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ORIGINAL RESEARCH

Trait-based analyses reveal the recovery of riverine fish communities after a fishing ban

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Abstract Setting reserves or implementing fishing bans in certain areas has become a popular approach to enhance the recovery of disturbed populations and communities due to overfishing. Evaluating the effectiveness of such management measures primarily relies on taxonomic diversity, yet changes in taxonomy-based metrics may not be easily visible even in decadal periods. It has been suggested that functional diversity could outperform taxonomic diversity in capturing early signs of community changes following fishing bans. Here, using a before-and-after comparison methodology, we assessed the recovery of fish communities in the Chishui River basin, an important tributary of the Yangtze River, after seven years of implementation of the "10-year fishing ban" policy. Following the ban, fish community composition and abundance showed no significant changes, but biomass increased significantly. Taxonomic α-diversity (species richness, Simpson, and Margalef indices) and functional α-diversity (functional richness, imbalance, and dispersion indices), as well as taxonomic and functional β-diversity (including turnover and nestedness components), did not change significantly after the ban. Moreover, results from single-trait-based community-weighted mean (CWM) implied an initial recovery of fish communities after the ban, with a significant increase in CWM of maximum body length, age and length at first maturation, and lifespan, while CWM of growth rate showing

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a declining trend. This study provides a necessary empirical assessment of the efficiency of a fishing ban in restoring fisheries resources in freshwater ecosystems. Furthermore, single-trait-based functional diversity is a useful tool to detect early fish community changes, enabling a robust evaluation of conservation outcomes.

Keywords Biomass · β-diversity · Community-weighted mean · Functional diversity · Sustainable fishing · Yangtze River

Introduction

Freshwater ecosystems cover nearly 2% of the planet's surface but harbor more than 12% of all known species and are thus invaluable for the maintenance of biodiversity (Albert et al. 2021). In the Anthropocene, however, freshwaters are facing a more rapid decline in biodiversity than their terrestrial and marine counterparts due to various human disturbances, such as overfishing, pollution, land-use alteration, and climate change (Dudgeon et al. 2006; Heino and Koljonen 2022; Heino et al. 2009; Reid et al. 2019). Of these stressors, overfishing, often causing substantial changes at the population, community, and ecosystem levels, has emerged as one of the most serious threats to biodiversity (Allan et al. 2005). Firstly, fishing activities would selectively remove targeted species with high commercial value, thereby making their populations more prone to depletion and sometimes resulting in species local, regional, or global extinction (Lotze et al. 2011). Secondly, under increased fishing pressures, large-bodied (typically piscivorous) species may be successively replaced by smaller species that can better cope with high fishing pressures due to shorter life history strategies, leading to the so-called "fishing down the food web" (Dunlop et al. 2019). Meanwhile, such species replacement may alter community structure and biotic interactions (e.g. predator–prey relationships and competitive interactions) (Babcock et al. 2010). Finally, overfishing could affect ecosystem-level processes because fishes play a critical role in supporting key ecosystem functions (e.g. productivity and stability) and providing irreplaceable services (e.g. provisioning, regulating, and cultural services) to human societies (Olden et al. 2020).

Globally, riverine reserves or fishing bans have become a popular approach to mitigate the adverse impacts of overfishing and recover fishery resources (Dugan and Davis 1993; Ziegler et al. 2022). Generally, taxonomic metrics (e.g. species richness or abundance) are used to assess the effectiveness of such management actions (Pipitone et al. 2000). Nevertheless, changes in these metrics are usually slow, with direct changes of abundance taking five to 20 years to become apparent (Babcock et al. 2010). Hence, the absence of changes in taxonomic diversity following protection may not imply a failure to meet conservation targets, but rather the inability of these metrics to detect early or subtle community-level changes (Coleman et al. 2015). In this context, functional diversity, accounting for biological and ecological traits of organisms (Petchey and Gaston 2006), may be complementary to a taxonomy-based approach to ecological monitoring (Li et al. 2020; Mouillot et al. 2013). Indeed, functional diversity could be sensitive to environmental fluctuations or human disturbances because of the tight linkages assumed between habitat conditions and functional traits (Heino et al. 2013; Li et al. 2019). For instance, the declines of rare species with distinctive traits might have significant impacts on functional diversity but no major influence on taxonomic metrics. Importantly, a major focus of a fishing ban or reserve is to restore ecosystem functions, and functional diversity is assumed to be more important in explaining variation in ecosystem functioning than taxonomic metrics (Flynn et al. 2011). Moreover, as species around the world could share a suite of traits, functional approaches are independent of taxonomy, allowing the comparison of results from multiple studies composed of distinct species (García-Girón et al. 2023; Heino et al. 2013). Currently, better performance of functional diversity has been proved in the evaluation of terrestrial (Gorczynski et al. 2022), marine (Coleman et al. 2015), and freshwater (Britton et al. 2017) reserves.

β-diversity, one intrinsic component of biodiversity, measures differences in community composition across sampling units (Whittaker 1960). Recent conceptual advances have proposed that β-diversity could be decomposed into two additive components often called, turnover and nestedness (Baselga 2010). Turnover refers to the substitution of species between sites, while nestedness considers a situation where species in low-diversity sites are a subset of those in high-diversity sites, a special case of richness differences. This β-diversity decomposition approach has also been extended to functional diversity (Villéger et al. 2013). The two components might reveal different ecological processes acting on biotic communities. For example, turnover might be closely associated with deterministic processes, such as environmental filtering and biotic interactions, whereas nestedness may inform us about stochastic dispersal or extinction processes shaping biotic communities (Baselga 2010; Heino and Tolonen 2017). Despite its wide application in examining community assembly (Heino et al. 2021), empirical studies exploring the usefulness of β-diversity measures in assessing the effectiveness of a fishing ban are scarce (Wang et al. 2021; Xie et al. 2022). For instance, Xie et al. (2022) found that fish β-diversity in a floodplain lake did not change significantly after a pen culture ban but recovered a natural seasonal variation with β-diversity being lower in the high-water period than in the low-water period. Nonetheless, after a trawl ban, Wang et al. (2021) showed that macroinvertebrate communities in Hong Kong marine areas became more homogenized due to reduced habitat fragmentation. Therefore, it is unclear how a fishing ban would affect β-diversity of freshwater taxa, especially in large human-impacted rivers.

The Yangtze River, the largest river in Asia, historically supports 416 fish species, among which 178 species are endemic to this river (Liu et al. 2019). Meanwhile, this river serves as the cradle of capture fisheries in China, accounting for approximately 60% of national inland fisheries production (Liu and Cao 1992). Additionally, it is the germplasm resource bank of China's freshwater fisheries, with most aquaculture species deriving from it (Cao 2011). Thus, the Yangtze River has dual attributes of biodiversity conservation and fishery development in China. However, due to overfishing and other human activities, fish resources declined sharply in this river during the past decades (Chen et al. 2020). First, more than 90 fish species, including the iconic Chinese paddlefish (*Psephurus gladius* Martens, 1862), Chinese sturgeon (*Acipenser sinensis* Gray, 1835), and Yangtze sturgeon (*Acipenser dabryanus* Duméril, 1869), have been listed as (functionally) extinct or seriously threatened (Liu et al. 2019; Zhang et al. 2020; Zhou et al. 2020). Second, fisheries yields dropped from 430,000 tons in 1954 to less than 100,000 tons at present, with a particularly marked decrease in migratory species (Wang et al. 2022). Third, major commercial fishes demonstrated a body size miniaturization trend with an increase of small fish abundance but a decline in maximum body length and age (Liu et al. 2019). To restore aquatic biodiversity, the Chinese Government implemented a spring fishing ban (three months) in the middle and lower reaches of the Yangtze River in 2002. In the following year, the banned area was expanded to encompass the upper reach and several major tributaries. Since 2016, this ban has further expanded to cover more tributaries and surrounding lakes and extended from three months to four months (Liu et al. 2021). Nevertheless, the effectiveness of such a seasonal fishing ban is considered limited because of an increase of fishing intensity and of the usage of illegal fishing gears during legal fishing periods (Chen et al. 2020). Consequently, a complete fishing ban is urgently needed. In 2017, the "10-year fishing ban" policy was implemented in the Chishui River basin, an important tributary of the Upper Yangtze River, with all activities concerning harvesting fish being strictly prohibited from January 2017 to December 2026. The main aim was to explore the feasibility of initiating a complete fishing ban in the Yangtze River (Liu et al. 2021). However, regarding the outcomes of a fishing ban, there is a global variation with positive (Mak et al. 2021), neutral (Bergman et al. 2015), and negative (Xu et al. 2022) responses being recorded. However, no study, to date, has measured the effects of a fishing ban by simultaneously considering multiple facets (i.e., taxonomic and functional) and levels (α and β) of diversity.

Here, taking the Chishui River basin as a natural laboratory, we performed a before-and-after comparison to determine if fish communities exhibited signs of recovery after seven years of implementation of the "10-year fishing ban" policy. Specifically, utilizing fish data collected before (2016) and after (2023) the fishing ban, we tested temporal changes of several community metrics (i.e., abundance and biomass), taxonomic and functional α-diversity, and taxonomic and functional β-diversity indices. Building on the conclusions of previous studies (Feng et al. 2023; Liu et al. 2023), we expected positive changes in community metrics and α-diversity indices. For β-diversity, no formal hypothesis was proposed due to the paucity of relevant research. Furthermore, we anticipated that functional diversity would outperform taxonomic diversity in detecting early community changes after the cessation of fishing.

Materials and methods

Study area

This study was conducted in the Chishui River basin (27°20′–28°50′N, 104°45′–106°51′E), southwestern China. The Chishui River basin originates from Zhenxiong County and flows for nearly 437 km before being discharged into the Upper Yangtze River in Hejiang County. The study area experiences a subtropical monsoon climate with an annual average precipitation of approximately 1000 mm (Xia et al. 2023). The main land use types in this basin are farmland, forest, shrubland, and grassland. Along the longitudinal gradient, the topography changes from deep valleys and mountaintop tablelands to flat plains. Soil types in the watershed mainly consist of yellow loam in the upstream and midstream reaches, as well as purple soil in the downstream.

Sampling protocol

Twenty-five sites covering the mainstem and several tributaries of the Chishui River basin were consistently surveyed in 2016 and 2023 (Fig. 1). Fish samplings were conducted in the spring to facilitate fish collections due to high per-unit-area fish abundance in the low water period. These sites were selected following two major criteria. First, sampling sites should be easily accessible and possess the maximum diversity of habitats. Second, to avoid the confounding

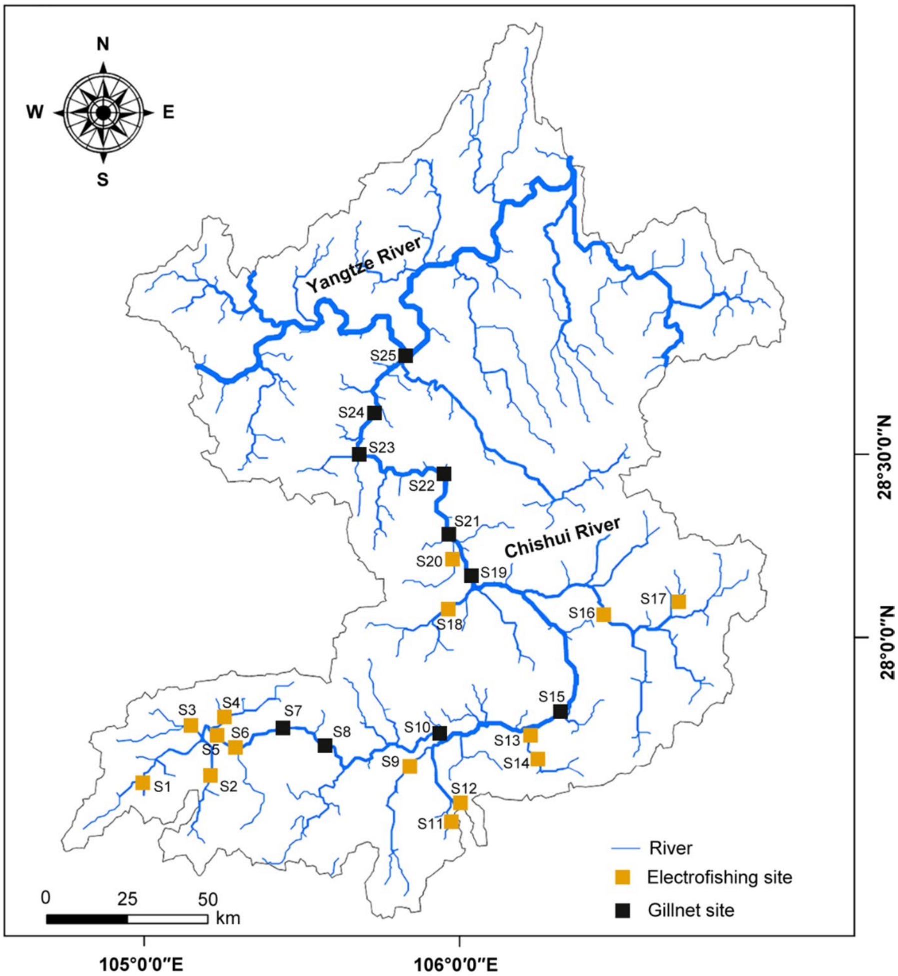

Fig. 1 Map of the Chishui River basin with 25 sampling sites

influence of dam removal in several large tributaries after the ban, we did not set sampling sites in these tributaries. Given the high topographic heterogeneity and complex hydrological regimes in large rivers, it is necessary to use a combination of different fishing gears to maximize the capture of fishes (Xia et al. 2023). In this study, at wadable sites (i.e., tributaries and the headwater), hired fishermen sampled a 200 m reach (30–40 min) using a backpack electrofishing protocol (CWB-2000P; 12 V import; 250 V export), slowly walking upstream with a single pass of the whole river width. For non-wadable sites, gillnets with a mesh size ranging from 3 to 5 cm (100 m long and 1.5 m high) were exposed to the water and fished overnight for 12 h. The deployed gillnets were only retrieved and emptied once the next day morning to avoid disturbing fishes around. To reduce the catch and mortality of juveniles, gillnets with smaller meshes were not used in this study. Besides, the specific method used for each site was kept consistent between 2016 and 2023, enabling the comparability of obtained data. All captured fishes were sorted, identified to species level, measured (1 mm), and weighed (0.1 g). Live fishes were released into the water in situ, while injured or dead individuals were deposited at Institute of Hydrobiology, Chinese Academy of Sciences as voucher specimens.

Functional traits

Here, we compiled six continuous (age and length at maturation, growth rate, lifespan, maximum body length, and trophic level) and three categorical traits (body shape, trophic guild, and vertical position) that could reflect five functions (i.e., food acquisition, mobility, nutrient budget, reproduction, and defense against predation) outlined by Villéger et al. (2017). Body shape was categorized into six classes (anguilliform, compressed, oval, cylindrical, dorso-ventrally flattened, and fusiform), trophic guild with six classes (detritivore, herbivore, invertivore, omnivore, piscivore, and planktivore), and vertical position with two classes (benthopelagic and demersal). These traits were selected because of their well-known sensitive responses to environmental changes and widespread application in recent literature (Wang et al. 2019; Xia et al. 2023). The detailed trait information was retrieved from FishBase (Froese and Pauly 2014) and given in Table S1.

Data analysis

Calculation of diversity indices

Before formal data analysis, non-native fish species were excluded. Five of seven species possibly came from artificial release and thus cannot be regarded as local members of ecological communities. Additionally, because they only accounted for a small fraction of total fish abundance ($<0.1\%$) and occurred in one or two sites, they do not significantly influence the observed results. Then, to evaluate temporal changes in fish communities, we calculated 35 indices that could be classified into six groups: community metrics (abundance and biomass), taxonomic α diversity (4 indices), functional α-diversity (3 indices), community-weighted mean (CWM) of each trait (20 indices) (Grime 1974; Lavorel et al. 2008), taxonomic β-diversity (3 indices), and functional β-diversity (3 indices).

First, abundance and biomass were estimated as the number and body weight of all fishes respectively.

Second, to characterize taxonomic α-diversity, we calculated species richness, Shannon-Weiner index, Simpson, and Margalef index using the vegan package (Oksanen et al. 2019). Species richness is the number of species, while Shannon–Wiener index combines the number and evenness of species within communities (Shannon and Weaver 1949). Simpson index measures the probability that two individuals selected at random within a site belong to the same species (Simpson 1949), and Margalef index assesses fish species dominance degree (Margalef 1958).

Third, before calculating functional diversity, we first calculated the multi-trait distance between each pair of species using the gawdis package, as this approach could produce a more balanced contribution between continuous and categorical traits (de Bello et al. 2021). Then, a principal coordinate analysis (PCoA) was undertaken on the multi-trait distance to derive trait vectors describing trait similarity (Heino and Tolonen 2017). We kept the first two trait vectors for subsequent diversity computation as a few sites only had three fish species. Additionally, Euclidean distance based on the two trait vectors was strongly correlated with “gawdis” distance based on the original nine traits (Pearson correlation, $r=0.7$, $p<0.05$). Subsequently, based on the two created trait vectors, functional trait space was constructed using the convex hull volume algorithm (Villéger et al. 2008). Three complementary functional α-diversity indices were quantified. Functional richness summarizes the area of functional space occupied by all species within a community, functional imbalance measures how regularly species relative abundance is distributed in functional space, and functional dispersion measures the mean distance of individual species to the centroid of all species in the functional space (Laliberté and Legendre 2010; Ricotta et al. 2022). Functional richness and dispersion were determined using the FD package (Laliberté and Legendre 2010), while functional imbalance was achieved via the adiv package (Pavoine 2020).

Fourth, we calculated CWM for each trait through the FD package:

$$\mathrm{CWM}_{\mathrm{jk}} = \sum_{i=1}^{n} P_{\mathrm{ik}} \times t_{\mathrm{ij}}$$

where p_{ik} is the relative abundance of species i in community k, t_{ij} is the value of trait j for species i, and n is the total number of species. Therefore, for the six continuous traits, CWM is the mean trait value of all species within a community, weighted by their relative abundance. For individual classes of the three categorical traits, CWM is measured as the relative abundance of focal species.

Finally, pairwise taxonomic β-diversity (based on Sørensen dissimilarity) was calculated using community data and further decomposed into turnover and nestedness components using the betapart package (Baselga et al. 2021). Functional β-diversity, functional turnover, and functional nestedness were produced following a similar methodology, but additionally using two trait vectors. Note that the estimation of the dissimilarity coefficient was based on intersections of functional space instead of species richness.

Statistical analysis

To assess the difference of fish communities before and after the fishing ban, non-metric multidimensional scaling (NMDS) ordination was performed based on Bray–Curtis dissimilarity index. Fish abundance was log $(x+1)$ transformed to down-weight the contribution of dominant species before computing Bray–Curtis index (Mak et al. 2021). Permutational multivariate analysis of variance (PERMANOVA) was run to examine the difference in community composition before and after the ban, utilizing the vegan package ($\alpha = 0.05$) (Anderson 2001). If significant differences in fish communities were detected, similarity percentage (SIMPER) analyses were run to identify the species responsible for most of the inter-period differences. Temporal changes of community abundance, biomass, taxonomic and functional α-diversity, and CWM of single traits were compared by applying Wilcoxon test or paired t-test. The choice of a specific method depends on the normality of examined indices, which was determined by Shapiro–Wilk test. For β-diversity, a permutational analysis of multivariate dispersion (PERMDISP) was performed to examine if there are differences between the two periods (Anderson 2001). All statistical analyses were accomplished in R 4.3.1 (R Core Team 2023).

Results

In total, 109 fish species (88 and 93 species in 2016 and 2023, respectively), belonging to seven orders and 20 families, were captured (Table S2). Among these species, 32 were endemic to the Upper Yangtze River and seven were exotic. For native fish, 70 species were captured in both 2016 and 2023, with 15 and 17 unique species being identified in 2016 and 2023, respectively. The three most diverse orders were Cypriniformes (85 species, accounting for 77.98% of the total richness), Siluriformes (13 species, 11.93%), and Gobiiformes (5 species, 4.59%), whereas other orders were only represented by less than four species. The most abundant species in 2016 were *Squalidus argentatus* (Sauvage and Dabry de Thiersant, 1874), *Rhinogobius giurinus* (Rutter, 1897), and *Hemibarbus labeo* (Pallas, 1776), while *Pseudobrama simoni* (Bleeker, 1864), *Pseudobagrus vachellii* (Richardson, 1846), *Tachysurus nitidus* (Sauvage and Dabry de Thiersant, 1874), and *Squalidus argentatus* (Sauvage and Dabry de Thiersant, 1874) were dominant fish species in 2023.

According to the NMDS ordination plot (Fig. 2), fish communities in 2016 showed a high degree of overlap with those in 2023. PERMANOVA test further confirmed that fish community composition did not change significantly following the fishing ban (pseudo-$F_{1,\ 49} = 1.06$, $p = 0.34$). Community abundance did not change significantly

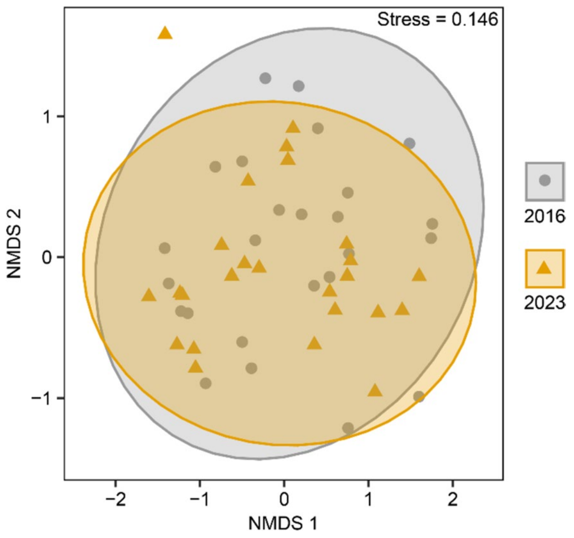

Fig. 2 Plot of non-metric multidimensional scaling (NMDS) of fish communities before (2016; grey dots) and after the fishing ban (2023; yellow triangles) in the Chishui River basin. The ellipses represent the 95% confidence interval for the two time periods

after the fishing ban with mean abundance per site being 596.32 ± 1862.35 individuals in 2016 and 897.72 ± 2263.59 individuals in 2023, respectively (Wilcoxon test, $p = 0.25$; Fig. 3a). In contrast, biomass showed a strong and significant increase with on average 17,395.90 ± 43,692.75 g per site in 2016 and 72,017.07 ± 165,967 g per site in 2023, respectively (Wilcoxon test, $p < 0.05$; Fig. 3b).

Species richness, Shannon–Wiener, Simpson, and Margalef indices respectively increased by 29.09%, 23.13%, 13.85%, and 21.86% between 2016 and 2023, but only Shannon–Wiener index exhibited a significant response (t-test, $p < 0.05$; Fig. 3c-f). Functional richness (Wilcoxon test, $p = 0.14$; Fig. 3g), functional imbalance (Wilcoxon test, $p = 0.94$; Fig. 3h), and functional dispersion (t-test, $p = 0.40$; Fig. 3i) were all higher in 2023 than in 2016, but no significant difference was observed between 2016 and 2023.

For continuous traits, CWM of age at maturation (Fig. 4a), lifespan (Fig. 4c), length at maturation (Fig. 4d), and maximum body length (Fig. 4e) showed a significant increasing trend after the fishing ban (t-test, $p < 0.05$), whereas CWM of growth rate declined significantly (Wilcoxon test, $p < 0.05$; Fig. 4b). Besides, there was no significant difference between 2016and 2023 for CWM of trophic level (t-test, $p = 0.19$; Fig. 4f). For categorical traits, CWM of body compressed fishes (Fig. 4g) and detritivores (Fig. 4h) significantly increased after the ban (Wilcoxon test, $p < 0.05$), while other classes of body shape, trophic guild, and vertical position did not differ significantly between 2016 and 2023 (Wilcoxon test, $p > 0.15$; Fig. 4g–i).

Taxonomic β-diversity (2016: 0.75 ± 0.24; 2023: 0.69 ± 0.26), taxonomic turnover (2016: 0.61 ± 0.30; 2023: 0.53 ± 0.31), functional β-diversity (2016: 0.61 ± 0.28; 2023: 0.50 ± 0.28), and functional turnover (2016: 0.32 ± 0.34; 2023: 0.21 ± 0.22) showed a decreasing trend after the fishing ban (Fig. S1a, b and d, e), while taxonomic nestedness (2016: 0.13 ± 0.16; 2023: 0.17 ± 0.17) exhibited an increasing trend (Fig. S1c). Besides, functional nestedness remained consistent between 2016 (0.29 ± 0.26) and 2023 (0.29 ± 0.26; Fig. S1f). Overall, PERMDISP analyses revealed that the six β-diversity measures did not significantly change after the ban ($p > 0.14$).

Discussion

Sensitive response of CWM to the fishing ban

Human disturbances such as overfishing impact freshwater ecosystems in varying ways, among which resetting biotic communities to initial successional stage is the most evident (Song and Saavedra 2018). Fishing activities selectively remove large, piscivorous individuals, resulting in the dominance of smaller species with fast growth and low trophic levels (Allan et al. 2005). For instance, using fishes in the North Sea as a case study, Jennings et al. (1999) revealed that larger species with later maturation were more susceptible to fishing pressures than smaller species with earlier maturation. Similarly, under increased fishing pressures, marine vertebrates exhibited faster growth (also lower maximum length and shorter lifespan and maturation time) and lower fecundity and trophic levels (McKeon et al. 2024). Thus, it could be predicted that, in the Chishui River basin, the cessation of fishing activities would lead to the opposite changes in fish functional structure (e.g. increase of species with slow growth, high trophic level, large size, and late maturation) from the above studies. As expected, CWM of maximum body length, age

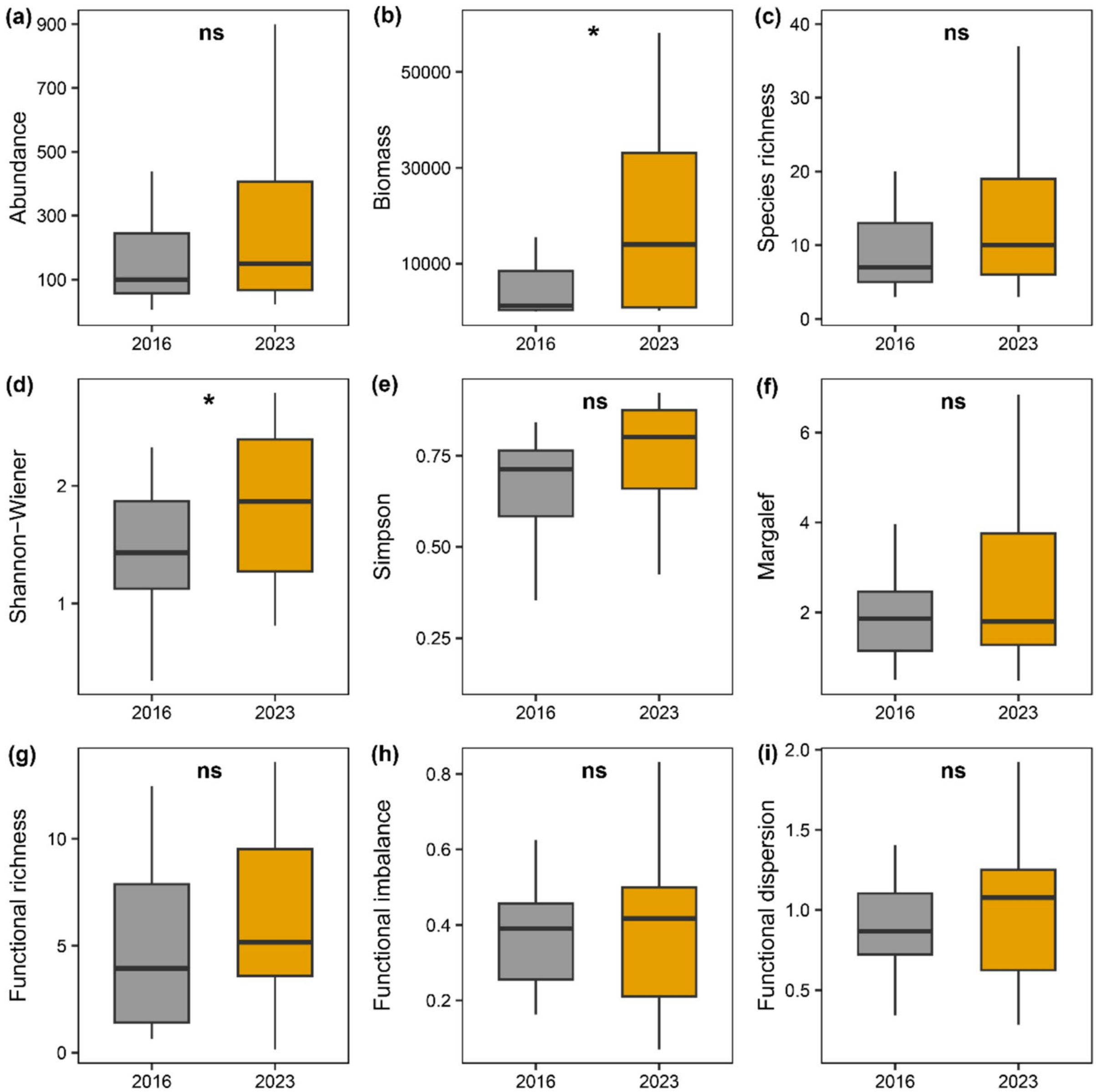

Fig. 3 Boxplots showing **a** abundance, **b** biomass, **c** species richness, **d** Shannon–Wiener indices, **e** Simpson, **f** Margalef, **g** functional richness, **h** functional imbalance, and **i** functional dispersion indices of fish communities before (2016; grey) and after the fishing ban (2023; yellow) in the Chishui River basin. Asterisk (*) represents statistically significant results ($p < 0.05$), whereas ns denotes not significant

and length at maturation, and lifespan significantly increased, while CWM of growth rate declined after the ban, suggesting an effective improvement of fish resources. During the overfishing period, the main fishery targets in the Chishui River basin are fishes with high commercial value such as *Acrossocheilus yunnanensis* (Regan, 1904), *Procypris rabaudi* (Tchang, 1930), *Spinibarbus sinensis* (Bleeker, 1871), and *P. vachellii*. These species are characterized by large body size (e.g. > 30 cm for body length), late age at maturation, and low growth rate. These fish stocks are prone to be overexploited owing to high fishing efforts and should therefore benefit strongly from the fishing ban. Besides,

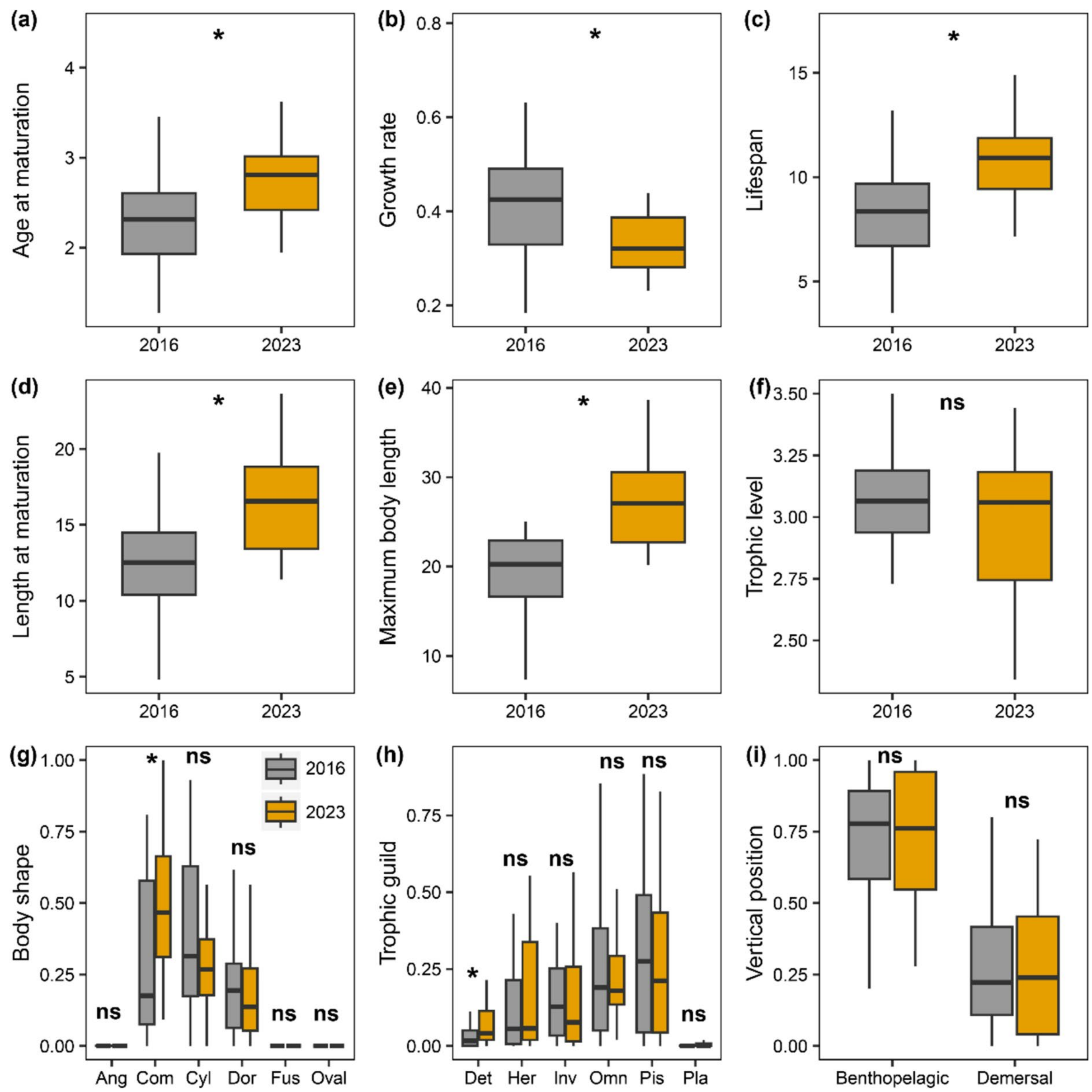

Fig. 4 Boxplots showing community-weighted means (CWM) of **a** age at maturation, **b** growth rate, **c** lifespan, **d** length at maturation, **e** maximum body length, **f** trophic level, **g** body shape, **h** trophic guild, and **i** vertical position of fish communities before (2016; grey) and after the fishing ban (2023; yellow) in the Chishui River basin. Asterisk (*) represents statistically significant results ($p < 0.05$), whereas ns denotes not significant. Note that, for categories such as Ang, Fus, Oval, and Pla, most sampling sites had zero values, thereby causing their median values equal to zero in the boxplot. Abbreviations: Ang = Anguilliform, Com = Compressed, Cyl = Cylindrical, Dor = Dorso-ventrally flattened, Fus = Fusiform. Det = Detritivore, Her = Herbivore, Inv = Invertivore, Omi = Omnivore, Pis = Piscivore, Pla = Planktivore

several key protected species (e.g. *A. dabryanus* and *Schizothorax kozlovi* Nikolskii, 1903) with large body size reappeared in the river, further strengthening the observed pattern. Noting that functional traits used in the present study are species-level features, and thus the detected patterns represent a variation in abundance of species with specific traits. In a parallel study, our team revealed that the measured body length of the dominant species increased significantly after the fishing ban (Liu et al. 2023). These results together demonstrate the recovery of fish populations and communities after the fishing ban.

A surprising finding of the present study is CWM of trophic level did not change significantly after the ban, which disagrees with theoretical expectations and several empirical studies (Feng et al. 2023; Mak et al. 2021). For example, Mak et al. (2021) found that compared with the period before the trawl ban, the mean trophic level of marine fishes was higher after the ban in Hong Kong coastal waters. Similarly, Feng et al. (2023) revealed an immediate post-fishing-ban recovery of high-trophic level fish species from Liangzi Lake (Yangtze River). Differences in the trophic level of primary fisheries targets may have contributed to the divergence between our findings and the two above-cited studies. In Hong Kong coastal waters, biomass of several fish families (e.g. Muraenesocidae, Synanceiidae, and Sciaenidae) at high trophic levels notably increased after the trawl ban. Similarly, in Liangzi Lake, piscivorous fishes (e.g. *Culter alburnus* Basilewsky, 1855, *Chanodichthys erythropterus* Basilewsky, 1855, and *Chanodichthys dabryi* Bleeker, 1871) are also the most targeted by fishermen. This situation contrasts with the fishing activities in the Chishui River basin where targeted species belong to various trophic levels. For instance, the most targeted species account for not only piscivores (e.g. *P. vachellii*) but also low-trophic level omnivores (e.g. *A. yunnanensis*, *P. rabaudi*, *S. sinensis*, and *A. dabryanus*). Hence, the simultaneous changes of both high- and low-trophic level fish abundance might explain why trophic level did not increase significantly after the ban. The response of trophic guild trait further confirmed such reasoning, as only CWM of the detritivore class increased significantly following the ban. Another possibility is that the sampling methods we used (i.e., electrofishing and gillnets) are not selective for fish species and thus underestimate the changes in trophic level. In this sense, stable isotope data may reveal a more nuanced variation in fish trophic level, as evidenced by previous studies (Tao et al. 2021). For body shape classes, compressed showed an increasing trend for CWM value due to its strong relationships with maximum body length and age at maturation (i.e., common targets of fishing activities), whereas for other classes no significant responses were found.

Other metrics were and were not significantly affected by the fishing ban

Unexpectedly, we found fish community structure was similar before and after the fishing ban, which is inconsistent with prior studies on lake fish (Xie et al. 2022) and macroinvertebrates (Yang et al. 2023) in the Yangtze River. Although rivers and lakes are intrinsically different, different intensities of human disturbance in these areas are likely the main reason for the discrepancy between our findings and the literature. Indeed, as no dam has been built in the mainstem, the Chishui River basin experiences relatively few human disturbances and sustains a high level of habitat heterogeneity. Moreover, this river has been incorporated into the "National Natural Reserve for the Rare and Endemic Fishes in the Upper Yangtze River" in 2005. Although commercial fishing was not completely prohibited until 2017 for social and economic reasons, fishing intensity was comparatively lower than in other rivers and lakes of the Yangtze River (Liu and Liu 2023). Hence, fishing activities in this area may cause compositional variation in fish abundance but might not induce significant changes in community structure. Contrastingly, in other rivers and lakes, overfishing, combined with multiple human activities such as habitat degradation or river–lake isolation (Chen et al. 2020), may lead to a distinct community structure. Overall, since few studies have investigated temporal variation in communities following the fishing ban in freshwaters, this reasoning needs further empirical support.

Abundance showed an increasing, albeit not significant, trend, yet biomass was higher after the fishing ban, indicating an initial recovery of fish communities. The results concur with a study on lake macroinvertebrates (Yang et al. 2023). Specifically, due to reduced physical disturbance on the substrate after the trawl ban, there was a significant increase in abundance of aquatic insects, yet oligochaetes and mollusks illustrated no significant change, which together resulted in no change in macroinvertebrate abundance. In the present study, the main dominant species before the fishing ban were *R. giurinus* and *S. argentatus*, accounting for about 50% of total abundance. This is because constant fishing pressure is less detrimental to these fast-growing species that are highly resilient and able to cope with high fishing mortality. However, their abundance intended to decline rapidly after the ban, and abundance of some species from Bagridae and Xenocyprididae started to increase, leading to no significant change in fish abundance. Furthermore, given that the latter is typically larger than the former two species, community biomass demonstrated a significant increase. The increase of biomass in our study reaches nearly 400%, which is more than the 65–300% increase observed in Hong Kong coastal waters (Mak et al. 2021), but much less than the eightfold increase in the Gulf of Castellammare of the Mediterranean Sea (Pipitone et al. 2000). Such variable responses to the fishing ban are likely determined by the peculiarity of each system, including the potential for recovery (e.g. initial population size), time since the fishing ban, and the intensities of other human disturbances (Mak et al. 2021).

All taxonomic and functional α-diversity indices, except for Shannon–Wiener index, did not differ significantly before and after the ban. This is a common finding in studies assessing the effectiveness of reserves or fishing bans in freshwater (Liu et al. 2021) and marine ecosystems (Coleman et al. 2015). It is suggested that changes in these different diversity indices might manifest at a longer timescale such as decades (Coleman et al. 2015). For instance, a consistent increase in species richness and functional diversity of benthic taxa in the Lyme Bay marine protected area was only observed after a decade (Davies et al. 2022). Indeed, both meta-analysis (Claudet et al. 2008) and collaborative fisheries research (Ziegler et al. 2024) revealed a positive association between the efficiency of marine protected areas and their age. Although the Chishui River basin has been included in a national natural reserve for almost 20 years, a complete fishing ban was initiated seven years ago. Such a medium-length time interval might explain why only Shannon–Wiener index exhibited a significant increase after the ban. Hence, we speculate that it will need more time to detect changes in multiple measures of community diversity. Importantly, we deemed that single-trait based CWM indices could be a useful compliment to species diversity in detecting community changes after the fishing ban. On the other hand, other human disturbances probably impede the recovery process. For example, after 6 years fishing ban, fish diversity of Liangzi Lake still did not show a sign of recovery because of habitat destruction caused by harvesting mollusks (Feng et al. 2023). Anecdotes from riverside dwellers during our fieldwork suggested that illegal fishing activities such as electric trawl, which is detrimental to the substrate, have been performed in several mountainous reaches of the Chishui River basin. Yet, considering the small spatial extent of its application, the extent of habitat degradation resulting from these activities is limited at the basin scale.

Turnover and nestedness components of fish β-diversity showed a decreasing and an increasing trend, respectively, yet these responses were not statistically significant. Similar to α-diversity, the short duration since the fishing ban, the influence of other human disturbances, and the potential for recovery could serve as viable explanations for the weak responses of β-diversity. To our knowledge, only one study has recorded significant changes in β-diversity after a fishing ban. Specifically, Wang et al. (2021) found that, after a trawl ban, β-diversity of marine benthos decreased significantly due to a reduced degree of habitat fragmentation and increased species occupancy. In the present study, occupancy of several species (e.g. *Onychostoma simum* Sauvage and Dabry de Thiersant, 1874, *T. nitidus*, and *S. sinensis*) increased sharply, while occupancy of most species did not show substantial changes. Different from marine systems with high connectivity, a prior study has revealed that fish communities in the study area are collectively determined by environmental filtering and dispersal limitation (Xia et al. 2023). Thus, fish species cannot freely disperse to each suitable habitat, leading to a non-significant change of β-diversity after the ban. However, given that few studies have employed β-diversity to evaluate the efficiency of a fishing ban, empirical tests on this topic should be strengthened in the future.

Caveats

A possible caveat is this study did not strictly follow the principle of the Before-After Control-Impact (BACI) design (Stewart-Oaten and Bence 2001). Typically, in the evaluation of marine protected areas, researchers would additionally select a nearby open area with similar environmental conditions and not be subjected to the fishing ban as a reference. Hence, any sign of recovery detected in the protected area instead of the open area may prove the effectiveness of the marine protected area (Coleman et al. 2015). Since our study only used a before-and-after comparison without control, it could be inferred that the fishing ban is beneficial to the recovery of fish species conferring traits vulnerable to overfishing, but the influence of environmental variation cannot be excluded (Feng et al. 2023). Unlike in marine ecosystems, it is often impossible to find a non-managed reference river or lake near the studied areas. Besides, the "10-year fishing ban" policy prohibited all forms of harvesting activities in all waterbodies of the Yangtze River. Thus, it is almost impossible to select an open area not subjected to the fishing ban and apply the BACI design in this study. Additionally, a previous study in the Yangtze River suggested that changes in environmental variables were not the main reasons for macroinvertebrate community changes after the fishing ban (Yang et al. 2023). We therefore suppose this also holds for fishes, although no formal proofs are available.

Implications

Our study has direct implications for biodiversity conservation and ecological monitoring in aquatic ecosystems facing overfishing. Utilizing a before-and-after comparison methodology, our results emphasized that the fishing ban is effective in promoting the restoration of fish resources in the Chishui River basin. Nonetheless, the effectiveness of this conservation and management approach is challenged by multiple threats, among which illegal fishing is the most prominent. First, despite seven years of implementation of the ban in this river, there are still rampant illegal fishing activities in some mountainous stretches (Liu et al. 2023), raising the need for more stringent protection actions from the fishery administration. Second, shifts in economic forces could contribute to the recovery (Lotze et al. 2011). People living in the Chishui River basin have long regarded wild fishes as the best delicacy, providing a market for illegal fishing. As such, it is recommended to develop the aquaculture industry to decrease the market value of wild fishes and achieve the goal of biodiversity conservation. This management measure could be efficient, but still requires a careful evaluation of the potential impacts of aquaculture development on wildlife, including disease spread, eutrophication, and non-native fish invasion risk (Cao et al. 2007). Third, the participation of local human communities is of crucial importance. In this sense, fisheries co-management, referring to cooperative management of aquatic resources by user groups and the government, is an increasingly recognized approach to maintaining sustainable resource utilization (Sen and Nielsen 1996). It aims to involve the community in the decision-making processes to increase adherence to the regulations developed by the government and the ultimate successful rate of fisheries management. Finally, recreational fishing, which has experienced rapid development after the ban, poses a growing threat to the restoration of fish stocks and thus needs proper management (Liu et al. 2023).

Researchers have realized that the depletion of fishing resources in the Yangtze River results from the combined effect of various human disturbances (Chen et al. 2020; Wang et al. 2022). Thus, a fishing ban alone is not probably sufficient to stop the current biodiversity decline, and comprehensive conservation and restoration plans are necessary. Although the Chishui River basin faces less severe human activities than the rest of the Yangtze River, several environmental problems are also outstanding. First, 373 dams have been constructed in its tributaries during the past decades, leading to a sharp decline in aquatic diversity. Hydropower development alters the hydrological rhythm, destroys running water habitats, and results in habitat fragmentation, especially for migratory species (Wu et al. 2019). Fortunately, nearly 72.4% of dams have been removed in the last three years and most large tributaries are reconnected with the mainstem river (Liu and Liu 2023). Yet, this process is still lagging in some regions and requires further restoration and mitigation efforts. Second, the number of exotic species, originating from fish ponds or are released artificially in the river, is increasing and deserves attention. Although most exotics were not established in riverine habitats, their adverse impacts cannot be ignored (Liu et al. 2023). We thus advocate a standardized management of the aquaculture industry and the development of better fish-release strategies. Third, the liquor industry in the Chishui River basin is world-renowned, but the sewages produced by many factories could cause mass fish kills or chronic influence on fish fitness. Furthermore, the rapid development of tourism would inevitably affect water quality and terrestrial landscapes (e.g. construction of roads and viewing platforms), which may indirectly exert an influence on aquatic diversity. Thus, water pollution treatment and habitat restoration programs should also be on the agenda (Liu et al. 2023).

Past studies conducted in young marine protected areas (e.g. less than 10 years old) have shown limited ability of species diversity indices to reveal subtle changes in biotic communities, implying that such a time scale is too short to allow scientific studies to detect meaningful biological changes (Coleman et al. 2015). However, because policy changes often occur in three to four years, researchers need sufficient evidence to demonstrate the efficiency of conservation measures in response to pressures from the public and governments (Coleman et al. 2015). In this scenario, functional diversity might be a promising approach to capturing early changes in communities after a fishing ban. Indeed, after seven years of the fishing bans, we found an initial recovery of fish communities using single-trait-based functional diversity metrics. Yet, it might take longer, sometimes even several decades, to achieve a full recovery of depleted resources (Lotze et al. 2011). Hence, long-term monitoring programs should be implemented to evaluate the effectiveness of the ban. Overall, this study will help build references for studies examining the effectiveness of management interventions (e.g. fishing ban) and provide invaluable guidance for the development of adaptive management for not only the Yangtze River but also other large rivers worldwide.

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