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Can habitat enhancement limit the ecological impacts of predatory fish stocking? An experimental approach

Marie Gimenez*  and Julien Cucherousset 

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Abstract – Fish stocking is a ubiquitous management measure in freshwater fisheries but it can induce important ecological impacts on communities and recipient ecosystems. Habitat enhancement might limit the ecological impacts of fish stocking by directly supporting biodiversity and helping to maintain ecosystem functioning. In the present, we used a mesocosm experiment to assess whether habitat enhancement, through the addition of coarse woody habitat (CWH) in the form of thin branches bundled or within an iron cage, can limit the impact of stocking of a predatory fish, juvenile largemouth bass *Micropterus nigricans*, on prey communities and ecosystem functioning. Results demonstrated that, prior to stocking, there was overall no significant effect of habitat enhancement on zooplankton communities and a strong effect on benthic macroinvertebrate communities that was associated with a decrease in the decomposition rate of organic matter in mesocosms containing caged-CWH. We also found that the stocking of juvenile largemouth bass significantly affected the structure of zooplankton communities while we did not observe significant effects on macroinvertebrate communities and ecosystem functioning. This effect on zooplankton community structure was compensated by habitat enhancement, notably when using caged-CWH. This study showed that habitat enhancement alone may not be sufficient to compensate the potential effects of predatory fish stocking, and that the choice of materials used to enhance habitats is fundamental in driving the efficiency.

Keywords: Ecosystem-based management / species-oriented management / *Micropterus nigricans* / coarse woody habitat / freshwater fisheries management

1 Introduction

Stocking programs are primarily designed to enhance fish stocks by releasing hatchery-reared or wild-borne individuals (Lorenzen *et al.*, 2012; Sass *et al.*, 2017) to optimize the angling experience (Cowx, 1994). In addition, to satisfy catch-challenge motivations of anglers, they often involve the release of fish species, especially non-native predators, which represent a fishing challenge, but are also known to affect recipient communities and ecosystems (Eby *et al.*, 2006; Rudman *et al.*, 2016). In fact, the stocking of predatory fish can result in a trophic cascade due to increased top-down control (Eby *et al.*, 2006), and lead to altered trophic linkages through changes in prey community structure (Tiberti *et al.*, 2014) that can subsequently affect ecosystem functions such as nutrient cycling and primary production (Schindler *et al.*, 2001). Furthermore, individuals used in stocking programs often come from fish farms and are therefore reared in conditions

that are very different from the ecosystems where they are released. These differences have multiple consequences on stocked fish (Milla *et al.*, 2021), including change in foraging behavior of predatory fish fed with artificial diets in hatchery (Huntingford, 2004; Milla *et al.*, 2021). Thus, stocking of predatory fish species, and especially hatchery-reared individuals, can be a possible threat to the long-term sustainability of freshwater biodiversity and ecosystems. However, stocking can also contribute to the recovery of fish stocks and provide benefits for fisheries (Lorenzen *et al.*, 2012; Amoroso *et al.*, 2017; Johnston *et al.*, 2018), but this depends on the ecological characteristics of the recipient ecosystem, which is rarely considered (Claussen and Philipp, 2023).

Habitat enhancement measures that aim to improve fish stocks have received less consideration by freshwater managers than stocking (Lorenzen, 2014; Schindler and Hilborn, 2015; Sass *et al.*, 2017). Nearshore habitats are often impacted by recreational activities or intentionally removed by fishery managers (Jennings *et al.*, 2003), although it can affect the growth and cause a decline of fish populations (Sass *et al.*, 2006). Increased investment in habitat enhancement and

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protection could have beneficial effects for the ecosystems, by increasing its carrying capacity, and for the fisheries, by improving the productivity of exploited fish stocks (Radinger *et al.*, 2023) through increased natural recruitment in some popular fish species (Roni *et al.*, 2008; Nilsson *et al.*, 2014). In fact, structured habitat are particularly important for freshwater fishes because they can be used for foraging and predator avoidance (Sass *et al.*, 2023). Compared to stocking, habitat enhancement appears to be a more integrative and sustainable management, because adding habitats can directly support biodiversity and contribute by extension to the ecosystem functioning and services (Dobson *et al.*, 2006; Harrison *et al.*, 2014; Radinger *et al.*, 2023). In lake, littoral habitats such as coarse woody habitat (CWH), including for example logs, root wads and stumps, provide key habitats not only for fish, but also for invertebrates or periphyton, and affect a wide range of ecological functions (Harmon *et al.*, 2004), such as ecosystem productivity and nutrient cycling (Czarnecka, 2016). Furthermore, the addition of this type of physical habitat structure represents one of the most common methods used to restore freshwater habitats (Cooke *et al.*, 2023), and it is especially beneficial in ecosystem lacking habitats (Sass *et al.*, 2023). The deployment of physical habitat structures is not limited to the addition of woody habitats, and many structures made from artificial materials have also been used, particularly in recreational fisheries (Bolding *et al.*, 2004). Such structure are also subjected to debate because of a potential release of contaminants (*e.g.*, with plastic habitats Cooke *et al.*, 2023). Thus, enhancing the quality and quantity of littoral habitats might limit some of the negative effects of predatory fish stocking by providing refuge to prey community and maintaining some important ecosystem functions, but this remains to be tested.

The main objective of the present study was to determine whether habitat enhancement can limit the ecological impacts of predatory fish stocking. To study the effect of stocking, we used an experimental mesocosm approach and hatchery-reared juvenile largemouth bass *Micropterus nigricans*, a predator and a popular game fish for anglers (Donaldson *et al.*, 2011), as a model species. We assessed the ecological consequences of two different habitat enhancements, a habitat made of natural materials and a habitat made of natural and artificial materials (*i.e.*, CWH and CWH within an iron cage), prior and after fish stocking. First, we predicted that stocking will have a strong impact on the composition of prey communities through predation, and consequently modify ecosystem functioning. Then, we predicted that habitat enhancement will limit the ecological impacts of stocking by supporting prey communities (*i.e.*, refuge from predation and additional physical habitat), thereby maintaining some important ecosystem functions. Finally, we have also predicted that the effect of habitat enhancement will differ depending on the materials used and the complexity of the artificial structure.

2 Materials and methods

2.1 Model system

We used the stocking of non-native largemouth bass in gravel pit lakes in southwestern France as a case study for this experiment. In many European countries, gravel pit lakes are becoming more and more common in the landscape and represent valuable ecosystems for recreational fisheries

(Matern *et al.*, 2019; Meyerhoff *et al.*, 2019), but the availability of structured littoral habitats for fish is often limited. In the study area, stocking is an important driver of fish community structure in gravel pit lakes (Zhao *et al.*, 2016; Gimenez *et al.*, 2023; Garcia *et al.*, 2023). Largemouth bass is one of the most notorious and highly introduced species in freshwater ecosystems (Brown *et al.*, 2009; Donaldson *et al.*, 2011) and its introduction can affect recipient community through trophic cascade (Drenner *et al.*, 2002; Jackson, 2002). Largemouth bass is well distributed in the study area, targeted by many recreational anglers and local angling authorities have recently implemented a regulation whereby catch-and-release angling is mandatory for this non-native species. The littoral habitat is particularly important for the all life stages of the species (Brown *et al.*, 2009), but gravel pit lakes are usually characterized by steep slopes and higher littoral depth with a lack of macrophytes and deadwood compared to natural lakes (Emmrich *et al.*, 2014). Thus, littoral habitat enhancement could be particularly efficient in such ecosystems (Radinger *et al.*, 2023), and this is particularly true for this species.

2.2 Experimental design

We used an experimental approach (24 outdoors mesocosms, circular cattle tanks, 550 L) based on four treatments: i) no fish stocking or habitat enhancement (hereafter “no stocking”), ii) fish stocking and no habitat enhancement (“stocking only”), iii) fish stocking and habitat enhancement with a coarse woody habitat (CWH) (“stocking and CWH”) and iv) fish stocking and habitat enhancement with a caged-CWH (“stocking and caged-CWH”). Each treatment was replicated six times and we used a block design with six blocks with each block containing the four treatments (Závorka *et al.*, 2020) (Fig. S1). CWH habitat enhancement consisted in a brush pile consisting of 2 kg of deadwood (thin branches < 1.5 cm diameter of downy oak *Quercus pubescens*) grouped into circular bundles (40 × 20 × 20 cm) (Fig. S2a). Caged-CWH habitat enhancement consisted in the same bundle of deadwood that was placed within an iron cage (40 × 40 × 30 cm, Biohut®, ECOCEAN, Montpellier, France) (see details of the structure in Fig. S2b). Specifically, the cage was made of iron coated with a zinc-aluminum alloy. This device is deployed to restore nurseries in marine ecosystems and was used here to increase habitat complexity and verticality compared to CWH.

On April 29, 2021, 5 cm of gravel and 500 L of unfiltered water from a nearby gravel pit lake were added to each mesocosm. On June 10, 2021, each mesocosm was inoculated with phytoplankton and zooplankton collected from three gravel pit lakes (Téoula, Sou lance and Lamartine lakes) located in the floodplain of the Garonne river (Haute-Garonne, France) (Zhao *et al.*, 2016). Phytoplankton and zooplankton inoculum were collected using nets with a mesh size of 10 and 50 μm, respectively. From May 18, 2021 to July 15, 2021, several additions of multiple macroinvertebrate taxa were made. In each mesocosm, 12 pond snails (immature *Lymnaea stagnalis*) reared in aquarium and two mesh bags containing 5 g of leaves of black poplar *Populus nigra* that have been placed in a nearby gravel pit lake for 21 days were added to each mesocosm. On June 28 and July 15, 2021, two additional

inoculums of macroinvertebrates collected in the Ariège river using a dip net (500 µm mesh size) were added.

The experiment was composed of two periods. The first period (before stocking) started on November 22, 2021, when habitat enhancements were installed and lasted 34 weeks. The second period (after stocking) started on July 20, 2022 with fish stocking and ended on September 6, 2022 (duration: eight weeks). From July 4, 2022 until the end of the experiment, nets (1.5 mm mesh size) were placed on the mesocosms to prevent fish escapes and potential predations. Summer 2022 was particularly warm and dry with multiple heat waves. Therefore, water was added to all mesocosms during the warmest period to compensate evaporation and an air bubbling system was placed in each mesocosm to avoid hypoxia.

2.3 Fish stocking

For all mesocosms with stocking, five hatchery-reared young-of-the-year (YOY) largemouth bass were introduced ($n_{total} = 90$ individuals) on July 20, 2022. In the hatchery, they were fed daily with pelletized food. To avoid handling stress, the total mass of largemouth bass introduced in each mesocosm was measured as a batch (mean = 33.6 g ± 2.4 SD) and did not differ significantly between treatments (LMM, $\chi^2_{(2,17)} = 0.11$, $p = 0.95$, Fig. S3).

2.4 Mesocosm monitoring and sampling

On September 6, 2022, fish were collected from each mesocosm and subsequently euthanized individually using an overdose of anesthetic (benzocaine, 25 mg.L⁻¹). The number of fish in each mesocosm was counted and individual size (nearest mm) and mass (nearest 0.01 g) were measured. Then, the survival rate was calculated based on the number of fish introduced and the number of fish found alive at the end of the experiment. We also calculated the scaled-mass index as an index of body condition following Peig and Green (2009):

$$\text{Scaled - mass index(SMI)} = W_i \left[\frac{L_0}{L_i} \right]^{b_{SMA}}$$

where W_i and L_i are the weight and length of each fish, respectively. In our case, L_0 was the arithmetic mean of the length of all fish measured. To compute the b_{SMA} , we applied an SMA regression (using the 'lmodel2' function in R) to log-transformed weight and length values to determine the slope of the fitted line.

Regarding prey communities, zooplankton was sampled by filtering 20 and 40 L of water using a 80 µm mesh sieve, respectively for each period (i.e., before stocking on July 19, 2022, and after stocking on September 5, 2022). Samples were stored in 96% ethanol and subsequently filtered again through a 160 µm mesh sieve prior to counting. Zooplankton was identified to the lowest taxonomic level using a binocular magnifier (Leica MZ7.5 StereoZoom Microscope). A total of eight taxa (Chaoboridae, Cyclopoïda, Calanoïda, Ceriodaphnia, Simocephalus, Daphnia, Bosminidae, Chydoridae and Nauplii) were identified and counted. We then calculated zooplankton richness (number of taxa) and density (ind.L⁻¹). Benthic macroinvertebrates were sampled using three plastic

trays buried in the substrate installed in the mesocosms on June 10 and July 22, 2022, respectively. Macroinvertebrates were collected using a sieve (before stocking on July 19, 2022, and after stocking on September 5, 2022) and stored in 96% ethanol before laboratory analysis. Macroinvertebrates inhabiting CWH and caged-CWH were also collected, but only at the end of the experiment (September 6, 2022) to avoid overly destructive sampling before fish introduction. Macroinvertebrates were then identified to the lowest taxonomic level (mainly Family) using a binocular magnifier (Leica MZ7.5 StereoZoom Microscope). A total of 16 macroinvertebrate taxa (*Lymnaea*, *Physa*, Ancylidae, Asellidae, Gammaridae, Planarian, Chironomidae, Culicidae, Dytiscidae, Hydrachnidia, Annelida, Ceratopogonidae, Baetidae, Corixidae, Corbicula, Mesovellidae) were identified and counted. We then calculated macroinvertebrate richness (number of taxa) and density (ind. mesocosm⁻¹).

Regarding ecosystem functioning, parameters were measured the day before community sampling to limit potential perturbations. Pelagic primary production was assessed by measuring total chlorophyll-*a* concentration (µg chl-*a*.L⁻¹) using a portable fluorometer (AlgaeTorch; BBE moldaenke GmbH) before fish stocking. After stocking, chlorophyll-*a* concentration (µg chl-*a*.L⁻¹) was quantified by filtering water samples (250 mL) due to high concentration in some mesocosms. Benthic primary production was assessed by measuring chlorophyll-*a* concentration (µg chl-*a*.cm⁻²) on three ceramic tiles (20 × 10 cm) using a portable fluorometer (BenthosTorch; BBE moldaenke GmbH; Kahlert and McKie, 2014). The decomposition rate of leaf litter was quantified by measuring breakdown of 3 g (± 0.02 g) of air-dried black poplar leaves (details in Alp et al., 2016; Závorka et al., 2020) placed into mesocosms. Leaf decomposition corresponded to the decomposition rate for each tank, which was calculated as follows (Lecerf et al., 2005):

$$k = \frac{-\ln \frac{M_f}{M_i}}{T}$$

where M_f is final and M_i is initial oven-dried mass of leaf litter, T the duration of leaf exposure in mesocosms (39 and 45 days for each period, respectively).

2.5 Statistical analyses

Overall, a similar general approach was used to test the effects of treatment on each response variables. We used mixed effects models (LMM and GLMM depending on data distribution, see details in Tab. S1) using treatment as a fixed variable and experimental block as a random variable. The response variables used in the models were those measured directly during the sampling campaign and community identification, except for community structures, where non-metric multidimensional scaling (nMDS with untransformed densities of each taxa and Bray-Curtis index; Kruskal, 1964) were performed and the first two axes used as response variables (Tab. S1). When response variables were significant, pairwise comparisons were subsequently used to identify differences between treatments (Tukey post-hoc test). All analyses were performed with R v. 4.2.2 (R Core Team, 2022)

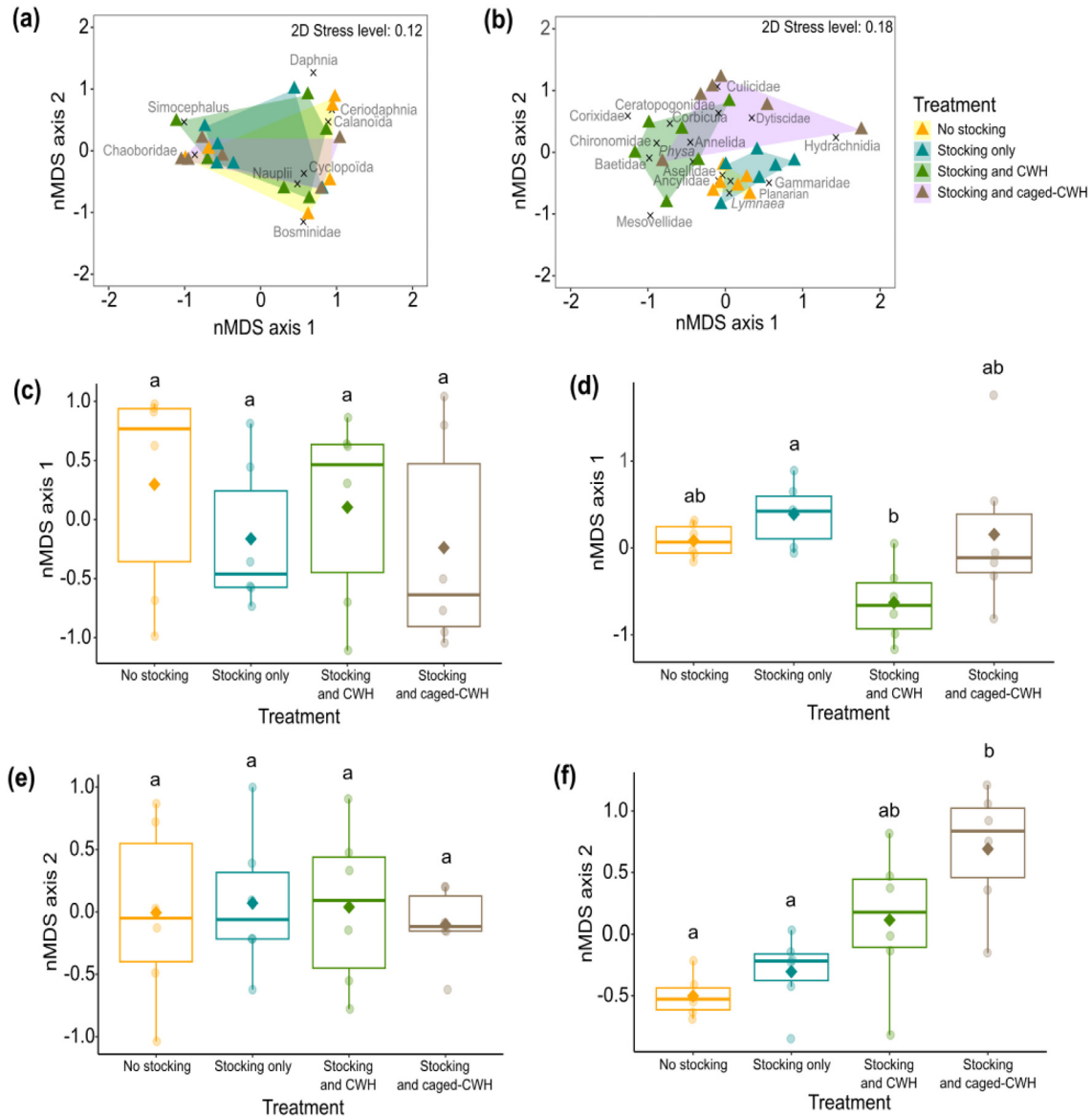


Fig. 1. Effects of management practices before stocking on community structure quantified using (a-b) a non-metric multidimensional scaling (nMDS) analysis and analyzed along the (c-d) first and (e-f) second axes. Zooplankton communities are represented on the left side of the panel and macroinvertebrate communities on the right side. Different letters indicate significant difference between treatments (Tukey post hoc test, $p < 0.05$).

using *lme4* v. 1.1-32 (Bates *et al.*, 2015) for LMM and GLMM, *emmeans* v.1.8.5 (Lenth *et al.*, 2023) for pairwise comparisons, *vegan* v. 2.6-4 (Oksanen *et al.*, 2022) for nMDS.

3 Results

3.1 Ecological effects before fish stocking

Zooplankton communities were dominated by Cyclopoida (mean = 128.2 ind.L⁻¹ ± 316.6 SD), Bosminidae (mean = 114.2 ind.L⁻¹ ± 391.5 SD) and Ceriodaphnia (mean = 83.3 ind.L⁻¹ ± 303.0 SD) (Fig. S4a). There were significant differences between treatments in the richness and density (LMM, $\chi^2_{(3,23)} = 10.52$, $p < 0.05$ and $\chi^2_{(3,23)} = 29.78$, $p < 0.0001$, respectively), with a significantly lower richness in stocking

and caged-CWH treatment compared with stocking only treatment (Tukey post hoc test, $p < 0.05$, Fig. S5a). Density was significantly lower in caged-CWH treatment compared to no stocking and, stocking and CWH treatments (Tukey post hoc test, $p < 0.01$, Fig. S5b). There were no significant difference between treatments in zooplankton community structure (LMM, $\chi^2_{(3,23)} = 1.62$, $p = 0.65$ and $\chi^2_{(3,23)} = 0.43$, $p = 0.93$, for the two axes, respectively, Figs. 1a, 1c, and 1e).

Macroinvertebrate communities were largely dominated by Asellidae (mean = 3376.7 ind.mesocosm⁻¹ ± 4765.7 SD), followed by Chironomidae (mean = 274.2 ind.mesocosm⁻¹ ± 786.5 SD) and Annelida (mean = 250.4 ind.mesocosm⁻¹ ± 1182.6 SD) (Fig. S6a). Richness and density differed significantly between treatments (LMM, $\chi^2_{(3,23)} = 12.57$, $p < 0.01$ and $\chi^2_{(3,23)} = 14.14$, $p < 0.01$, respectively), and both

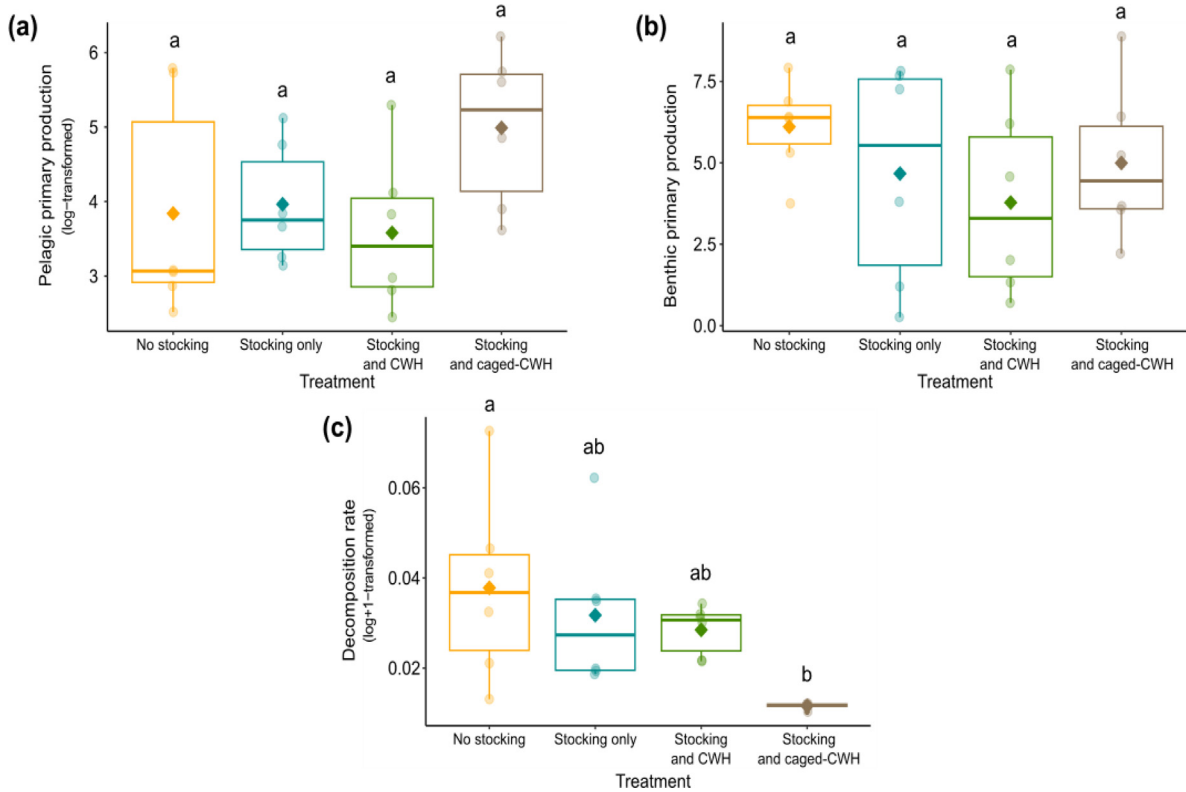


Fig. 2. Ecological effects of treatments before stocking on (a) pelagic primary production, (b) benthic primary production and (c) decomposition rate. Different letters indicate significant difference between treatments (Tukey post-hoc test, $p < 0.05$).

were significantly lower in the stocking and caged-CWH compared with no stocking and stocking only treatments (Tukey post hoc test, $p < 0.05$, Fig. S7 a-b). Community structure significantly differed between treatments (Fig. 1b) along the two axis (LMM, $\chi^2_{(3,23)} = 11.82, p < 0.01$ and $\chi^2_{(3,23)} = 28.37, p < 0.0001$, respectively for the two axes, Fig. 1d and f). Along the first axis, stocking only and stocking and CWH treatments differed significantly (Tukey post hoc test, $p < 0.05$, Fig. 1d), and along the second axis, stocking and caged-CWH treatment differed significantly with treatments without habitat enhancement (Tukey post hoc test, $p < 0.01$, Fig. 1f).

Treatments did not differ significantly for the pelagic and benthic primary production (LMM, $\chi^2_{(3,23)} = 5.64, p = 0.13$ and $\chi^2_{(3,23)} = 3.54, p = 0.32$, respectively, Fig. 2a-b). However, decomposition of organic matter differed significantly between treatments (LMM, $\chi^2_{(3,23)} = 15.37, p < 0.01$), with a significant lower decomposition rate in the stocking and caged-CWH treatment compared with the no stocking treatment (Tukey post-hoc test, $p < 0.01$, Fig. 2c).

3.2 Ecological effects after fish stocking

At the end of the experiment, there was a significant difference in scaled-mass index between treatments (GLMM, $\chi^2_{(2,70)} = 10.64, p < 0.01$, Fig. 3a), with fish displaying significantly lower scaled-mass index in mesocosms with caged-CWH compared to stocking only (Tukey post-hoc test, $p < 0.01$, Fig. 3a). The survival rate did not differ significantly between treatments (LMM, $\chi^2_{(2,16)} = 3.56, p = 0.17$, Fig. 3b).

Zooplankton communities were largely dominated by Bosminidae (mean = 147.7 ind.L⁻¹ ± 267.6 SD), followed by Cyclopoïda (mean = 36.5 ind.L⁻¹ ± 76.2 SD) and Ceriodaphnia (mean = 21.9 ind.L⁻¹ ± 66.5 SD) (Fig. S4b). There were no significant difference between treatments in zooplankton richness and density (LMM, $\chi^2_{(3,23)} = 6.15, p = 0.10$ and $\chi^2_{(3,23)} = 5.59, p = 0.15$, respectively, Fig. S5 c-d). Community structure significantly differed between treatments (Fig. 4a) along the first axis of the nMDS, (LMM, $\chi^2_{(3,23)} = 22.16, p < 0.0001$, Fig. 4c), with no stocking and stocking and caged-CWH treatments significantly different with stocking only treatment (Tukey post hoc test, $p < 0.01$ and $p < 0.05$, respectively, Fig. 4c). There was no significant difference between treatment along the second axis of the nMDS (LMM, $\chi^2_{(3,23)} = 3.19, p = 0.36$, Fig. 4e).

Macroinvertebrate communities were largely dominated by Asellidae (mean = 2022.1 ind.mesocosm⁻¹ ± 2896.5 SD), followed by Annelida (mean = 479.2 ind.mesocosm⁻¹ ± 1382.8 SD) and Physa (mean = 52.9 ind.mesocosm⁻¹ ± 178.5 SD) (Fig. S6b). Richness differed significantly between treatments (LMM, $\chi^2_{(3,23)} = 49, p < 0.0001$), with a significantly lower richness in the stocking and caged-CWH treatment compared to all other treatments (Tukey post hoc test, $p < 0.01$, Fig. S7c). However, density did not differ significantly between treatments (LMM, $\chi^2_{(3,23)} = 7.20, p = 0.07$, Fig. S7d). Community structure significantly differed between treatments (Fig. 4b), but only on the first axis of the nMDS (LMM, $\chi^2_{(3,20)} = 64.58, p < 0.0001$ and $\chi^2_{(3,20)} = 2.40, p = 0.49$, respectively for the two axes, Fig. 4d and f), with the stocking and caged-CWH treatment being significantly

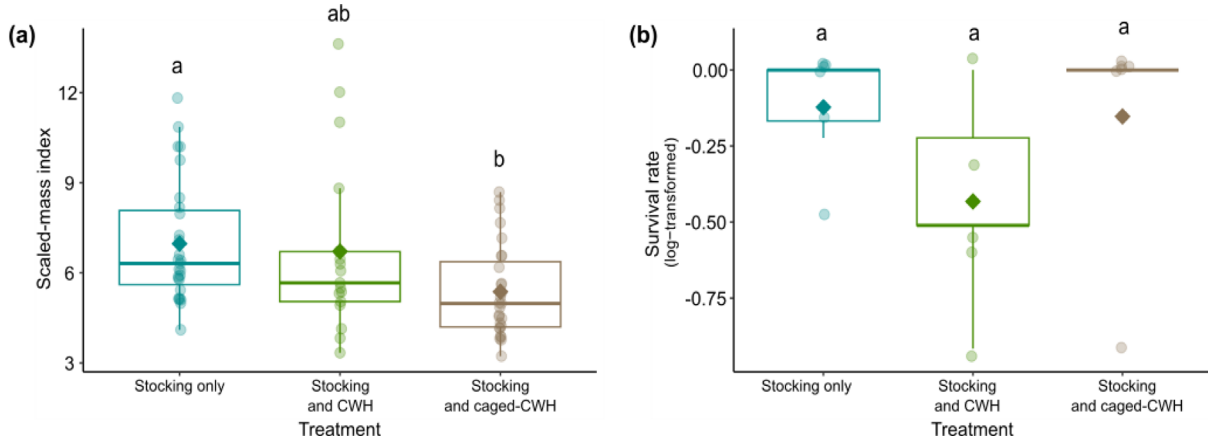


Fig. 3. Treatment effects on (a) scaled-mass index and (b) survival rate of juvenile largemouth bass *Micropterus nigricans*, at the end of the experiment. Different letters indicate significant difference between treatments (Tukey post-hoc test, $p < 0.05$).

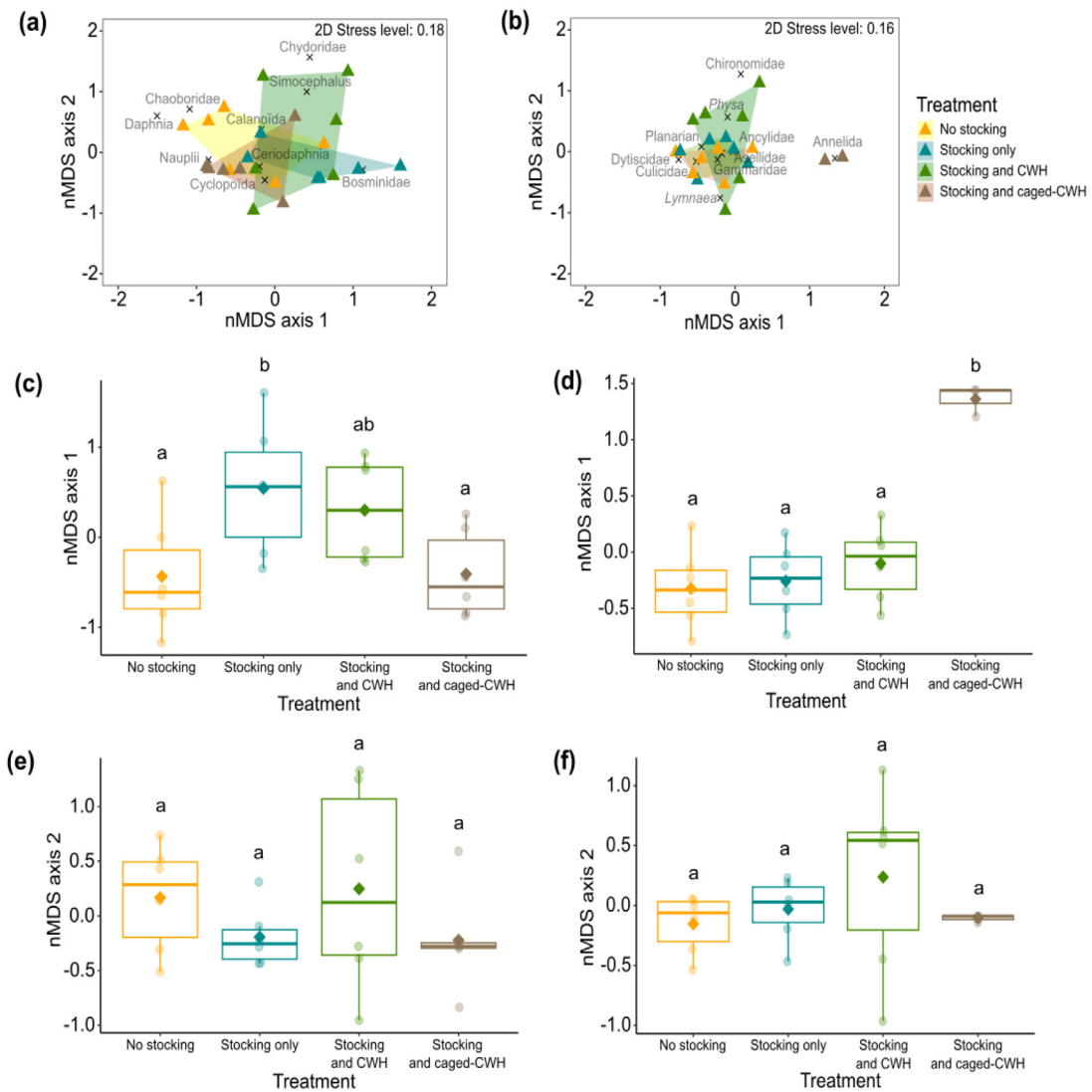


Fig. 4. Effects of management practices after stocking on community structure quantified using (a-b) a non-metric multidimensional scaling (nMDS) analysis and analyzed along the (c-d) first and (e-f) second axes. Zooplankton communities are represented on the left side of the panel and macroinvertebrate communities on the right side. Different letters indicate significant difference between treatments (Tukey post hoc test, $p < 0.05$).

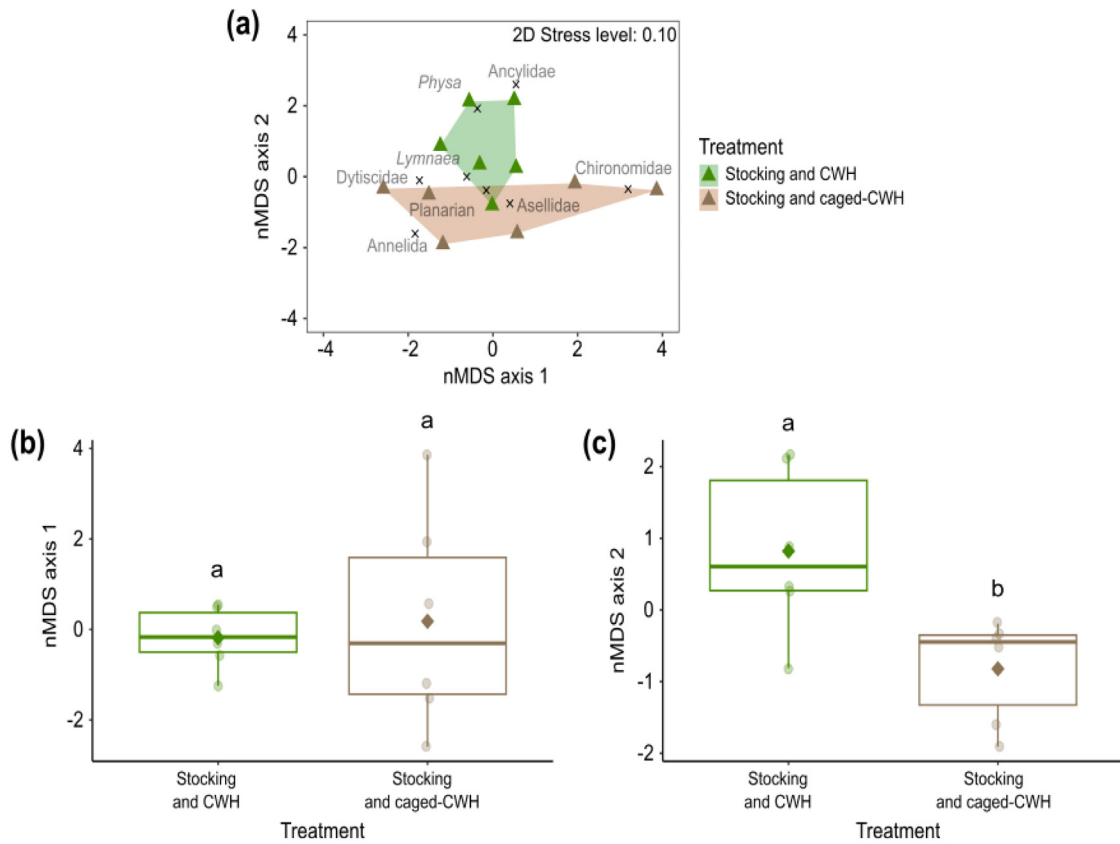


Fig. 5. Macroinvertebrate community structure within the added habitats after stocking quantified using (a) a non-metric multidimensional scaling (nMDS) analysis and analyzed with the (b) first and (c) second axes. Different letters indicate significant difference between treatments (ANOVA, $p < 0.05$).

different from all other treatments (Tukey post hoc test, $p < 0.001$, Fig. 4d).

Macroinvertebrate communities in habitat were largely dominated by *Physa* (mean = 171.7 ind.hab⁻¹ ± 370.1 SD) and Asellidae (mean = 59.5 ind.hab⁻¹ ± 130.1 SD) (Fig. S8). For the two treatments with habitat enhancement action, a large proportion of the macroinvertebrates sampled were found within the habitat, despite a high variability between samples (for stocking and CWH treatment: mean = 82.4 ± 19.4% and ranging from 45.7 to 96.9%; for stocking and caged-CWH treatment: mean = 50.2 ± 47.8% and ranging from 6.0 to 100%). No significant difference in richness was found between the two habitat devices (LMM, $\chi^2_{(1,11)} = 1.71$, $p = 0.19$, Fig. S9a), but density of macroinvertebrates in caged-CWH was lower compared to density in CWH (LMM, $\chi^2_{(1,11)} = 8.96$, $p < 0.01$, Fig. S9b). There was no significant difference in macroinvertebrate community structure in the added habitats (Fig. 5a) along the first axis (LMM, $\chi^2_{(1,11)} = 0.13$, $p = 0.72$, Fig. 5b) while a significant difference was found between CWH and caged-CWH along the second axis (LMM, $\chi^2_{(1,11)} = 24.92$, $p < 0.0001$, Fig. 5c).

Regarding ecosystem functioning, pelagic primary production differed significantly between treatments (LMM, $\chi^2_{(3,23)} = 52.78$, $p < 0.0001$) with higher values observed in stocking and caged-CWH than in other treatments (Tukey post-hoc test, $p < 0.001$, Fig. 6a). Benthic primary production did not differ significantly between treatments (LMM, $\chi^2_{(3,23)} = 0.59$, $p = 0.90$,

Fig. 6b). The decomposition rate of organic matter differed significantly between treatments (LMM, $\chi^2_{(3,23)} = 14.70$, $p < 0.01$), with a significant lower decomposition rate in the stocking and caged-CWH treatment compared to the no stocking treatment (Tukey post-hoc test, $p < 0.01$, Fig. 6c).

4 Discussion

Using an experimental approach, this study aimed to assess whether habitat enhancement, as a management practice, can help limiting the ecological impacts caused by the introduction of a non-native predatory species. First, we found that, prior to fish stocking, habitat enhancements had a contrasted effect on prey communities in mesocosms with coarse woody habitat (CWH) having no significant effect on zooplankton communities but a significant effect on macroinvertebrate community structure while caged-CWH had a significant effect on richness and density of zooplankton and on the richness, density and structure of benthic macroinvertebrate communities. In addition, the presence of caged-CWH was associated with a decrease in the decomposition rate of organic matter. We then found that stocked young-of-the-year largemouth bass induced significant changes in the structure of zooplankton communities, while macroinvertebrate communities and ecosystem functioning were not significantly impacted by stocking. We then found that the impacts of stocking on zooplankton community structure were compensated by habitat enhance-

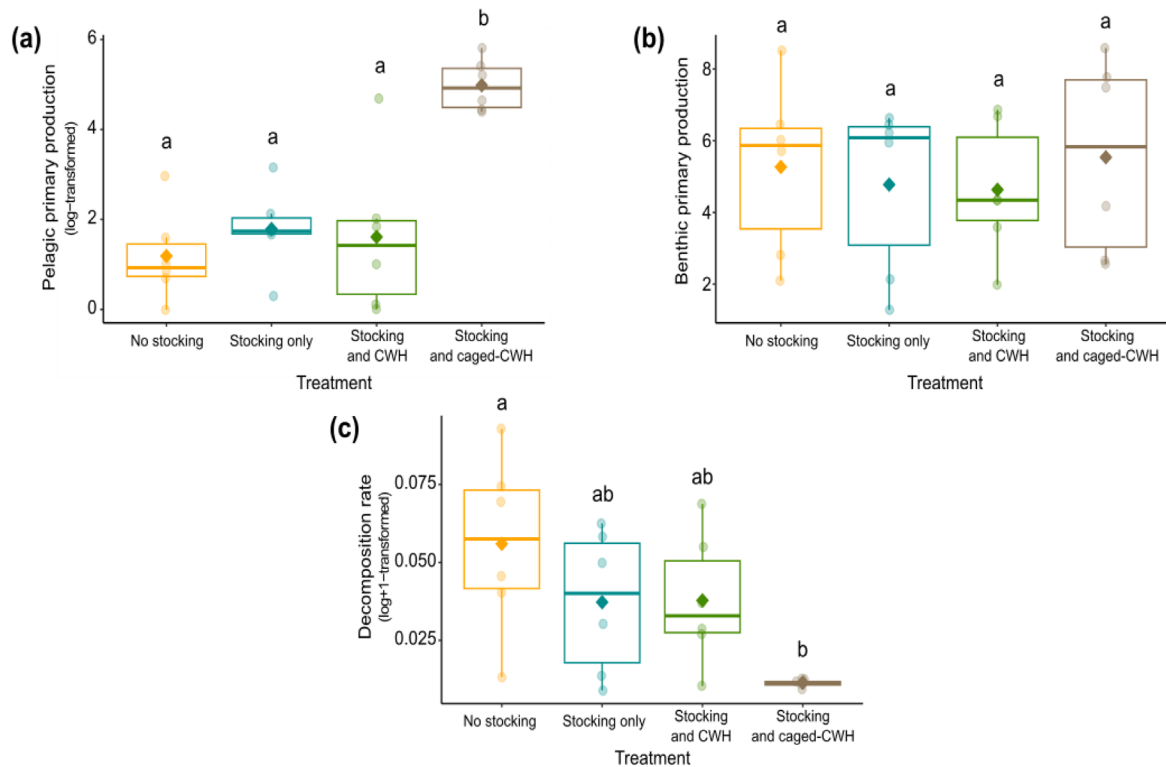


Fig. 6. Ecological effects of management practices after stocking on (a) pelagic primary production, (b) benthic primary production and (c) decomposition rate. Different letters indicate significant difference between treatments (Tukey post-hoc test, $p < 0.05$).

ment. However, we also found that habitat enhancement with caged-CWH had a significant impact on fish body condition.

While predatory fish stocking has been reported to induce important trophic cascade (Eby *et al.*, 2006; Rudman *et al.*, 2016), we found a significant effect of stocking on zooplankton community structure but limited cascading effect on ecosystem functioning. Specifically, in presence of largemouth bass, we found that the density of some important zooplankton taxa strongly decreased (*e.g.*, *Daphnia* and Chaoboridae), while the density of some small-bodied cladocerans (*e.g.*, Bosminidae) increased. Such changes in the zooplankton community have already been observed in lakes after largemouth bass introduction (Baca and Drenner, 1995). By consuming large zooplankton taxa, largemouth bass have likely enabled smaller zooplankton to dominate. Surprisingly, we observed an increased phytoplankton with caged-CWH while zooplankton community did not differ from the control without stocking. This might be explained by the fact that food webs in this treatment were already weakened before stocking, with a different community structure and, in particular, a lower richness and density of organisms.

Regarding the benthic habitat, stocking of young-of-the-year bass did not affect, in our experiment, macroinvertebrate community, although they represent potential prey for them (Post, 2003; Brown *et al.*, 2009). The introduction of predatory game fish into fishless lakes has been reported to strongly affect benthic macroinvertebrates (Knapp *et al.*, 2005) and particularly largemouth bass (Jackson, 2002). The lack of effects measured here might be caused by the fact that largemouth bass used in this experiment were reared in a hatchery and fed with pelletized food prior to their introduction

in the mesocosms. They may have exhibited different feeding behavior due to rearing conditions (Huntingford, 2004), such as surface feeding with limiting experience in consuming benthic prey. This could also explain why we only observed a consumption effect of largemouth bass on zooplankton without a cascading top-down effect on primary producers.

Contrary to a previous work conducted in a boreal lake (Theis *et al.*, 2022), habitat enhancement did not increase macroinvertebrate productivity in the present study. This result is surprising as the presence of CWH should have provided a prime habitat for benthic macroinvertebrates and a potential refuge from predators (Everett and Ruiz, 1993; Smokorowski *et al.*, 2006; Czarnicka, 2016). A previous study in stream (Bond *et al.*, 2006) showed a very rapid colonization of habitats by macroinvertebrates, within a month, but followed by a drastic drop in abundance and richness after several months. When adding an iron cage with the idea to increase habitat complexity, deleterious effects on the invertebrate community were observed, contrary to previous studies (Schmude *et al.*, 1998; Taniguchi *et al.*, 2003). We found that the presence of cage increased water conductivity (Fig. S10) and this might explain the effect on communities compared to CWH without cage (Cormier *et al.*, 2013). The changes observed in zooplankton diversity and density can also be explained by this change in water quality (Yan *et al.*, 1996). Macroinvertebrate communities found in the two added habitats differed in terms of diversity and structure, indicating that the choice of materials is crucial. We also observed that habitat enhancement did not have positive effects on fish body condition, and we even found significantly lower body mass in fish in the treatment with caged-CWH. This difference can be

explained by the fact that the addition of the cage resulted in a significant decrease in the density and richness of zooplankton, thereby reducing the abundance of potential food resources for YOY largemouth bass (Post, 2003; Brown *et al.*, 2009). Specifically, cages might release potential contaminants (*e.g.*, zinc, aluminum) and previous studies have shown that metallic pollution can affect the health and behavior of fish (Javed and Usmani, 2019; Jacquin *et al.*, 2020). It can also have an impact on the structure and functioning of freshwater communities, although its effect can be modulated by other factors such as temperature (Van de Perre *et al.*, 2016). Therefore, further investigations are needed to ensure the absence of ecological effects of the materials used for habitat enhancement (Cooke *et al.*, 2023).

In conclusion, our experience has provided some insights on the capacity of habitat enhancement in potentially limiting the ecological impacts of stocking predatory fish. We have demonstrated that habitat enhancement can partially compensate the predatory effect of fish, but that it can also alter water quality and key ecosystem functions. Ecosystem-based management is promising (Feng *et al.*, 2023; Radinger *et al.*, 2023), but remains complex to implement, particularly in the choice of materials used to ensure a sustainable and beneficial outcome (Cooke *et al.*, 2023). The effects of habitat enhancement occur over the long-term whereas the effects of stocking may occur in the short term, indicating that the impacts of stocking with non-native predators are difficult to reverse, despite investment in habitat enhancement. This study suggests that the outputs of habitat enhancement are complex, and that the use of habitat enhancement alone might not be sufficient to compensate the rapid consequences induced by fish stocking.

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Supplementary material

Figure S1. Block design of the experiment with each block ($n = 6$) containing each of the four treatments.

Figure S2. Additional habitats used in the experiment: (a) coarse woody habitat (CWH) composed of a deadwood bundle (downy oak, *Quercus pubescens*) and (b) caged-CWH composed of a deadwood bundle (downy oak, *Quercus pubescens*) installed within an iron cage (Biohut®, ECOCEAN, Montpellier, France).

Figure S3. Initial stocking biomass of largemouth bass *Micropterus nigricans* in treatments with stocking. For all treatments, five hatchery-reared young-of-the-year (YOY) largemouth bass were introduced in each mesocosm ($n_{total} = 90$ individuals). There was no significant difference between treatments in initial stocking biomass (Tukey post-hoc test, $p > 0.05$).

Figure S4. Density (ind.L^{-1}) of each taxon zooplankton sampled in each treatment (a) before and (b) after fish stocking.

Figure S5. Effect of management practices (a-b) before and (c-d) after fish stocking on zooplankton richness and density (ind.L^{-1}). Different letters indicate significant difference between treatments (Tukey post hoc test, $p < 0.05$).

Figure S6. Density (ind.mesocosm^{-1}) of sampled macroinvertebrate per taxon and for each treatment (a) before stocking and (b) after fish stocking.

Figure S7. Effect of management practices (a-b) before and (c-d) after fish stocking on macroinvertebrate richness and density (ind.mesocosm^{-1}). Different letters indicate significant difference between treatments (Tukey post hoc test, $p < 0.05$).

Figure S8. Density (ind.hab^{-1}) of each taxon of macroinvertebrates for each treatment with a habitat enhancement device (CWH only and caged-CWH) after fish stocking.

Figure S9. Macroinvertebrate (a) richness and (b) density (ind.hab^{-1}) within the CWH and the caged-CWH. Different letters indicate significant difference between treatments (ANOVA, $p < 0.05$).

Figure S10. Effects of treatments (a) before and (b) after stocking on conductivity ($\mu\text{S.cm}^{-1}$). Different letters indicate significant difference between treatments (Tukey post hoc test, $p < 0.05$).

Tab. S1. Details on the models, transformation and distributions used for each response variable before and after stocking.

The Supplementary Material is available at <https://www.kmae-journal.org/10.1051/kmae/2024004/olm>.

References

- Alp M, Cucherousset J, Buoro M, Lecerf A. 2016. Phenological response of a key ecosystem function to biological invasion. *Ecol Lett* 19: 519–527.
- Amoroso RO, Tillotson MD, Hilborn R. 2017. Measuring the net biological impact of fisheries enhancement: pink salmon hatcheries can increase yield, but with apparent costs to wild populations. *Can J Fish Aquat Sci* 74: 1233–1242.
- Baca RM, Drenner RW. 1995. Do the effects of piscivorous largemouth bass cascade to the plankton? *Hydrobiologia* 316: 139–151.
- Bates D, Mächler M, Bolker B, Walker S. 2015. Fitting Linear Mixed-Effects Models Using lme4. *J Stat Softw* 67: 1–48.
- Bolding B, Bonar S, Divens M. 2004. Use of artificial structure to enhance angler benefits in lakes, ponds, and reservoirs: a literature review. *Rev Fish Sci* 12: 75–96.
- Bond NR, Sabater S, Glaister A, Roberts S, Vanderkruk K. 2006. Colonisation of introduced timber by algae and invertebrates, and its potential role in aquatic ecosystem restoration. *Hydrobiologia* 556: 303–316.
- Brown TG, Runciman B, Pollard S, A.D.A. 2009. Biological synopsis of largemouth bass. *Can Manuscr Rep Fish Aquat Sci* 2884 V 27 P.
- Claussen JE, Philipp DP. 2023. Assessing the role of supplementation stocking: a perspective. *Fish Manag Ecol* 30: 583–591.
- Cooke SJ, Piczak ML, Vermaire JC, Kirkwood AE. 2023. On the troubling use of plastic ‘habitat’ structures for fish in freshwater ecosystems – or – when restoration is just littering. *FACETS* 8: 1–19.
- Cormier SM, Suter II GW, Zheng L, Pond GJ. 2013. Assessing causation of the extirpation of stream macroinvertebrates by a mixture of ions. *Environ Toxicol Chem* 32: 277–287.
- Cowx. 1994. Stocking strategies. *Fish Manag Ecol* 1: 15–30.
- Czarnecka M. 2016. Coarse woody debris in temperate littoral zones: implications for biodiversity, food webs and lake management. *Hydrobiologia* 767: 13–25.

- Dobson A, Lodge D, Alder J, Cumming GS, Keymer J, McGlade J, Mooney H, Rusak JA, Sala O, Wolters V, Wall D, Winfree R, Xenopoulos MA. 2006. Habitat loss, trophic collapse, and the decline of ecosystem services. *Ecology* 87: 1915–1924.
- Donaldson MR, O'Connor CM, Thompson LA, Gingerich AJ, Danylchuk SE, Duplain RR, Cooke SJ. 2011. Contrasting global game fish and non-game fish species. *Fisheries* 36: 385–397.
- Drenner RW, Baca RM, Gilroy JS, Ernst MR, Jensen DJ, Marshall DH. 2002. Community responses to piscivorous largemouth bass: a biomanipulation experiment. *Lake Reserv Manag* 18: 44–51.
- Eby LA, Roach WJ, Crowder LB, Stanford JA. 2006. Effects of stocking-up freshwater food webs. *Trends Ecol Evol* 21: 576–584.
- Emmrich M, Schällicke S, Hühn D, Lewin C, Arlinghaus R. 2014. No differences between littoral fish community structure of small natural and gravel pit lakes in the northern German lowlands. *Limnologia* 46: 84–93.
- Everett RA, Ruiz GM. 1993. Coarse woody debris as a refuge from predation in aquatic communities. *Oecologia* 93: 475–486.
- Feng K, Yuan J, Zhang Y, Qian J, Liu J, Li Z, Lek S, Wang Q. 2023. Application of artificial spawning substrates to support lacustrine fish recruitment and fisheries enhancement in a Chinese lake. *Front Ecol Evol* 10.
- García F, Paz-Vinas I, Gaujard A, Olden JD, Cucherousset J. 2023. Multiple lines and levels of evidence for avian zoochory promoting fish colonization of artificial lakes. *Biol Lett* 19: 20220533.
- Gimenez M, Villéger S, Grenouillet G, Cucherousset J. 2023. Stocking practices shape the taxonomic and functional diversity of fish communities in gravel pit lakes. *Fish Manag Ecol* 30: 603–614.
- Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, Lienkaemper GW, Cromack K, Cummins KW. 2004. Ecology of coarse woody debris in temperate ecosystems. *Advances in Ecological Research*, Academic Press, pp. 59–234.
- Harrison PA, Berry PM, Simpson G, Haslett JR, Blicharska M, Bucur M, Dunford R, Ego B, Garcia-Llorente M, Geamana N, Geertsema W, Lommelen E, Meiresonne L, Turkelboom F. 2014. Linkages between biodiversity attributes and ecosystem services: a systematic review. *Ecosyst Serv* 9: 191–203.
- Huntingford FA. 2004. Implications of domestication and rearing conditions for the behaviour of cultivated fishes. *J Fish Biol* 65: 122–142.
- Jackson DA. 2002. Ecological effects of Micropterus introductions: the dark side of black bass. *American Fisheries Society Symposium*, pp. 221–232.
- Jacquin L, Petitjean Q, Côte J, Laffaille P, Jean S. 2020. Effects of pollution on fish behavior, personality, and cognition: some research perspectives. *Front Ecol Evol* 8.
- Javed M, Usmani N. 2019. An overview of the adverse effects of heavy metal contamination on fish health. *Proc Natl Acad Sci India Sect B Biol Sci* 89: 389–403.
- Jennings MJ, Emmons EE, Hatzenbeler GR, Edwards C, Bozek MA. 2003. Is littoral habitat affected by residential development and land use in watersheds of wisconsin lakes? *Lake Reserv Manag* 19: 272–279.
- Johnston FD, Allen MS, Beardmore B, Riepe C, Pagel T, Hühn D, Arlinghaus R. 2018. How ecological processes shape the outcomes of stock enhancement and harvest regulations in recreational fisheries. *Ecol Appl* 28: 2033–2054.
- Kahlert M, McKie BG. 2014. Comparing new and conventional methods to estimate benthic algal biomass and composition in freshwaters. *Environ Sci Process Impacts* 16: 2627–2634.
- Knapp RA, Hawkins CP, Ladau J, McClory JG. 2005. Fauna of Yosemite national park lakes has low resistance but high resilience to fish introductions. *Ecol Appl* 15: 835–847.
- Kruskal JB. 1964. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 29: 115–129.
- Lecerf A, Dobson M, Dang CK, Chauvet E. 2005. Riparian plant species loss alters trophic dynamics in detritus-based stream ecosystems. *Oecologia* 146: 432–442.
- Lenth RV, Bolker B, Buerkner P, Giné-Vázquez I, Herve M, Jung M, Love J, Miguez F, Riebl H, Singmann H. 2023. *emmeans: Estimated Marginal Means*, aka Least-Squares Means.
- Lorenzen K. 2014. Understanding and managing enhancements: why fisheries scientists should care. *J Fish Biol* 85: 1807–1829.
- Lorenzen K, Beveridge MCM, Mangel M. 2012. Cultured fish: integrative biology and management of domestication and interactions with wild fish. *Biol Rev* 87: 639–660.
- Matern S, Emmrich M, Klefoth T, Wolter C, Nikolaus R, Wegener N, Arlinghaus R. 2019. Effect of recreational-fisheries management on fish biodiversity in gravel pit lakes, with contrasts to unmanaged lakes. *J Fish Biol* 94: 865–881.
- Meyerhoff J, Klefoth T, Arlinghaus R. 2019. The value artificial lake ecosystems provide to recreational anglers: implications for management of biodiversity and outdoor recreation. *J Environ Manage* 252: 109580.
- Milla S, Pasquet A, Mohajer LE, Fontaine P. 2021. How domestication alters fish phenotypes. *Rev Aquac* 13: 388–405.
- Nilsson J, Engstedt O, Larsson P. 2014. Wetlands for northern pike (*Esox lucius* L.) recruitment in the Baltic Sea. *Hydrobiologia* 721: 145–154.
- Oksanen J, Simpson GL, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Solymos P, Stevens MHH, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, Caceres MD, Durand S, Evangelista HBA, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill MO, Lahti L, McGlenn D, Ouellette M-H, Cunha ER, Smith T, Stier A, Braak CJFT, Weedon J. 2022. *vegan: Community Ecology Package*.
- Peig J, Green AJ. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos* 118: 1883–1891.
- Post DM. 2003. Individual variation in the timing of ontogenetic niche shifts in largemouth bass. *Ecology* 84: 1298–1310.
- R Core Team. 2022-. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.r-project.org/>.
- Radinger J, Matern S, Klefoth T, Wolter C, Feldhege F, Monk CT, Arlinghaus R. 2023. Ecosystem-based management outperforms species-focused stocking for enhancing fish populations. *Science* 379: 946–951.
- Roni P, Hanson K, Beechie T. 2008. Global review of the physical and biological effectiveness of stream habitat rehabilitation techniques. *North Am J Fish Manag* 28: 856–890.
- Rudman SM, Heavyside J, Rennison DJ, Schluter D. 2016. Piscivore addition causes a trophic cascade within and across ecosystem boundaries. *Oikos* 125: 1782–1789.
- Sass GG, Kitchell JF, Carpenter SR, Hrabik TR, Marburg AE, Turner MG. 2006. Fish community and food web responses to a whole-lake removal of coarse woody habitat. *Fisheries* 31: 321–330.
- Sass GG, Rypel AL, Stafford JD. 2017. Inland fisheries habitat management: lessons learned from wildlife ecology and a proposal for change. *Fisheries* 42: 197–209.
- Sass GG, Shaw SL, Fenstermacher CC, Porreca AP, Parkos III JJ. 2023. Structural habitat in lakes and reservoirs: physical and biological considerations for implementation. *North Am J Fish Manag* 43: 290–303.
- Schindler DE, Hilborn R. 2015. Prediction, precaution, and policy under global change. *Science* 347: 953–954.
- Schindler DE, Knapp RA, Leavitt PR. 2001. Alteration of nutrient cycles and algal production resulting from fish introductions intomountain lakes. *Ecosystems* 4: 308–321.
- Schmude KL, Jennings MJ, Otis KJ, Piette RR. 1998. Effects of habitat complexity on macroinvertebrate colonization of artificial substrates in north temperate lakes. *J North Am Benthol Soc*.
- Smokorowski KE, Pratt TC, Cole WG, McEachern LJ, Mallory EC. 2006. Effects on periphyton and macroinvertebrates from removal of submerged wood in three Ontario lakes. *Can J Fish Aquat Sci* 63: 2038–2049.
- Taniguchi H, Nakano S, Tokeshi M. 2003. Influences of habitat complexity on the diversity and abundance of epiphytic invertebrates on plants. *Freshw Biol* 48: 718–728.

- Theis S, Ruppert JLW, Shirton JR, Poesch MS. 2022. Measuring beta diversity components and beneficial effects of coarse woody habitat introduction on invertebrate and macrophyte communities in a shallow northern boreal lake; implications for offsetting. *Aquat Ecol* 56: 793–814.
- Tiberti R, von Hardenberg A, Bogliani G. 2014. Ecological impact of introduced fish in high altitude lakes: a case of study from the European Alps. *Hydrobiologia* 724: 1–19.
- Van de Perre D, Roessink I, Janssen CR, Smolders E, Van Regenmortel T, Van Wichelen J, Vyverman W, Van den Brink PJ, De Schampelaere KAC. 2016. The effects of zinc on the structure and functioning of a freshwater community: a microcosm experiment. *Environ Toxicol Chem* 35: 2698–2712.
- Yan ND, Keller W, Somers KM, Pawson TW, Girard RE. 1996. Recovery of crustacean zooplankton communities from acid and metal contamination: comparing manipulated and reference lakes. *Can J Fish Aquat Sci* 53: 1301–1327.
- Závorka L, Lassus R, Britton JR, Cucherousset J. 2020. Phenotypic responses of invasive species to removals affect ecosystem functioning and restoration. *Glob Change Biol* 26: 5693–5704.
- Zhao T, Grenouillet G, Pool T, Tudesque L, Cucherousset J. 2016. Environmental determinants of fish community structure in gravel pit lakes. *Ecol Freshw Fish* 25: 412–421.

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