ; mean/max water transparency:  $1.9/2.7 \text{ m}$ ; data from the Povodí Vltavy State Enterprise, for 20,062,009). For more details, see Křolová et al. (2012). The study site was in the middle part of the reservoir, in Hadí Luka Bay

(Fig. 1;  $48^{\circ}74' \text{ N}$ ,  $14^{\circ}04' \text{ E}$ ; 5 m max. depth). Aquatic macrophytes in the Lipno reservoir can hardly grow in the upper littoral (eulittoral) disturbed by water-level fluctuations and ice. Due to the brown coloured water with low transparency (usually 1–3 m), the macrophytes cannot colonize bottom in the deeper littoral (Křolová et al., 2012; Křolová & Hejzlar, 2013). Therefore, several prototypes of AFI were installed on this reservoir as a pilot compensation measure for low habitat complexity and macrophyte absence. Of several prototypes tested, the most promising designs (four AFI-M1 and four AFI-M2, see Fig. 2 and below) were chosen for investigating

**Fig. 2** Artificial floating island (AFI) models (M1 area: 10 m<sup>2</sup>; M2 area: 14 m<sup>2</sup>) used in this experiment and measurement of each island's unit on the right top. On the bottom right point abundance sampling electrofishing (PASE) sites (black rectangles)



the fish assemblages using the AFI. Fish community of the Lipno reservoir is represented mainly by roach (*Rutilus rutilus* (L., 1758)), white bream (*Blicca bjoerkna* (L., 1758]), carp (*Cyprinus carpio* L., 1758), perch (*Perca fluviatilis* L., 1758), bleak (*Alburnus alburnus* (L., 1758)), and pikeperch (*Sander lucioperca* (L., 1758))—(De Moraes et al., 2023; Vehanen et al., 2020, p. 81–85).

#### Design of AFIs

The AFIs used in this study were constructed from five or seven elementary units (each 2×1 m) that were tightly connected in two combinations (AFI-M1 and four AFI-M2, Fig. 2). One island unit represented

our registered prototype (Kubečka et al., 2020), which was designed as a sandwich gabion structure filled with geotextiles. The hard outer layers of each unit consisted of two galvanically coated gabion panels (each 1×2 m with 10 cm mesh) connected with gabion spirals. The core consisted of a coconut fibre bed (0.05×1×2 m) lying on the water surface to keep the roots of plants grown on it in a wet or aquatic environment (Fig. 3). AFIs buoyancy was provided by two PVC tubing's (0.2×1.4 m each) per island unit. Four concrete anchors (0.2×0.5×0.5 m each) held each AFI in place. AFIs were planted with four emergent species, namely *Carex acuta* Linnaeus 1753, *Eleocharis palustris* (L.) Roemer & Schultes 1817, *Phalaris arundinacea* Linnaeus

**Fig. 3** Details of floating islands construction. **A** Freshly made elementary units of AFI before planting the plants. **B** Complete AFI-M2 in summer during the experiments. **C** Roots of plants hanging down from the AFI in April 2019 with the eggs of roach



1753, *Scirpus radicans* Schkuhr 1793, and/or three amphibious species, namely *Alopecurus aequalis* Sobol. 1799, *Glyceria fluitans* (L.) R. Brown 1810, *Potentilla palustris* (L.) Scopoli 1771. Both groups of plants are native to the region. Species composition was primarily set to achieve 30–50% coverage and maximum biomass of several large species of grasses and sedges during the vegetative season, while allowing other species to cover only a small portion of the AFIs. Several other species colonized the AFIs spontaneously.

Some AFIs were damaged by storms over the winter and had to be reshaped and/or replanted during spring 2020. During surveys of fish communities in August 2019 and 2020, extensive roots of dominant grasses and sedges in particular grew through 43–85% of the AFI bottom area and created structured habitats for fish to the depths of 0.5–0.8 m (Fig. 3).

#### AFI deployment

The islands were aligned with the shore in a straight line and deployed approximately 50 m apart (Fig. 1) in spring 2019 (late April, early May). Because the rough conditions of the winter, the islands were heavily damaged and new ones were deployed again in spring 2020. A total of eight individual AFIs were deployed between the two types of AFIs, four smaller AFI-M1 (10 m<sup>2</sup>) and four larger AFI-M2 (10 m<sup>2</sup>, Fig. 2) were alternating along the shoreline of the bay, in each year (Fig. 1). The eight control areas were located between the installed AFIs (yellow colour at Fig. 1) and were exposed to identical environmental and ecological conditions.

#### Electrofishing sampling

Point Abundance Sampling (PASE) (Copp, 2010) was carried out using

an electroshocker (Hans Grassel, Schönau am Königsee, Germany; 13 kW, 300/600 185 V) from a 7-m boat with an outboard motor on the side opposite to the electrodes. The power output was adjusted according to the conductivity of the surrounding water by manipulating the cycle frequency 80–90 HZ, 600 V (Miranda & Kratochvíl, 2008). A spherical anode attached to a 4-m-long fibreglass rod was used for PASE, while a second circular dip net was used for fish capture. Depth during fish sampling was between 1.5 and 1.7 m with approximately 30 m distance from shore.

The AFIs were rectangular in shape and each of them were sampled at four AFI margins, in the middle section of each side (analogically to compass positions East, South, West, North, Fig. 2), and the sum of 4 points would constitute a sampling unity for this experiment (= island sample consisting of four electrofishing points). The control sites were sampled in the areas between the AFIs, and the sampling points followed the same protocol as the AFIs (four points around imaginary AFI centre, control sample consisting of four electrofishing points each). Overall sampling effort is given in Table 1. For sampling, the anode was submerged in the water (0.2–0.5 m deep), and an electric field was activated for a duration of 15 s per point. PASE surveys were conducted from 26 to 28 August 2019 and 27 to 28 August 2020, in two diel periods: around 11:00–13:00 h (noon) at the highest light intensity and around 23:00–01:00 (midnight) at the lowest light intensity. These sampling periods were chosen to avoid an undefined fish distribution change during evening/morning migration between the pelagic and littoral zones (Muška et al., 2013). We sampled only one day and night in 2020, because the 3rd day of 2019 showed a lower result than the others, most likely that the fish got used with the boat sound and moved away from the AFI when sampling boat approached.

**Table 1** Design of sampling of AFI and control sites in 2019 and 2020. Every Island and control sample represents a sampling unity from the statistical point of view and contains four electrofishing points

Date	Number of island samples day	Number of control samples day	Number of island samples night	Number of control samples night
2019 August 26/27	8	8	8	8
2019 August 27/28	8	8	8	8
2019 August 28/29	8	8	8	8
2020 August 27/28	8	8	8	8

The catch was sorted by species; standard length was measured to the nearest mm for each fish. Weight was calculated using the weight-length model with catches from standard sampling for fish stocks in Lipno Reservoir (Soukalová et al., 2020).

The field sampling and experimental protocols used in this study were performed in accordance with the guidelines and permission of the Experimental Animal Welfare Commission under the Ministry of Agriculture of the Czech Republic (Ref. No. CZ 01,679). All methods were approved by the Experimental Animal Welfare Commission of the Biology Centre, Czech Academy of Sciences.

### Data analysis

The catch of each of four sampling points were clustered to a sampling unit (AFI or control) and the treatment means were calculated for these clusters. Mean value per unit of effort (VPUE) was calculated using the abundance (CPUE, catch per unit of effort) or the weight (BPUE, biomass per unit of effort) per sampling point of the treatment. The means of VPUE were calculated for the different models of the AFIs, treatments, periods of time, and year of sampling. The Standard lengths of the fish were calculated for different treatments, periods of time, and year of sampling.

We checked whether the different sizes of the surface area on the AFIs (AFI-M1 and AFI-M2) in the experiment would influence the CPUE, BPUE, and diversity indices of the total fish community catch between small and big AFIs, also using the negative binomial generalized linear models.

Negative binomial generalized linear models were applied to describe differences in the values of fish VPUE values (abundance and biomass) and size of the fish (standard length) between treatments (AFI and control sites), diel periods (day and night), and years of sampling (2019–2020).

$Model = Value \sim Treatment + Period + Year.$

The negative binomial generalized linear model was chosen because it can handle a large number of zeros and over dispersed data (Zuur et al., 2009). The MASS package (Ripley et al., 2013) was used to compute all negative binomial generalized linear models.

We calculated taxonomic diversity indices to understand how AFIs locally influenced the biodiversity. The Shannon–Wiener diversity, Simpson's diversity, Pielou's evenness, and Richness indices were calculated by treatments, periods of time, and year of sampling using the Vegan package (Oksanen et al., 2018). The generalized linear negative binomial model was also used to compare the diversity index values using the structure as the previous models.

All statistical analyses were performed using R software (R Core Team, 2020).

## Results

### AFI size analyses

The analyses to test the influence of the size of the area of the AFIs, in relation to the fish community showed no significant difference between the catches by smaller (AFI-M1 10 m<sup>2</sup>) and larger (AFI-M2 14 m<sup>2</sup>) AFI configurations in terms of CPUE ( $P=0.666$ ), BPUE ( $P=0.823$ ), and diversity (Shannon  $P=0.949$ ; Simpson's  $P=0.963$ ; Pielou's  $P=0.934$ ; Richness  $P=0.886$ ). Therefore, the differences in AFI designs were further neglected in the following analysis.

### Catch results

In 2019, a total of 623 fish were captured (70 in control and 553 in AFIs), belonging to 9 different species, while in 2020, a total of 513 fish were caught (17 in control and 496 in AFIs) from 8 different species (Table 2).

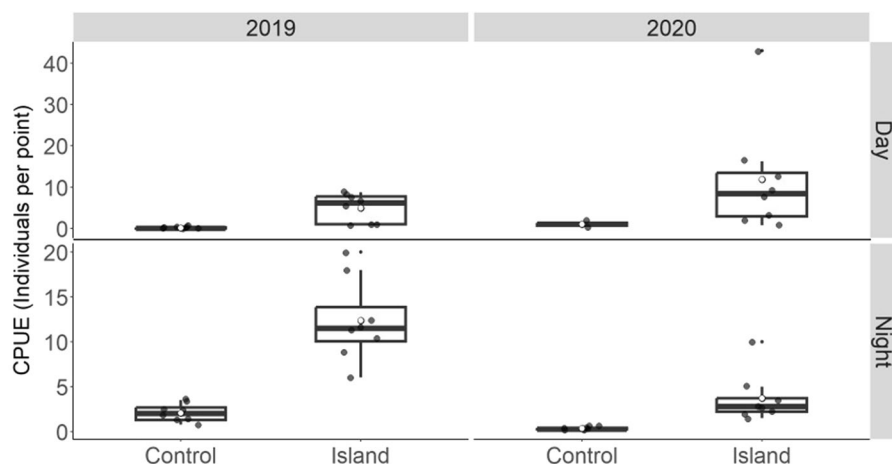
The total CPUE was significantly higher in AFIs ( $P \leq 0.001$ ; Table 2, Fig. 4). At species level, only perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) showed significant difference in CPUE between the years (perch  $P \leq 0.001$ , roach  $P < 0.05$ ), for the AFIs and control ( $P \leq 0.001$  both species), and diel period (perch  $P < 0.01$ , roach  $P < 0.05$ ); bleak (*Alburnus alburnus*) was the only other species that had significantly different values of CPUE between years ( $P < 0.05$ ).

The total BPUE was significantly higher in control ( $P < 0.01$ ; Table 3, Fig. 5) and for the night period ( $P < 0.05$ ). Perch had significantly higher BPUE values in AFIs ( $P \leq 0.001$ ), at night ( $P < 0.01$ )

**Table 2** Mean and standard error (SE) of the fish CPUE (mean catch per electrofishing point at treatment—AFI or control, time of day and year)

Sp	2019												2020											
	Control				Island				Control				Island				Control				Island			
	Day	Night	Mean ± SE	Time	Day	Night	Mean ± SE	Time	Day	Night	Mean ± SE	Time	Day	Night	Mean ± SE	Time	Day	Night	Mean ± SE	Time	Day	Night	Mean ± SE	Time
A.b	0 ± 0	0.38 ± 0.17	0 ± 0	0.19 ± 0.08	0 ± 0	0 ± 0	0 ± 0	0.09 ± 0.07	ns	ns	ns	ns	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.09 ± 0.07	ns	ns	ns	ns	ns	ns	ns
A.sp.	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	ns	ns	ns	ns	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	ns	ns	ns	ns	ns	ns	ns
A.a	0 ± 0	0.47 ± 0.15	0.03 ± 0.03	0.44 ± 0.11	0.12 ± 0.12	0.21 ± 0.07	0.12 ± 0.05	0.12 ± 0.05	*	*	*	*	0.12 ± 0.05	0.12 ± 0.05	0.12 ± 0.05	0.12 ± 0.05	0.12 ± 0.05	*	*	*	*	*	*	*
B.b	0 ± 0	0.09 ± 0.05	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	ns	ns	ns	ns	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	ns	ns	ns	ns	ns	ns	ns
C.c	0 ± 0	0.03 ± 0.03	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	ns	ns	ns	ns	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	ns	ns	ns	ns	ns	ns	ns
E.l	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	ns	ns	ns	ns	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	ns	ns	ns	ns	ns	ns	ns
P.f	0.06 ± 0.04	0.22 ± 0.07	3.16 ± 0.88	7.91 ± 1.66	0.5 ± 0.5	0 ± 0	0.5 ± 0.5	0.03 ± 0.03	ns	ns	ns	ns	0.03 ± 0.03	0.03 ± 0.03	0.03 ± 0.03	0.03 ± 0.03	0.03 ± 0.03	ns	ns	ns	ns	ns	ns	ns
R.r	0.06 ± 0.04	0.75 ± 0.26	1.72 ± 0.44	3.59 ± 0.57	0.38 ± 0.37	0.07 ± 0.07	0.38 ± 0.37	1.53 ± 0.56	****	****	****	****	0.88 ± 0.48	1.53 ± 0.56	1.53 ± 0.56	1.53 ± 0.56	1.53 ± 0.56	*	*	*	*	*	*	*
S.l	0 ± 0	0.12 ± 0.07	0 ± 0	0.03 ± 0.03	0 ± 0	0 ± 0	0 ± 0	0.03 ± 0.03	ns	ns	ns	ns	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.03 ± 0.03	ns	ns	ns	ns	ns	ns	ns
S.e	0 ± 0	0 ± 0	0 ± 0	0.06 ± 0.04	0 ± 0	0 ± 0	0 ± 0	0 ± 0	ns	ns	ns	ns	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	ns	ns	ns	ns	ns	ns	ns
S.g	0 ± 0	0 ± 0	0.03 ± 0.03	0.12 ± 0.09	0 ± 0	0 ± 0	0 ± 0	0 ± 0	ns	ns	ns	ns	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	ns	ns	ns	ns	ns	ns	ns
TC	0.12 ± 0.07	2.06 ± 0.35	4.94 ± 1.23	12.34 ± 1.63	1 ± 0.75	0.32 ± 0.05	1 ± 0.75	3.69 ± 0.97	ns	ns	ns	ns	11.81 ± 4.84	3.69 ± 0.97	3.69 ± 0.97	3.69 ± 0.97	3.69 ± 0.97	ns	ns	ns	ns	ns	ns	ns

Significance level: \*\*\* =  $P < 0.001$ , \*\* =  $P < 0.01$ , \* =  $P < 0.05$  and ns =  $P \geq 0.05$ . Species abbreviation: *Abramis brama* (A.b), *Abramis sp.* (A.sp.), *Alburnus alburnus* (A.a), *Blicca bjoerkna* (B.b), *Cyprinus carpio* (C.c), *Esox lucius* (E.l), *Perca fluviatilis* (P.f), *Rutilus rutilus* (R.r), *Sander lucioperca* (S.l), *Scardinius erythrophthalmus* (S.e), *Silurus glanis* (S.g), and Total of the Catch (TC)



**Fig. 4** Average values of catch-per-unit effort (CPUE; individuals per point) of fish from electrofishing at eight control sites and eight artificial floating islands (AFIs) in Luka Bay, separated by year and period of sampling. The boxplot

represents the quartile value of CPUE, the grey dots represent the mean of individual AFIs, the thick middle line represents the median, and the white dot represents the overall mean of all measurements

and in the year 2019 ( $P < 0.01$ ); roach for the time of sampling ( $P < 0.01$ ) and year 2019 ( $P \leq 0.001$ ). Bream (*Abramis brama*,  $P \leq 0.001$ ), white bream (*Blicca bjoerkna*;  $P \leq 0.001$ ), and pikeperch (*Sander lucioperca*;  $P < 0.01$ ) showed differences between years only.

There were significant differences in perch standard lengths between time of sampling ( $P < 0.01$ ), years ( $P < 0.01$ ), and AFIs and control sites ( $P \leq 0.001$ ). Roach also showed significant differences between time of sampling ( $P < 0.01$ ) and years ( $P \leq 0.001$ ). Bream ( $P \leq 0.001$ ), white bream ( $P \leq 0.001$ ), and pikeperch ( $P \leq 0.001$ ) showed differences between years only (Table 4). In general, fish were smaller at AFIs. Abundant species (perch and roach) were mainly present in the 0+ age group. These 0+ fish were extremely abundant, so when an overall size structure on the catch is displayed, it is possible to see mainly 0+ fish in the results at the AFIs (Fig. 6).

Most diversity indices showed no difference between the AFIs and control sites, except for richness, which was significantly higher in AFIs, at night and during 2019 sampling. The Shannon–Weiner index was significantly higher in night samplings (Table 5).

## Discussion

Our results showed that even relatively simple artificial floating islands are highly attractive especially for the young of the year individuals of roach and perch. The dominance of age 0+ fish is most likely because these smaller fish are exposed to a high predation pressure and come to the AFIs for protection. Shorelines of waterbodies with extensive water level fluctuations lack a macrophyte belt and structural complexity (Kalf, 2001; Krolová et al., 2012; Říha et al., 2015). The presence or absence of a structured macrophyte littoral has a profound effect on the recruitment and survival of many fish species (Duncan & Kubečka, 1995), and different composition of macrophyte community can influence upon fish composition (Pelicice et al., 2005; Dibble & Pelicice, 2010). When structured habitats are scarce, artificial habitats can provide community benefits such as shelter, shade, and food (Nakamura et al., 1997; Gatz, 2008; Santos et al., 2008), or even become successful spawning habitats for some species (Byeon, 2014).

Possible factors that can explain the fish attraction to AFIs include cover, shielding from aerial predators such as herons or kingfishers, and shading. Reducing light levels could reduce the effectiveness of aquatic predator vision (Helfman, 1981, 1986; Verweij et al., 2006). These factors are most important to

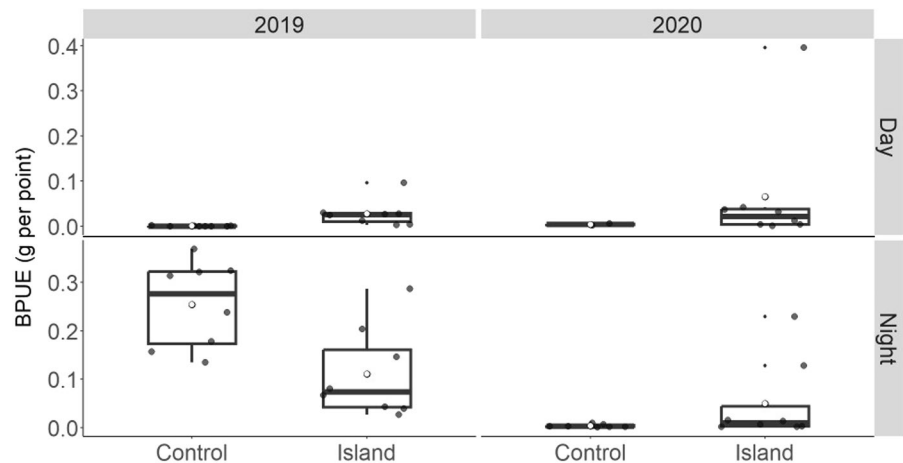
**Table 3** Mean and standard error (SE) of the fish BPUE (mean biomass in g per electrofishing point at treatment—AFI or control, time of day and year)

Sp	2019												2020											
	Control						Island						Control						Island					
	Day			Night			Day			Night			Day			Night			Day			Night		
	Mean ± SE	Mean ± SE	SE	Mean ± SE	Mean ± SE	SE	Mean ± SE	Mean ± SE	SE	Mean ± SE	Mean ± SE	SE	Mean ± SE	Mean ± SE	SE	Mean ± SE	Mean ± SE	SE	Mean ± SE	Mean ± SE	SE	Mean ± SE	Mean ± SE	SE
<i>A.b</i>	0 ± 0	73.07 ± 34.86	0 ± 0	0 ± 0	39.3 ± 21.27	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Asp.</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>A.a</i>	0 ± 0	5.53 ± 2.22	1.11 ± 1.11	0 ± 0	5.92 ± 2.02	0.73 ± 0.73	0 ± 0	0 ± 0	2.71 ± 1.22	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>B.b</i>	0 ± 0	41.75 ± 21.33	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.97 ± 0.97	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>C.c</i>	0 ± 0	26.16 ± 26.16	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>E.l</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>P.f</i>	0.14 ± 0.1	1.31 ± 0.74	20.61 ± 10.08	0 ± 0	29.06 ± 7.25	0.71 ± 0.71	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>R.r</i>	0.16 ± 0.11	25.31 ± 12.78	5.66 ± 1.49	0 ± 0	10.13 ± 1.97	2.25 ± 2.25	0 ± 0	0 ± 0	0.09 ± 0.09	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>S.l</i>	0 ± 0	81.19 ± 42.43	0 ± 0	0 ± 0	25.5 ± 25.5	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>S.e</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.72 ± 0.48	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>S.g</i>	0 ± 0	0 ± 0	0.17 ± 0.17	0 ± 0	0.55 ± 0.42	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
TC	0.03 ± 0.02	254.32 ± 10.4	27.55 ± 2.3	111.18 ± 5.01	3.69 ± 0.3	3.77 ± 0.3	65.55 ± 4.9	50.05 ± 3.8	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

Species abbreviation: *A.b* *Abramis brama*, *A.sp.* *Abramis sp.*, *A.a* *Alburnus alburnus*, *B.b* *Blicca bjoerkna*, *C.c* *Cyprinus carpio*, *E.l* *Esox lucius*, *P.f* *Perca fluviatilis*, *R.r* *Rutilus rutilus*, *S.l* *Sander lucioperca*, *S.e* *Scardinius erythrophthalmus*, *S.g* *Silurus glanis*, *TC* Total of the Catch

Significance level: \*\*\* $P < 0.001$ , \*\* $P < 0.01$ , \* $P < 0.05$  and ns =  $P \geq 0.05$

**Fig. 5** Average values of biomass-per-unit effort (BPUE; g per point) of fish from eight control sites and eight artificial floating islands (AFIs) in Luka Bay, separated by year and period of sampling. The boxplot represents the quartile value of BPUE, the grey dots represent the mean of kg AFIs, the thick middle line represents the median, and the white dot represents the overall mean of all measurements



juveniles, as they need them most to avoid predators. The benefits of artificial habitats on fish populations have been documented in several studies (Karstens et al., 2021; Nakamura et al. 1997). Fish communities can use and likely benefit from all types of artificial or natural structures as new habitats (Dempster & Taquet, 2004; Feger & Spier, 2010; Campbell et al., 2016). Our findings confirmed the prediction on the attractivity of AFIs to juvenile fish showing that they had an impact on the fish community. A similar result, but on a higher scale than ours, was documented by Nakamura et al. (1997) who studied the fish of Lake Kasumigaura, Japan, where they found that AFIs had 100 times more fish than control sites. In our surveys, we recorded 9–30 times more fish at AFIs. Unfortunately, other studies lack control samples, so it is not possible to demonstrate the attraction effect of AFIs.

There may be further benefits even from our simple constructions of AFIs. The attractiveness of the AFI for the age 0+ fish is a first step for helping the population of fish grow to a more sustainable size by the protection of the root complexity (Karstens et al., 2021). The complexity created by the roots of the macrophytes can increase the area for biofilm, that is food for zooplankton and some fish, increasing the residence of fish in the AFI area (Karstens et al., 2021). Spatial extent of roots seems to be in fact larger than the extent of emerged plant parts (Fig. 3) and created a nursery habitat for age 0+ perch, roach, and wels catfish (*Silurus glanis* L., 1758) and foraging habitat for the northern pike (*Esox Lucius*, L., 1758). Another very important benefit comes for

fish reproduction. Many species are limited by the plant spawning substratum and the roots of plants of AFIs provide very suitable alternative. Besides roach (Fig. 3c) eggs of northern pike, perch, and wels catfish were found at the roots of macrophytes dwelling in the AFIs in Lipno (Kubečka, J., unpublished data). Clear advantage of AFIs for reproduction is that they are almost not affected by water-level fluctuation (Prashant & Billore, 2020).

Large bream, pikeperch, and carp individuals were less abundant in AFIs than in control areas, and therefore the biomass in control areas were overall larger than in the AFIs, due to the smaller body size of the individuals captured in AFIs. Artificial structures with abundant age 0+ fish could attract predators such as large piscivorous fish (e.g. wels catfish, northern pike, pikeperch, and asp (*Leuciscus aspius* (L., 1758))). The AFI structures used in this study were also monitored with DIDSON acoustic cameras, and large northern pike were recorded swimming and ambushing under the AFIs (Muška, M., unpublished data). The northern pike was found in AFIs in 2020, likewise with catfish, they show preference for complex habitat for ambush predation (Casselmann & Lewis, 1996). With AFIs increasing the complexity of the habitat, northern pike can be attracted to the shadows and root system created by the vegetation under AFIs which are preferred for ambush predation strategy of this species (Sepulveda et al., 2013; Říha et al., 2021). Catfish was the only truly predatory fish captured by PASE in AFIs in 2019. This was also seen in a study in Sweden by Spange (2018), where the author observed in his tracking experiment that



**Table 4** Mean of the standard length, standard error (SE), in millimetres, and number of individual catches (Ind.) of the fish from the experiment with PASE from Luka Bay

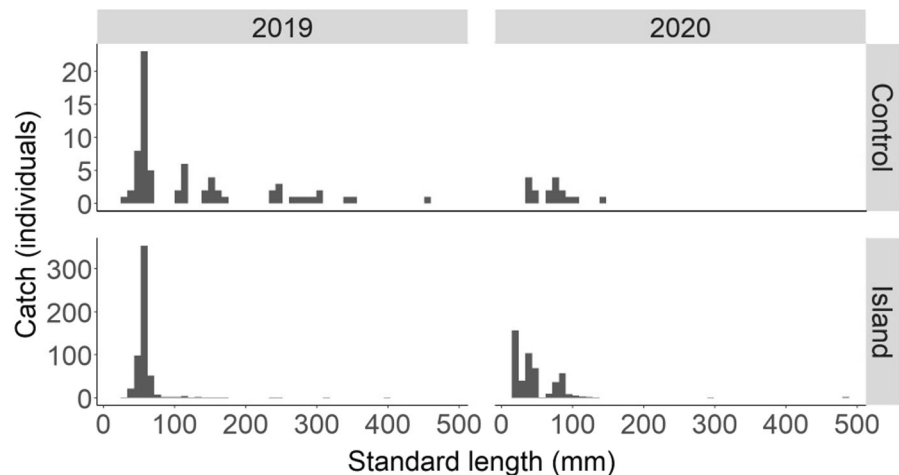
Sp	2020											
	2019				Control				Island			
	Control		Island		Control		Island		Control		Island	
Day	Night		Day		Night		Day		Night		Day	
	Mean ± SE	Ind	Mean ± SE	Ind	Mean ± SE	Ind	Mean ± SE	Ind	Mean ± SE	Ind	Mean ± SE	Ind
A.b	-	0	187.08 ± 20.23	12	-	0	190 ± 31.22	6	-	0	-	0
Asp.	-	0	-	0	-	0	-	0	-	0	20.03 ± 0.23	190
A.a	-	0	83.33 ± 8.43	15	135	1	90 ± 8.09	14	77	1	92.5 ± 9.81	6
B.b	-	0	253.33 ± 13.33	3	-	0	-	0	-	0	105	1
C.c	-	0	290	1	-	0	-	0	-	0	-	0
E.l	-	0	-	0	-	0	-	0	-	0	480	1
P.f	50 ± 5	2	63.57 ± 7.05	7	59.6 ± 1.94	101	58.06 ± 0.41	253	43.25 ± 1.38	4	-	0
R.r	50 ± 5	2	76.46 ± 11.51	24	54.27 ± 0.91	55	51.3 ± 0.7	115	68.33 ± 2.6	3	41 ± 1	2
S.l	-	0	361.25 ± 33.06	4	-	0	400	1	-	0	-	0
S.e	-	0	-	0	-	0	82.5 ± 2.5	2	-	0	-	0
S.g	-	0	-	0	80	1	75 ± 2.04	4	-	0	-	0

P value significance

Sp	Year		Treatment		Time
	Year	Treatment	Year	Treatment	
A.b	***	ns	ns	ns	ns
Asp.	ns	ns	ns	ns	ns
A.a	ns	ns	ns	ns	ns
B.b	***	ns	ns	ns	ns
C.c	ns	ns	ns	ns	ns
E.l	ns	ns	ns	ns	ns
P.f	***	***	***	***	***
R.r	***	ns	ns	ns	***
S.l	***	ns	ns	ns	ns
S.e	ns	ns	ns	ns	ns
S.g	ns	ns	ns	ns	ns

Significance level: \*\*\* =  $P < 0.001$ , \*\* =  $P < 0.01$ , \* =  $P < 0.05$  and ns =  $P \geq 0.05$ . Species abbreviation: *Abramis brama* (A.b), *Abramis sp.* (A.sp.), *Alburnus alburnus* (A.a), *Blicca bjoerkna* (B.b), *Cyprinus carpio* (C.c), *Exox lucius* (E.l), *Perca fluviatilis* (P.f), *Rutilus rutilus* (R.r), *Sander lucioperca* (S.l), *Scardinius erythrophthalmus* (S.e), and *Silurus glanis* (S.g)

**Fig. 6** Standard whole fish community length comparisons from the catches from the eight controls and artificial floating islands (AFIs), separated by year and treatment



catfish showed preferential behaviour in choosing habitats associated with floating mats. The control areas studied in Lipno Reservoir are not complex habitats. Rather, the control areas are characterized by a bare, soft substrate without macrophytes (Krolová & Hejzlar, 2013). This may be one of the reasons that catfish use the AFI in our study. Moreover, catfish is a voracious piscivore, even when very young, and eats other small juveniles. Therefore, the presence of juvenile catfish in AFIs may also be related to the higher density of its prey in the area.

In our study we detected a strong diel dissimilarity in the use of AFIs by associated fish. During the day, the fish abundances and biomasses of perch and roach were much lower than during the night, with the species composition changing little. The higher abundance of these two species during the night coincides with their shelter seeking and activity in most lakes (Muška et al., 2013). During the day shoals of fry (roach, perch, bream) swim around the AFI or under the core of AFIs. These shoals are fairly active and some of them may not be encountered by PASE due to their increased activity or position far from the electrode. They can be observed by Didson acoustic camera (Muška, M., unpublished data). At night, juvenile fish are inactive and hide in overhanging plant material and thus, the potential of sampling avoidance is much smaller.

The size and shape of artificial habitat can influence biotic and abiotic effects on community composition of an area (Harlan & Paradise, 2006; Woolnough et al., 2009). Madhavan & Neethiselvan (2002) studied the effects of size and shape of FADs

on the fish community. Their results showed that differences between the shapes and sizes of FADs affected fish size and fish community diversity. However, our results did not show the same pattern. In our case, this result could be explained by the similarity of the AFI designs and sizes used. Overall, point abundance sampling proved to be fairly effective and simple way to assess the fish community associated with AFIs. Two to three days and nights were able to capture sufficient numbers of fish and clear picture of the community present. We have also sampled different AFI sites in the same reservoir with Nordic multimesh gillnets, and the results were much less conclusive as the gillnets catches contained much higher background catch irrespective of AFI treatment. Some other studies have used nets (Oliver & McKaye, 1982; Nakamura et al., 1997; Suresh, 2000), but our experience indicated that PASE electrofishing is more effective for detecting benefits of AFIs. The time span of the current study was limited to sampling in late August. We wanted to observe the effect of AFIs at the period of culminating summer, which is best for sampling temperate fish communities (fish are active and not reproducing, young of the year are large enough to be safely identified to the species level, and fish distribution is not yet affected by approaching winter). So, the peak summer has been a standard sampling period to sample fish communities by many methods (Jůza et al., 2014; CEN, 2015; Kubečka et al., 2022) and it was an obvious choice for the initial snapshot study. Long-term seasonal observations may be

**Table 5** Mean and standard error of the diversity indexes from the gillnet and PASE experiment, divided in day, night, and total. Significance level: \*\*\* =  $P < 0.001$ , \*\* =  $P < 0.01$ , \* =  $P < 0.05$ , and ns =  $P \geq 0.05$

Indexes	2019						2020						P value significance		
	Control			Island			Control			Island					
	Day	Night	Mean ± SE	Day	Night	Mean ± SE	Day	Night	Mean ± SE	Day	Night	Mean ± SE		Year	
Shannon	0.09 ± 0.09	1.2 ± 0.06	0.62 ± 0.11	0.89 ± 0.13	0.34 ± 0.34	0 ± 0	0.45 ± 0.11	0.78 ± 0.13	0.46 ± 0.07	0.57 ± 0.14	2 ± 0.33	2.88 ± 0.3	ns	ns	*
Simpson	0.69 ± 0.16	0.65 ± 0.03	0.42 ± 0.07	0.5 ± 0.05	0.24 ± 0.24	0 ± 0	0.3 ± 0.08	0.46 ± 0.07	0.49 ± 0.49	0 ± 0	1.5 ± 0.5	1 ± 0	ns	ns	ns
Pielou's	0.12 ± 0.12	0.88 ± 0.04	0.77 ± 0.12	0.65 ± 0.04	0.49 ± 0.49	0 ± 0	0.57 ± 0.14	0.74 ± 0.08	0.49 ± 0.49	0 ± 0	1.5 ± 0.5	1 ± 0	ns	ns	ns
Richness	0.5 ± 0.27	4 ± 0.27	2.12 ± 0.23	4 ± 0.5	1.5 ± 0.5	1 ± 0	2 ± 0.33	2.88 ± 0.3	0.49 ± 0.49	0 ± 0	1.5 ± 0.5	1 ± 0	*	**	***

recommended if more complex insights into AFI benefits are needed.

### Conclusions

Our study demonstrated that even relatively simple and cheap Artificial Floating Islands (AFIs) are an efficient fish attraction device for age 0+ fish juveniles. The addition of structural complexity in an ecosystem lacking a macrophyte belt provides refuge and shelter to fry of species such as perch and roach, and hence, may enhance survival and recruitment; research for this hypothesis could be done in the future. AFIs also provide habitat for apex predators which is otherwise scarce in a reservoir environment with frequent changes in water level. We recommend point abundance sampling electrofishing as a simple and efficient approach to sample fish community associated with AFIs.

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**Data availability** The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

### Declarations

**Conflict of interest** There are no conflicts of or competing interests.

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### **3. Conclusion and future prospects**





During our studies, the main goal was to test different methodologies to study fish distribution and improve reservoir habitats. Each one of them focus on methods to help understand and increase the fish stock abundance and diversity. Our distinct experiments have shown positive results and can be seen as guidelines for helping other water bodies around the world. However, these examples cannot be seen as one fit for every case, as every waterbody is a unique environment and proper research should be done with this in mind.

Our experiments were conducted on water bodies with few fish species (approximately 10), with even fewer species dominating general abundance on each experiment. It would be recommended to conduct similar studies on other types of environmental systems where the diversity and abundance would be higher. A higher diversity in the ecosystem can increase interactions for the factors that were studied in our three case studies and could help with validation of these results.

The **PAPER I**, with the delimitation of the littoral is important for the assessment of health of the fish community and the rest of the environment. The results show that fish are very well aware of the difference between benthic and the poorer and less diverse pelagic habitats starts consequently very closely after the sampling effort departed from the bottom. This has huge consequences for volume weighted fish estimates in larger lakes and reservoirs. The findings were used to create weighted composition of the fish community at long termed study of Tesfaye et al., 2022, that help balance the abundance and biomass estimation between pelagic and benthic habitats. Furthermore, it would be very appealing to further scrutinize the vertical dimension if the fish distribution pattern, in deeper layers, would still have the same strong and spatially limited affinity to the bentic habitat, as we observed in the shallowest layer. With the telemetry real-time positioning of bottom bound fish, it would be possible to validate the true range of the littoral area with diverse slope inclinations and different habitat complexities (Slavík & Bartoš, 2001; Radinger et al., 2017; Cucherousset et al., 2018).

**PAPER II** has an extensive problem with the openness of the investigated protected area (PA). Fish can freely move between the protected and fished areas, and many of them are captured just outside the PA; in fact, some anglers are attracted by the PA and prefer to fish just outside the PA. The possibility of free exchange makes it difficult to distinguish between the real resident population of the protected area and the fish that are passing by. Compared to the large Lipno reservoir, the PA is relatively small, so the differences in fish communities were either non-significant or significant. The use of electrofishing combined with sonar cameras and telemetry would help improve the understanding of fish behaviour and migration in protected and surrounding areas. With telemetry home range and residence time of the fish community in the PA, we could determine whether the fish stay permanently, seasonally, or use the protected area as migratory paths (Slavík & Bartoš, 2001; Horký et al., 2008; Cooke et al., 2016; Říha et al., 2021).

During the original deployment of the floating islands for **PAPER III**, significant damage occurred to the previous models because of less sophisticated design, extreme weather conditions (storms, frozen lake, ice collisions, etc...) and relatively exposed installations. Many constructions, materials and designs were tested during the project (Hladík, 2018). The models used in our experiments were the most resilient to weather conditions, but improvements are still possible to surpass these conditions

and to support large-scale applications. The possible increment in size can be one solution, the increment can help with robustness and extra weight can endure some of the weather conditions.

On our first attempts to sample the floating islands, multimesh gillnets were used. But we found that the instantaneous picture of the fish community obtained by electrofishing is much more indicative than the picture obtained by the multimesh gillnets. The most likely reason for this is a high-level background catch of gillnets. CEN gillnets catch a lot of fish always irrespective of the treatment (island presence). So, the reviewer strongly recommended to abandon gillnet results of floating islands in the paper. However, this case study may serve as an experience for further studies showing that the gillnets are not very useful when the effect of local habitat improvement has to be documented.

Other problem that we faced with the survey conducted in the floating islands was that just the borders of the islands could be sampled directly, and the more central areas of the islands could harbour more abundant and diverse fish community. Techniques such as echosounders, acoustic cameras, or underwater camera monitoring could help identify the true picture of the fish community under the islands in the early stages of root development. In fact, Muška et al (unpublished) recorded interesting records of artificial islands use by predatory fish species sampled rarely during our point abundance electrofishing.

Fish stock recovery and improvement have been proven to be possible on a small scale, but there is a need for subsequent steps. Constant monitoring of the fish stock is one of the most important steps; these data can help determine what is right or wrong. Another step is further research on possible causes of the decline of fish stock, as said before it is quite rare that overfishing collapse the stock alone. The management decisions for the recovery of the stock are also dependent on previous research, to focus remediating the causes for the decline. Good management plan needs to be inclusive and comprehensive in space, time and multi-species. Furthermore, it takes couple of years for fish habitat restoration to reach self-sustainability and ecological balance. Therefore, a great amount of effort, recourses and know how is needed to fully understand and plan the effects of restoration measures.

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## **5. *Curriculum vitae***





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2003 – 2006 Bachelor's degree in Biology, Unimodulo, Caraguatatuba, SP, Brazil

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2018 – present Researcher at Fish Ecology Unit (FishEcU), Department of Fish and Zooplankton Ecology, Institute of Hydrobiology, Biology Centre CAS.

2015 – 2018 Marine Research Team Coordinator, Archipelagos Institute of Marine Conservation, Pythagorio, Samos, Greece.

2013 – 2014 Research assistant at NIOZ Koninklijk Nederlands Instituut voor Onderzoek der Zee, Texel, Netherlands.

2010 – 2012 Researcher in Food Quality, Researcher Associate in Immuno-biotechnology & Histo-pathology CESAM - The University of Aveiro (EU), Aveiro.

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