



Original Article

Fish diversity reduction and assemblage structure homogenization in lakes: A case study on unselective fishing in China

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ABSTRACT

Unselective fishing involves activities that target the entire assemblage rather than specific fish species, size classes, or trophic levels. This common fishing approach has been in practice for decades in inland waters in China but its implications for biodiversity remain unclear. We addressed this issue by studying fish assemblages in freshwater lakes (five fishing lakes, one reference lake, and a total of 51 sampling sites) between pre- and post-fishing time-periods in Eastern China during 2017–2019. The effects of lake, fishing period, and their interactions on fish abundance, biomass, and diversity indices were assessed. Multivariate analysis was conducted to test for differences in fish assemblages among lakes and between fishing periods. After the implementation of fishing activities, significant reductions in fish species richness, abundance, biomass, and all three life-history strategies (opportunistic, equilibrium, and periodic) were observed in fishing lakes, whereas opposite trends were observed in the reference lake. Compositional similarity of fish assemblages among fishing lakes increased over the three-year monitoring period. Our results suggest that unselective fishing reduces fish diversity and homogenizes fish assemblage structure in lakes. These findings have important implications for protecting both biodiversity and fisheries in inland waters in China and are applicable to other countries or regions that rely on fish as a major food source.

1. Introduction

Fisheries, including capture fisheries and aquaculture, play an essential role in food security and provide many socio-economic opportunities (FAO, 2020). For example, inland freshwater capture fisheries account for 12.5% of global fish production, and China is the top producer, accounting for 16% (FAO, 2020). Inland fisheries provide much-needed protein, employment, and income for poor rural areas in developing countries (McIntyre et al., 2016). However, fishing and other human activities have led to population changes of freshwater

vertebrates (Chen et al., 2017; Reid et al., 2019; Su et al., 2021), with an average decline in abundance of 84% since the 1970s, more than double the rate of decline observed in marine or terrestrial populations (Tickner et al., 2020).

Recognized as a major human stressor on aquatic ecosystems, overfishing often leads to dramatic changes in the structure of natural populations, with sometimes irreversible losses (Walsh et al., 2004; Allan et al., 2005; Hsieh et al., 2010; Britten et al., 2014). The consequences of overfishing include substantial declines in long-lived, low fecundity individuals and species (Botsford et al., 1997; Walsh et al., 2004). The

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selection effects of fishing-net mesh size can artificially increase the abundance of smaller species with higher fecundity (Pauly et al., 1998; Claireaux et al., 2018; Dunlop et al., 2019), leading to a decline in the average trophic level of the fish assemblage over time (Dunlop et al., 2019).

The use of species traits in freshwater ecology is expanding rapidly because trait-based approaches have promise to increase our mechanistic understanding of biological responses (Verberk et al., 2013). This is particularly the case for freshwater fish, where traits, rather than species entities, have been proven powerful. Among these are the three primary life-history strategies for freshwater fishes: opportunistic, equilibrium, and periodic strategists (Winemiller and Rose, 1992), describing the inherent trade-offs between the basic demographic parameters of survival, fecundity, and reproductive onset/duration in relation to environmental change (Olden et al., 2006). The 'opportunistic' life-history strategy in fishes places a premium on early maturation, frequent reproduction over an extended spawning season, rapid larval growth, and rapid population turnover rates, all of which lead to a large intrinsic rate of population increase (Winemiller, 1989, 1992). For fishes of the 'equilibrium' strategy, large eggs and parental care result in the production of relatively small clutches of larger or more advanced juveniles at the onset of independent life, which is largely consistent with the suite of characteristics often associated with the traditional K-strategy of adaptation to life in resource-limited or density-dependent environments (Pianka, 1970). A 'periodic' strategy identifies fishes that delay maturation to attain a size sufficient for production of a large clutch and adult survival during periods of suboptimal environmental conditions (e.g. winter, dry season, periods of reduced food availability) (Winemiller, 1992). Because life-history strategies are fundamental determinants of population performance, investigation of these characteristics is central to both theoretical ecology and resource management (Winemiller and Rose, 1992). Previous studies have shown that fishes with either periodic or equilibrium life-history strategies are less tolerant of fishing pressure than those with an opportunistic life history strategy (King and McFarlane, 2003). Thus, under high fishing intensity, the relative abundance of fishes with an opportunistic life-history strategy would be expected to gradually increase. For fishes with a periodic or equilibrium life-history strategy, a medium to low fishing intensity needs to be maintained when formulating sustainable fishing practices (Jennings and Kaiser, 1998; Mao et al., 2019).

Two major types of fishing practices occur in inland waters: one is intensive fishing of targeted species, and the other is non-discriminatory fishing of entire assemblages (Allan et al., 2005). Intensive fishing of targeted species is mainly to catch certain species whereas assemblage fishing is to catch the entire assemblage without selecting for fish species, size, or trophic level (Allan et al., 2005). Assemblage or unselective fishing is common in countries or regions where local people have a high reliance on fish harvests (Allan et al., 2005). For instance, in the Tonle Sap River basin (a part of the Mekong River Basin), the number of fishers increased from 0.36 million in the 1940s to an estimated 1.2 million in 1995 (Hortle et al., 2004). During the same period, catches per fisher decreased by 50%, but total catches nearly doubled. While large and medium-sized fish dominated the catch in the 1940s, by 1996 the catch was dominated by small fish, largely because of increased fishing pressure and assemblage overfishing (Allan et al., 2005). This unselective fishing, using multiple gear types (e.g. gillnets with different mesh sizes, night spear fishing, trawls, and baited hooks) and varying effort (e.g., time, number of gears), is also a common fishing approach that has been practiced in Chinese inland waters since the 1950s (Lian et al., 2016; Chen et al., 2017). In China, more than 70% of the 18 million registered fishers are engaged in capture fisheries and aquaculture in inland waters (CMARA, 2020). Thus, heavy dependence on fishing and assemblage fishing has led to increased exploitation of a wide variety of species from the entire assemblage (Allan et al., 2005; Chen et al., 2020).

Overfishing is a major threat to inland waters (Allan et al., 2005), but a full account of its impacts on ecosystems (e.g., changes in all biota and

food webs) is still in progress (Reid et al., 2019; Chen et al., 2020). Most studies rely primarily on fisheries landing data (e.g. Pauly et al., 1998, 2001; Wang et al., 2014) rather than quantitative stock assessments, which are essential for evaluating the ecological impacts of fishing activities (Branch et al., 2010; Dunlop et al., 2019).

There are many large shallow lakes in the Eastern Plain of China (Fig. 1). With the growth of the regional population and economy over the years, these lakes have become important bases for freshwater fisheries (Lian et al., 2016), and they also play an important role in water supply, flood control, tourism, navigation, trade, and other ecosystem services (Wang and Dou, 1998). Most of these lakes have been unselectively fished since the 1950s (Lian et al., 2016), but there is little understanding of the potential effects this is having on lake ecosystems.

Building on existing understanding of these lakes (e.g. Guo et al., 2019a, 2020; Qu et al., 2020), we assessed fish assemblages between pre- and post-fishing time periods. Specifically, we assessed potential influences of unselective fishing on (1) fish abundance, biomass, diversity, and trait composition (in terms of life history strategies), and (2) similarity of fish assemblage structures across these lakes.

2. Materials and methods

2.1. Study lakes and fishing activities

We studied six lakes in eastern China: Gaoyou Lake (GY), Hongze Lake (HZ), Luoma Lake (LM), Nansi Lake (NS), Dongping Lake (DP), and Donghu Lake (DH) (Fig. 1). These lakes had mean littoral water depths ranging from 2.0 to 4.9 m, which were measured with a portable water depth sensor (Speedtech SM-5, Japan) where we set the nets. Lake areas were obtained from the lake management agencies and ranged from 5 to 2152 km². The lakes are partially connected through a water diversion canal system. GY, HZ and LM are in Jiangsu Province, and NS, DP, DH are in Shandong Province. More details about these lakes have been provided in previous studies (Guo et al., 2020; Qu et al., 2020) and Table S1.

From July to October each year, tens of thousands of commercial fishermen employ a variety of gears and fishing methods (e.g., gill nets, ground cages, trap nets and trawls, pocket nets, cormorant fishing, and electrofishing) to intensively fish five of these lakes (GY, HZ, LM, NS, DP). As with typical unselective fishing, there is almost no size or species selection in catches because of the different mesh sizes and gears used. According to statistical records from lake management agencies and our field surveys, the annual catch per fishing lake ranges from 5.5 to 27.0 kilotons, which supports from 12,000 to 92,000 commercial fishers and 103,000 to 198,000 fishery-related jobs varying by lake area and fishery resources (Liu et al., unpublished data). According to the lake management agency, the sixth lake (DH) has never been fished, and could thus serve as a reference lake for the current study.

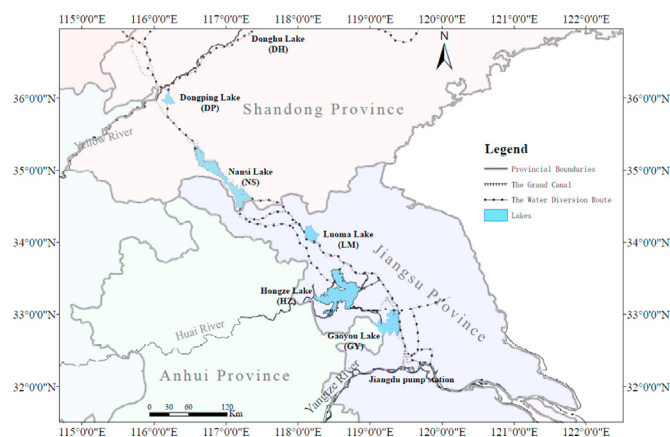


Fig. 1. Location of studied lakes in Eastern China.

2.2. Fish sampling

We sampled fish from April to May prior to the opening of the commercial fishing season (i.e., the pre-fishing period) and from November to December after the commercial fishing season closed (i.e., the post-fishing period) in 2017. To further track potential fishing influences, we sampled during two additional post-fishing periods from November to December in 2018 and 2019. In each sampling period, a total of 51 sites were sampled across these lakes (GY = 8, HZ = 13, LM = 8, NS = 11, DP = 8, DH = 3), which included littoral, near shore, and open water areas. The number of sampling sites per lake varied by lake area and habitat heterogeneity to represent the overall lake condition, which was determined by following a standard protocol for sampling lakes and reservoirs (Huang, 2000). The same number and locations of sampling sites were sampled for both periods. In each of the 51 sites, both pelagic and benthic multi-mesh gillnets (with mesh sizes ranging from 5 to 55 mm), and a ground trap net (with a mesh size of 5 mm) were employed. These nets were deployed overnight for 12 h at each site. The collected fishes were identified, counted, measured, and weighed. More details about the sampling gears and procedures were presented in a previous study (Guo et al., 2020). We attempted to keep the sampling effort (i.e., sampling frequency, gears used) consistent among these lakes. However, DH was drawn down to a very low water level in late 2019 by the lake management agency, so no post-fishing sampling was conducted in this lake in 2019.

2.3. Data analysis

To calibrate for the differing sampling efforts among lakes, fish abundances, biomasses, and dominant species were quantified for each sampling site first and then we averaged the results from the multiple sites for each lake. Fish abundance and biomass were calibrated as CPUE-a and CPUE-b for later analysis, respectively. The dominance index (DI) was used to determine the dominant species of each lake, which was calculated by counting the relative abundance (RA), relative biomass (RB), and frequency of occurrence (f) of each species in the lake, where $DI = (RA + RB) \times f$. Species with the top six DI values in a given lake were defined as dominant species. Fish α -diversity and equitability were measured using species richness (SR) and the Pielou evenness (J) index, respectively. We used the Scheiner-Ray-Hare test to assess the effects of lake, fishing period, and their interactions on abundance, biomass, and diversity indices. If there was an interaction between lake and fishing period, then a Kruskal-Wallis test and multiple comparison test were conducted separately to identify group differences.

Fish life-history traits were obtained from the published literature (Winemiller and Rose, 1992; Li, 2012; Pecuchet et al., 2017) and Fishbase (www.fishbase.org). A total of 7 trait parameters were used for the analysis of fish life-history strategies: egg size, fecundity, age at maturity, body length at maturity, longevity, maximum body length, and parental care (Winemiller and Rose, 1992; Li, 2012). For some species lacking data, we referred to species of the same genus. Principal Component Analysis (PCA) based on a covariance matrix was used to analyze life history parameters and screen important variables. The life history parameters of each species were analyzed by hierarchical clustering. The tri-lateral continuum model proposed by Winemiller and Rose (1992) was used to verify the life history strategy of fish in this study. Using the results of cluster analysis, the life history strategies of different groups of fish were compared, and the least-range method was used to quantify variance of the mean value (Winemiller and Rose, 1992; Li, 2012). Based on clustering results, fish life history strategies in the studied lakes were divided into: periodic, equilibrium, and opportunistic strategies (Winemiller and Rose, 1992; Li, 2012, Pecuchet et al., 2017 Table S2). Fish with high absolute fecundity and late age at maturity were assigned to the periodic strategy. Species with high energy allocation to each pre-larva and a small number of pre-larva were assigned to the equilibrium strategy. Species with short initial sexual maturity, low energy

allocation to each pre-larva, and low absolute reproductive capacity were assigned to the opportunistic strategy (Winemiller and Rose, 1992; Li, 2012). Both a ternary graph and boxplots were used to detect life history strategy patterns of fish assemblages and the differences between the pre- and post-fishing periods. The relative abundances of fish with the three different life history strategies at each sampling site were used as a coordinate point on the ternary plot, and the clustering trend of the coordinate points was used to reveal the composition pattern of fish life history strategies in different lakes between the pre- and post-fishing periods. The ternary graph and boxplot were developed in R (R Core Team, 2019) with the “ggtern” and “ggplot2” packages.

We first conducted multiple comparison tests to assess differences among lakes across each fishing period and used Non-metric Multidimensional Scaling (NMDS) to display differences in assemblage structure among lakes. We then performed two-way Permutational Multivariate Analyses of Variance (perMANOVA) tests with 999 permutations based on Bray-Curtis dissimilarity matrices of species relative abundances to test for differences in fish assemblages among lakes and between fishing periods. We ran a permutation test for homogeneity of multivariate dispersions by using the “betadisper” function in the R package “vegan” (Jari et al., 2019) to test that the perMANOVA result did not occur because of differences in group dispersions. To assess the similarity of fish assemblages amongst lakes over time, analysis of similarities (ANOSIM) with 999 permutations based on Bray-Curtis distance was used to test for differences within lakes and among lakes between fishing periods. We finally used coefficients of Adonis models to identify the key species that determined differences in fish assemblage structure between fishing periods, and a heat map was developed to detect the contribution of each species. A statistical difference was considered as significant when $P < 0.05$. Analysis of perMANOVA and NMDS were carried out using the “vegan” package in R.

3. Results

3.1. Fish abundance, biomass, diversity, and life history strategy

In 2017, a total of 14,368 fish specimens were collected from the six lakes, comprising 44 species, 6 orders, 13 families, and 36 genera (Table S2). A total of 39 and 30 species were collected in the pre- and post-fishing periods, respectively. GY, HZ, LM, NS, DP, and DH had a total of 22, 22, 19, 24, 18, and 15 species in the pre- and 16, 18, 14, 19, 18, and 18 species in the post-fishing periods, respectively. The most diverse families collected were Cyprinidae (26 species, accounting for 59.1%) and Bagridae (4 species, accounting for 9.1%) in these lakes. All other families were represented by one or two species in each lake. With respect to life history strategies, a total of 20 species belonged to the opportunistic strategy (mainly small-bodied fish such as *Toxabramis swinhonis* and *Coilia nasus*). A total of 11 species belonged to the equilibrium strategy (such as *Tridentiger bifasciatus* and *Sarcocheilichthys nigripinnis*). Lastly, 13 species belonged to the periodic strategy (mainly large-bodied, piscivorous fish, such as *Culter alburnus* and *Siniperca chuatsi*). In the pre-fishing period, fish with the opportunistic strategy accounted for 85.14% of the total abundance, while fish with equilibrium and periodic strategies accounted for 13.56% and 1.30%, respectively. In the post-fishing period, the abundance of fish with the opportunistic strategy accounted for 75.39%, while those with equilibrium and periodic strategies accounted for 20.43% and 4.18%, respectively. For all fishing lakes (AF), both abundance and biomass significantly decreased after fishing (Fig. 2a and b). For the non-fishing lake, DH, both abundance and biomass significantly increased in the post-fishing period (Fig. 2a and b).

No significant differences in fish species richness were found among lakes, but there was a significant difference between fishing periods (Table 1). Abundance differed between fishing periods and among lakes, but biomass differed significantly only between fishing periods (Table 1; Fig. 2a and b). The Pielou index differed significantly among lakes and

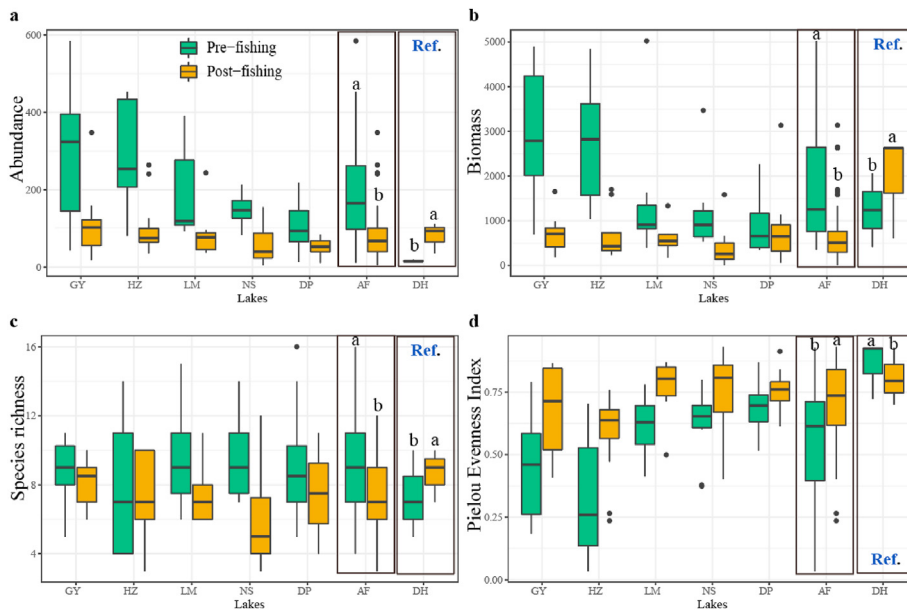


Fig. 2. Comparisons of fish (a) abundance as individuals per unit effort, (b) biomass as weight in grams per unit effort, (c) species richness, and (d) Pielou evenness index between pre- and post-fishing periods of studied lakes. Note: Different letters above the boxes indicate a significant difference between fishing periods; GY, HZ, LM, NS, DP, AF, and DH refer to Gaoyou Lake, Hongze Lake, Luoma Lake, Nansi Lake, Dongping Lake (all fishing lakes), and non-fishing reference Donghu Lake, respectively. The non-fished reference lake DH is highlighted as Ref. in blue text.

Table 1

Effects of fishing period, lake, and their interactions on fish abundance, biomass, and diversity indices. H is the Scheirer-Ray-Hare test.

	Fishing period		Lake		Fishing period * Lake	
	H	P	H	P	H	P
Abundance	52.257	<0.001	17.306	0.008	8.438	0.208
Biomass	57.230	<0.001	11.693	0.069	9.893	0.129
Species richness	10.859	<0.001	2.527	0.866	6.452	0.374
Pielou	26.644	<0.001	25.183	<0.001	2.498	0.869

Significant *P* values (*P* < 0.05) are in bold font.

between fishing periods (Table 1). In all fishing lakes, species richness significantly decreased while the Pielou index significantly increased after fishing (Fig. 2c and d). In the non-fishing lake, species richness, abundance, and biomass significantly increased while the Pielou index significantly decreased in the post-fishing period (Fig. 2c and d).

Small-bodied fishes (mostly with the opportunistic life history strategy) dominated samples and varied among lakes and fishing periods (Table S3). The most abundant species were *Coilia nasus* (Engraulidae) (36.41% of total catch), *Toxabramis swinhonis* (Cyprinidae) (23.39% of total catch), *Pseudorasbora parva* (Cyprinidae) (12.48% of total catch), and *Hemiculter leucisculus* (Cyprinidae) (6.76% of total catch) (Table S3).

Both richness and abundance of large-bodied or piscivorous fishes (mostly with the periodic life history strategy, e.g. *Culter alburnus* (Cyprinidae), *Channa argus* (Channidae) in all fishing lakes were higher in the pre- (in total, 7 species and 42 individuals) than the post-fishing (in total, 5 species and 24 individuals) periods. In the non-fishing lake, their richness remained the same (2 species), but abundance was lower for pre- (3 individuals) than for post-fishing (26 individuals) periods.

In both the pre- and post-fishing periods, fishes of the opportunistic life-history strategy were dominant, followed by the equilibrium life-history strategy (Fig. 3a). In fishing lakes, fishes of all three life-history strategies were significantly less common during the post-fishing period (Fig. 3b). In the reference lake, fishes with both the opportunistic and periodic life-history strategies were significantly more common during the post-fishing period (Fig. 3c).

3.2. Similarity of fish assemblage structure

Multivariate ordination (NMDS) showed only partial overlaps in fish

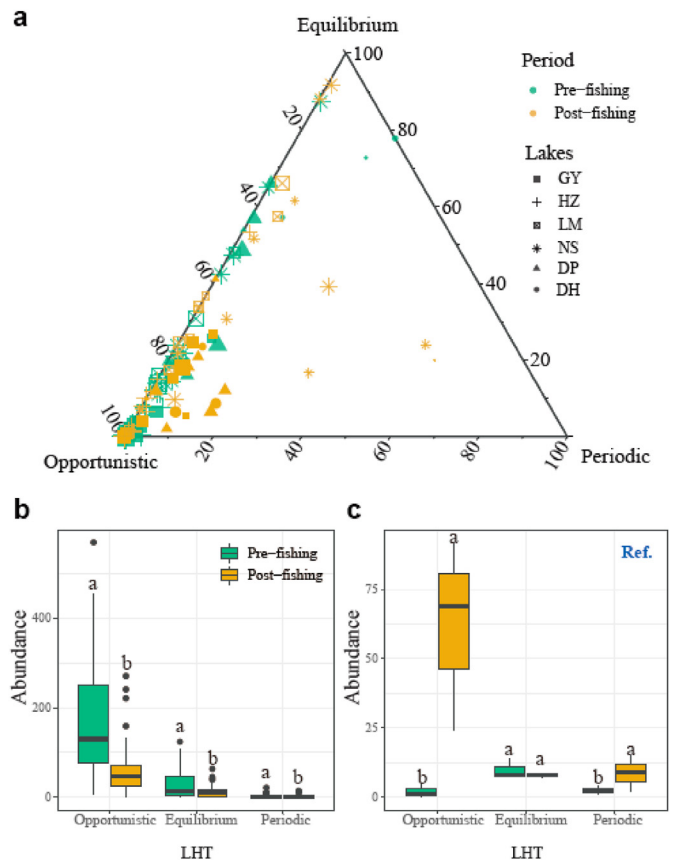


Fig. 3. A ternary plot and boxplots illustrating fish species in (a) relative proportions of opportunistic, periodic, and equilibrium life-history strategies, and their changes in abundance in (b) fishing lakes and (c) the reference lake between pre- and post-fishing periods. In the ternary plot, the different symbols represent sampling sites of different lakes, and the symbol sizes represent the mean fish abundance at each site.

assemblages among fishing lakes during the pre-fishing period in 2017 (Fig. 4a). Most of these overlaps were only observed between adjacent lakes, i.e., between HZ and GY, GY and LM, between LM and NS, and between NS and DP (Fig. 4a). During the post-fishing period in 2017, fish

assemblages became overlapped among all studied lakes, except between HZ and NS (Fig. 4b). Fish assemblages had more overlap among lakes following two post-fishing periods in 2018 and 2019 such that differences between lakes became smaller over the years (Fig. 4c and d). The ANOSIM showed the similarity of fish assemblages between lakes increased from 2017 to 2019 (i.e., $R_{\text{pre-fishing 2017}} > R_{\text{post-fishing 2017}} > R_{\text{post-fishing 2018}} > R_{\text{post-fishing 2019}}$) (Fig. 4a–d).

There were significant lake and fishing period effects on fish assemblage structure (two-way perMANOVA: Table 2). Fish assemblages significantly differed between pre- and post-fishing periods in all five fishing lakes, but no significant difference was detected in the non-fishing lake (Table 2), and betadisper results showed that the assemblage structure difference between fishing periods was statistically stable except for Nansi Lake. The decreases of *Hemiculter leucisculus* (Cyprinidae), *Rhinogobius giurinus* (Gobiidae), *Salanx chinensis* (Salangidae), *Hyporhamphus intermedius* (Hemiramphidae), *Toxabramis swinhonis* (Cyprinidae), *Acheilognathus chankaensis* (Cyprinidae), *Carassius auratus* (Cyprinidae), *Coilia nasus* (Engraulidae), *Tridentiger bifasciatus* (Gobiidae), and *Hemiculter bleekeri* (Cyprinidae) were key factors contributing to differences between fishing periods in fishing lakes. The increase of *Hemiculter leucisculus* (Cyprinidae), *Toxabramis swinhonis* (Cyprinidae), *Acheilognathus macropterus* (Cyprinidae), and *Hemibarbus maculatus* (Cyprinidae) was the key factor contributing to differences between fishing periods in the non-fishing lake (Fig. S1).

4. Discussion

4.1. Fish abundance, biomass, diversity, and life-history strategy

Fish abundance, biomass, and species richness in all fishing lakes were significantly reduced in the post-fishing period compared to the pre-fishing period, while the non-fishing lake showed opposite trends. This result indicates that current unselective fishing practices deplete fishery resources of fishing lakes as reported by others (Allan et al., 2005; Kantoussan et al., 2018). We observed a decrease in species richness such that some species were not observed at all after fishing despite the same sampling effort, which may indicate significant declines in the

Table 2

Two-way perMANOVA analysis of lake and fishing period effects on fish assemblage structure, and comparisons between fishing periods for each lake and permutation test for homogeneity of multivariate dispersions.

Analysis	Parameter	Adonis		Betadisper	
		F	P	F	P
Main effect	Lake	8.291	0.001	2.674	0.008
	Fishing period	9.711	0.001	0.978	0.323
Between fishing periods	GY	2.887	0.010	1.833	0.212
	HZ	3.470	0.012	0.101	0.758
	LM	5.249	0.001	0.235	0.635
	NS	5.944	0.001	13.931	0.001
	DP	6.911	0.001	0.617	0.449
	DH	7.673	0.100	4.232	0.201

Note: Significant P values ($P < 0.05$) were highlighted.

populations of these species.

Although fishing in our fishing lakes was unselective, large-bodied species or individuals showed a greater change compared to smaller species. High long-term fishing mortality of large individuals may reduce breeding stocks in lakes because egg production or quality, sustainability, and recruitment are positively correlated with the age, size, and experience of egg-laying females (Britten et al., 2014; Kantoussan et al., 2018; Dunlop et al., 2019). Reducing the size of large individuals within a stock not only affects recruitment success, but also affects the structure and dynamics of fish stocks (Kantoussan et al., 2018). In the fishing lakes studied, the high annual fishing pressure may have increased the mortality rate of larger more economically valuable individuals and directly decreased their abundance, leading to an indirect reduction in the predation of small-bodied fishes.

Under the effects of long-term overexploitation, species that can better balance adult mortality with compensatory responses (e.g., early sexual maturation, increased fertility) may show more sustainable population dynamics over time (Kantoussan et al., 2018; Claireaux et al., 2018). In fishing lakes, high exploitation pressure led to a decrease in larger individuals, and the dominant species were small, short-lived fish. Our analyses of life-history strategies suggest that the fish assemblages in

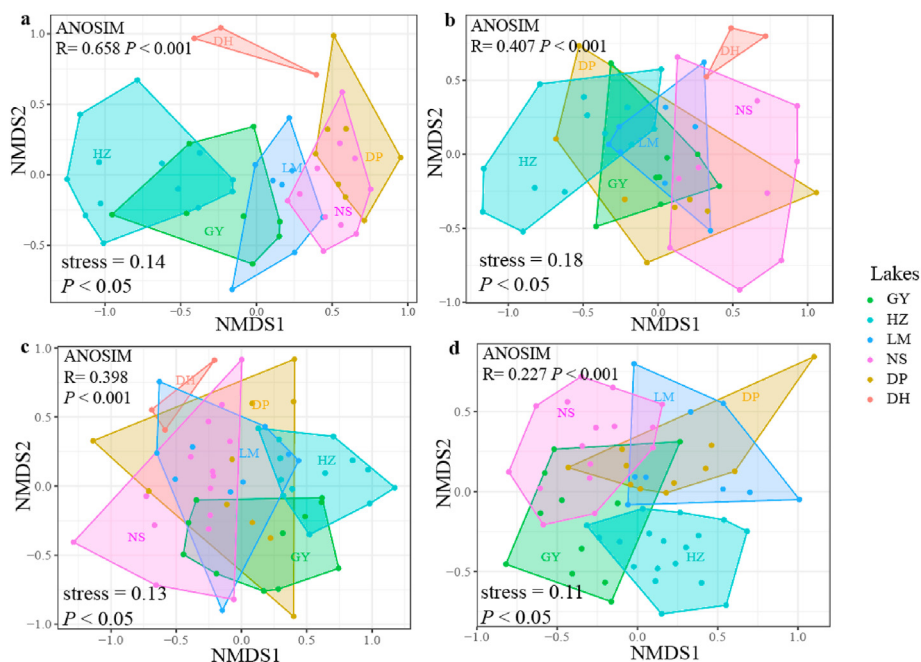


Fig. 4. Non-metric multidimensional scaling on the relative abundance of species at sampling sites in studied lakes during (a) the 2017 pre-fishing period, (b) the 2017 post-fishing period, (c) the 2018 post-fishing period, and (d) the 2019 post-fishing period. Note: Dots represent sites and shaded polygons are the convex hulls of lakes. The ANOSIM results are shown in the upper left corner. $p < 0.05$ indicates a significant difference.

the fishing lakes were subjected to high fishing pressure in two ways. 1) There was a significant reduction of fish species with the periodic strategy (e.g., *Culter alburnus*, *Cyprinus carpio*) in fishing lakes but a significant increase of these fish species in the reference lake. 2) There was an absolute dominance of fish species with the opportunistic (e.g., as *Coilia nasus*, *Toxabramis swinhonis*) and equilibrium (e.g., *Abbottina rivularis*, *Mylopharyngodon piceus*) strategies in the fishing lakes. Our results indicate that unselective fishing practices may not sustain fish populations and could potentially lead to significant decreases of fishery resources and fish diversity in these fishing lakes and others managed similarly (Walsh et al., 2004).

Fish species richness was reduced and more evenly distributed in fishing lakes after fishing. In previous studies, high fishing pressure led to a loss of biodiversity (Bianchi et al., 2000; Dulvy et al., 2003), which could compromise the capacity for population renewal for species most vulnerable to intense and constant fishing pressure (Greenstreet et al., 1999; Dulvy et al., 2003). In addition, fishing pressure could lead to a disproportionate decrease in the abundance of individual species and increase evenness between species, as the removal of more abundant species could increase evenness and lead to the anomalous conclusion that high fishing pressure improves diversity (Rice, 2000).

The composition and dominance of life-history traits did not show significant changes after fishing, which is consistent with previous studies on freshwater systems. For example, Wang et al. (2014) found no significant difference in mean trophic levels of fish in several freshwater lakes based on commercial fishing catch surveys. Pauly et al. (2001) also reported that inland waters did not show the same decline in trophic levels as observed in fish landings from marine systems. This is likely because the fish stocks in many freshwater lakes have already been overexploited or depleted because of their small size and greater accessibility by fishers (Pauly et al., 2001).

We observed increased species richness in the reference lake. This may have been a result of the difficulties of collecting rare or spatially rare (patchily occurring) fish species (Hughes et al., 2021) or a function of insufficiently employed sampling gears (Dunn and Paukert, 2020). Because there was no fishing pressure in DH, some uncommon fish species could have become more abundant, and thus more likely detected, during the post-fishing period.

4.2. Similarity of fish assemblage structure

There was a significant change in the fish assemblage structure after fishing in studied lakes, which was driven by changes in the abundance of dominant species and absence of some fish species compared to the pre-fishing period. Among these, the average abundance of the main dominant species; *Coilia nasus*, *Toxabramis swinhonis*, and *Hemiculter leucisculus*, decreased by 39.6%, 39.8%, and 69.8%, respectively. The 2017 catch data in these lakes showed that these species were the main targets of catches, accounting for 10–30% of the total annual catch. In addition, there were many discarded and uncounted catch yields for those low economic value species through bycatch, so fishing mortality in these lakes could be much higher than reported (Hall et al., 2000; Lescauwae et al., 2013).

Analysis of the fish assemblage structure also indicated that current unselective fishing practices could homogenize fish assemblage in the studied lakes. Historically, fish composition among the studied lakes was significantly different (Guo et al., 2015, 2019b). The current study indicated that unselective fishing in these lakes can change fish assemblage structure and reduce their diversity, in addition to the possibility of increasing biological homogeneity (described previously by Qin et al., 2019). The current unselective fishing in the studied lakes has led to the decline of natural fishery resources and an increase in evenness, and may ultimately have long-term implications on the entire lake ecosystems (McIntyre et al., 2016; Lian et al., 2016).

During the pre-fishing period, water diversions were occurring and high-water levels flooded the littoral zone of these lakes. This increased

habitat heterogeneity and organic matter in the water, provided more suitable habitats and food for fish, and supported greater fish assemblage abundance and biomass (Amoros and Bornette, 2002; Jin et al., 2019). After the water diversions ceased, water levels decreased and the hydrological connectivity between the lakes decreased, which reduced the suitable habitat for fish and potentially increased interspecific competition (Thomaz et al., 2007; Winemiller et al., 2016). In the current study, fishing occurred during a period when the water level dropped after the diversion. Intense fishing pressure tends to reduce the population of large piscivorous fish which decreases their predation and regulation of small-sized fish populations. Fish with opportunistic life history strategies such as *C. nasus* and *T. swinhonis* have stronger compensatory and adjustment capacities in the face of intense fishing pressure. Thus, intense fishing can lead to irreversible impacts on the overall structure of fish assemblages (Mao et al., 2019). Although fishing clearly results in fish assemblage changes, impacts to hydrological connectivity through water diversion and decreases in water quality could still play important roles in homogenizing fish assemblages among these lakes (Guo et al., 2020).

4.3. Management implications

Based on our results, managers may want to consider two strategies if they wish to sustain the fish assemblages in these lakes. (1) They could reduce the scale and intensity of current unselective fishing practices by extending the fishing closure period, setting strict target species and size limits, and formulating a fixed catch quota. Such changes would mitigate the degradation of fish stocks in these lakes (Chen et al., 2020). For instance, starting January 2021, lakes of GY, HZ, and LM have temporarily banned fishing for the whole year in accordance with the Chinese Ministry of Agricultural and Rural Affairs (CMARA) fishing ban policy in the Yangtze River Basin. (2) Transition to recreational fisheries in these lakes. Recreational fisheries have shown some advantages in the recovery of freshwater fish assemblages over traditional commercial fisheries in some countries (Ayllón et al., 2018; Dunlop et al., 2019). The transition from traditional unselective fishing to recreational fisheries at appropriate time periods could be a way to preserve the biodiversity and sustainability of fishery resources in the lakes studied. This approach is actually promising because the above-mentioned long-term commercial fishing bans of CMARA have recently been implemented for the Yangtze River Basin. It could be extended to the entire current study area as well as other major Chinese river basins (Chen et al., 2020). Moreover, freshwater recreational fisheries have been expanding in China recently, providing increased economic benefits (CMARA, 2020).

5. Conclusions

The potential assemblage-wide impacts of unselective fishing on freshwater lakes were assessed. We found that:

- (1) Unselective fishing decreased fishery resources, with significant reductions in fish species richness, abundance, and biomass in fishing lakes.
- (2) Unselective fishing reduced the abundance of dominant species and homogenized fish assemblages among fishing lakes.

One limitation of the current study is that only one reference lake was available, and this reference lake was smaller in surface area and had a deeper littoral area than the fishing lakes. This is often a common challenge in nature-based observational studies compared with laboratory or manipulative experiments, because natural systems are not completely controllable or lack sufficiently replicated reference systems (e.g., Schindler et al., 2008; Downes, 2010; Dunlop et al., 2019). The sampling locations and gears used in this study could potentially have introduced selection bias in the fish assemblage sampling. To minimize this bias, we kept sampling the same locations in each lake in different fishing periods. Also, the sampling gears were tested in previous studies (Guo et al., 2020).

and we kept them consistent across fishing periods and lakes. Another point worth mentioning is that the current study only assessed influences over three years of fishing. The potential for long-term fishing impacts on lake ecosystems calls for continued monitoring and assessment of fish assemblages in these lakes whether the current unselective fishing practices persist or not.

The current study has improved our understanding of ecosystem impacts associated with unselective fishing in inland waters. These findings have important implications for protecting both fisheries and biodiversity in inland waters of China, and could also potentially be applied to other countries or regions that rely on fish as major food sources while experiencing overfishing and biodiversity reduction.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.watbs.2022.100055>.

References

- Allan, J.D., Abell, R., Hogan, Z., Revenga, C., Taylor, B.W., Welcomme, R.L., Winemiller, K.O., 2005. Overfishing of inland waters. *Bioscience* 55, 1041–1051. [https://doi.org/10.1641/0006-3568\(2005\)055\[1041:OOIW\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2005)055[1041:OOIW]2.0.CO;2).
- Amoros, C., Bornette, G., 2002. Connectivity and biocomplexity in waterbodies of riverine floodplains. *Freshw. Biol.* 47, 761–776. <https://doi.org/10.1046/j.1365-2427.2002.00905.x>.
- Ayllón, D., Railsback, S.F., Almodóvar, A., Nicola, G.G., Vincenzi, S., Elvira, B., Grimm, V., 2018. Eco-evolutionary responses to recreational fishing under different harvest regulations. *Ecol. Evol.* 8, 9600–9613. <https://doi.org/10.1002/ece3.4270>.
- Bianchi, G., Gislason, H., Graham, K., Hill, L., Jin, X., Koranteng, K., et al., 2000. Impact of fishing on size composition and diversity of demersal fish communities. *ICES J. Mar. Sci.* 57, 558–571. <https://doi.org/10.1006/jmsc.2000.0727>.
- Botsford, L.W., Castilla, J.C., Peterson, C.H., 1997. The management of fisheries and marine ecosystems. *Science* 277, 509–515. <https://doi.org/10.1126/science.277.5325.509>.
- Branch, T.A., Watson, R., Fulton, E.A., Jennings, S., McGilliard, C.R., Pablico, G.T., et al., 2010. The trophic fingerprint of marine fisheries. *Nature* 468, 431–435. <https://doi.org/10.1038/nature09528>.
- Britten, G.L., Dowd, M., Minto, C., Ferretti, F., Boero, F., Lotze, H.K., 2014. Predator decline leads to decreased stability in a coastal fish community. *Ecol. Lett.* 17, 1518–1525. <https://doi.org/10.1111/ele.12354>.
- Chen, Y., Qu, X., Xiong, F., Lu, Y., Wang, L., Hughes, R.M., 2020. Challenges to saving China's freshwater biodiversity: fishery exploitation and landscape pressures. *Ambio* 49, 926–938. <https://doi.org/10.1007/s13280-019-01246-2>.
- Chen, Y., Zhang, S., Huang, D., Li, B., Liu, J., Liu, W., Wang, H., 2017. The development of China's Yangtze River Economic Belt: how to make it in a green way? *Sci. Bull.* 62 (2017), 648–651. <https://doi.org/10.1016/j.scib.2017.04.009>.
- Claireaux, M., Jørgensen, C., Enberg, K., 2018. Evolutionary effects of fishing gear on foraging behavior and life-history traits. *Ecol. Evol.* 8, 10711–10721. <https://doi.org/10.1002/ece3.4482>.
- CMARA (China Ministry of Agriculture and Rural Affairs), 2020. *China Fishery Statistical Yearbook*. Beijing, China.
- Core Team, R., 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL: <https://www.R-project.org/>.
- Downes, B.J., 2010. Back to the future: little-used tools and principles of scientific inference can help disentangle effects of multiple stressors on freshwater ecosystems. *Freshw. Biol.* 55, 60–79. <https://doi.org/10.1111/j.1365-2427.2009.02377.x>.
- Dulvy, N.K., Sadovy, Y., Reynolds, J.D., 2003. Extinction vulnerability in marine populations. *Fish Fish.* 4, 25–64. <https://doi.org/10.1046/j.1467-2979.2003.00105.x>.
- Dunlop, E.S., Goto, D., Jackson, D.A., 2019. Fishing down then up the food web of an invaded lake. *Proc. Natl. Acad. Sci. U. S. A.* 116, 19995–20001. <https://doi.org/10.1073/pnas.1908272116>.
- Dunn, C.G., Paukert, C.P., 2020. A flexible survey design for monitoring spatiotemporal fish richness in nonwadeable rivers: optimizing efficiency by integrating gears. *Can. J. Fish. Aquat. Sci.* 77, 978–990. <https://doi.org/10.1139/cjfas-2019-0315>.
- FAO, 2020. *The State of World Fisheries and Aquaculture*. Rome.
- Greenstreet, S.P.R., Spence, F.B., Shanks, A.M., McMillan, J.A., 1999. Fishing effects in northeast Atlantic shelf seas: patterns in fishing effort, diversity and community structure. V. Changes in structure of the North Sea groundfish species assemblage between 1925 and 1996. *Fish. Res.* 40, 153–183. [https://doi.org/10.1016/S0165-7836\(98\)00210-0](https://doi.org/10.1016/S0165-7836(98)00210-0).
- Guo, C., Lek, S., Ye, S., Li, W., Liu, J., Chen, Y., Li, Z., 2015. Predicting fish species richness and assemblages with climatic, geographic and morphometric factors: a broad-scale study in Chinese lakes. *Limnologia* 54, 66–74. <https://doi.org/10.1016/j.limno.2015.08.002>.
- Guo, C., Chen, Y., Liu, H., Lu, Y., Qu, X., Yuan, H., et al., 2019a. Modelling fish communities in relation to water quality in the impounded lakes of China's South-to-North Water Diversion Project. *Ecol. Model.* 397, 25–35. <https://doi.org/10.1016/j.ecolmodel.2019.01.014>.
- Guo, C., Chen, Y., Gozlan, R.E., Li, Z., Mehner, T., Lek, S., Paukert, C.P., 2019b. Biogeographic freshwater fish pattern legacy revealed despite rapid socio-economic changes in China. *Fish Fish.* 20, 857–869. <https://doi.org/10.1111/faf.12380>.
- Guo, C., Chen, Y., Gozlan, R.E., Liu, H., Lu, Y., Qu, X., et al., 2020. Patterns of fish communities and water quality in impounded lakes of China's south-to-north water diversion project. *Sci. Total Environ.* 713, 136515. <https://doi.org/10.1016/j.scitotenv.2020.136515>.
- Hall, M.A., Alverson, D.L., Metzuzal, K.I., 2000. By-catch: problems and solutions. *Mar. Pollut. Bull.* 41, 204–219. <https://doi.org/10.1016/S0025>.
- Hortle, K.G., Lieng, S., Valbo-Jørgensen, J., 2004. An introduction to Cambodia's Inland Fisheries. Phnom Penh (Cambodia): Mekong River Commission. In: *Mekong Development Series* no. 4.
- Hsieh, C., Yamauchi, A., Nakazawa, T., Wang, W., 2010. Fishing effects on age and spatial structures undermine population stability of fishes. *Aquat. Sci.* 72, 165–178. <https://doi.org/10.1007/s00027-009-0122-2>.
- Huang, X., 2000. *Ecological Investigation, Observation, and Analysis for Lakes*. Standards Press of China, Beijing, China, pp. 95–96.
- Hughes, R.M., Herlihy, A.T., Peck, D.V., 2021. Sampling efforts for estimating fish species richness in western USA river sites. *Limnologia* 87, 125859. <https://doi.org/10.1016/j.limno.2021.125859>.
- Jari, O., Blanchet, F.G., Michae, F.L., Roeland, K., Pierre, L., Dan, M., Wagner, H., 2019. vegan: community ecology package. R package version 2.5-6. <https://CRAN.R-project.org/package=vegan>.

- Jennings, S., Kaiser, M.J., 1998. The effects of fishing on marine ecosystems. *Adv. Mar. Biol.* 34, 201–352. [https://doi.org/10.1016/S0065-2881\(08\)60212-6](https://doi.org/10.1016/S0065-2881(08)60212-6).
- Jin, B.S., Winemiller, K.O., Shao, B., Si, J., Jin, J., Ge, G., 2019. Fish assemblage structure in relation to seasonal environmental variation in sub-lakes of the Poyang Lake floodplain, China. *Fish. Manag. Ecol.* 26, 131–140. <https://doi.org/10.1111/fme.12333>.
- Kantoussan, J., Raymond, L., Mbaye, T., 2018. Review of the fisheries indicators for monitoring the impacts of fishing on fish communities. *Rev. Fish. Sci. Aquac.* 26, 1–19. <https://doi.org/10.1080/23308249.2018.1458282>.
- King, J.R., McFarlane, G.A., 2003. Marine fish life history strategies: applications to fishery management. *Fish. Manag. Ecol.* 10, 249–264. <https://doi.org/10.1046/j.1365-2400.2003.00359.x>.
- Lescrauwaet, A.K., Torrelee, E., Vincx, M., Polet, H., Mees, J., 2013. Invisible catch: a century of bycatch and unreported removals in sea fisheries, Belgium 1929–2010. *Fish. Res.* 147, 161–174. <https://doi.org/10.1016/j.fishres.2013.05.007>.
- Li, M.Z., 2012. Study on the Life History Strategies of Fishes in the Yangtze River and its Adaption to Environment during Early Life History Stage. Institute of Hydrobiology, Chinese Academy of Sciences. PhD Thesis.
- Lian, Y., Liu, J., Chen, Y., Yuan, J., Li, Z., 2016. Development and reform of lake commercial fisheries in the Yangtze River Basin, China. Pages 79–90. In: Chen, Y., Chapman, D.C., Jackson, J.R., Chen, D., Li, Z., Kilgore, K.J., Phelps, Q., Eggleton, M.A. (Eds.), *Fisheries Resources, Environment, and Conservation in the Mississippi and Yangtze (Changjiang) River Basins*, vol. 84. *Am. Fish. Soc. Symp.*, Bethesda, Maryland.
- Mao, Z., Gu, X., Gong, Z., Zeng, Q., Chen, H., Li, H., et al., 2019. The structure of fish community and changes of fishery resources in Lake Hongze. *J. Lake Sci.* 31, 1109–1119 (in Chinese with English abstract).
- McIntyre, P.B., Reidy Liermann, C.A., Revenga, C., 2016. Linking freshwater fishery management to global food security and biodiversity conservation. *Proc. Natl. Acad. Sci. U. S. A.* 113, 12880–12885. <https://doi.org/10.1073/pnas.1521540113>.
- Olden, J.D., Poff, N.L., Bestgen, K.R., 2006. Life-history strategies predict fish invasions and extirpations in the Colorado River Basin. *Ecol. Monogr.* 76, 25–40.
- Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres Jr., F., 1998. Fishing down marine food webs. *Science* 279, 860–863. <https://doi.org/10.1126/science.279.5352.860>.
- Pauly, D., Palomares, M.L.D., Froese, R., Sa-a, P., Vakily, M., Preikshot, D., Wallace, S., 2001. Fishing down Canadian food webs. *Can. J. Fish. Aquat. Sci.* 58, 51–62. <https://doi.org/10.1139/cjfas-58-1-51>.
- Pecuchet, L., Lindegren, M., Hidalgo, M., Delgado, M., et al., 2017. From traits to life-history strategies: deconstructing fish community composition across European seas. *Global Ecol. Biogeogr.* 26, 812–822. <https://doi.org/10.1111/geb.12587>.
- Pianka, E.R., 1970. On r - and K -selection. *Am. Nat.* 104, 592–597.
- Qin, J., Cheng, F., Zhang, L., Schmidt, B.V., Liu, J., Xie, S., 2019. Invasions of two estuarine gobiid species interactively induced from water diversion and saltwater intrusion. *Manag. Biol. Invasion.* 10, 139–150. <https://doi.org/10.3391/mbi.2019.10.1.09>.
- Qu, X., Chen, Y., Liu, H., Xia, W., Lu, Y., Gang, D.D., Lin, L.S., 2020. A holistic assessment of water quality condition and spatiotemporal patterns in impounded lakes along the Eastern Route of China's South-to-North Water Diversion Project. *Water Res.* 185, 116275. <https://doi.org/10.1016/j.watres.2020.116275>.
- Reid, A.J., Carlson, A.K., Creed, I.F., Eliason, E.J., Gell, P., Johnson, P.T.J., et al., 2019. Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biol. Rev.* 94, 849–873. <https://doi.org/10.1111/brv.12480>.
- Rice, J.C., 2000. Evaluating fishery impacts using metrics of community structure. *ICES J. Mar. Sci.* 57, 682–688. <https://doi.org/10.1006/jmsc.2000.0735>.
- Schindler, D.W., Hecky, R.E., Findlay, D.L., Stainton, M.P., Parker, B.R., Paterson, M.J., et al., 2008. Eutrophication of lakes cannot be controlled by reducing nitrogen input: results of a 37-year whole-ecosystem experiment. *Proc. Natl. Acad. Sci. U. S. A.* 105, 11254–11258. <https://doi.org/10.1073/pnas.0805108105>.
- Su, G., Logez, M., Xu, J., Tao, S., Villéger, S., Brosse, S., 2021. Human impacts on global freshwater fish biodiversity. *Science* 371, 835–838. <https://doi.org/10.1126/science.abd3369>.
- Thomaz, S.M., Bini, L.M., Bozelli, R.L., 2007. Floods increase similarity among aquatic habitats in river-floodplain systems. *Hydrobiologia* 579, 1–13. <https://doi.org/10.1007/s10750-006-0285-y>.
- Tickner, D., Opperman, J.J., Abell, R., Acreman, M., Arthington, A.H., Bunn, S.E., et al., 2020. Bending the curve of global freshwater biodiversity loss – an emergency recovery plan. *Bioscience* 70, 330–342. <https://doi.org/10.1093/biosci/biaa002>.
- Verberk, W.C.E.P., van Noordwijk, C.G.E., Hildrew, A.G., 2013. Delivering on a promise: integrating species traits to transform descriptive community ecology into a predictive science. *Freshw. Sci.* 32 (2), 531–547.
- Walsh, M.R., Munch, S.B., Chiba, S., Conover, D.O., 2004. Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. *Ecol. Lett.* 9, 142–148. <https://doi.org/10.1111/j.1461-0248.2005.00858.x>.
- Wang, S., Dou, H., 1998. *Lakes of China*. Science Press, Beijing, China.
- Wang, Y., Xu, J., Yu, X., Lei, G., 2014. Fishing down or fishing up in Chinese freshwater lakes. *Fish. Manag. Ecol.* 21, 374–382. <https://doi.org/10.1111/fme.12088>.
- Winemiller, K.O., 1989. Patterns of variation in life history among South American fishes in seasonal environments. *Oecologia* 81, 225–241.
- Winemiller, K.O., 1992. Life-history strategies and the effectiveness of sexual selection. *Oikos* 63, 318–327. <https://doi.org/10.2307/3545395>.
- Winemiller, K.O., Rose, K.A., 1992. Patterns of life history diversification in North American fishes: implications for population regulation. *Can. J. Fish. Aquat. Sci.* 49, 2196–2218. <https://doi.org/10.1126/science.aac7082>.
- Winemiller, K.O., McIntyre, P.B., Castello, L., Fluet-Chouinard, F., Giarrizzo, T., et al., 2016. Balancing hydropower and biodiversity in the Amazon, Congo, and Mekong. *Science* 351, 128–129. <https://doi.org/10.1126/science.aac7082>.