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Stocking practices shape the taxonomic and functional diversity of fish communities in gravel pit lakes

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Abstract

Freshwater fishes are widely stocked to enhance existing stocks and create new fishery opportunities, but quantification of ecological effects of stocking on recipient communities is still limited. Here, we quantified recent stocking practices in geographically close gravel pit lakes with contrasting history and management, and measured effects of stocking on fish community structure (taxonomic and functional diversity and body-size structure). Between 2011 and 2017, 50% of managers stocked fish into gravel pit lakes at least once. However, stocking density (1.6 $kg.year^{-1}.ha^{-1}$ to 907 $kg.year^{-1}.ha^{-1}$), stocking diversity, and species stocked (from rainbow trout-dominated to cyprinid-dominated) were highly variable. Stocking intensity and choice of stocked species were primarily driven by management objectives and lake size. Stocking intensity was associated with changes in the recipient fish community, with an increase in taxonomic and functional richness and nonlinear changes in community size spectrum. Our findings demonstrate that recent stocking practices can modulate ecological dynamics of fish communities in gravel pit lakes with important consequences on functional characteristics that should be incorporated into management practices.

KEYWORDS

artificial lakes, community structure, fishery management, functional traits, recreational fisheries, size spectrum

1 | INTRODUCTION

Freshwater ecosystems provide countless services to humans (Reid, 2005), but have been strongly altered by anthropogenic activities (Dodds et al., 2013; Dudgeon, 2019). In inland waters of developed countries, recreational anglers are important to the management of freshwater ecosystems (Arlinghaus et al., 2016). Most angling is recreational, with 220 million anglers worldwide (Arlinghaus et al., 2019), but some also harvest species for subsistence (Nyboer et al., 2022). To overcome declining fish stocks while maintaining recreational fisheries, several management strategies have been implemented in freshwater ecosystems, such as habitat restoration and pollution reduction, but one of the most widespread is stocking to enhance fish abundance by releasing farmed or wild-borne individuals (Arlinghaus et al., 2016; Guillerault et al., 2018). Although fish are also stocked for conservation of endangered species (Roques et al., 2018) or for biomanipulation (Jeppesen et al., 2012; Lathrop et al., 2002), the main purpose of stocking is fishery management (Aprahamian et al., 2003; Cowx, 1994). Based on species status, stocking can be categorized as enhancement stocking when native species are stocked to maintain or improve existing fisheries (Claussen & Philipp, 2022; Cowx, 1994) or as introduction stocking when non-native species are stocked to create a new fishery (Cowx, 1994; Eby et al., 2006).

Anglers appreciate fishing challenges and trophy fish (Lewin et al., 2006) and commonly target large-bodied individuals such as top predators (Eby et al., 2006). Decision-makers often try to meet these expectations (Birdsong et al., 2021) by maintaining high catch rates and large body sizes of fish (Arlinghaus et al., 2020). Fishing-rights holders usually define stocking practices in ecosystems they manage but their decisions are highly influenced by multiple interacting determinants, including psychological disposition, economic situation, and socio-cultural environment (Aas et al., 2018; Fujitani et al., 2020; Riepe et al., 2017). Global records of stocking practices by managers are lacking (Aas et al., 2018), thereby making the assessment and monitoring of stocking practices complex (Cucherousset et al., 2021; Hunt & Jones, 2018). Although values vary among countries (Halverson, 2008; Hunt & Jones, 2018; Lorenzen, 2014), numerous fish are stocked worldwide every year. For instance, in France, 1.5 kg of fish (about 64 fish individuals) are released per angler per year, totaling 90 million individual fish stocked across the country (Cucherousset et al., 2021). Identifying main drivers of stocking practices and how stocked fish subsequently affect recipient communities is therefore crucial to improve management strategies of freshwater ecosystems and recreational fisheries.

Stocking can play an important role in structuring fish communities by introducing a large number of individuals with novel phenotypes (i.e., native species from aquaculture), or by introducing non-native species (Cucherousset & Olden, 2020). In general, stocking programs rarely take into account the carrying capacity of recipient ecosystems, which could result in increased competition that affects growth and mortality rates of fish (Claussen & Philipp, 2022; Cowx, 1994; Lorenzen et al., 2012; van Poorten et al., 2011). A recent study in small lakes revealed that regular stocking can increase fish species richness (Matern et al., 2022) and that small artificial lakes, such as gravel pit lakes, managed for recreational fisheries through fish stocking can host similar fish abundance and richness as natural lakes (Matern et al., 2022). In particular, gravel pit lakes are usually disconnected from other permanent aquatic ecosystems, so human activities have a fundamental role in shaping biological diversity of these ecosystems. Gravel pit lakes are extremely common in many industrialized landscapes (Blanchette & Lund, 2016; Oertli, 2018), where they provide refuges or substitutes for lost habitats for endangered or rare species (Emmrich et al., 2014; Lenda et al., 2012; Santoul et al., 2004). Because they are often located near densely populated areas (Mollema & Antonellini, 2016), gravel pit lakes also offer many cultural services, such as recreational angling or water sports (Soni et al., 2014). Because gravel pit lakes are managed for different purposes (Zhao et al., 2016), and because their fish communities are strongly influenced by human activities, they provide a unique opportunity to investigate the causes and consequences of fish stocking intended for different purposes.

The present study aimed to determine whether stocking affected recipient fish communities in a network of geographically close gravel pit lakes with different management purposes. The first objective was to quantify recent stocking practices, including species composition and density of fish stocked, and to identify primary determinants of these practices. We hypothesized that stocking practices would strongly differ among gravel pit lakes and would be driven by the primary use of lakes and the type of fishing-rights holders managing lakes. The second objective was to assess consequences of stocking practices on taxonomic and functional diversity and body-size structure of fish community. We hypothesized that stocked species would have different ecological characteristics than non-stocked species (i.e., species present in the community but not recently stocked) and that fish community structure in gravel pit lakes would be affected by recent stocking practices.

2 | METHODS

2.1 | Study area

The study area included 34 gravel pit lakes located in the central part of the Garonne floodplain, Haute-Garonne, France (Figure 1). These gravel pit lakes were located within a 55-km radius and disconnected

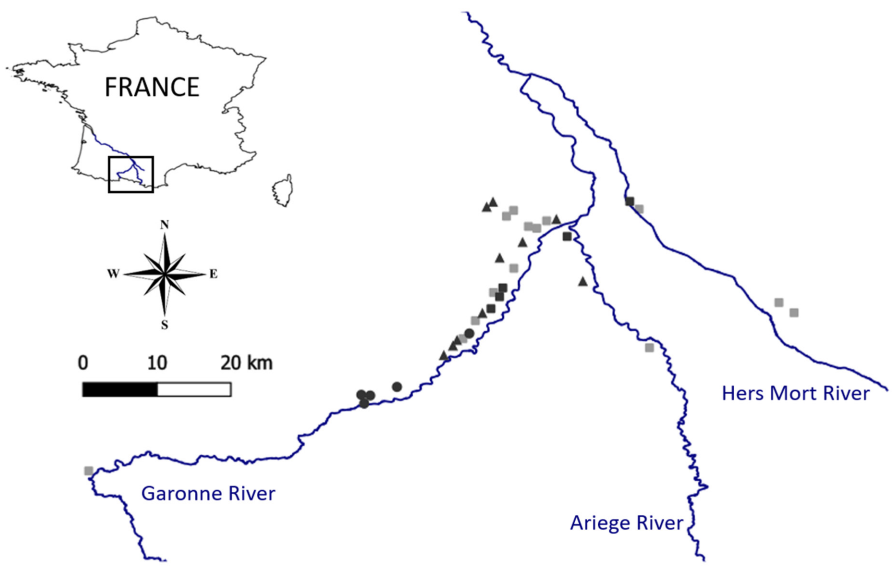

FIGURE 1 Locations of 34 gravel pit lakes located in the central part of the Garonne floodplain, Haute-Garonne, France. Shapes indicate the management type: ● gravel exploitation, ▲ leisure activities, ■ private fishery, and ■ public fishery.

from the hydrographical network and other gravel pit lakes (Alp et al., 2016; Paz-Vinas et al., 2021; Zhao et al., 2016) (Figure 1 and Table S1). Study lakes were distributed along a gradient of maturity (from 17 to 56 years following excavation), maximum depth (ranging from 1.7 to 22.4 m), and surface area (ranging from 0.73 to 47.43 ha; Colas et al., 2021; Table S1). Lakes were selected to represent different fishing-rights holders (i.e., private, communal, and public) and main use (from gravel exploitation to water sports and recreational fisheries) in the study area (Evangelista et al., 2015; Zhao et al., 2016). Overall, lakes were categorized into four management types (i.e., lake use describing the main management objective and structure): (i) gravel exploitation ($n = 5$, 15%), defined as gravel pit lakes managed by private companies for gravel extraction where angling and public access was prohibited; (ii) leisure activities ($n = 10$, 29%), defined as gravel pit lakes managed by private companies or private organizations for water sports and other recreational activities, with angling prohibited and restricted public access; (iii) private fishery ($n = 5$, 15%), defined as lakes with fishing rights owned by private companies or municipality and dedicated to recreational fisheries; and (iv) public fishery ($n = 14$, 41%), defined as lakes managed by federal angling clubs with high accessibility to the public (Figure 1).

In the study area, fish communities of gravel pit lakes follow predictable changes associated with ecosystem maturity (i.e., age and productivity) and management practices that tend to increase over time (Zhao et al., 2016). Young, oligotrophic lakes are usually colonized by a limited number of native species such as European perch (*Perca fluviatilis*) and roach (*Rutilus rutilis*). When ecosystem maturity increases, more fish species are observed, including more cyprinids and some predators such as northern pike (*Esox lucius*). Older and eutrophic lakes usually host more non-native species including pumpkinseed (*Lepomis gibbosus*) and black bullhead (*Ameiurus melas*) (Zhao et al., 2016). Unfortunately, information about historical management practices and history of fish colonization in each lake is lacking. This process is likely to be complex and variable depending on lake age, lake history, lake location, and also fish species. Multiple pathways can act simultaneously to explain the colonization of gravel pit lakes, including legal and illegal stocking or introduction as stowaway during the stocking of other species (Paz-Vinas et al., 2021). For this reason, we focused our investigations on recent stocking events and current fish communities.

2.2 | Fish community and lake monitoring

Fish communities were sampled between 2016 and 2019 (except one lake sampled in 2013) using a standardized protocol based on two complementary approaches, electrofishing, and gillnetting (details in Zhao et al., 2016). All sampled fishes were identified to species and total length was measured to the nearest mm. Body mass was subsequently estimated using length–weight relationships for each species in the study area (Zhao et al., 2019). For each sampled lake, five environmental variables describing lake morphology were measured: lake perimeter (m), surface area (ha), shoreline development ($SLD = \frac{Pr}{2\sqrt{\pi SA}}$; Hutchinson, 1959), where Pr is the lake perimeter (m) and SA is the lake surface area (m^2), maximum depth (m) and lake volume (m^3).

2.3 | Recent stocking practices

Recent stocking practices were assessed for each lake using questionnaires conducted in person or by phone in 2018 and 2019 and completed by the person responsible for (or able to report) stocking practices performed between 2011 and 2017, prior to fish community sampling. We focused on recent stocking events because, as observed in most ecosystems worldwide (e.g., Aas et al., 2018), records of historical stocking (if any) were not available in the studied gravel pit lakes. We used this period because it was relatively recent, thereby allowing managers to answer the questionnaire, and ecologically relevant. When stocking occurred, data on stocking date and stocked fishes, including species name, body size or body mass of stocked individuals, and quantity (biomass or number of individuals), were collected. Complementary information on management type was also collected.

2.4 | Community descriptors and structure metrics

Species richness (i.e., the number of species) was calculated to describe taxonomic diversity in each lake and a functional approach was used (Mouillot et al., 2013; Villéger et al., 2008) to assess the ecological role of species using their functional traits (Violle et al., 2007) and the diversity of roles in the community. Sampled individuals were classified into functional entities defined as life stages (i.e., young-of-the-year (YOY), juvenile, and adult) and discriminated by body size (i.e., fork length), within each species following Zhao et al. (2019). Accounting for intraspecific variability is important because it can provide a better understanding of variation of functional diversity patterns in communities facing human-induced perturbations (Zhao et al., 2019). The use of different life stages is appropriate to capture ontogenetic shifts that could be strong and ecologically important (e.g., Zhao et al., 2014). Functional entities richness (i.e., the number of functional entities), following the same principle as species richness, was also calculated to describe functional entities diversity within communities. Then, a set of 16 morpho-functional traits describing food acquisition and locomotion functions (Albouy et al., 2011; Mason et al., 2008) was used to describe functional entities (Zhao et al., 2019). On average, 21 individuals (±20 SD; ranging from 4 to 119 individuals) were measured for each functional entity. To compute functional diversity indices, a multidimensional functional space was built using a principal component analysis (PCA) based on scaled traits (Villéger et al., 2008). The first four principal components were used to build a 4D functional space. Then, three functional diversity indices (functional richness, functional evenness, and functional divergence) describing complementary facets of functional diversity were computed (Mouillot et al., 2013) using functional entities' position in the 4D functional space and functional entities abundance. Within a given community, the functional richness corresponds to the range of ecological strategies present, the functional evenness corresponds to the regularity of abundance distribution among ecological strategies, and the functional divergence corresponds to the proportion of the total abundance supported by functional entities with the most extreme trait values (Mouillot et al., 2013). All the selected lakes (n = 34) had at least five functional entities, allowing to calculate functional diversity metrics that require more functional entities in a given community than the number of axes in the computed functional space, that is, four in the present study (Villéger et al., 2008). Four very rare species sampled in the lakes, namely barbel (*Barbus barbus*) (one adult and one juvenile), goldfish (*Carassinus auratus*) (two adults), stone loach (*Barbatula barbatula*) (two adults), and European catfish (*Silurus glanis*) (five YOYs), were not included because morphometric data were not available. In total, 15,294 individuals from 22 species were analyzed (11 native and 11 non-native species) and categorized into 52 functional entities.

A community size-spectrum approach, based on the log-linear relation between fish abundance and body-size class (Trebilco et al., 2013), was used. In each lake, all sampled individuals were grouped according to their mass (g) into 10 size classes following a binned method based on a geometric series of base 2 (Sprules & Barth, 2016) and considering the size interval from 4 g to 1024 g. The smallest individuals were accumulated into the first size class and the largest ones into the 10th size class (Table S2). Then, fish abundance in each size class was normalized by dividing it by the size width of the associated size class. Size-spectrum parameters (slope, intercept, and regularity) were determined using linear regression between $\log_2$ normalized abundance and $\log_2$ body mass midpoint of each size class (Sprules & Barth, 2016). To avoid a strong correlation between the intercept and the slope, midpoints of size classes were centered (Sprules & Barth, 2016). The resulting slope quantifies the rate of decline in abundance with the increase in body size, the normalized intercept informs about the carrying capacity of the recipient ecosystem, and the regularity reflects the potential heterogeneous responses from different components of community (Heneghan et al., 2019). All selected lakes (n = 34) had at least 50 individuals to minimize potential biases in size-spectrum calculation (Arranz et al., 2021).

2.5 | Statistical analyses

To assess recent stocking practices, annual stocking (kg.year^{-1}) was calculated for each lake and species and divided by lake size to obtain annual stocking density (in kg.year^{-1}.ha^{-1}). Species representing less than 1% of total annual stocking for all lakes combined were grouped. To summarize stocking practices, a PCA was performed on annual stocking density (log $x+1$ transformed) of the most commonly stocked species and on combined annual stocking density of other species. Stocking practices were summarized with a PCA to address the issue of high collinearity among variables. The first two axes were used for subsequent analyses.

Hydromorphological variables (i.e., perimeter, surface, SLD, maximum depth, and volume) were also summarized using a PCA, due to high collinearity among variables (Figure S1). The first two principal components were used for subsequent analyses. Linear models were used to assess whether the first two PCA axes describing stocking practices varied according to management type, and along the first two axis of PCA describing lake hydromorphology. The first axis of PCA describing stocking practices was log $x+2$ transformed prior to analysis to meet normality assumption of residuals of linear models, and a Tukey post hoc test was used when the factor variable was significant.

To investigate effects of stocking practices on communities, linear regressions with quadratic terms were considered to assess monotonic changes (i.e., linear relations) or non-monotonic changes (i.e., density-dependent relations) in community descriptors (species and functional entities richness) and community structure metrics (functional richness, functional evenness, functional divergence, slope, intercept, and regularity) along the first two PCA axes on stocking practices. Functional richness and divergence were Box–Cox transformed prior to analysis to meet normality assumption of residuals in linear models. For all models, quadratic and interaction terms were removed when not significant ($p > 0.05$). Differences in the number of species and functional entities (taxonomic richness), functional richness, total abundance, and total biomass were compared between lakes with and without recent stocking management using Student or Wilcoxon rank-sum tests. Finally, a permutational multivariate analysis of variance (PERMANOVA, Anderson, 2017) was used to test for differences in species traits between stocked and non-stocked species. Non-stocked species were defined as fish species not recently stocked by managers but sampled in gravel pit lakes (Table S3). Statistical analyses used R 4.0.2 (R Core Team, 2020). Specifically, functional space and functional diversity indices used the *mFD* package (Magneville et al., 2022).

3 | RESULTS

3.1 | Recent stocking practices

Half of all lake managers (n = 17) reported having stocked fish at least once between 2011 and 2017. Fourteen fish species (six native and eight non-native) were stocked, including six predatory and eight nonpredatory species (Table 1). Six species accounted for 99% of total annual stocking in all lakes combined, including rainbow trout (*Oncorhynchus mykiss*), roach, common carp (*Cyprinus carpio*), rudd (*Scardinius erythrophthalmus*), northern pike, and tench (*Tinca tinca*; Table 1). Annual stocking across all lakes ranged among species from 8675.5 kg.year^{-1} for rainbow trout to 0.6 kg.year^{-1} for grass carp (*Ctenopharyngodon idella*). On average, 3.4 (±1.6 SD) species were stocked into each lake and ranged from one to seven species. Roach was the most commonly stocked species (76.5%), followed by rainbow trout (47.1%) and pikeperch (*Sander lucioperca*) (35.3%; Table 1). Adults represented 88.5% of stocking (kg.year^{-1}). Seven species were only stocked as adults (i.e., rainbow trout, common carp, rudd, northern pike, pikeperch, bleak, *Alburnus alburnus*, and European eel, *Anguilla anguilla*), and two species (i.e., Prussian carp, *Carassius gibelio*, and grass carp) were only stocked as YOY. The other five species (i.e., roach, tench, European catfish, European sturgeon, *Huso huso*, and largemouth bass, *Micropterus salmoides*) were stocked at different life stages (Table S4). Stocking densities averaged 27.7 kg.year^{-1}.ha^{-1} (±239.1 SD) and ranged among lakes from 1.6 kg.year^{-1}.ha^{-1} to 907 kg.year^{-1}.ha^{-1}. Non-native species were 73.2% of stocking (kg.year^{-1}).

3.2 | Drivers of recent stocking practices

In the PCA describing stocking practices, the first axis (36.5%) described stocking intensity (Figure 2), with increasing values indicating higher stocking density, and the second axis (28.5%) contrasted two stocking types, with negative values indicating rainbow trout-dominated stocking and positive values indicating cyprinid-dominated stocking. Regarding lake hydromorphology, the first PCA axis described lake size (50.4% of total variability) and the second PCA axis described lake depth (36.7% of total variability used). Hydromorphological conditions did not differ significantly between lakes from different management types, except maximum depth differed significantly between public fishery and gravel exploitation (Dunn test, $Z = 2.86$, $p < 0.05$, Table S1).

Stocking intensity differed significantly between management types ($F_{(3,28)} = 6.77$, $p < 0.01$), with higher annual stocking densities in gravel pit lakes managed for fishing activities (i.e., private and public fisheries) than in lakes managed for other activities (Tukey post hoc test, $p < 0.05$; Figure 3a). Stocked fish (stocking type) did not differ significantly between management types (Figure 3b). Stocking type increased significantly along the first PCA axis describing lake size (linear model, $F_{(1,28)} = 4.95$, $p < 0.05$; Figure 3d). The second PCA axis describing lake depth had no significant effect on stocking intensity or type (Figure S2).

3.3 | Consequences of recent stocking on recipient communities

The number of fish species (species richness) and the number functional entities (functional entities richness) sampled in gravel pit lakes significantly increased with stocking intensity ($F_{(1,31)} = 9.50$ and $F_{(1,31)} = 8.37$, $p < 0.01$, respectively; Figure 4a,b). Stocking type had no significant effect on the two facets of taxonomic diversity (Figure S3). In addition, gravel pit lakes recently stocked displayed a higher number of species and functional entities (Student test, $t = -2.81$ and $t = -2.21$, $p < 0.01$ and $p < 0.05$, respectively) than gravel pit lakes not recently stocked (Figure S4a,b). However, fish total abundance and biomass did not differ significantly between gravel pit lakes with or without recent stocking (Figure S4c,d).

The first four principal components of the PCA, used to build the 4D functional space, explained 67.8% of total variance (PC1 = 25.1%,

TABLE 1 Fish species (Latin and common names), status (native or non-native), occurrence (%), stocking quantity (kg.year^{-1}), and body mass of individuals (g) stocked in studied gravel pit lakes located in the central part of the Garonne floodplain, Haute-Garonne, France between 2011 and 2017. Species are listed in decreasing order of stocking quantity.

Latin name	Common name	Status	Occurrence (%)	Quantity (kg/year)	Body mass (g) Mean (±SD)	Body mass (g) Min-max
Oncorhynchus mykiss	Rainbow trout	Non-native	47.1	8675.5	193.5 (±27.3)	180–250
Rutilus rutilus	Roach	Native	76.5	1868.7	18.4 (±11.5)	7–81
Cyprinus carpio	Common carp	Non-native	23.5	756.4	9213.4 (±5880.7)	1500–15,500
Scardinius erythrophthalmus	Rudd	Native	17.7	715.5	34.9 (±1.3)	22–35
Esox lucius	Northern pike	Native	29.4	628.5	2274.8 (±743.5)	600–2633
Tinca tinca	Tench	Native	23.5	305.0	100.5 (±6.8)	100–200
Silurus glanis	European catfish	Non-native	23.5	68.6	3273.0 (±1033.7)	3000–7000
Sander lucioperca	Pikeperch	Non-native	35.3	54.4	1082.1 (±69.8)	800–1099
Carassius gibelio	Gibel carp	Non-native	11.8	35.7	21.0 (±0)	21–21
Huso huso	European sturgeon	Non-native	17.7	28.9	6491.7 (±12340.8)	100–25,000
Alburnus alburnus	Bleak	Native	5.9	4.8	16.0 (±0)	16–16
Anguilla anguilla	European eel	Native	5.9	3.2	2220.0 (±0)	2220–2220
Micropterus salmoides	Largemouth bass	Non-native	11.8	2.4	72.2 (±32.8)	64–200
Ctenopharyngodon idella	Grass carp	Non-native	5.9	0.6	20.0 (±0)	20–20

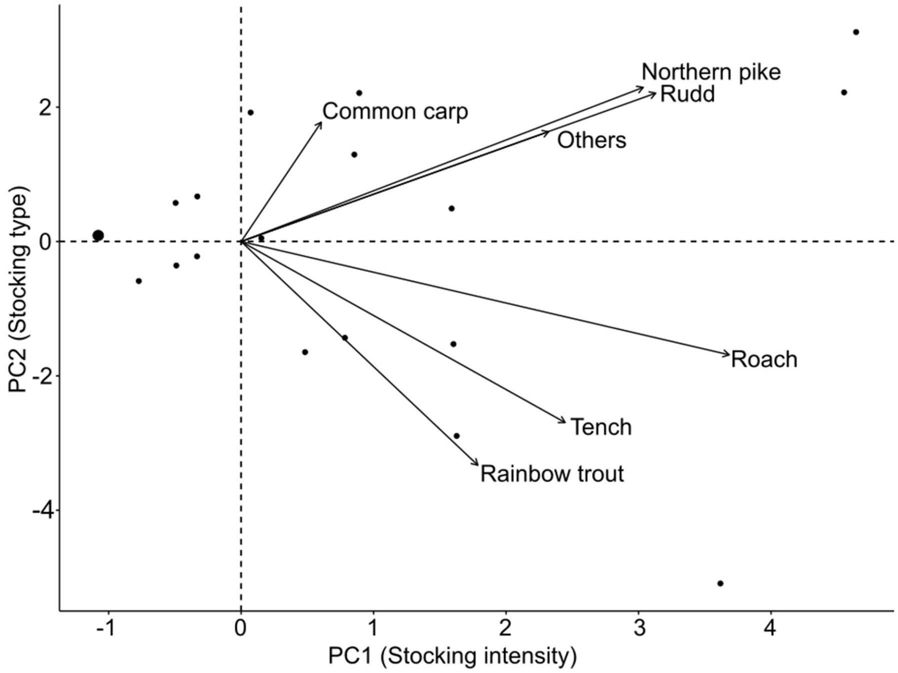

FIGURE 2 Principal component analysis (PCA) based on the log-transformed annual stocking density (log+1) of the most commonly stocked species (PC1: 36.5%, PC2: 28.5%) in 34 gravel pit lakes located in the central part of the Garonne floodplain, Haute-Garonne, France between 2011 and 2017. Each small dot represents a gravel pit lake that has been recently stocked ($n = 17$) and the large dot represents gravel pit lakes that have not been recently stocked ($n = 17$).

PC2 = 21.5%; PC3 = 13.1%, PC4 = 8.1%; respectively). Species recently stocked by managers differed significantly in functional traits from species not stocked by managers (PERMANOVA, $F_{(1,50)} = 2.31$, $p < 0.05$), especially for traits related to body size (e.g., mass), prey acquisition (e.g., oral gape surface), and locomotion (e.g., caudal peduncle throttling; Figure 5). Functional richness increased linearly (linear model, $F_{(1,31)} = 7.63$, $p < 0.01$) with stocking intensity (Figure 6a). In addition, gravel pit lakes recently stocked were higher in functional richness (Wilcoxon rank-sum test, $W = 83$, $p < 0.05$) than gravel pit lakes not recently stocked (Figure S4e). Stocking intensity was not significantly related to functional evenness and divergence (Figure 6b,c). Functional diversity was not significantly related to stocking type (Figure 6d–f). The size-spectrum slope displayed a U-shaped relationship with stocking intensity (linear model, $F_{(1,30)} = 6.05$ and $F_{(1,30)} = 5.14$, $p < 0.05$ for linear and quadratic terms, respectively; Figure 7a). The size-spectrum intercept displayed a significant hump–shape relationship with stocking intensity (linear model, $F_{(1,30)} = 7.12$ and $F_{(1,30)} = 6.15$, $p < 0.05$ for linear and quadratic terms, respectively; Figure 7b). Regularity was not significantly related to stocking intensity (Figure 7c). Size-spectrum parameters were not significantly related to stocking type (Figure 7d–f).

4 | DISCUSSION

Our findings provide novel insight into effects of recent stocking activities on fish community structure in gravel pit lakes and identify a key role of management practices and lake attributes in driving these practices. Our results supported the initial hypothesis that stocking practices differed significantly among gravel pit lakes despite the small size of the study area. Specifically, management type describing the fishing-rights holders and the main use of the lake significantly affected stocking intensity. In addition, lake size affected stocked species. Our study also provides strong evidence of important effects of recent stocking on recipient communities in gravel pit lakes. Indeed, we found increases in both taxonomic (species and functional entities richness) and functional richness in fish communities with increasing stocking intensity. Body-size structure in the communities was also affected by stocking intensity, while stocking type did not significantly affect the recipient community.

Variability in recent stocking practices, both in terms of density and species stocked, could be explained by the fact that, in France, fish stocking can be independently carried out by each fishing-rights holder (Fujitani et al., 2017). In addition, choice of species stocked by managers appears to be influenced by size of the system they manage. Thus, to better understand their practices, managers should be questioned about their perception of the environment. Based on the list of species stocked and their quantity, stocking into gravel pit lakes is relatively similar to stocking by angling clubs at a national scale (Cucherousset et al., 2021). In our study, the most commonly stocked species were likely stocked to meet angler expectations. Indeed, four of the six most-stocked species in our study (i.e., rainbow trout, common carp, northern pike, and tench) are popular game fish (Donaldson et al., 2011) and three (i.e., rainbow trout, common carp, and northern pike) were stocked only as adults (i.e., at large body size). Accordingly, we also observed that most species were stocked only as adults when aiming to improve the quality of fisheries. Some species were, however, stocked at multiple life stages to meet different management objectives. For instance, roach and rudd can serve as both prey for stocked predators (e.g., northern pike, pikeperch, and largemouth bass) and targeted by some anglers. Other species targeted by anglers, such as largemouth bass and grass carp, could also be introduced to control invasive crayfish or reduce macrophyte

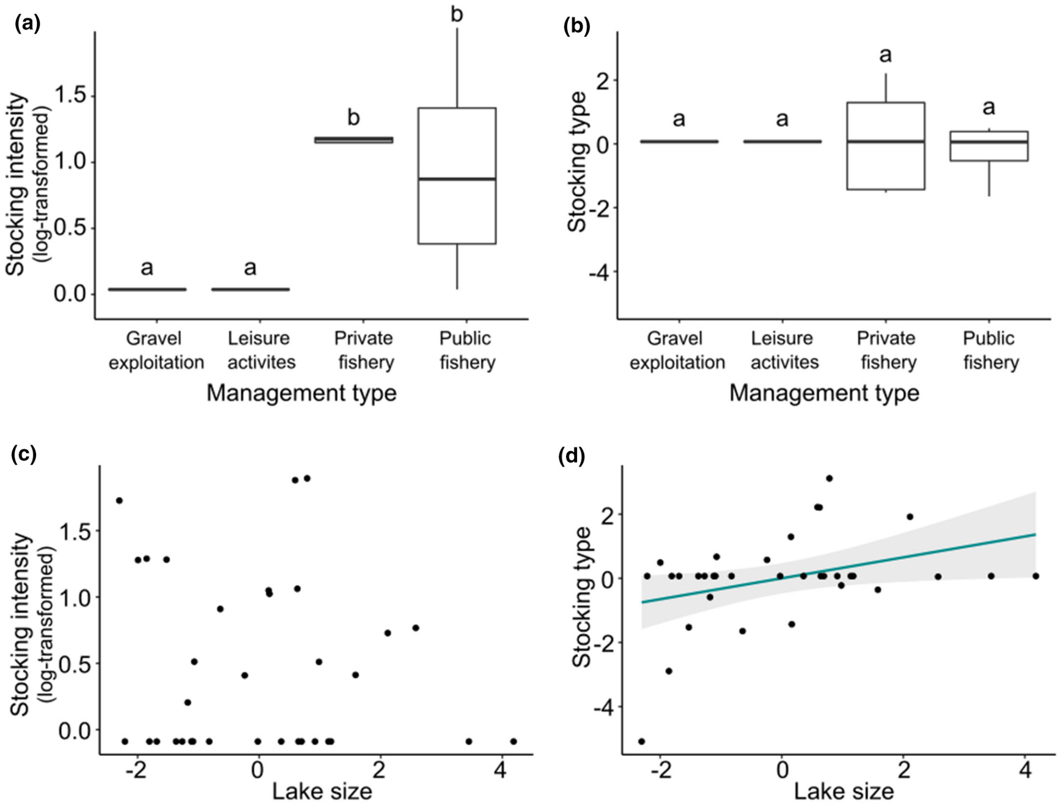

FIGURE 3 Comparison of (a) log-transformed stocking intensity (log+2) and (b) stocking type between management types and relationship between lake size (corresponding to the first axis of the PCA performed on hydromorphological variables) and (c) log-transformed stocking intensity (log+2) and (d) stocking type in 34 gravel pit lakes located in the central part of the Garonne floodplain, Haute-Garonne, France. Different letters indicate a significant difference between management types (Tukey post hoc test, $p < 0.05$). Solid line represents a significant relationship ($p < 0.05$).

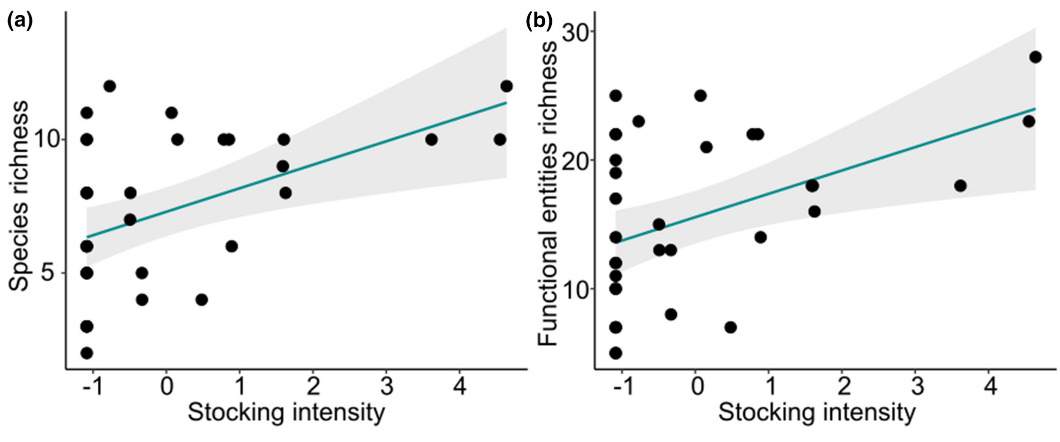

FIGURE 4 Relationship between stocking intensity and (a) species richness and (b) functional entities richness in 34 gravel pit lakes located in the central part of the Garonne floodplain, Haute-Garonne, France. Solid lines represent significant relationships ($p < 0.05$).

abundance. Importantly, all lakes recently stocked, except one, were stocked simultaneously for both enhancement (i.e., stocking of native species) and introduction (i.e., stocking non-native species), which highlights the multifaceted nature of stocking.

Gravel pit lakes are usually disconnected from hydrographic networks (Mollema & Antonellini, 2016), so fish colonization relies primarily on stocking. We found that gravel pit lakes managed by stocking had a higher species richness than gravel pit lakes not recently stocked, and stocking mainly occurred in gravel pit lakes managed for fisheries. Previous studies also found that fishery management promoted a higher species richness, particularly a higher number of piscivorous species, especially sport fishing species and cyprinid prey species (Matern et al., 2019; Zhao et al., 2016). We also found that taxonomic richness increased with

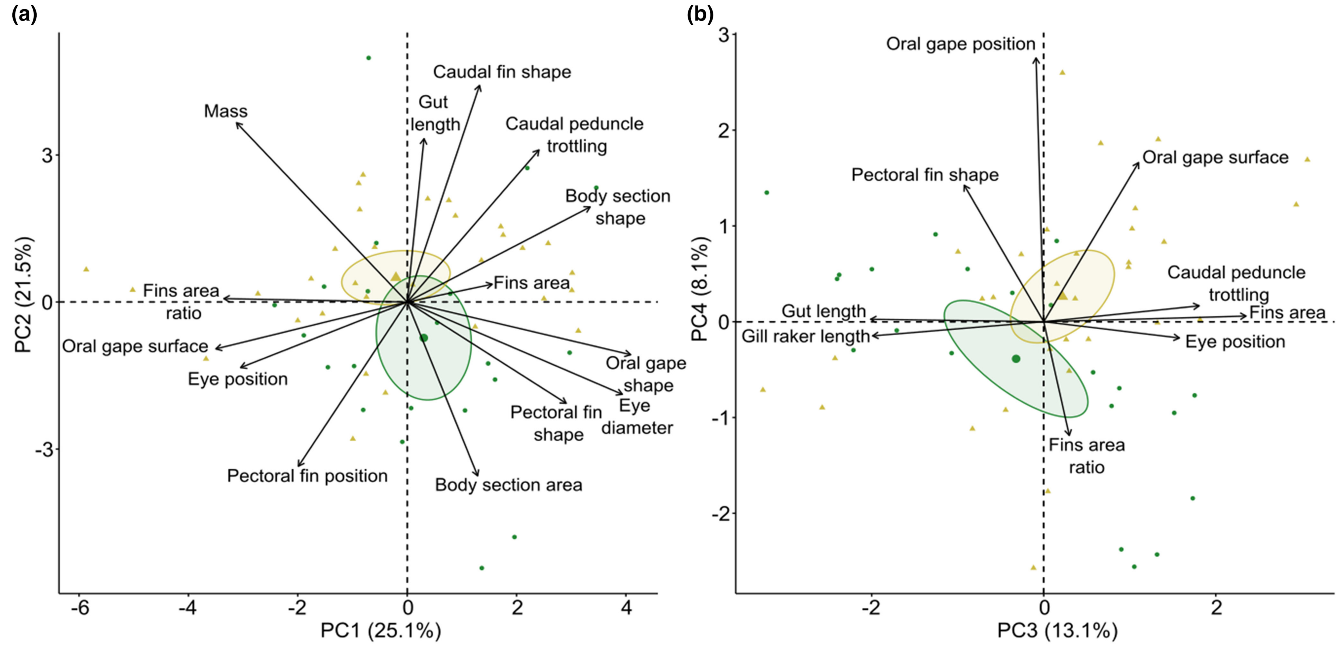

FIGURE 5 Functional space based on 16 functional traits for 52 functional entities (a = PC1 and PC2) and (b = PC3 and PC4) for species sampled in 34 gravel pit lakes located in the central part of the Garonne floodplain, Haute-Garonne, France. Stocked species are displayed with yellow triangles and non-stocked species in green circles. Only functional traits that are significantly correlated with the displayed principal components are represented by arrows.

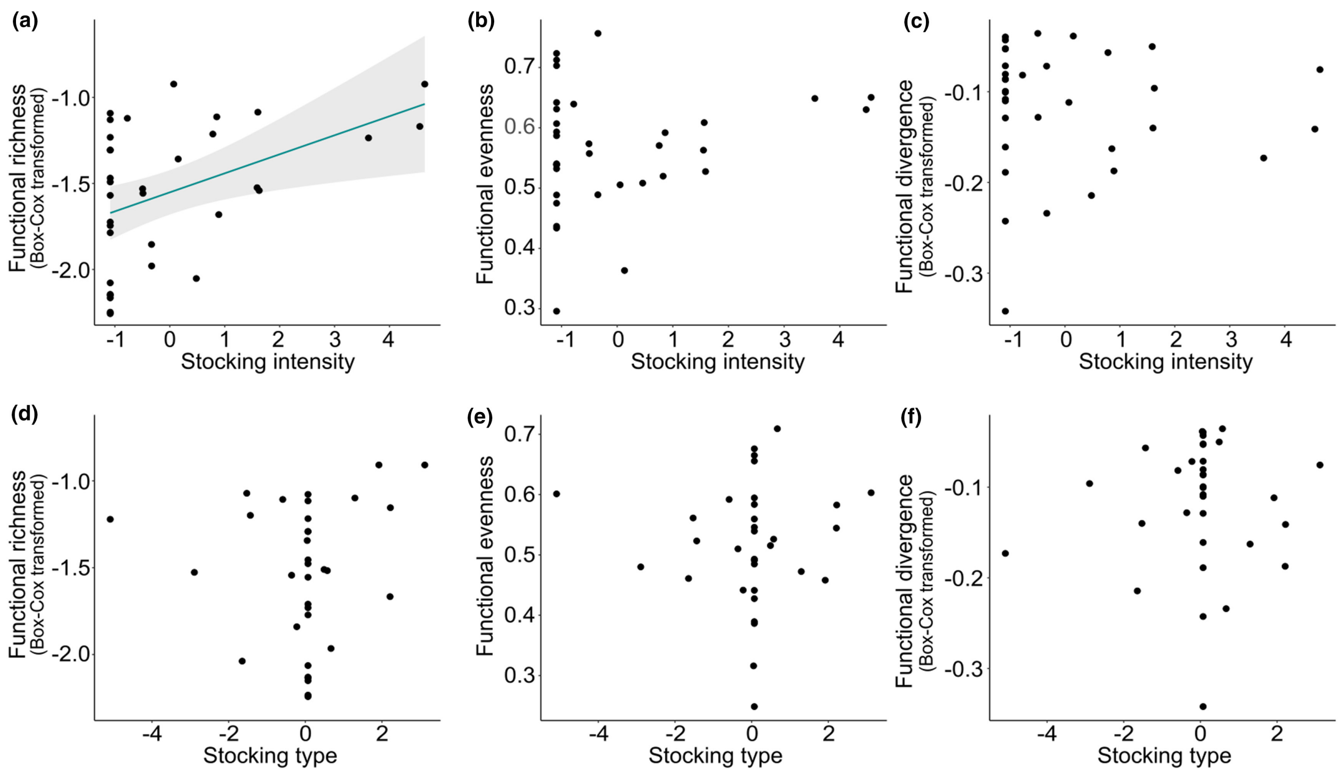

FIGURE 6 Effect of stocking intensity (a–c) and stocking type (d–f) on functional diversity of 34 gravel pit lakes located in the central part of the Garonne floodplain, Haute-Garonne, France. Functional richness and functional divergence were Box–Cox transformed. Solid line represents significant relationships ($p < 0.05$).

increasing stocking intensity, perhaps because higher stocking densities represent higher propagule pressures to facilitate species establishment. The same pattern was observed for functional richness, thereby confirming the establishment of self-sustaining populations of stocked species with multiple life stages sampled. Our findings confirm the importance of fishery management in

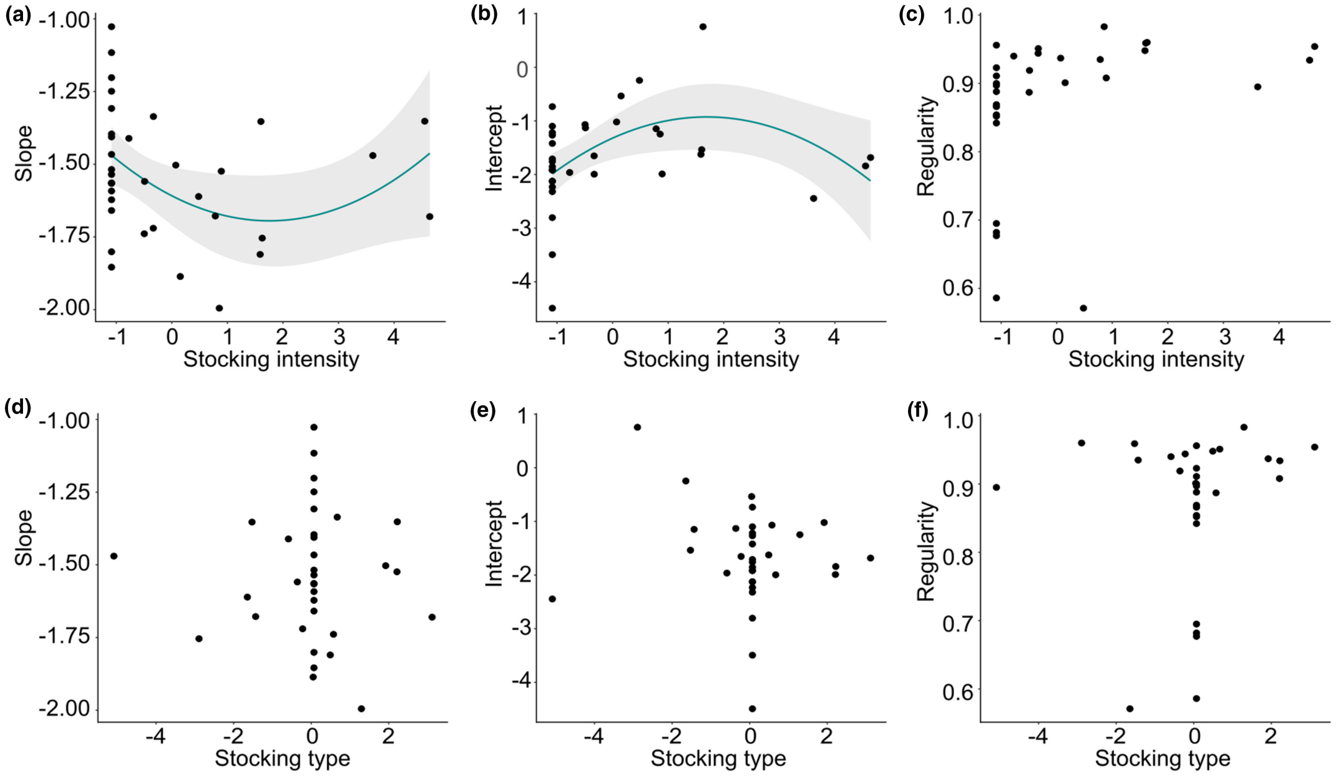

FIGURE 7 Effect of stocking intensity (a–c) and stocking type (d–f) on community size spectrum of 34 gravel pit lakes located in the central part of the Garonne floodplain, Haute-Garonne, France. Solid lines represent significant relationships ($p < 0.05$).

shaping fish community composition in gravel pit lakes (Matern et al., 2019, 2022; Zhao et al., 2016).

The functional structure of fish communities was also affected by intensity of recent stocking. As observed for taxonomic richness, we found that gravel pit lakes managed by stocking had a higher functional richness than gravel pit lakes not recently stocked, indicating that gravel pit lakes managed by stocking support fish communities with a wider range of ecological strategies. In addition, functional richness increased with increasing stocking intensity, and we hypothesize that higher propagule pressures can facilitate the establishment and persistence of species with particular ecological strategies. This finding was likely caused by differences in functional traits between stocked and non-stocked species, which were caused by stocking of non-native species that differ functionally from native species (Zhao et al., 2019). Such differences have already been observed at the global scale (Blanchet et al., 2010; Toussaint et al., 2018) and were associated with important changes in the functional structure of communities (i.e., an increase in functional richness and functional divergence; Toussaint et al., 2018). We found that recent stocking practices were not associated with changes in functional evenness and divergence, which may have been caused by simultaneous introduction and enhancement stockings that blurred the independent effects of introduction and enhancement stocking. However, stocked native species can also have different traits than wild conspecifics due to domestication (Teletchea & Fontaine, 2014). Unfortunately, accounting for differences in functional traits between hatchery-reared and wild individuals (Cucherousset & Olden, 2020; Gross, 1998) would require more data. Stocking can modulate the dynamics of interactions between organisms (i.e., prey and predators), thereby resulting in a substantial density-dependent change in the proportion of individual sizes within the community and the carrying capacity of recipient ecosystem. In our study, however, recent stocking practices were not associated with increased total abundance or biomass of fish between gravel pit lakes managed with or without stocking. Although this remains to be measured empirically, our findings suggest that stocking might induce a replacement of individuals rather than an addition of individuals in recipient communities.

Colonization of fish in young gravel pit lakes (i.e., following gravel exploitation) remains unknown in many cases, and in our study, the colonization history of fish was not known in these artificial ecosystems. Knowledge of the composition of fish communities at the start of our study was limited, with no information about management history. Fish could have been introduced legally, illegally, or as stowaways during fish releases (Paz-Vinas et al., 2021), before our study, so we focused on recent stocking practices and their effects on current communities. Our results are consistent with a predictable shift in community composition previously observed in gravel pit lakes (Zhao et al., 2016) and confirm the influence of fishery management and stocking on the trajectory of community assembly in these ecosystems. Nevertheless, repeated stocking of a limited number of species could lead to biotic homogenization of taxonomic (Matern et al., 2019, 2022; Radomski & Goeman, 1995) and functional diversity among lakes managed for fishery purposes. Fishery managers must account for this potential risk of loss of community diversity at the regional level, especially because gravel pit lakes are primarily managed for recreational fisheries, as in Central Europe (Matern et al., 2019; Nikolaus et al., 2021).

In conclusion, integrative management of social-ecological systems, such as gravel pit lakes, requires an understanding of complex interactions between users, managers, and the environment (Mee et al., 2016). Moreover, gravel pit lakes can, in some cases, represent valuable habitats for conservation with important socio-economical values (Nakahashi et al., 2022), so management practices should account for ecological consequences of stocking. Integration of ecological principles is crucial to achieve long-term sustainability of recreational fisheries (Claussen & Philipp, 2022), particularly for stocking in small lakes that can have important effects on fish communities. Although recreational fisheries, through stocking, actively participate in colonization of new ecosystems, fish stocked in these programs have different characteristics than wild native fish communities. In the future, stocking could impact functioning of these ecosystems and their associated ecosystem services.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest for this article.

DATA AVAILABILITY STATEMENT

Data are available on request from the authors.

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SUPPORTING INFORMATION

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