The past and potential antagonistic effects of fishing ban against nutrient loading control on eutrophication restoration in Lake Hongze

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ABSTRACT

Integrated management strategies are often implemented to achieve comprehensive environmental restoration; however, the potential antagonistic effects among such measures are seldom examined. For instance, fishing bans, aimed at enhancing fish biodiversity in eastern China, may counteract the effectiveness of nutrient control measures in mitigating eutrophication. This study employs a dual modeling approach to evaluate this hypothesis in Lake Hongze, the fourth largest shallow lake in China. The PCLake model was calibrated using observational data from Lake Hongze collected between 2016 and 2020. The calibrated model was subsequently applied in a hindcast analysis from 2020 to 2024 and a forecast simulation from 2025 to 2030 to assess the impacts of fishing bans. Combined with structural equation modeling (SEM) path analysis, the results support the hypothesis that fishing bans can exhibit antagonistic effects on nutrient loading control by enhancing top-down regulation relative to bottom-up processes. Specifically, the fishing ban led to increased fish biomass, phytoplankton abundance, and nutrient levels over the past four years, while reducing the abundance of submerged macrophytes, zoobenthos, and zooplankton. Projections further indicate that such antagonistic effects would persist through 2030 if the fishing ban remains in place as planned. Additionally, model forecasts suggest that even with adjustments to the duration and intensity of fishing bans, antagonistic effects could be amplified under more stringent nutrient control scenarios. This study provides valuable insights into maximizing the net benefits of combined environmental management strategies through a systematic framework that evaluates both the effects and underlying processes of different interventions.

Keywords: Lake restoration, Nutrient loading control, Fishing bans, PCLake model, Structure Equation Model

1. Introduction

Degradations of freshwater lakes, including cultural eutrophication and biodiversity loss, have impeded global sustainable development since last century (Albert et al. 2020, Ho, Michalak and Pahlevan 2019). Major drivers of these degradations include, but are not limited to, enhanced nutrient enrichment, over-exploitation, hydrological modification, and climate change (Sinha, Michalak and Balaji 2017, Jenny et al. 2020). Achieving relevant Sustainable Development Goals (e.g.SDGs 6 and 14) requires concerted efforts from multiple stakeholders, implying that integrated management strategies targeting diverse drivers are essential (Birk et al. 2020, Reed 2008). While the synergistic effects of combined management measures have been widely studied, less attention has been given to potential antagonistic effects—which also represent critical information for policy-making.

The shallow lakes in the eastern plain region of China have experienced severe cultural eutrophication and biodiversity degradation (Qin et al. 2013, Wang et al. 2023, Chen et al. 2022). Controlling external nutrient loading is considered the primary approach for mitigating eutrophication, as it restricts phytoplankton growth and influences higher trophic levels through bottom-up resource limitation (Schindler 2012, Jeppesen et al. 2007, Tigli et al. 2024). In China, policies such as the Action Plan for Water Pollution Prevention and Control (2015) and the River and Lake Chief System (2016) are expected to facilitate the restoration of eutrophic lakes as regulations become stricter and more widespread (Yu et al. 2020, Hu et al. 2024). Concurrently, an unprecedented ten-year fishing ban has been implemented since 2020 in the Yangtze River and its connected lakes—one of the most stringent biodiversity conservation initiatives globally (Wang et al. 2022a). This year-round prohibition comprehensively restricts all harvest of natural fishery resources in designated areas. Classic biomanipulation techniques, such as removing planktivorous and benthivorous fish and introducing piscivorous species, are often applied alongside nutrient control in eutrophic lakes (Søndergaard et al. 2007, Søndergaard et al. 2008). These measures enhance zooplankton biomass by reducing grazing pressure, thereby suppressing phytoplankton proliferation. However, subtropical lakes in eastern China support more omnivorous and planktivorous-benthivorous fish and fewer piscivorous species compared to temperate systems(Jeppesen et al. 2010, Mao et al. 2020). Consequently, the fishing ban may produce effects contrary to traditional biomanipulation: by increasing planktivorous fish stocks, it could intensify predation on zooplankton and indirectly promote phytoplankton growth (Figure 1B). Although recent studies report positive effects in water quality, fish abundance, and network stability in certain lakes after fishing ban (Huang et al. 2025a, Yu et al. 2020, Zhang et al. 2024, Yao et al. 2024), the existence and magnitude of such antagonistic effects remain uncertain.

The process-based lake ecosystem model, a widely-used tool for evaluating the efficacy of restoration measures (Janssen et al. 2015), can help assess such antagonistic effects resulting from fishing bans. As a model specifically designed for shallow lakes, PCLake represents a fully mixed water body and incorporates key biological components such as phytoplankton, zooplankton, and three functional groups of fish (Janse 2005) (Figure S1). It has been applied globally to study the causes and characteristics of eutrophication (Kuiper 2011, Janssen et al. 2021), the effectiveness of restoration measures (Qin et al. 2022, Hilt et al. 2018),and the potential impacts of climate change (Qin et al. 2025, Rolighed et al. 2016) across case-specific, regional, and global scales. Interactions between ecological processes should be taken into account in order to understand the balance of feedbacks (Dakos et al. 2019). Although PCLake is built upon a rigorous theoretical framework, the complexity of biological processes often complicates direct and concise representation of trophic cascades. In contrast, structural equation modeling (SEM), grounded in a strong theoretical foundation, allows for the estimation of trophic cascade strength and other causal networks through a series of multiple regression analyses (Grace 2006, Su et al. 2019). Thus, integrating both approaches enables a

comprehensive assessment of both the outcomes and underlying processes associated with combined management strategies.

This study employed two modeling approaches to evaluate the potential antagonistic effects between nutrient control measures and fishing bans in Lake Hongze, the fourth largest shallow lake in China (Figure 1). As a key storage reservoir for the Eastern Route of the South-North Water Diversion Project, Lake Hongze plays a vital role in climate regulation, flood control, and water resource management, and is currently in a critical phase of restoration (Zhang et al. 2024). Monthly observational data from 2016 to 2020, collected prior to the implementation of the fishing ban, were used to calibrate the PCLake model. A hindcast simulation based on the calibrated model was then conducted to assess the ecological impacts of the fishing ban, the trophic cascades of which were further examined using structural equation modeling (SEM). Finally, a forecast analysis was performed to identify strategies for maximizing management effectiveness. The results confirm the hypothesized antagonism through a novel research framework, and the implications and limitations of these findings for lake conservation and management are discussed.

2. Material and methods

2.1 Study Area.

Lake Hongze (33°06'-33°40'N, 118°10'-118°52'E), the fourth largest freshwater lake in China, has a surface area of 1793 km^2 and a drainage basin of 160000 km^2. With a mean depth of 1.7 m and a water volume of 3.0 billion m^3 (Cai et al. 2016a), the lake exhibits a rapid hydrological cycle and a short water retention time of approximately 35 days. The region experiences a monsoon-influenced climate, with a mean annual precipitation of 925.5 mm, an average wind speed of 3.7 $m \cdot s^{-1}$, and mean temperatures of 2.5°C in January and 28.8°C in July. Major inflows enter from the west and exit toward the east (Figure 1A; Table S1). The Huaihe River, the primary inflow, accounts for about 70% of total inflow and more than half of the external nutrient load. The main outflow occurs through the Sanhe River, which connects Lake Hongze to the Yangtze River and conveys 60%–70% of the total discharge.

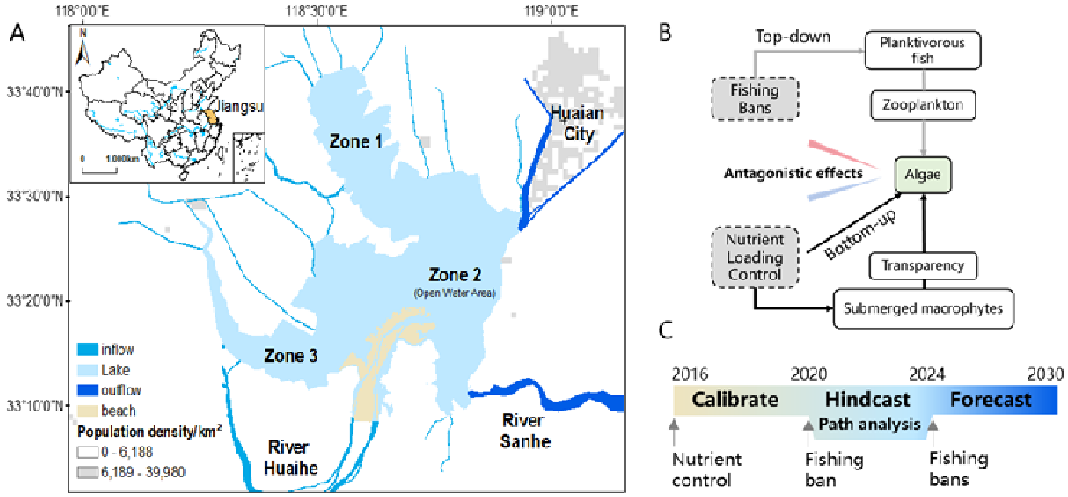

Figure 1 - Location of study area, hypothesis and modelling approach of this study. (A) Zones 1 and 3 exhibit relatively high vegetation coverage, whereas Zone 2 is an open water area largely devoid of aquatic vegetation. (B) The conceptual diagram illustrates the hypothesis that fishing bans and external nutrient loading controls may exert antagonistic effects on phytoplankton dynamics, as they operate through distinct ecological mechanisms. (C) Model

parameter calibration, hindcast simulation, and forecast analysis will be conducted across different temporal phases. A subsequent structural equation modeling (SEM) path analysis will be performed following the hindcast to elucidate causal pathways.

Since the 1980s, Lake Hongze has undergone eutrophication following marked declines in water quality and aquatic biodiversity (Li and Pu 2003). It was listed under the Regulations of Jiangsu Province on Protection of Lakes in 2004 to mitigate pollution and manage resource use. Between 2017 and 2019, nine algal blooms were recorded, with affected areas expanding from 16 km^2 to 36 km^2 (Cui et al. 2021). Spatial heterogeneity characterizes the lake's water quality and ecological conditions (Figure 1A, S2). Zone 1 (Chengzi District) in the north has restricted hydrologic exchange, while Zone 3 (Lihewa District) in the west functions as a wetland reserve with shallow water. These regions support relatively abundant populations of aquatic macrophytes, zooplankton, and macroinvertebrates (Li et al. 2019, Ni et al. 2023, Cai et al. 2016b). In contrast, Zone 2 is an open-water area largely devoid of submerged vegetation and exhibits higher nutrient levels, strongly influenced by inputs from the Huaihe River.

2.2 Sampling and Measurement of Lake Variables.

Monthly field investigations were conducted from January 2016 to December 2019 at ten sampling sites distributed across three zones (Figure 1A). These sites are characterized by very shallow conditions, with annual average water depths ranging between 1.9 m and 2.9 m. At each site, Secchi depth (SD) was measured in situ, and dissolved oxygen was determined using a YSI 6600 V2-4 Multi-Parameter Water Quality Sonde. Vertically integrated water samples were collected using acid-cleaned 5 L plastic containers, stored under cool and shaded conditions, and transported to the laboratory for subsequent analysis. Total nitrogen, total phosphorus, and chlorophyll-a concentrations were measured following standard methods described in APHA (2012). Zoobenthos samples were collected at all sites, where the substratum predominantly consisted of muddy sediment. Sampling was performed using a 0.05 m^2 modified Peterson grab, with three grabs combined to form a composite sample. The collected material was sieved in situ through a 250 μm mesh sieve. Retained residues were stored in a low-temperature incubator and transported to the laboratory on the same day. There, samples were sorted on a white tray, and organisms were preserved in 7% buffered formalin. Specimens were identified to the lowest practicable taxonomic level, enumerated, blotted dry, and weighed for wet mass determination using an electronic balance (Sartorius BS-124, precision: 0.1 mg). Taxonomic identification and classification of zoobenthos followed the references of Liu et al. (1979) and Tang (2006).

2.3 Lake Ecosystem Model Configuration and Calibration.

To achieve adequate model performance for Lake Hongze during 2016–2024, key model inputs were adjusted. Fixed inputs included a mean water depth of 1.9 m, maximum depth of 4.5 m, wind fetch of 60,600 m (Janssen et al. 2014), lightly clayish soil (Janse 2005) and no wetland zone. Time-series inputs of PCLake model, including wind speed ($m \cdot s^{-1}$), solar radiation ($J \cdot m^{-2} \cdot d^{-1}$), water temperature (°C), water inflow, evaporation ($mm \cdot d^{-1}$), outflow ($mm \cdot d^{-1}$), and nutrient loading ($g \cdot m^{-2} \cdot d^{-1}$), were derived from multiple sources: (1). Monthly wind speed, precipitation, air temperature, and radiation from 2016 to 2024 were obtained from National Meteorological Information Center (https://m.data.cma.cn/data) at a meteorological station (Xuyi, 32.98°N,118.52°E, 40.8 m a.s.l) located 3 km from the lake. (2) Water temperature from the Huaihe River (2016–2019) was used directly; an empirical air–water temperature relationship extended these data to 2020–2024. (3). Monthly river inflow (2016–2019) was investigated (Table S1), with the Huaihe River contributing 88.5% of total inflow. Inflow for 2020–2024 was estimated using precipitation and historical discharge. Daily water level (Jiangba station) ranged from 11.5 m to 13.7 m. Mean daily evaporation was set to 2.5 mm (variance: 1.3 mm). Outflow was computed from total inflow, water level change, and evaporation. (4). Monthly nutrient inputs (2016–2021) from the Huaihe River averaged 4×10^5 kg N and 2×10^4 kg P (Meng. F. J. et al.

2023), showing a general decline, especially after December 2018. A ratio of 0.8 was applied to estimate total nutrient loading based on Huaihe inputs (Ji et al. 2014).

Two modifications were made to the PCLake model to better represent Lake Hongze's ecosystem and address the research objectives. First, while the original model includes three functional fish groups—zooplanktivorous juvenile whitefish, benthivorous adult whitefish, and piscivorous fish—with benthivorous adults (sDFiAd) dominating (~80% in both clear and turbid states), we introduced an additional group: zooplanktivorous adult whitefish. This adjustment reflects the prevalence of zooplanktivorous and omnivorous fish in local catches. All equations for this group were adapted from those of benthivorous adults, except for the food limitation function, which was derived from zooplanktivorous juveniles. Second, the original model represents fishing intesity as a first-order rate constant, which is inadequate for simulating variable fishing pressures. To improve temporal realism, we converted fishery intensities into time-series inputs based on annual fish yield and composition data (Mao et al. 2019), allowing dynamic simulation of fishing effort over time.

Default model parameters were initially derived from observations in over 40 lakes (Janse et al. 2010). Both original and newly introduced parameters were adjusted to enhance the performance of the modified PCLake model for Lake Hongze. Calibration was performed over a four-year period (2016–2020) using monthly observed data for total nitrogen, total phosphorus, dissolved oxygen, Secchi depth, chlorophyll-a, and zoobenthos, along with annual records of macrophyte coverage and fish harvest from published sources. Although the vegetation presence frequency (VPF) ranges between 0.24 and 0.37 (Li et al. 2019), submerged macrophytes remain scarce, with a peak coverage of only 11.80 km^2 (approximately 0.8% of the lake area) between 2013 and 2023 (Huang et al. 2025b). Fish catch data from 2016 to 2019 were provided by the Jiangsu Province Hongze Lake Fisheries Management Committee, indicating that zooplanktivorous and omnivorous fish collectively accounted for over 75% of the total catch (Lin. et al. 2013, Mao et al. 2019).

Simulations were conducted using a C++ compiled version of PCLake called via GRIND for MATLAB (Mooij et al. 2014). Each simulation began from a default turbid state and was run for a 20-year "burn-in" period under 2016 input conditions to achieve seasonal equilibrium before calibration. Key parameters were manually calibrated based on model outputs. The coefficient of determination (R^2) and root-mean-square error (RMSE) were employed to evaluate model performance across whole-lake averages (Bennett et al. 2013). A higher R^2 indicates better predictive accuracy, while a lower RMSE reflects smaller deviations between simulated and observed values. Given the absence of abrupt ecological shifts during the calibration period, the objective was to achieve simulations where most variables exhibited similar ranges and seasonal dynamics to the observations.

2.4 Hindcast and SEM analysis.

Following calibration, the model simulation was extended from 2020 to 2024 to conduct a hindcast analysis. Due to the unavailability of nutrient loading data for this period, values from 2020 were applied to the subsequent four years. Fishing intensity was set to zero to reflect the implementation of the fishing ban (FB scenario). For comparative purposes, a no-fishing-ban scenario (no FB) was also simulated using the average fishing intensity from 2016 to 2020. Monthly and annual averages were computed for eight model outputs. Dissolved oxygen was excluded due to its limited influence in the food web of this large, shallow lake, whereas zooplankton—a key group linking fish and phytoplankton dynamics—was included. Although additional time-series observations were unavailable, further validation was supported through comparison with previously published findings in the discussion.

Structural equation modeling (SEM) was employed to analyze trophic cascades under scenarios with and without the fishing ban. A conceptual path model was developed based on the PCLake framework (Figure S1), incorporating seven variables; total nitrogen was excluded due to its correlation with total phosphorus. Monthly outputs from both simulations were used to ensure sufficient data. The model was fitted to the covariance structure of the data, beginning

with a full model that included all possible pathways, which was subsequently refined by removing nonsignificant paths. Standardized path coefficients were used to quantify the strength and direction of direct relationships between consecutive trophic levels. The overall cascade strength was evaluated through the indirect effect from top to bottom of the food web, derived from the product of sequential path coefficients. Model fit was assessed using the chi-square/degrees of freedom ratio (CMIN/df) (Karin Schermelleh-Engel and Helfried Moosbrugger 2003), to assess how well the proposed network structure explains the simulated data from PCLake. All SEM analyses were performed in AMOS 21.0 (IBM 2012).

2.5 Forecast.

According to the Environmental Quality Standards for Surface Water in China, the total phosphorus level in Lake Hongze in 2023—though the lowest in recent years—still exceeded the drinking water threshold by 46% (Zhang et al. 2024). In addition, while fish stocks increased significantly, imbalanced fish community structure was also reported. Above facts imply that continued measures are further needed for Lake Hongze in the near future. To evaluate potential management outcomes, we designed eight scenarios combining different levels of external nutrient loading and fishing intensity to simulate conditions from 2025 to 2030. Two nutrient loading scenarios were defined: the highest level over the past five years (NP-, control) and the lowest level (NP--, approximately half of NP-). Four fishing scenarios were established: continued full fishing ban (F0, control); a biennial ban alternating between prohibition and permission (F0/1); full resumption of fishing at the 2020–2024 average intensity (F1); and continuous fishing at half of F1 intensity (F0.5). Other model inputs used 2020 data as boundary conditions. As the ten-year fishing ban is scheduled to end in 2030, we focused on the relative changes between 2030 and 2025. Differences in annual model outputs were calculated and compared against the control scenario to standardize units across variables.

3. Results

3.1 Lake States and PCLake Model Performance.

The average nutrient concentrations in the lake water from 2016 to 2020 were 1.72 g·m-3 for total nitrogen (TN) and 0.08 g·m-3 for total phosphorus (TP) (Figure S2). While TP exhibited a slight increase, TN declined significantly after 2017. The mean Secchi depth was 0.35 m and dissolved oxygen averaged 0.35 g·m-3, both remaining relatively stable throughout the period. The chlorophyll-a concentration averaged 8 mg·m-3, with occasional peaks observed. At the class level, Oligochaeta dominated in Zone 1, whereas Polychaeta were more abundant in Zone 2 (Figure S3). Since the PCLake model does not explicitly include large zoobenthos, the total dry weight of the five major classes was used to represent zoobenthos biomass.

The performance of the calibrated PCLake model for Lake Hongze was assessed using two statistical indices based on six monthly and two annual observational variables (Figure 2). The simulated trajectories (solid lines) generally captured both the range and seasonal dynamics of the whole-lake observations (dots). The coefficient of determination (R^2) ranged from 0.3 (zoobenthos) to 0.8 (dissolved oxygen), with an average of 0.53. The root-mean-square error (RMSE) varied between 0 (fish catch) and 3.7 (chlorophyll-a), averaging 0.73. Although the annual observations (macrophyte coverage and fish catch) were limited in number, their simulations were deemed acceptable due to agreement in mean values. Monthly water quality variables were better reproduced than biological variables (phytoplankton and zoobenthos). The modified and calibrated model exhibited generally higher R^2 and lower RMSE compared to the original model (Figure S4, Table S2), particularly for biological components. Overall, the model demonstrated acceptable performance during the 2016–2020 calibration period and was considered suitable for further analysis.

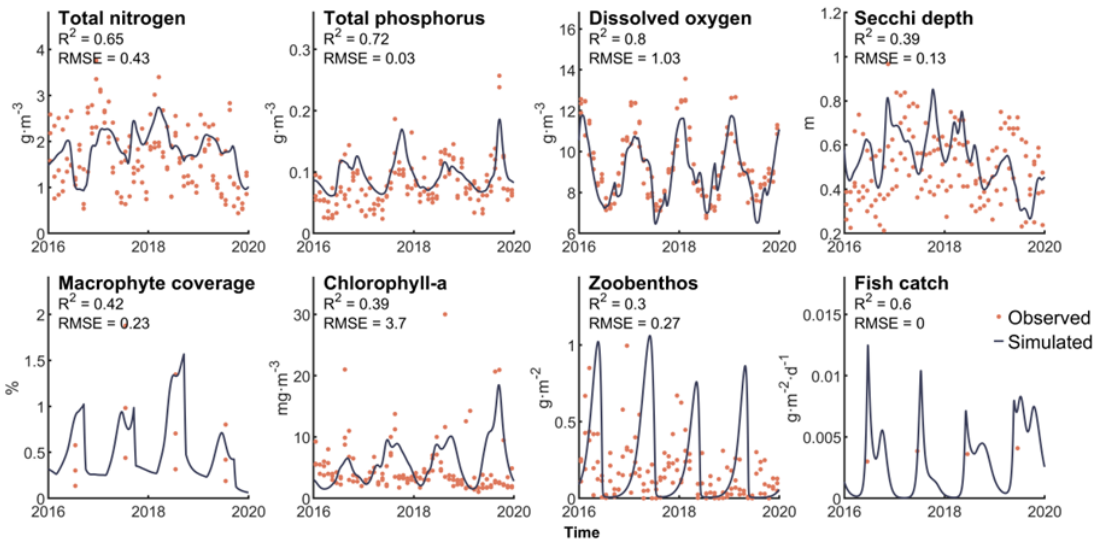

Figure 2 - The result of PCLake model calibration between 2016 and 2020. Monthly observational data from Lake Hongze comprised total nitrogen, total phosphorus, dissolved oxygen, Secchi depth, chlorophyll-a, and zoobenthos, while macrophyte coverage and fish harvest were recorded annually. Data from different lake zones are presented; however, the coefficient of determination (R^2) and root mean square error (RMSE) were calculated based on whole-lake averages and corresponding model simulations.

3.2 Hindcast on Fishing Ban and Trophic Cascade.

The calibrated PCLake model was applied to conduct a hindcast analysis for the period 2020–2024 (Figure 3A). Under the fishing ban scenario (FB), total fish biomass and chlorophyll-a showed an increasing trend, while macrophyte coverage declined slightly; other variables remained largely stable. Compared to the no-fishing-ban scenario (no FB), the FB scenario resulted in higher levels of total nitrogen, total phosphorus, chlorophyll-a, and total fish biomass, but lower values of Secchi depth, macrophyte coverage, zoobenthos, and zooplankton.

Monthly hindcast outputs were further analyzed using structural equation modeling (SEM) to quantify trophic interactions (Figure 3B; Table S3). Both SEM models exhibited acceptable fit ($\chi^2/df < 5$). Under the fishing ban, the path coefficients ranged from –0.91 to 0.6 (average: –0.38), with dominant negative relationships (red lines) across most variables except total phosphorus and macrophyte coverage. Strong top-down effects were evident through significant negative paths from fish to zooplankton (–0.62) and zoobenthos (–0.58). In contrast, without the fishing ban, positive pathways (black lines) prevailed among total phosphorus, macrophyte coverage, Secchi depth, phytoplankton, and zooplankton. Bottom-up effects were indicated by positive sequential coefficients from total phosphorus to phytoplankton (0.42) and phytoplankton to zooplankton (0.63).

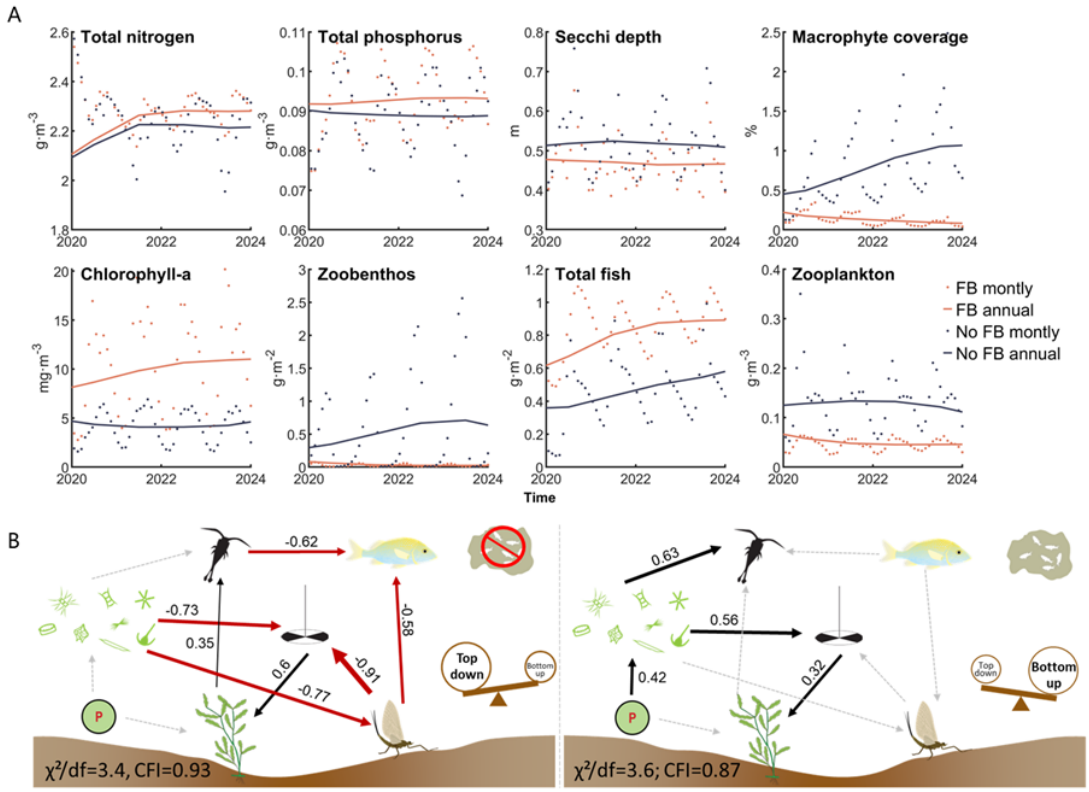

Figure 3 - The result of PCLake hindcast and SEM path analysis between 2020 and 2024. (A) "FB" denotes the control scenario with a full fishing ban (fishing intensity = 0), while "no FB" represents the scenario without fishing restrictions. Results are presented both monthly and annually. (B) Two SEM analyses were performed using monthly data from seven variables. Symbols representing these variables were sourced from https://ian.umces.edu/media-library/. Both SEM models exhibited acceptable fit according to the chi-square/degrees of freedom ratio (χ^2/df), and revealed contrasting dominant trophic cascades under fishing ban (left) and no ban (right) conditions. Red lines indicate negative relationships, black lines positive relationships, with line width corresponding to effect strength. Non-significant paths are shown as dashed grey lines.

3.3 Forecast Under Potential Managements.

To evaluate potential regulatory effects from 2025 to 2030, a scenario analysis was conducted using the Hongze Lake PCLake model. Relative changes in annual outputs by 2030 reveal distinct response patterns across scenarios compared to the control (NP- and F0). Variables in group A show greater sensitivity to nutrient control (differences between NP- and NP--) than to fishing intensity. In contrast, variables in group B exhibit a vertical gradient across fishing scenarios (F0, F0/1, F0.5, F1), indicating stronger influence from fishing pressure. Chlorophyll-a displays discernible variation along both nutrient and fishing gradients.

Stricter nutrient control significantly reduced nutrient concentrations and increased oxygen levels, whereas fishing bans had minimal impact on these variables. Chlorophyll-a also decreased under lower external loading. Compared to continued fishing ban (F0), scenario F1 (no ban) resulted in markedly lower total fish biomass and chlorophyll-a, but higher zooplankton, zoobenthos, and macrophyte levels. Intermediate fishing scenarios (F0/1 and F0.5) led to moderate effects, with F0.5 yielding slightly lower fish stock and chlorophyll-a, yet higher macrophyte coverage than F0/1. Moreover, differences between F0 and F1 were amplified under stricter nutrient control for chlorophyll-a and all group B variables except for zooplankton.

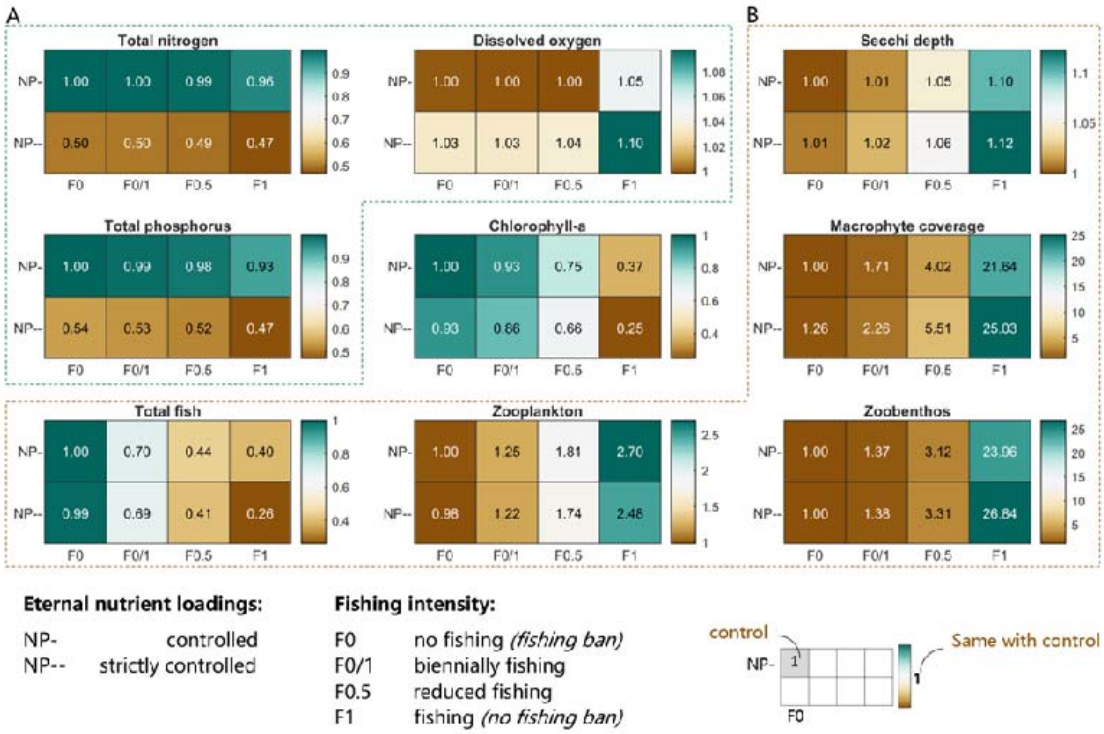

Figure 4 -The result of PCLake forecast between 2025 and 2030. The eight scenarios resulted from combining two external nutrient loading conditions (controlled, NP-; strictly controlled, NP--) with four fishing regimes (continuous ban, F0; biennial ban, F0/1; reduced effort, F0.5; no ban, F1). The color bar indicates the relative change compared to the control scenario (NP- and F0), with values above 1 denoting an increase relative to control. Variables are grouped into (A) and (B) based on similar response patterns across scenarios.

4. Discussion

4.1 The Past and Potential antagonistic Effects of Nutrient Control and Fishing Ban.

Despite the well-acknowledged negative effect of zooplankivorous fish stocking on water quality, such impact remains neglected in the combination of fishing ban and nutrient control. This neglection was mainly due to the difficulties in conducting process evaluations and the separation of the effectiveness evaluation system. Here, we sought to fill in the gap by combining a process-based modeling and path analysis approach in a lake with consistent observations. We confirmed the hypotheses that fishing ban can trigger enhanced top-down control to compromise the effectiveness of nutrient loading control on lake water quality and such antagonism would continue until 2030 if fishing ban will be implemented as planned. Thus, we anticipate that, in the context of comprehensive management, eutrophication restoration would slow down due to more enhanced trophic cascade from fish.

One advantage of combining the PCLake model and SEM analysis is to disentangle both the independent contributions and the indirect causal-effect pathways of combined managements in lake foodweb.

First, the model revealed divergent trends in lake variables under fishing ban (FB) and non-ban (no FB) conditions (Figure 3). From 2020 to 2024, the FB scenario was characterized by increases in fish biomass and chlorophyll‑a concentration. These findings align with reported rises in fish biodiversity and phytoplankton density by Zhang et al. (2024). The expansion of fish stocks resulted from the cessation of fishing, particularly under sufficient availability of

zooplankton and zoobenthos as food sources. This also implies that the likelihood of fishing bans leading to an increase in predatory fish populations and a decrease in other fish populations is low. Although macrophytes could offer refuge for zooplankton against predation, their limited coverage—remaining consistently low—rendered this effect negligible. Consequently, zooplankton declined slightly, reducing grazing pressure and contributing to phytoplankton increase. Even under no FB, a modest rise in fish biomass was simulated, attributable to the preexisting seasonal fishing ban (February–June annually since 2012) (Liu 2015), which had already lowered baseline fishing pressure. Continued implementation of such partial bans could enable gradual fish recovery, as reflected in the hindcast. Zoobenthos also increased, likely due to greater stocking of zooplanktivorous over benthivorous fish. Notably, studies such as Ren et al. (2022) indicate that benthic fish can promote sediment nutrient release, stimulating phytoplankton and periphyton growth, which in turn shades and suppresses submerged macrophytes. In our hindcast, Secchi depth remained largely stable despite correlations with other variables, suggesting that factors such as hydrodynamics and mining activities—exacerbated by the lake's shallow depth and short retention time (Li et al. 2019)—may exert stronger influence on light penetration and macrophyte development.

Second, our simulations demonstrate that fishing bans can intensify top-down control, thereby undermining the effectiveness of nutrient reduction measures in improving water quality—an effect projected to persist until 2030 if the ban continues as scheduled (Figure 4). Phytoplankton, positioned at the interface of bottom-up nutrient effects and top-down predation pressure (Figure 3), exhibits complex responses under combined management regimes (Figure 4). Lower phytoplankton levels under non-ban conditions may be attributed to nutrient removal through fishery activity, which enhances bottom-up control. Under fishing bans, however, phytoplankton abundance closely tracked fish biomass, as increased predation reduced zooplankton grazing pressure. Our results indicate that stringent nutrient control (NP--) combined with maintained fishing activity (F1) could optimize water quality by achieving the lowest nutrient and phytoplankton levels alongside the highest transparency, macrophyte coverage, and zoobenthos biomass (Figure 4). However, this scenario also resulted in the lowest fish stock, illustrating a classic ecosystem service trade-off (Rodríguez et al. 2006, Xu et al. 2017). Partial fishing restrictions (e.g., biennial F0/1 or reduced effort F0.5) also attenuated the benefits of nutrient control, reflecting intermediate ecological outcomes. This may result from rapid fish stock expansion during initial ban years, leading to structural surplus (Zhang et al. 2024).

Generally, a 40%–75% reduction in nutrient inputs can result in a regime shift from a turbid, algal-dominated state to a clear, macrophyte-dominated state (Søndergaard, Jensen and Jeppesen 2005, Me et al. 2018). Although Lake Hongze is nearing this critical threshold (Zhang et al. 2024) and both external and internal nutrient levels have declined in recent years, no significant macrophyte recovery has been observed yet. The restoration of Lake Hongze, which is in a critical phase of regime shift, would slow down due to more enhanced trophic cascade from fish. With adjustments to the duration and intensity of fishing bans, antagonistic effects could be amplified under more stringent nutrient control scenarios (Figure 4).Therefore, complementary strategies—such as reconnecting migratory pathways, restoring habitats, and targeted species stocking (Wang et al. 2022b, Mao et al. 2020, Feng et al. 2023)—should be integrated to simultaneously support biodiversity and eutrophication mitigation.

4.2 Evaluations and Limitations of the Modeling.

Based on model performance during calibration (2016–2020) and hindcasting (2020–2024), we conclude that the boundary conditions and parameter values of the PCLake model were appropriately configured. The calibrated simulation captured both the magnitude (RMSE) and seasonal dynamics (R^2) of observed variables comparably to other studies (Figure 2; Table S2). Relatively low R^2 values for zoobenthos and chlorophyll-a may be attributed to insufficient zooplankton data, leading to uncertain estimates of grazing pressure on phytoplankton and zoobenthos food availability. Although biological variables showed lower fit than water quality parameters, the modified model exhibited improved performance over the original version

(Figure S4; Table S2). Hindcast simulations under the fishing ban (2020–2024) aligned with trends reported in independent studies (Z. H. Huang et al., 2025), further supporting model validity. Additionally, a 4.5% increase in fish species richness (Huang et al. 2025b) and a projected 30% recovery of aquatic animal resources by 2031 (Wang et al. 2022a) corroborate the model's ecological relevance. Structural equation modeling (SEM) was employed for trophic cascade analysis. Although a χ^2/df ratio below 3 is ideal, values under 5 are considered acceptable (Karin Schermelleh-Engel and Helfried Moosbrugger 2003); both models in this study (Figure 3B) fell within this range. Potential sources of uncertainty include simplification of model structure, assumption of fixed pathways and directions—which may vary temporally—and possible nonlinear relationships among variables not captured in the SEM.

The limitations of this study primarily concern the absence of uncertainty analysis and the generalizability of the results. First, uncertainties stemming from the PCLake model structure and the selection of forcing functions for the control scenarios were not quantitatively evaluated. Although originally designed for temperate lakes (Janse 2005), the model for Lake Hongze was adapted to represent omnivorous fish indirectly by incorporating zooplanktivorous fish and adjusting their balance with benthivorous species. Nevertheless, the explicit absence of true omnivorous fish may reduce the reliability of simulations, particularly for biological variables. Second, while the choice of forcing functions—such as average nutrient loading from 2020 to 2024—likely preserves relative differences between scenarios, it may affect the absolute values of predicted variables. Third, the mismatch in temporal scales between lower and higher trophic levels in process-based modeling could influence the simulated responses of certain functional groups. Additionally, although a mutually antagonistic effect between fishing bans and nutrient reduction was identified in Lake Hongze, synergistic outcomes might occur in lakes dominated by piscivorous fish.

4.3 Implications.

Our findings hold relevance for a broad range of lakes globally. First, shallow freshwater lakes with food web structures comparable to Lake Hongze are widespread. Many of these systems experience severe eutrophication and water quality degradation, primarily due to pollution and resource overexploitation. The quantitative insights provided here regarding the contributions of different management strategies can support more informed decision-making. Although fishing bans are not traditionally classified as biomanipulation measures, they represent a direct policy approach to mitigating biodiversity loss by addressing key anthropogenic pressures (Wang et al. 2022a). Such targeted interventions, aimed at eliminating specific local stressors, are increasingly relevant in the context of achieving Sustainable Development Goals (SDGs). While the specific antagonistic effects identified here may be most applicable to lakes resembling Lake Hongze in physical and biological characteristics, the proposed research framework offers a transferable methodology for optimizing net benefits from multiple environmental policies. Importantly, the integration of process-based modeling and path analysis enables simultaneous evaluation of management outcomes and underlying mechanisms—an approach especially critical under future climate change.

Our modeling approach reveals the presence and mechanisms of antagonistic effects between external nutrient control and fishing bans in the restoration of eutrophic freshwater lakes. We project that this antagonism will persist until 2030 if the fishing ban continues as planned, and may intensify under stricter nutrient reduction. Within integrated management frameworks, eutrophication mitigation is likely to slow due to strengthened trophic cascades originating from fish populations. These results highlight the need for complementary strategies that simultaneously support biodiversity recovery and water quality improvement. Furthermore, management combinations should be implemented within systematic frameworks—featuring quantifiable feedback mechanisms—to address inherent trade-offs among ecosystem services. This study also demonstrates how integrating process-based modeling with path analysis can help quantify the contributions and underlying processes of management measures with complex

interactions. Future improvements in model precision are necessary to enhance the reliability of strategies aimed at maximizing net benefits from multi-objective environmental policies.

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Conflict of interest disclosure

The authors of this article declare that they have no financial conflict of interest with the content of this article.

Data and code availability

All data will be made available on request. The code of the original model used in this study is available at https://github.com/pcmodel/PCModel.

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