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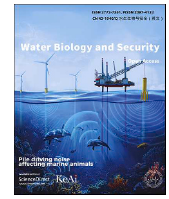

Research Article

Spatiotemporal dynamics and interrelationships of fish assemblages and environment under stocking-based ecological fisheries practices: Insights from Qiandao Lake

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ABSTRACT

Qiandao Lake, a key drinking water reservoir and a national model for Stocking-based Ecological Fisheries (SEF) in China, has been intensively managed to balance fishery productivity with ecological health. We investigated the spatiotemporal dynamics of its fish assemblage and its interactions with water quality, phytoplankton, zooplankton, and macrobenthos. Non-Metric Multidimensional Scaling (NMDS) and Analysis of Similarities (ANOSIM) highlighted seasonal and spatial disparities in fish assemblage structure. Machine learning models demonstrated that water quality variables were strong predictors of fish and assemblage composition than biotic indicators. Phytoplankton and zooplankton density and biomass predominantly influenced fish abundance. Non-native species have steadily increased in abundance and biomass, coupled with a decline in native piscivorous fish, indicating the need to change fishing bans and enhance protected areas.

1. Introduction

Fish play a pivotal role in lake ecosystems, influencing other components through food web control and nutrient cycling (Jeppesen et al., 2010; Birk et al., 2020). The structure and diversity of fish assemblages are fundamental to maintaining ecosystem functioning, biodiversity, and overall stability in aquatic systems (Villéger et al., 2017; Reid et al., 2019). Various factors, including water quality, hydrological conditions, adjacent land use, and other water-body uses collectively shape fish assemblage structure (Xiong et al., 2021). Among these, water quality directly affects fish life history traits, distribution, productivity, and interactions with other biota (Downing and Plante, 1993; Yang et al., 2023).

Freshwater fish stocking in lakes and reservoirs is a common strategy worldwide (Lorenzen, 2008). Although stocking aims to improve fishery production, restore fish populations, and manage aquatic ecosystems, it also raises ecological concerns, particularly when stocking is not conducted using evidence-based practices (Cucherousset and Olden, 2020). In China, fish stocking practices are extensively employed to enhance fishery yields, control phytoplankton biomass, and mitigate algal blooms, particularly through introducing filter-feeding species such as silver carp *(Hypophthalmichthys molitrix)* and bighead carp *(Hypophthalmichthys nobilis)* (Liu et al., 2020). Studies have shown that in many large water bodies, appropriate stocking levels of silver carp and bighead carp have effectively controlled phytoplankton biomass and helped prevent algal blooms (Chen et al., 2012; Li et al., 2017). Simultaneously, fish harvesting provides substantial amounts of high-quality protein and contributes economic value (Boyd et al., 2022; Song et al., 2022). However, inappropriate ratios or quantities can also disrupt aquatic ecosystems and pose ecological threats (Ke et al., 2009; Li et al., 2023). For instance, irrational stocking of filter-feeding fish can lead to reduced water transparency and phytoplankton proliferation. This primarily results from sediment suspension by bighead and silver carps, which decreases water clarity and increases phosphorus (P) levels in the water column, thereby promoting phytoplankton growth (Lin et al., 2020; Su et al., 2023). Given these considerations, the impacts of fish

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stocking on aquatic ecosystems should be analyzed comprehensively and comparatively, incorporating multiple perspectives such as the water environment, other aquatic organisms, and fish assemblages.

The Stocking-Based Ecological Fisheries (SEF) paradigm represents an integrated fisheries management strategy designed to balance aquaculture production with ecosystem health (Liu et al., 2020). SEF emphasizes the use of rational stocking and harvesting practices to enhance fishery yields while maintaining ecosystem stability. This approach has gained widespread application in China's lakes and reservoirs, which offer abundant large water surface resources well-suited for the development of stocking-based ecological fisheries (Liu et al., 2010; Wang et al., 2015). Effective implementation of such fisheries in these large water bodies can bring considerable ecological and economic benefits. However, there are still no uniform standards exist for fish stocking, harvesting types, quantities, or timings in stocking-based fisheries. Understanding the interactions between fish assemblages and water quality during stocking is crucial for developing effective fishery management plans (Liu et al., 2020). The interactions between fish assemblages and water quality under the SEF framework remain poorly understood. Furthermore, quantitative insights into the spatio-temporal dynamics of fish assemblages and their interactions with water quality are crucial for developing evidence-based SEF strategies applicable to other systems.

The core issue addressed in this study was: What are the spatio-temporal dynamics and interactions between the fish assemblages, water quality, phytoplankton, zooplankton, and macrobenthos in Qiandao Lake? We predicted that water quality would have a greater influence on fish assemblage structure than biotic indicators (phytoplankton, zooplankton, macrobenthos), but that prey density would significantly affect fish abundance and biomass.

2. Materials and methods

2.1. Study area

Qiandao Lake, located in Zhejiang Province, China, is a deep-water reservoir spanning approximately 580 km^2, with a storage capacity of around 17.8 billion m^3. Renowned for its good water quality, the lake serves as a tourist destination, a drinking water source for Eastern China, and a successful example of decades of SEF (Sun et al., 2020). The SEF in Qiandao Lake prioritizes the stocking of silver (*Hypophthalmichthys molitrix*) and bighead (*Hypophthalmichthys nobilis*) carp, aiming to balance fishery production, biodiversity support, and ecological functions. Qiandao Lake has achieved substantial fishery yields and good water quality via science-based stocking and harvesting, fish protection zones, and fishing moratoria, making it a national model for SEF (Deng et al., 2022; Gu et al., 2016, 2015).

This study encompassed five major lake zones: Northeast (NE), Northwest (NW), Central (CT), Southeast (SE), and Southwest (SW), each with three designated sampling sites, amounting to a total of 15 sites (Fig. 1). The CT zone is a year-round no-capture zone, whereas the other zones are subject to seasonal fishing bans (from March to June). Additionally, the SE zone has the highest average depth and is less influenced by surrounding human activities. The CT and NW zones are in the center of the lake, with more urbanization and tourism activities around them. In contrast, the NE and SW zones are near the inflow, where cage aquaculture activities are relatively prevalent.

2.2. Fish assemblage sampling

Each year between 2021 and 2023, we sampled in March, June, September, and December, representing spring, summer, autumn, and winter, respectively. We sampled fish for 1 night at all 15 sites for 12

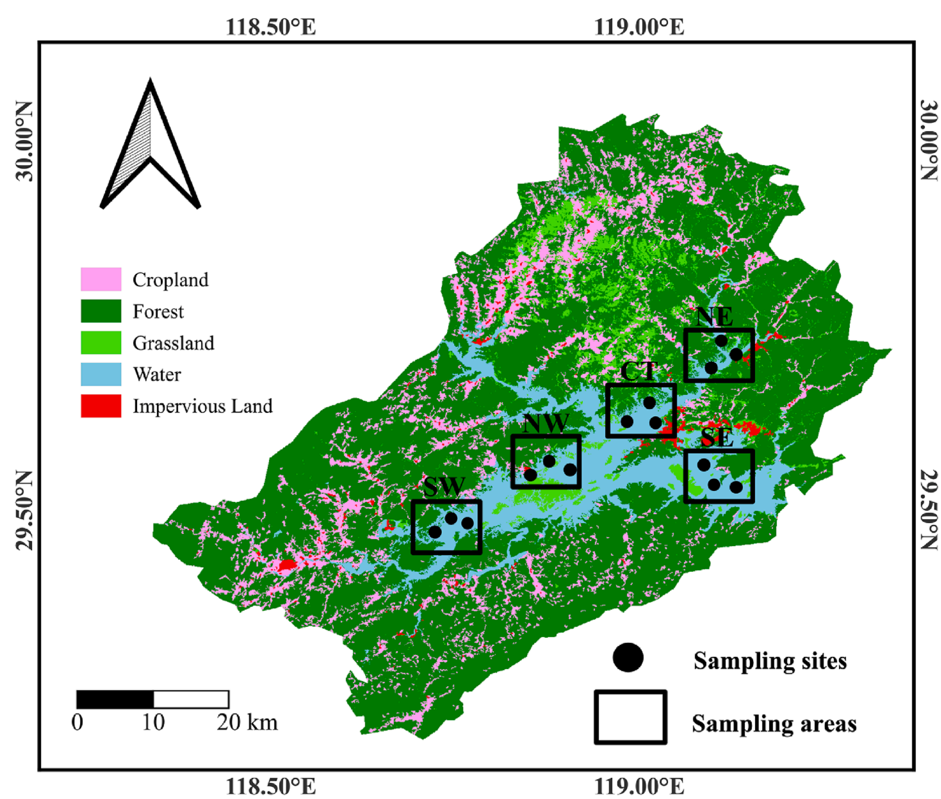

Fig. 1. Fish assemblage zones and sampling sites in Qiandao Lake.

quarters each. To do so, we used 3 gear types: pelagic multi-mesh gillnets, benthic multi-mesh gillnets, and fish traps. Each gillnet consisted of twelve 2.5-m-long mesh panels with 12 mesh sizes (8.5, 4.0, 12.5, 2.0, 11.0, 1.6, 2.5, 4.8, 3.1, 1.0, 7.5, and 6.0 cm) arranged in random order (Appelberg, 2000). The pelagic gillnet was 5-m high and 30-m long, whereas the benthic gillnet was 2-m high and 30-m long. The fish trap was 15-m long, 0.4-m wide, and 0.4-m high, with a 10-mm mesh. At each sampling site, three pelagic multi-mesh gillnets, three benthic multi-mesh gillnets, and two fish traps were deployed overnight from 6:00 p.m. until 6:00 a.m. Live individuals were identified to species, measured (total length & body length), and weighed on-site. Dead individuals were frozen and transported to the laboratory for identification, measurement, and weighing. The number of species captured per set of nets (3 pelagic gillnets, 3 benthic gillnets, 2 fish traps) was used to determine Species Richness (SR), number captured per unit effort (NPUE), and biomass per unit effort (BPUE).

2.3. Water quality monitoring

Water, phytoplankton, zooplankton, and macrobenthos were collected at the same sites as the fish. Water, phytoplankton, and zooplankton were collected using a 5-L plexiglass sampler at depths of 1 m, 6 m, and 11 m, with the samples then thoroughly mixed. The mixed water was placed in a 1 L sample bottle, frozen, and analyzed within 24 h in the laboratory for subsequent water quality analysis. Two types of samples were collected and processed separately. First, 1 L of well-mixed water was transferred into a 1-L sample bottle, and 10 mL of 10 % Lugol's solution was added for fixation of phytoplankton, protozoa, and rotifers. Second, 13 L of the same mixed water was filtered through a 13-μm mesh plankton net to concentrate zooplankton. The retained zooplankton were then transferred into a 100-mL plastic bottle and preserved with 4 % formalin for later identification and quantification. Three sediment samples were collected using a Petersen grab (surface area = 0.0625 m^2) and passed through a 500-μm sieve. The benthic macroinvertebrates were visually sorted from the sediments in a white porcelain pan, rinsed with water, weighed, and preserved in formalin.

In the laboratory, we quantified both density (individuals per cubic meter or square meter) and biomass (mg/m^3 or g/m^2) of phytoplankton, zooplankton, and macrobenthos using standard methods (Hu and Wei, 2006; Huang, 1999; Qu et al., 2018). Phytoplankton samples were settled for 48 h, and cells were counted under a microscope using a Sedgwick-Rafter counting chamber; biomass was estimated based on cell volume converted to wet weight (Hu and Wei, 2006; Zhang and Huang, 1991). Zooplankton samples were concentrated and counted under a stereomicroscope; biomass was calculated using published length–weight relationships (Jiang and Du, 1979; Shen and Du, 1979). Macrobenthos were counted; biomass was determined by wet weight after blotting surface moisture with filter paper (Qu et al., 2018).

At each site, we measured water depth (WD), and Secchi depth (SD). We determined pH, water temperature (WT), dissolved oxygen (DO), conductivity (Cond), and oxidation-reduction potential (ORP) by using a YSI ProPlus meter (Thermo Fisher Scientific, Waltham, USA). In the laboratory, we determined chemical oxygen demand (COD_{Mn}), total nitrogen (TN), total phosphorus (TP), ammonia nitrogen (NH_3-N), nitrite (NO_2^-), nitrate (NO_3^-), phosphate (PO_{4+}), and chlorophyll-a (Chl.a). COD_{Mn} was measured using the acidic potassium permanganate method. TN was analyzed by alkaline potassium persulfate digestion followed by UV spectrophotometry. TP was determined using the ammonium molybdate spectrophotometric method after digestion. NH_3-N was measured using the indophenol blue spectrophotometric method. NO_2^- was determined by the N-(1-naphthyl)-ethylenediamine spectrophotometric method, and NO_3^- was measured by UV spectrophotometry. PO_4^{3-} was analyzed directly by the molybdenum blue spectrophotometric method. Chl.a was extracted with 90 % acetone and quantified by spectrophotometry.

2.4. Data analyses

We used XGBoost modeling to determine relationships between fish response indicators and environmental predictors. The XGBoost model shows superior performance compared to traditional machine learning models (e.g., Random Forest) in handling complex nonlinear relationships, improving prediction accuracy, preventing overfitting, handling missing values, and providing interpretability (Khaira et al., 2024; Zhang et al., 2021; Xu et al., 2024; Sun et al., 2021). SHAP (SHapley Additive exPlanations) scores are based on the Shapley value from game theory and are considered an excellent tool for interpreting black-box machine learning models. SHAP values help one understand the magnitude and direction of the influence of input variables on output variables. The magnitude of SHAP values indicates the importance of each parameter in the XGBoost model (Parsa et al., 2020; Tseng et al., 2020; Lundberg and Lee, 2017). We developed 4 XGBoost models with fish NPUE, BPUE, SR, and SW as the response indicators. The potential predictor variables included 15 water quality variables, and the 6 density and biomass variables described above. The training data were based on 144 samples, with 36 samples used in the validation set. Model performance was evaluated using Coefficient of Determination (R^2), Root Mean Square Error (RMSE) and Mean Absolute Error (MAE). Additionally, the SHAP values for the water quality and density/biomass predictors were calculated for each of the 4 response indicators.

We used the Index of Relative Importance (IRI) to assess fish species numerical dominance. The IRI is calculated using the formula:

$$IRI = (N\% + W\%) \times F\% \times 10{,}000$$

where N% represents the percentage of the number of individuals of a given species relative to the total number of individuals, W% denotes the percentage of the biomass of a given species relative to the total biomass, and F% indicates the percentage of sample occurrences of a given species relative to the total number of samples. Species with an IRI $\geq$1000 were defined as dominant species.

The Kruskal-Wallis test (“FSA” package, R) was used to assess seasonal and spatial differences in NPUE, BPUE, species richness (SR), and Shannon-Wiener index (SW) values (Ogle et al., 2023), with post-hoc comparisons using different letter annotations. Non-Metric Multidimensional Scaling (NMDS) and Analysis of Similarities (ANOSIM) were performed using the “vegan” package to evaluate fish assemblage variations, followed by SIMPER analysis to identify species contributions (Oksanen et al., 2024). Spearman correlation (“linkET” package) was conducted to assess relationships between fish NPUE, BPUE, SR, and SW and water quality (Huang, 2021). Detrended Correspondence Analysis (DCA) was also performed, and due to a gradient length <3 SD, Redundancy Analysis (RDA) was selected over Canonical Correspondence analysis (CCA). Variation Partitioning Analysis (VPA) quantified the effects of environmental and biotic predictors. RDA and VPA were used to quantify the dynamics of predictor variables and fish assemblage response metrics, as well as their interactions. All computations employed the “tidyverse” package, visualizations were generated with “ggplot2” and composite figures were assembled using “patchwork” (Pedersen, 2024; Wickham, 2009). All statistical analyses were conducted in R version 4.3.3 (R Core Team, 2024) with significance set at $p < 0.05$.

3. Results

3.1. Spatial and temporal dynamics of fish assemblages

3.1.1. Fish species composition

Over the three-year study period, we captured 17,483 fish weighing 593.57 kg from the 180 samples, including 64 species, 13 families, and 5 orders. The Cyprinidae dominated 67.19 % of the total catch (Table S1), but *Lepomis macrochirus* (an introduced species from the North America) comprised 27.19 % of the total abundance. Although silver and bighead carp dominated the biomass composition, they were not abundant, so based on IRI calculations, the dominant species were *L. macrochirus*, *Pseudolaubuca sinensis*, *Toxabramis swinhonis*, and *Hemiculter leucisculus* (Table S1). The non-native fish species in Qiandao Lake, primarily *L. macrochirus*, *L. auritus*, and *Coptodon zillii*, increased in both density and biomass from 2021 to 2023 and were lower in the CT zone than in the SW and SE zones (Table 1). Piscivorous fish (*Culter alburnus*, *Chanodichthys mongolicus*, *Siniperca knerii*) made up a minor proportion of the assemblage; their densities and biomasses were greatest in the CT zone, but their density decreased significantly from 3.11 % in 2021 to 1.33 % in 2023 (Table 1).

3.1.2. Temporal dynamics of fish assemblage structure

NPUE, BPUE, SR, and SW all tended to show an upward trend from spring to summer, followed by a marked decline from summer to winter (Fig. 2), but no significant differences were found in any of the four metrics between years ($p > 0.05$) (Fig. 3a, b, c, d). However, significant seasonal differences existed for all four metrics with generally the highest values in Summer and the lowest ones in Winter ($p < 0.001$) (Fig. 3e, f, g, h).

3.1.3. Spatial dynamics of fish assemblage structure

NPUE and BPUE showed no significant differences among lake zones ($p > 0.05$), whereas SR and the SW showed significant differences (Fig. 4a and b) with significantly higher values in the CT zone than in the SW and SE zones ($p < 0.001$) (Fig. 4c and d).

3.1.4. Spatial-temporal patterns of fish assemblage

NMDS indicated significant differences in fish assemblage structure (Fig. 5a and b), but the high stress value (0.161) warrants caution in interpreting the results. ANOSIM also confirmed significant differences between seasons ($R = 0.266$; $p = 0.001$) and lake zones ($R = 0.241$; $p = 0.001$) (Fig. 5a and b), but the R^2 indicate weak explanatory power. The key contributors to seasonal differences in fish assemblage composition based on SIMPER included *T. swinhonis* (19.4 %), *H. leucisculus* (14.1 %), *S. argentatus* (10.4 %), *P. sinensis* (9.8 %), *L. macrochirus* (8.8 %), *Rhinogobius giurinus* (5.9 %), and *Tilapia zillii* (5.4 %) (Table S5). Key contributors to lake zone differences included *S. macrops* (12.3 %), *X. davidi* (10.8 %), *P. sinensis* (10.3 %), *S. argentatus* (7.3 %), *T. swinhonis* (7.1 %), *Acheilognathus macropterus* (6.5 %), *L. macrochirus* (6.4 %), and *C. alburnus* (5.2 %) (Table S6).

3.2. Water quality dynamics

The SD (3.74 m), DO (8.77 mg/L), NH_3-N (0.14 mg/L), COD_{Mn} (0.18 mg/L), and TP (21.04 μg/L) indicated good water quality (Table 2). Average phytoplankton, zooplankton, and macrobenthos biomasses were 1.27 mg/L, 0.59 mg/L, and 0.76 g/m^2, respectively (Table 2).

Compared to 2021, TN in 2023 decreased significantly ($p < 0.001$) (from 0.86 mg/L to 0.33 mg/L), whereas TP increased significantly ($p < 0.001$) (from 19.55 μg/L to 27.94 μg/L) (Table S2). Phytoplankton biomass also increased significantly (from 0.98 mg/L to 1.52 mg/L) ($p = 0.032$) (Table S2). Seasonally, TN and TP concentrations showed no significant differences ($p > 0.05$). However, phytoplankton biomass exhibited significant seasonal variation ($p < 0.001$), with higher values in summer and autumn (1.93 mg/L, 2.57 mg/L) compared to spring and winter (0.26 mg/L, 0.33 mg/L) (Table S3). Zooplankton biomass was significantly higher in spring and summer (0.78 mg/L, 1.02 mg/L) than in autumn and winter (0.30 mg/L, 0.25 mg/L) ($p < 0.001$; Table S3). TN, TP, phytoplankton biomass, and zooplankton biomass showed no significant differences among zones ($p > 0.05$). However, macrobenthos biomass in the CT and NE zones (1.52 g/m^2, 1.40 g/m^2) was significantly greater than in the other zones ($p < 0.001$; Table S4).

3.3. Interactions between fish assemblages and environment

We found significant positive correlations between WT, pH, NO_2^-, Cond, and COD and all four fish assemblage metrics ($p < 0.05$) (Fig. 6). Conversely, SD showed significant negative correlations with all four fish metrics ($p < 0.05$). Significant, but weak, negative correlations occurred between TP and SW ($p < 0.01$) ($r = -0.2$), and between DO and NPUE ($p < 0.001$) ($r = -0.26$). Chl.a was positively correlated only with NPUE, whereas NH_3^-N was positively correlated with BPUE and SR. Z-den and P-bio were significantly correlated with all four fish metrics ($p < 0.05$). P-den was significantly correlated with all but SW, and Z-bio was significantly correlated with BPUE, SR ($p < 0.05$) and SW, but B-bio and B-den were not significantly correlated with any fish indicator ($p > 0.05$; Fig. 6).

The VPA of the RDA results showed that the combined influence of environmental predictors explained only 30.7 % of the variation in fish assemblage composition (Fig. 7). The biotic predictors explained 4.9 % of that variation versus 18 % for the water quality predictors; their interaction explained 7.8 %. All values were statistically significant ($p < 0.001$).

The XGBoost models explained of 0.39 %, 0.50 %, and 0.28 % of the variation in NPUE, SR, and SW, respectively, with low RMSE and MAE, but only 1 % of the variation in BPUE (Fig. 8). The top 3 predictors for NPUE were P-den, Z-den, and P-bio, with SHAP (SHapley Additive exPlanations) values of 0.303, 0.190, and 0.173. The top 3 predictors for SR were Cond, WT, and Z-den (SHAP = 0.294, 0.184, 0.114). For SW, Cond, WT, and DO were the top 3 predictors (SHAP = 0.265, 0.120, 0.118). These findings suggest that biotic predictors had stronger predictive capability for NPUE, whereas water quality predictors were more influential for predicting SR and SW.

Table 1
NPUE and BPUE composition of different fish guilds by year, season, and zone.

Group		Year			Season				Zone				
		2021	2022	2023	Spring	Summer	Autumn	Winter	SW	NW	CT	NE	SE
Percentage of NPUE	Other fish	75.43 %	75.17 %	58.00 %	76.50 %	81.44 %	62.38 %	43.17 %	59.00 %	79.93 %	82.53 %	73.35 %	42.63 %
	Non-native fish	20.52 %	22.93 %	40.26 %	20.15 %	15.47 %	36.15 %	54.88 %	39.96 %	17.78 %	12.34 %	24.87 %	56.03 %
	Filter-feeding fish	0.94 %	0.82 %	0.41 %	0.64 %	1.27 %	0.20 %	0.51 %	0.38 %	1.45 %	0.73 %	0.57 %	0.09 %
	Piscivorous fish	3.11 %	1.08 %	1.33 %	2.71 %	1.82 %	1.27 %	1.44 %	0.67 %	0.85 %	4.39 %	1.20 %	1.25 %
Percentage of BPUE	Other fish	43.97 %	70.65 %	50.97 %	65.77 %	49.69 %	49.16 %	54.66 %	51.95 %	55.08 %	51.61 %	58.73 %	47.26 %
	Non-native fish	8.14 %	18.87 %	16.64 %	10.11 %	11.15 %	18.60 %	23.79 %	17.25 %	10.26 %	3.97 %	11.50 %	34.37 %
	Filter-feeding fish	43.66 %	7.23 %	26.71 %	20.88 %	36.64 %	25.75 %	7.75 %	28.41 %	32.15 %	36.79 %	27.84 %	12.35 %
	Piscivorous fish	4.23 %	3.25 %	5.68 %	3.23 %	2.52 %	6.49 %	13.80 %	2.39 %	2.50 %	7.64 %	1.93 %	6.02 %

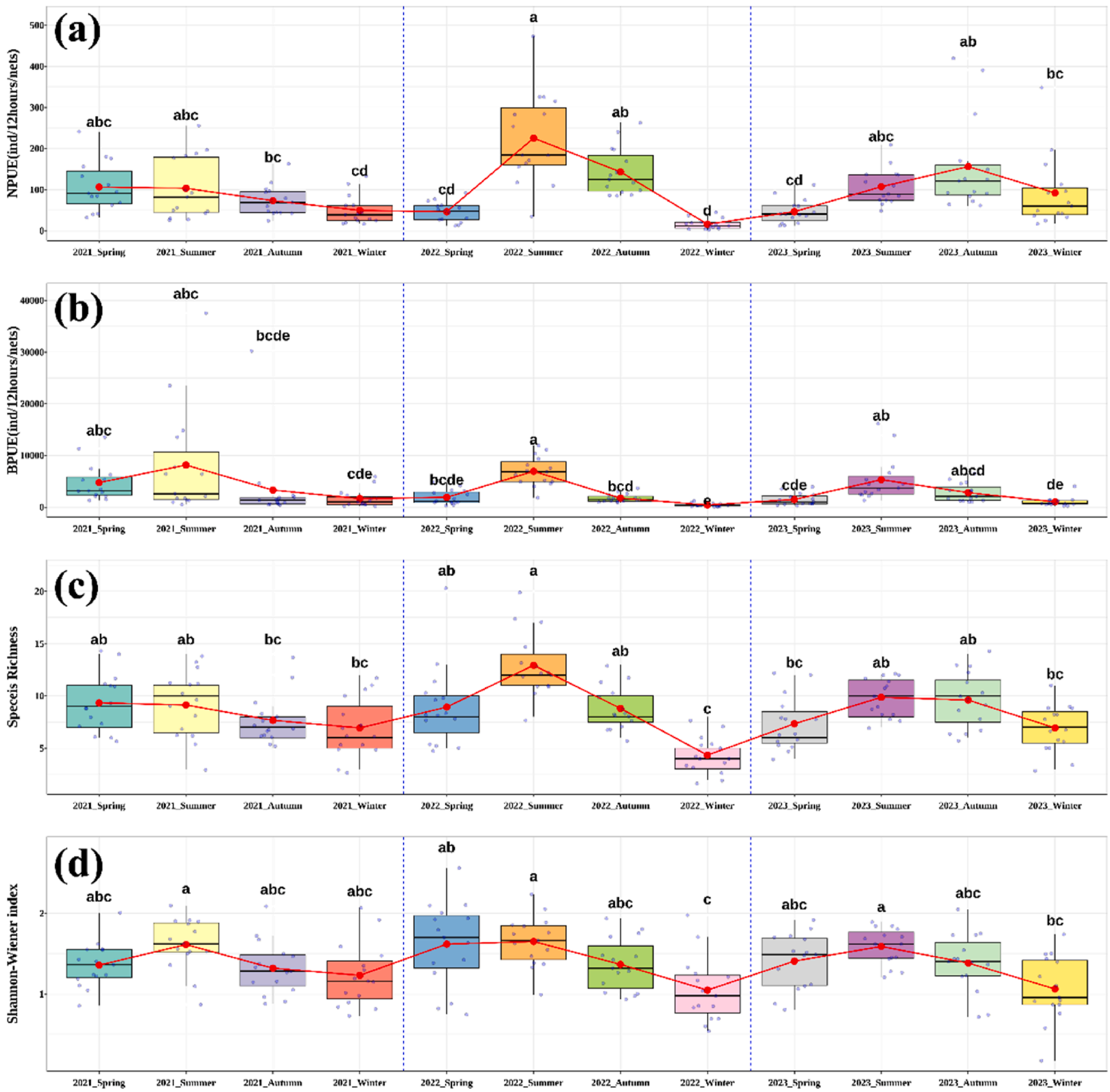

Fig. 2. Temporal variations in fish assemblage metrics from 2021 to 2023. The red dots and lines represent the means and trend of the data, and the boxplots show the quartiles for each season. The blue dashed vertical lines separate the different years. Letters (a, b, c, d, e) represent significant differences between seasons (Dunn's test).

4. Discussion

4.1. Historical changes in Qiandao Lake fishes

We collected 64 fish species compared to 54 species in 2010–2013 (Hou et al., 2014) and in 2016–2017 (43 species) (Hao et al., 2019), but fewer than the 102 species recorded in 2008–2010 (Liu et al., 2011). The primary reason for the higher species richness(102) is the difference in sampling areas, which included both Qiandao Lake and streams and reaches of the Xin'an River. (Liu et al., 2011; Hao et al., 2019; Hou et al., 2014). The dominant species in Qiandao Lake were omnivores such as *L. macrochirus*, *P. sinensis*, *T. swinhonis*, and *H. leucisculus* (Table S1). These species have robust r-strategy traits that facilitate rapid population growth and dominance (Lisi et al., 2018; Manfrin et al., 2019; Mims and Olden, 2012; Xu et al., 2022b). From 2021 to 2023, piscivorous fish density decreased, but their biomass proportion remained stable (Table 1). Compared to the 2010–2013 and 2016–2017 surveys, the density and biomass proportions of piscivorous fish decreased (Wen et al., 2024). This decrease may result from the fishing of *L. macrochirus*, *P. sinensis*, *T. swinhonis*, and *H. leuciscuslus* (Wen et al., 2023; Guo et al., 2022). Non-native fish species have become dominant, with a sampling frequency of 95 % (Table S1). The prolific reproduction of non-native fish species reduces survival space for native fish, because these invasive species occupy wider ecological niches and threaten the health and indigenous species diversity of Qiandao Lake (Gallardo et al., 2016; Liu et al., 2017a; Ndaleni et al., 2018; Shuai and Li, 2022). Further

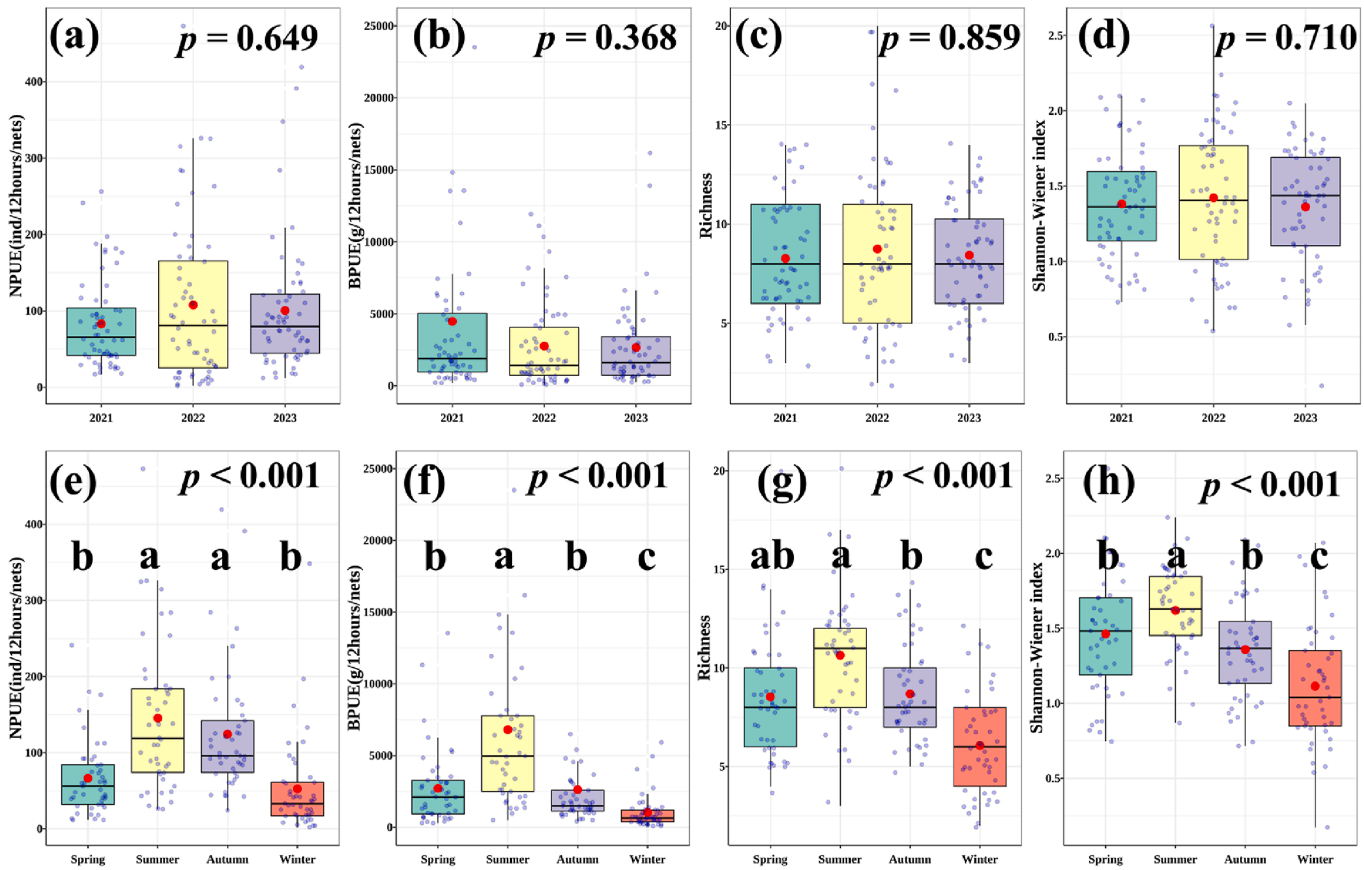

Fig. 3. Inter-annual and seasonal variations in fish assemblage metrics. The red dots represent the mean value of data, and the boxplots show the quartiles for each season. The p-value represent the significance levels from statistical tests (Kruskal-Wallis test). Letters (a, b, c) represent significant differences for year or season (Dunn's test).

measures are needed to mitigate invasive species impacts in Qiandao Lake.

4.2. Spatiotemporal dynamics in fish assemblages and environment

The stocking and fishing of silver and bighead carp indirectly influence phytoplankton and zooplankton biomasses through trophic cascades. No-fishing zones and fishing bans contribute to the recovery of fish populations, leading to improvements in fish population density, biomass, and diversity. Silver and bighead carp stocking and fishing are relatively evenly distributed in Qiandao Lake spatially and temporally, meaning that we could only evaluate the effects of no-fishing zones and fishing bans on fish assemblages. Significantly higher SR and SW were observed in the protected CT zone than in the SW and SE zones, contributing to greater SR and SW in the CT zone. Additionally, proximity to conservation areas in the NW and NE zones was negatively correlated with invasive fish species proportions. This finding aligns with previous research (Giakoumi et al., 2019; Gracida-Juárez et al., 2024; Jia et al., 2019), suggesting that the genetic resource conservation zone in the NW zone achieves conservation outcomes.

Significant seasonal variations were observed in NPUE, BPUE, SR, and SW, with peak values in summer, intermediate values in spring and autumn, and lowest values in winter (Fig. 3e–h). The increases in these indices from spring to summer may benefit from the March to June fishing bans, whereas the summer to winter declines are likely associated with intensive non-selective fishing practices. Previous studies have indicated that lifting seasonal fishing bans increases fishing pressure, resulting in fish biomass and diversity declines. (Li et al., 2023; Wang et al., 2015; Xu et al., 2022a). In contrast, non-native fish species showed higher abundance and biomass proportions during autumn and winter, possibly because those species experience less fishing pressure than other species (Table 1). The increase in algal biomass from 2021 to 2023 may be associated with declines in silver and bighead carp biomasses (Table 2). *L. macrochirus*, *P. sinensis*, *T. swinhonis*, and *S. argentatus* contributed significantly to the seasonal and spatial variations in fish assemblage composition because of their high abundances (Fig. 6).

4.3. Drivers of fish assemblage dynamics

The spatial distribution and composition of fish assemblages are influenced by biotic and abiotic factors (Huo et al., 2023; Liu et al., 2017b; Whiterod et al., 2021; Xiong et al., 2021). Spearman's correlations indicated positive relationships between NPUE, BPUE, SR, and SW with the density and biomass of phytoplankton and zooplankton (Fig. 6), indicating preferences for zones more abundant in these resources (Bartrons et al., 2020; Rogers et al., 2024; Vrba et al., 2024). In contrast, there was no significant relationship between NPUE, BPUE, SR, and SW and macrobenthos, indicating that the latter had little association with fish distribution (Fig. 6). This is attributed to the prevalence of pelagic and epipelagic fish species in the Qiandao Lake fish assemblages (Wang et al., 2022; Zhu et al., 2007). COD, ORP, Cond, NO_2^-, and pH were positively correlated with NPUE, BPUE, SR, and SW (Fig. 6), indicating that fish prefer areas with elevated nutrient concentrations, consistent with previous studies (Yang et al., 2023; Yin et al., 2024). SHAP values indicated that NPUE was mainly influenced by phytoplankton and zooplankton, whereas SR and the SW were mainly influenced by water quality (Fig. 8). This suggests that fish abundance was primarily influenced by aquatic prey, whereas fish diversity was mainly influenced by water quality. VPA revealed that fish assemblage composition was influenced more by water quality than by phytoplankton and

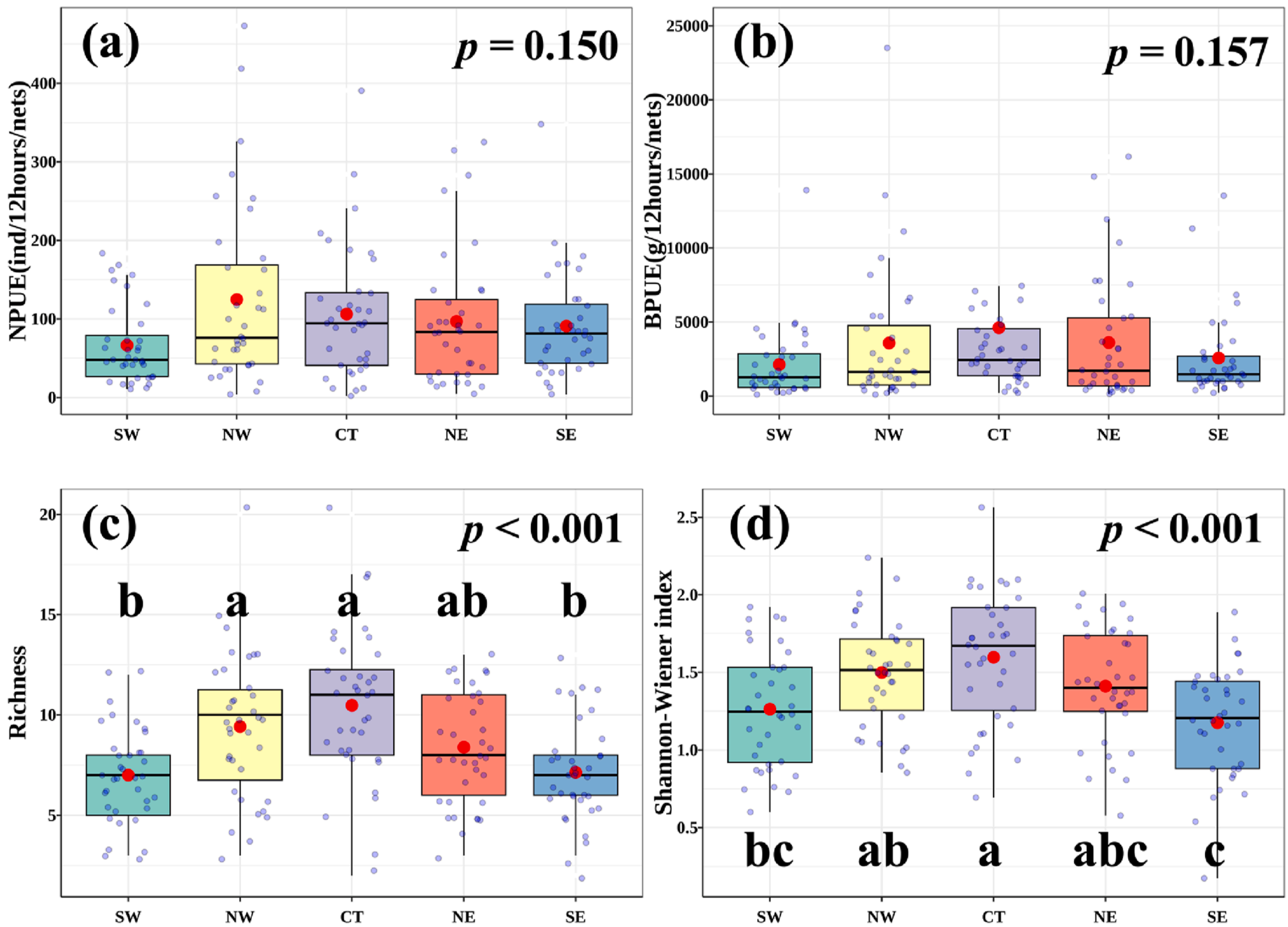

Fig. 4. Spatial variations in NPUE,、BPUE,、Species Richness, and Shannon-Wiener Index among lake zones. The red dots represent means and the boxplots show the quartiles for each season. The *p*-values represent significance levels (Kruskal-Wallis test). Letters (a, b, c) represent year or seasonal differences (Dunn's test).

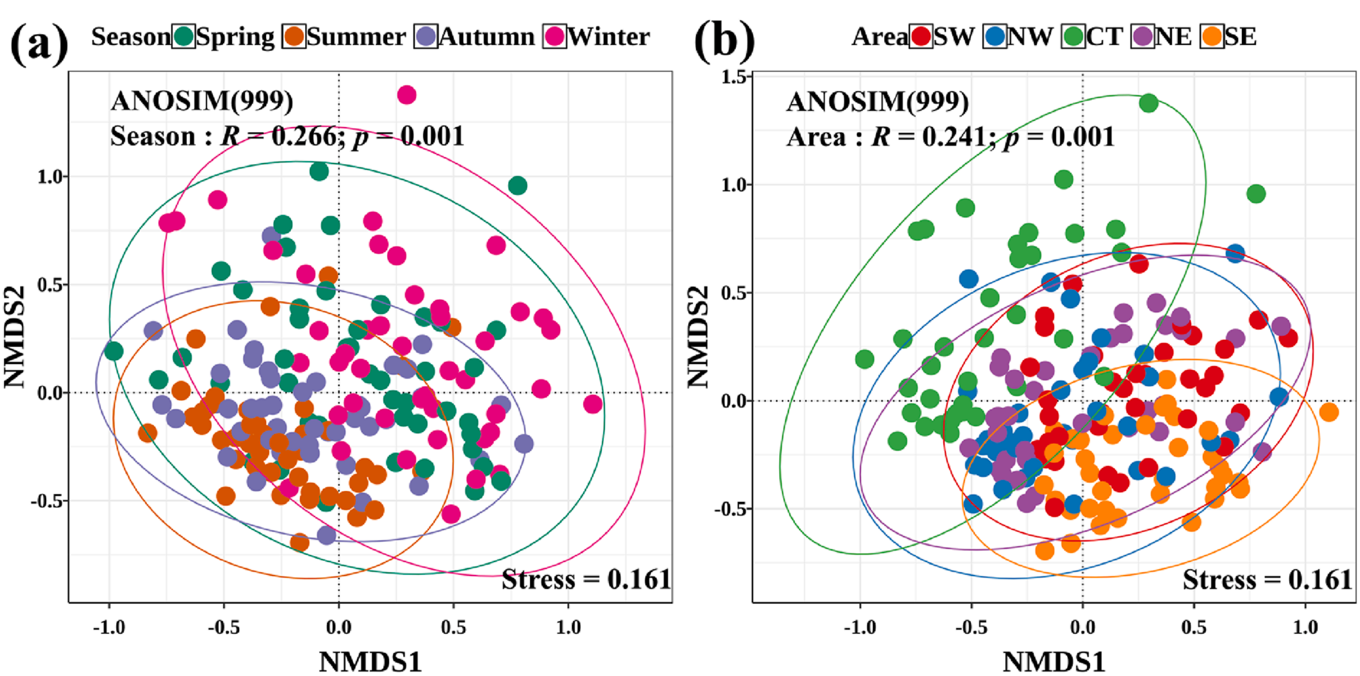

Fig. 5. NMDS analysis of (**a**) seasonal and (**b**) spatial differences in fish assemblage structure.

Table 2
Qiandao Lake water body condition.

Indicator		Mean ± SE	CV	Kruskal-Wallis test		
				Year	Season	Area
Water quality	**WT (°C)**	20.68 ± 0.53	0.32	$p < 0.001$	$p < 0.001$	$p = 0.889$
	WD (m)	42.29 ± 1.08	0.32	$p = 0.774$	$p = 0.874$	$p < 0.001$
	SD (m)	3.74 ± 0.12	0.39	$p = 0.039$	$p < 0.001$	$p < 0.001$
	TN (mg/L)	0.63 ± 0.03	0.50	$p < 0.001$	$p = 0.528$	$p = 0.196$
	TP (μg/L)	21.04 ± 1.91	1.13	$p < 0.001$	$p = 0.086$	$p = 0.092$
	pH	8.53 ± 0.05	0.07	$p < 0.001$	$p < 0.001$	$p = 0.578$
	DO (mg/L)	8.77 ± 0.12	0.18	$p < 0.001$	$p < 0.001$	$p = 0.615$
	NH4 (mg/L)	0.14 ± 0.01	0.84	$p = 0.735$	$p < 0.001$	$p = 0.431$
	NO2 (μg/L)	10.46 ± 0.57	0.68	$p = 0.649$	$p < 0.001$	$p < 0.001$
	NO3 (mg/L)	0.27 ± 0.02	0.71	$p < 0.001$	$p < 0.001$	$p = 0.007$
	ORP (mv)	179.94 ± 6.45	0.45	$p < 0.001$	$p < 0.001$	$p = 0.995$
	PO4 (μg/L)	4.24 ± 0.29	0.85	$p = 0.178$	$p = 0.003$	$p = 0.025$
	Chl.a (μg/L)	4.59 ± 0.32	0.86	$p < 0.001$	$p < 0.001$	$p = 0.404$
	Cond (S/m)	113.53 ± 1.14	0.13	$p = 0.005$	$p < 0.001$	$p = 0.060$
	COD_{Mn} (mg/L)	3.18 ± 0.11	0.42	$p < 0.001$	$p < 0.001$	$p = 0.619$
Biotic	**P-den (10^6 ind/L)**	16.93 ± 2.43	1.79	$p = 0.016$	$p < 0.001$	$p = 0.361$
	Z-den (10^2 ind/L)	12.00 ± 1.67	1.74	$p < 0.001$	$p < 0.001$	$p = 0.029$
	B-den (ind/m^2)	269.54 ± 39.5	1.83	$p < 0.001$	$p = 0.285$	$p < 0.001$
	P-bio (mg/L)	1.27 ± 0.11	1.07	$p = 0.032$	$p < 0.001$	$p = 0.331$
	Z-bio (mg/L)	0.59 ± 0.04	0.91	$p = 0.073$	$p < 0.001$	$p = 0.834$
	B-bio (g/m^2)	0.76 ± 0.11	1.81	$p < 0.001$	$p = 0.265$	$p < 0.001$

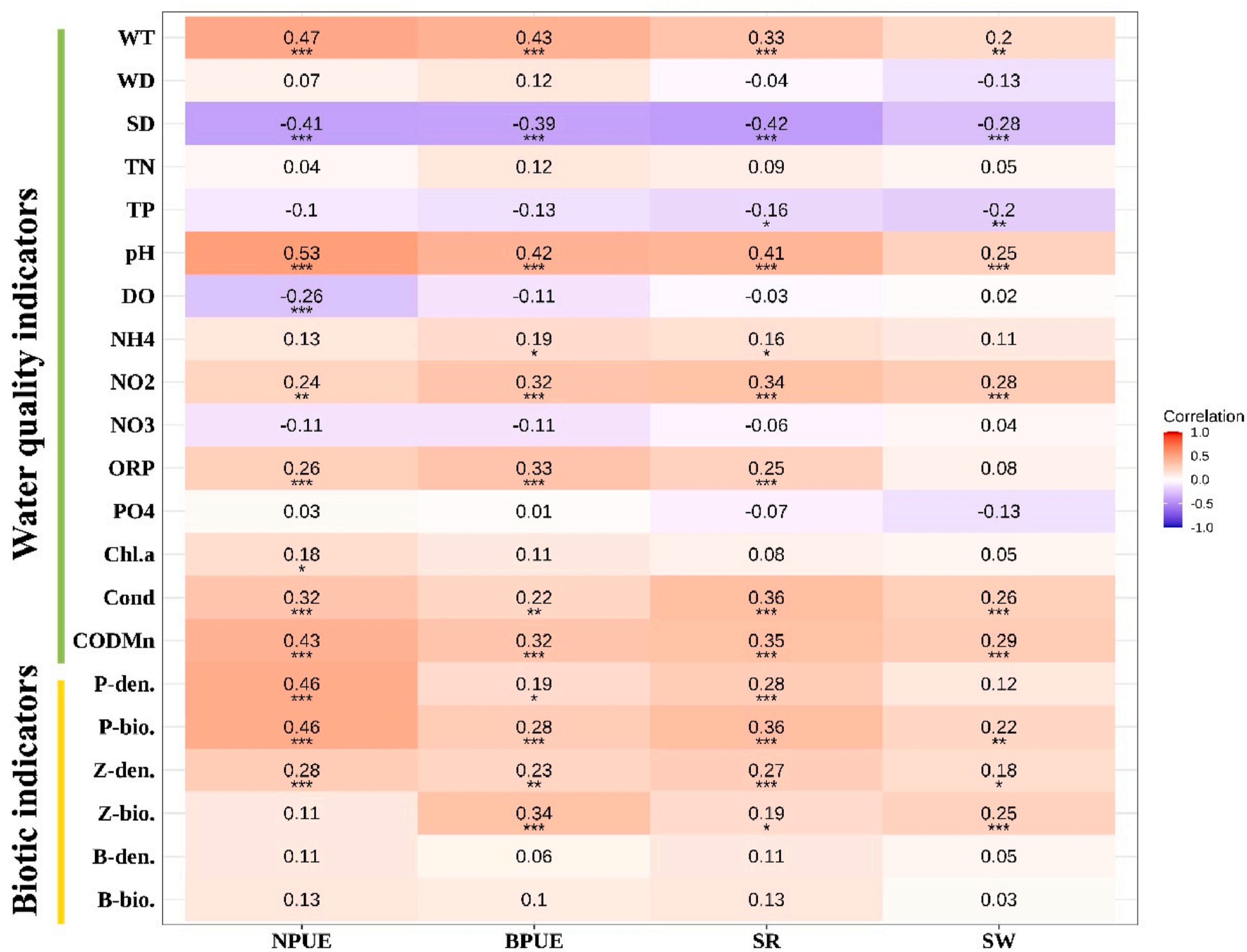

Fig. 6. Spearman correlations between environmental and fish assemblage metrics (NPUE, BPUE, Species richness, and Shannon-Wiener index). Asterisks indicate levels of statistical significance: $p < 0.05$ (*), $p < 0.01$ (**), $p < 0.001$ (***).

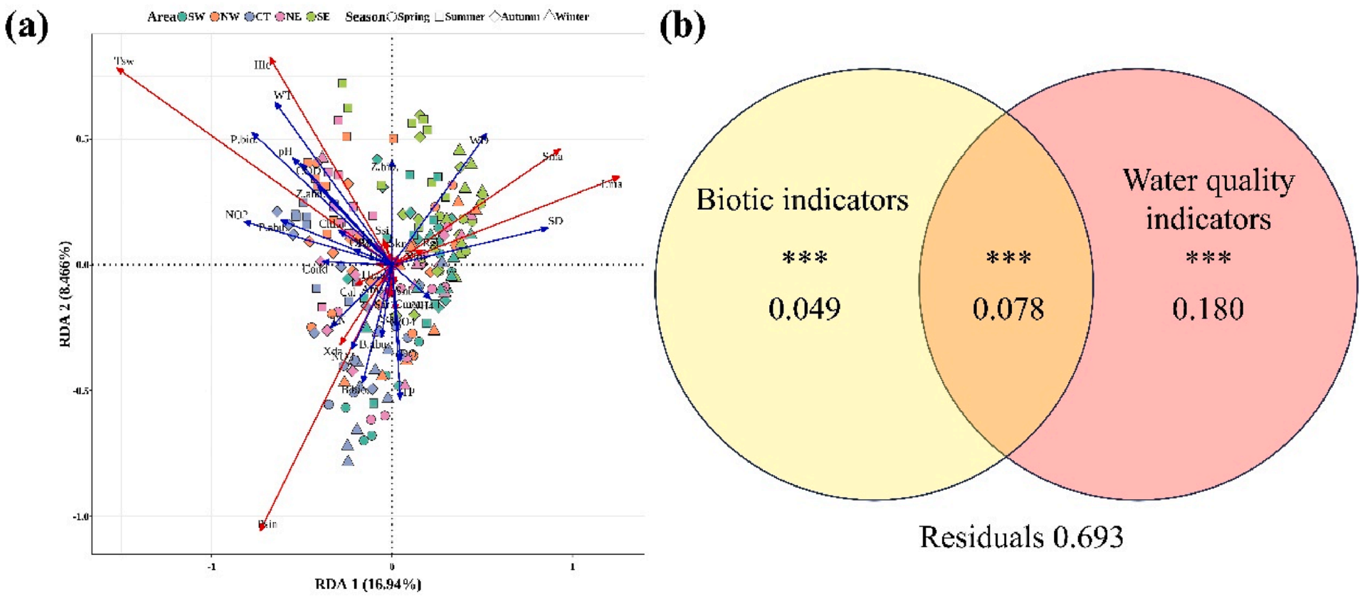

Fig. 7. RDA and VPA analysis of the relationships between fish assemblage indicators and environmental predictors.

zooplankton (18.0 % vs. 4.9 %) (Fig. 7). We did not assess the effects of physical habitat structure. However, Kaufmann et al. (2014) reported that intolerant fish species richness declined, and tolerant fish species richness increased, with increased shoreline human development and decreased abundance and structural complexity of riparian vegetation and littoral cover in northeast USA lakes. Studying two large Brazilian reservoirs, Becker et al. (2016) found that riverine zones in one produced greater fish diversity, richness, abundances of native species abundances, and long-distance migratory species. Lacustrine zones supported greater total and nonnative species abundances. In the other

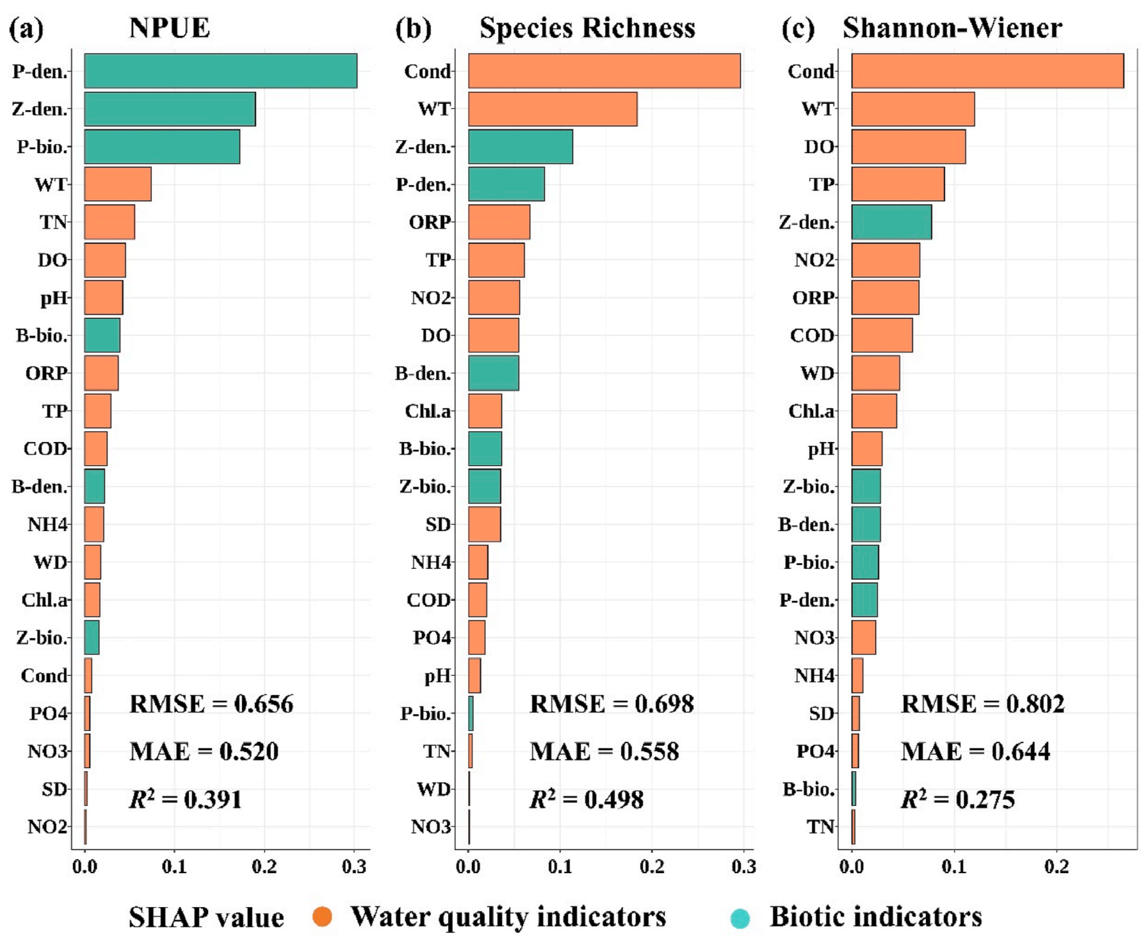

Fig. 8. Environmental predictor importance based on XGBoost modeling.

reservoir, riverine zones supported greater total and non-native species abundances. Subsequent Qiandao Lake studies should incorporate the effects of physical habitat structure on fish assemblages.

5. Summary

The Qiandao Lake fish assemblage exhibited seasonal and zonal variations. The Central (CT) zone supported higher fish diversity, likely because of its favorable habitat conditions and proximity to conservation areas. In contrast, the Southeast (SE) and Southwest (SW) zones experienced lower diversity and higher densities of invasive species. Non-native species have steadily increased in abundance and biomass. This proliferation, coupled with the decline in native piscivorous fish, indicates the need for targeted management interventions to mitigate invasive species impacts, perhaps by changing fishing bans and enhancing protected areas. Qiandao Lake fish assemblage structure was more strongly influenced by water quality indicators than by prey indicators; however, prey indicators were better predictors of abundance, whereas water quality indicators were better predictors of diversity.

Our study provides empirical support for managing Qiandao Lake fisheries, enhancing its ecosystem health, and serves as a reference for SEF management in other reservoirs. Although SEF is a cornerstone of fishery management in China's reservoirs, adaptive management is needed to mitigate ecological risks. For example, the stocking densities of filter-feeding fish, such as silver and bighead carp, must be optimized to regulate phytoplankton biomass, improve water quality, and prevent algal blooms. Additionally, strict enforcement of conservation measures and regular ecological monitoring are essential.

CRediT authorship contribution statement

Bo Xu: Writing – original draft, Investigation, Methodology, Validation, Conceptualization, Data curation, Visualization, Writing – review & editing. **Steven J. Cooke:** Methodology, Writing – review & editing. **Feng Wen:** Investigation, Data curation. **Yuxing Ma:** Investigation. **Chuansong Liao:** Investigation, Writing – review & editing. **Jiashou Liu:** Resources, Writing – review & editing, Project administration. **Chuanbo Guo:** Writing – review & editing, Conceptualization, Methodology, Resources, Project administration.

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Declaration of competing interest

The authors declare that they have no competing financial interests or personal relationships that could have appeared to influence the work reported in this paper. Chuanbo Guo and Steven J. Cooke are editorial board members for *Water Biology and Security* but were not involved in the editorial review or the decision to publish this article.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.watbs.2025.100458.

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