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Ambiguous influences of omnivorous fish on trophic cascade and alternative states: Implications for biomanipulation from an ecological model

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An ecological model was developed to systematically analyze the comprehensive influence of omnivory level and predation intensity of fish on the dynamic state and strength of trophic cascade of a lake ecosystem. Results showed that a higher fish omnivory level reduced the strength of trophic cascade and increased the occurrence of alternative states, while an increase in predation intensity resulted in opposite effects. With the combination of these two factors, the occurrence of alternative states was dependent on the relative increase in the predation intensity. The model was further applied to a subtropical shallow lake in China. Modeling results revealed that the heavy stock of omnivorous fish in the lake increased the occurrence of alternative states and decreased the strength of trophic cascade. Results indicated that the long-term effect of biomanipulation would be significant and therefore high rates of fish removal would be required. The information from this study indicated the importance of understanding the dynamic state and strength of trophic cascade when predicting the long-term effects of biomanipulation.

Keywords: omnivory, Asian Carp, predation intensity, dynamic state, Comprehensive Aquatic Simulation Model

Introduction

Biomanipulation through the artificial reduction of planktivorous fish biomass is a useful remediation method that has been widely applied to numerous eutrophic lakes (Hansson et al., 1998; Søndergaard et al., 2002). However, the effect of biomanipulation, especially the long-term effect, remains poorly understood. Omnivorous fish have

been reported as one of the important factors responsible for the difficulties in biomanipulation, especially in lower latitudes with rich filter-feeding species, such as Gizzard Shad (*Dorosoma cepedianum*), Silver Carp (*Hypophthalmichthys molitrix*) and Tilapia (*Oreochromis niloticus*) (Jeppesen et al., 2010). These fish selectively prey on detritus and planktonic algae besides zooplankton. The complex feeding habit reduces

trophic cascade and diminishes water quality improvements that would be obtained by the removal of planktivorous fish (Lazzaro, 1997; Pace et al., 1999). Therefore, the reduced trophic cascade makes biomanipulations less effective.

Nevertheless, at least two aspects need to be considered. First, omnivorous fish biomanipulation is also necessary to release predation pressure (Tátrai et al., 2003; Beklioglu et al., 2007). Attributed to their community structure, life history traits and feeding mode, omnivorous fish often have significant higher predation intensity (Okun et al., 2008; Jeppesen et al., 2010). For example, omnivorous fish in lower-latitude areas are with smaller sizes, substantially higher density, and therefore much higher zooplankton demand per unit of biomass. The strong predation intensity promotes negative cascading effects. Second, the existence of alternative states is another important factor affecting biomanipulation. If a system is monostable, the long-term effect of regime shifts would probably be limited (Hansson et al., 1998). Meanwhile, the alternative states are a possibility of the ecosystem behavior (Schröder et al., 2005). However, in several models incorporating the omnivory factor (Post et al., 2000; Faria and Costa, 2010), the effects of alternative states on biomanipulation have seldom been considered.

The aim of this study was to systematically analyze the comprehensive effects of omnivory and predation intensity of fish on the strength of trophic cascade and alternative states using an ecological model. The model was applied to predict biomanipulation effects through evaluating dynamic states and trophic cascade. Biomanipulation strategies were discussed based on the results.

Material and methods

The ecological model

The model used in the article is a modified version of the Comprehensive Aquatic Simulation Model (CASIM) (DeAngelis et al., 1989). It includes three trophic levels and nutrient (phosphorus) circulation from detritus to water, and is able to perform regime shifts triggered by sufficient perturbation under intermediate nutrient loading (Amemiya et al., 2005, 2007). The details of the model are shown in Appendix 1 in the supplementary information. To consider the omnivory

habit of fish, we expanded the model by including a prey-switching function (Post et al., 2000; Faria and Costa, 2010):

$$\begin{cases} \theta_i = iw_i / \sum iw_i & (i = Z, A, D) \\ \sum w_i = 1 \end{cases} \quad (1)$$

where w_i ($w_i \geq 0$) is the food preference degree of fish for zooplankton ($i = Z$), algae ($i = A$), and detritus ($i = D$). For example, if $w_Z = 1$ and $w_A = w_D = 0$, fish only prey on zooplankton; if $w_Z = w_A = w_D = 1/3$, fish feed on zooplankton, algae, and detritus without preference. By incorporating Equation (1), the modified model becomes

$$\begin{cases} \frac{dN}{dt} = I_N - r_N N - \frac{\gamma r_A N A}{k_N + N} + \gamma d_D D \\ \frac{dA}{dt} = \frac{r_A A N}{k_N + N} - \frac{f_Z A^2 Z}{k_A^2 + A^2} - \frac{\theta_A f_{FA} A F}{k_{FA} + A} - (d_A + e_A) A \\ \frac{dZ}{dt} = \frac{\eta f_Z A^2 Z}{k_A^2 + A^2} - \frac{\theta_Z f_F Z F}{k_Z + Z} - (d_Z + e_Z) Z \\ \frac{dF}{dt} = \eta \frac{\theta_Z f_{FZ} Z F}{k_Z + Z} + \eta \frac{\theta_A f_{FA} A F}{k_{FA} + A} + \eta \frac{\theta_D f_{FD} D F}{k_D + D} - (d_F + e_F) F \\ \frac{dD}{dt} = (1 - \eta) \frac{\theta_Z f_{FZ} Z F}{k_Z + Z} + (1 - \eta) \frac{\theta_A f_{FA} A F}{k_{FA} + A} + (1 - \eta) \frac{\theta_D f_{FD} D F}{k_D + D} + (1 - \eta) \frac{f_Z A^2 Z}{k_A^2 + A^2} - \frac{\theta_D f_{FD} D F}{k_D + D} + d_A A + d_Z Z + d_F F - (d_D + e_D) D \end{cases} \quad (2)$$

where the definitions and values of all variables and parameters are explained in Table 1. In the model, three growth terms with food preference (θ_Z , θ_A , θ_D) were used to account for the selective consumptions on zooplankton, algae, and detritus. We used Type II equations to reflect fish functional response instead of the type III equations in the original model, because the combination of preference term and type II equation can produce type-III-like functional response (Post et al., 2000; Attayde et al., 2010).

Table 1. Definitions and values of state variables and parameters of the ecological model. The value ranges are assigned for the calibration of the case study.

Symbol	Definition	Unit	Value
<i>State variables</i>			
N	Nutrient (phosphorus) concentration	g m^{-2}	—
A	Algal biomass	g m^{-2}	—
Z	Zooplankton biomass	g m^{-2}	—
F	Fish biomass	g m^{-2}	—
D	Detrital biomass	g m^{-2}	—
<i>Control parameters</i>			
I_N	Input rate of nutrient	$\text{g m}^{-2} \text{d}^{-1}$	0 – 0.002
<i>Parameters representing omnivory level</i>			
w_i	Preference degree of fish consuming zooplankton ($i = Z$), detritus ($i = D$) and algae ($i = A$), where $w_Z + w_A + w_D = 1$	—	0 (1 for $i = Z$) (0 – 0.5)
<i>Parameter representing predation intensity</i>			
f_{FZ}	Feeding rate of fish on zooplankton	1 d^{-1}	10 (7 – 34) ^{a, b}
k_Z	Half-saturation constant of zooplankton biomass for fish predation	g m^{-2}	1.4 (0.5 – 5) ^{a, b}
<i>Other parameters</i>			
r_N	Loss rate of nutrient	1 d^{-1}	0.005 ^{a, b}
r_A	Maximum growth rate of algae	1 d^{-1}	0.3 ^{a, b}
k_N	Half-saturation constant of nutrient	g m^{-2}	0.005 ^{a, b}
k_A	Half-saturation constant of algal biomass for zooplankton grazing	g m^{-2}	2.45 ^b
k_{FA}	Half-saturation constant of algal biomass for fish predation	g m^{-2}	3.7 ^c
k_D	Half-saturation constant of detrital biomass for fish predation	g m^{-2}	3 ^c
f_Z	Feeding rate of zooplankton on algae	1 d^{-1}	2 (0.24 – 10) ^{a, b, d}
f_{FA}	Feeding rate of fish on algae	1 d^{-1}	0.35 ^{c, e}
f_{FD}	Feeding rate of fish on detritus	1 d^{-1}	0.5 ^{c, e}
γ	Ratio of nutrient mass to biomass	—	0.02 ^{a, b}
η	Assimilation efficiency	—	0.5 ^{a, b}
d_i	Death rate of algae ($i = A$), zooplankton ($i = Z$) and fish ($i = F$); decomposition rate of detritus ($i = D$)	1 d^{-1}	0.1 (0.5 for $i = F$) ^{a, b}
e_i	Removal rate of algae ($i = A$), zooplankton ($i = Z$), fish ($i = F$) and detritus ($i = D$) from the system	1 d^{-1}	0.001 ^{a, b}

Sources: ^aDeAngelis et al. (1989); ^bAmemiya et al. (2005, 2007); ^cSagehashi et al. (2000); ^dSuzuki et al. (2000); ^eSagehashi et al. (2001).

Numerical analysis

A numerical linear stability analysis for the model was carried out with the input rate (I_N) being used as a control parameter. Coexisting solutions for same I_N values are identified as alternative equilibria. In the study, the I_N range assigned for the stability analysis was 0–0.002 g m⁻² d⁻¹, slightly larger than that in the original CASM (Amemiya et al., 2005, 2007). Based on the I_N range and the parameter values listed in Table 1, algal biomass ranged from 0.8 to 40 g m⁻² was obtained, which covered most of possible values in freshwater systems.

In the model, the omnivory level is determined based on phytoplanktivory (w_A) and detritivory (w_D). Higher w_A and/or w_D indicated higher omnivory levels. The predation intensity is estimated by the half-saturation constant of zooplankton biomass (k_Z) and the feeding rate of fish (f_{FZ}), that is, higher f_{FZ} and/or lower k_Z values represents higher predation intensity (Li et al., 2010). To examine the influence of fish omnivory and predation intensity on the dynamic state and trophic cascade of the system, different values of parameters w_A , w_D , f_F and k_Z (as listed in Table 1), were selected to perform the stability analysis. Other parameters were set to the default values. Four types of dynamic states were obtained by the analysis. Definitions and characteristics of the four types of dynamic states (S1 to S4) are listed in Table 2. In S2 and S3, regime shifts were most likely triggered by suitable perturbations.

Trophic cascades result in inverse patterns in abundance or biomass across more than one trophic link in a food web (Persson, 1999). For a three-level food chain, abundant top predators (fish) result in lower abundances of mid-level consumers (zooplankton) and higher abundance of basal producers (algae) (Pace et al., 1999). To evaluate the strength of trophic cascade, the trophic cascade index (TCI) was defined:

$$TCI = \frac{dA}{dF} = \frac{(A_2 - A_1)}{(F_2 - F_1)} \tag{3}$$

where A and F are the algal biomass and fish biomass, and subscripts 1 and 2 denote equilibria with low and high algal biomass, respectively. The stability analysis with the parameter values in Table 1 showed that the A value was ~0.8 g m⁻² with F close to zero and increase (> ~25 – 40 g m⁻²) quasi-linearly with high F values. According the sensitivity of TCI values, A_1 and A_2 were taken 1 and 30 g m⁻², respectively, and F_1 and F_2 were estimated through the stability analysis.

Case study: Wuhan East Lake

A case study was introduced to illustrate how to assess the feasibility of biomanipulation through evaluation of the dynamic states and trophic cascade. Wuhan East Lake (Lake Donghu) is a subtropical urban shallow lake located along the

Table 2. Definitions and characteristics of the four types of dynamic states.

Type	Definition	Alternative states	Example
S1	Stable equilibrium with the algal biomass linearly increasing with nutrient loading	Non-existent ^a	Figures 2a and g
S2	Stable equilibrium with low (high) algal biomass at low (high) nutrient loading; alternative equilibria at moderate nutrient loading	Existent	Figures 2b and f
S3	Stable equilibrium with low algal biomass at low nutrient loading; alternative equilibria at high nutrient loading	Existent	Figures 2c and e
S4	Stable equilibrium with low algal biomass at increasing nutrient loading ^b	Non-existent	Figure 2d

^aThe existence of alternative states means regime shifts are possibly triggered by suitable perturbations (e.g. biomanipulation);
^bmathematically, stable equilibrium with extremely high algal biomass (> ~200 g m⁻²) exists at high nutrient loading (> ~0.01 g m⁻² d⁻¹), as we tested on the parameter space of Table 1. However, such high magnitudes of algal biomass and nutrient loading are rarely observed in natural freshwater systems, and therefore not considered in this study.

middle reach of Yangtze River in central China (114°24'E, 30°32'N). It has an average depth of 2.2 m and a surface area of 27.9 km². Both acceleration and control of the eutrophication process in the lake are highly associated with commercial fisheries. Since the 1960s, typical omnivorous Asian Carps, Silver Carp (*Hypophthalmichthys molitrix*) and Bighead Carp (*Aristichthys nobilis*) have been heavily stocked in the lake. As a result, the community compositions of fish and zooplankton have been heavily altered to small and tolerant species, and nuisance blue-green algal blooms frequently occurred. Dramatically, the blooms have vanished since 1985, as the fish stocking has been intense enough to control the algae since then (Liu and Xie, 1999). However, the lake still has turbid water with low transparency and submerged macrophytes are extinct due to degradation of the ecosystem. Details of the lake's eutrophication are presented in Appendix 2.

Model (2) was applied to simulate the long-term ecological dynamics and evaluate the changes of omnivory level, predation intensity, trophic cascade and dynamic state. Data on total phosphorus concentrations and the biomass of algae, zooplankton and fish from 1980 to 2009 were extracted from published literature (Appendix 2). Essential model parameters, including I_N , f_Z , w_A , w_D , k_Z and f_{FZ} during every five-year periods were calibrated, among which w_A and w_D represent the omnivory level, k_Z and f_{FZ} represent the predation intensity, and I_N and f_Z are sensitive to environmental change and algal compositions, respectively. During the calibration process, 10^{10} sets of parameters (w_A , w_D , k_Z , f_F , I_N , f_F) were randomly generated within their ranges

(Table 1) through Latin hypercube sampling to run the model. Other parameters were set to their default values. Simulations (SV_{sim}) and observations (SV_{obs}) were compared by the average error (AE), maximum error (ME), mean sum of standard deviation (SD) and relative error (RE), which are calculated by (Li, 2012):

$$\begin{cases} AE = |\overline{SV_{sim}} - \overline{SV_{obs}}| / \overline{SV_{obs}} \\ ME = |\max(SV_{sim}) - \max(SV_{obs})| / \max(SV_{obs}) \\ SD = \sqrt{\sum (SV_{sim} - SV_{obs})^2 / \sum SV_{obs}} \\ RE = \sum |SV_{sim} / SV_{obs} - 1| \end{cases} \quad (4)$$

For the sets of parameters satisfying $AE < 0.1$, $ME < 0.1$ and $SD < 0.1$ for the state variables, the total relative error (TRE) was obtained by the sum of RE . The optimal parameters should result in the lowest TRE . The model was further used to evaluate the dynamic state and calculate the TCI , as described above.

Results and discussion

Influence of omnivory and predation intensity on trophic cascade and dynamic state

Numerical analysis showed that omnivory reduced the strength of trophic cascade and increased the occurrence of alternative states (Figure 1a), while the increase in predation intensity had opposite effects (Figure 1b) and their

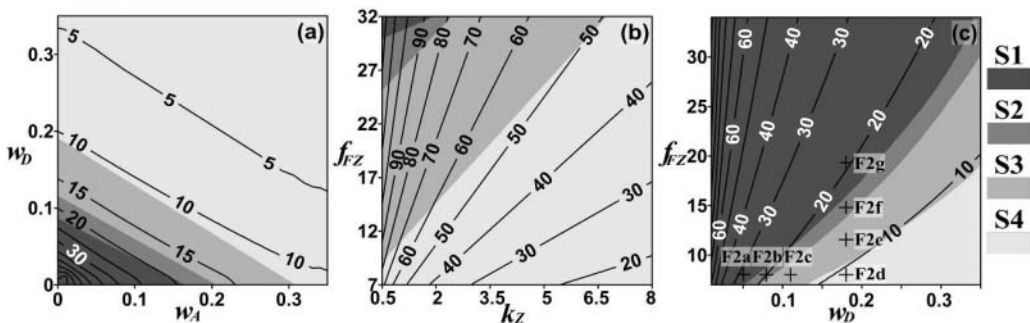


Figure 1. Dynamic states (shading) and TCI (contour) as functions of (a) omnivory (w_A , w_D), (b) predation intensity (k_Z , f_Z) and (c) their combinations (represented by w_D and f_Z). Other parameters were equal to the default values. The four states (S1 to S4) are explained in Table 2. Note that the omnivory levels are restrained by Equation (1). Typical examples of the detailed biomass dynamics are shown in Figure 2, with the crosses indicating the values of w_D and f_Z in Figure 1c.

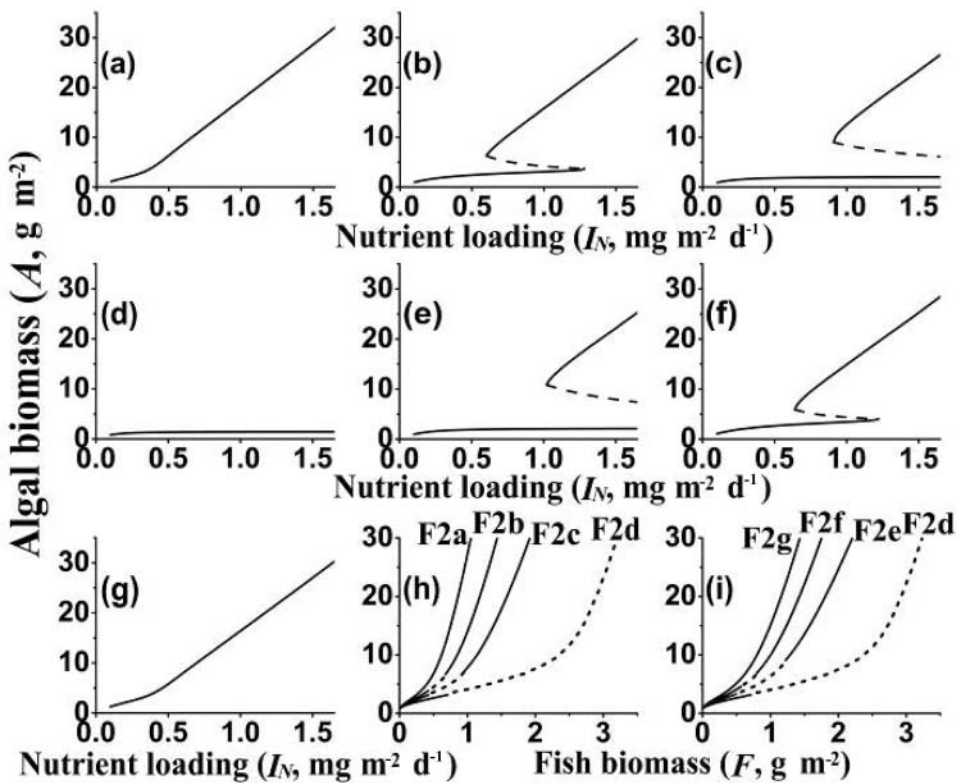


Figure 2. Algal biomass (A) as a function of (a–g) nutrient loading (I_N) and (h, i) fish biomass (F), with the levels of omnivory (w_D) and predation intensity (f_{FZ}) marked in Figure 1c. Other parameters were equal to the default values. Solid and dashed lines represent stable and unstable equilibria, respectively.

combination led to ambiguous influences (Figure 1c). For instance, at a low omnivory level, the dynamic state belonged to S1, where regime shifts were not likely to occur due to the absence of alternative equilibria (Figure 2a). With a higher omnivory level, the dynamic state became S2, where alternative equilibria existed under moderate nutrient loading, implying regime shifts were possible (Figure 2b). With increasing omnivory levels, alternative equilibria coexisted with increasing range of nutrient levels. When the range was wide enough to exclude the monostable equilibrium with high algal biomass, the system entered S3 (Figure 2c). When the omnivory level was high enough, the equilibrium with algal biomass became too high to be captured from our initial condition, and the system entered S4 (Figure 2d). In addition, the slopes of the $A - F$ dynamics decreased with the increasing omnivory level (Figure 2h), which revealed that more fish were required to control the same amount of algae, that is, a decrease in trophic cascade. Conversely,

with increasing predation intensity, dynamic state changed from S4, S3, S2 to S1, with trophic cascade increasing (Figures 2d–g, and i).

The ecological reasons for the model behavior can be attributed to the alteration of the “biological resistance” (Scheffer et al., 2001). The increase in predation intensity enhances the biological resistance (Beklioglu et al., 2011), which makes the system tend to behave in a monostable manner regime, whereas increased omnivory reduces the resistance by creating horizontal and vertical heterogeneity in food web structure with the potential for bistability (Mylius et al., 2001; Schröder et al., 2005). With respect to the comprehensive influence, Holt and Polis (1997) hypothesized that there was a potential for alternative states if the top predator was relatively inefficient at consuming the intermediate species. Our results support the hypothesis: if the predation intensity is low, the alternative states may exist in wide omnivory ranges; oppositely, the alternative states can only exist at sufficiently high omnivory levels

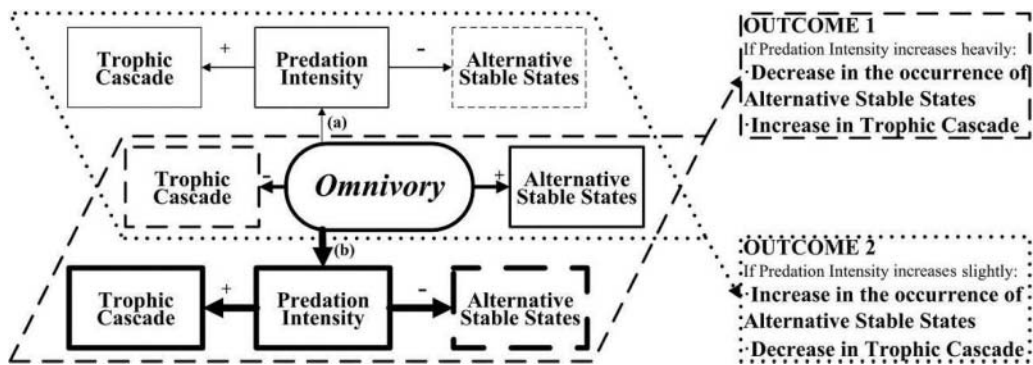


Figure 3. Conceptual diagram model depicting two possible outcomes of increases in omnivory and predation intensity based on the model. Predation intensity may either (a) slightly or (b) heavily increase with omnivory level, which leads to different influences on dynamic state and trophic cascade. The symbols “+” and “-” represent positive and negative effect; the solid and dashed boxes denote the increase and decrease of the variables; and the thickness of arrows and boxes indicate the degree of effect and variation, respectively.

(Figure 1c). In addition, the resistance can be further strengthened by bottom-up input at relative high I_N loading levels. The state variables are balanced by a high matter flux and the only source I_N decides the matter level of the system. For example, algal biomass increased linearly with I_N when the loading level was relatively high (Figures 2a–g), which was also observed in similar models (Scheffer, 1990; Scheffer et al., 2001).

Similar to Lazzaro (1997) and Pace et al. (1999), fish omnivory reduces trophic cascade but increases the occurrence of alternative states (Figure 1a). On the other hand, the increase in predation intensity enhances trophic cascade (Okun et al., 2008) but decreases the occurrence of alternative states (Figure 1b). As the results, omnivorous fish may either increase or decrease the occurrence of alternative states, depending on the relative increase level of predation intensity (Figure 3). The two outcomes compatibly explain the coexistence of the two distinct expectations when applying biomanipulation: one (Outcome 1) queried the unpredictable long-term effect due to the reduced cascading effect (Lazzaro, 1997; Pace et al., 1999), and the other (Outcome 2) emphasized the urgent need to release high predation pressure on zooplankton (Tátrai et al., 2003; Beklioglu et al., 2007).

Implications for biomanipulation with the case study

The ecological dynamics of Wuhan East Lake from 1980 to 2009 were simulated and the

modeling results were quite consistent with the observations, which indicated that the model was capable of reproducing the features and variability of the lake (Figures 4a–d). Furthermore, the results revealed that the heavy stocking of commercial fish had altered the internal properties of the lake system. Silver Carp and Bighead Carp, the main species stocked in the lake, are characterized by omnivorous feeding habit, high predation pressure on zooplankton and high efficacy of nutrient recycling (Datta and Jana, 1998; Zhang et al., 2006). These characteristics were evident in the calibrated parameters, which showed the omnivory level, the predation intensity and nutrient loading were generally increasing during the modeling period (Figures 4e–g). Moreover, these fish are capable of controlling blue-green algae (Datta and Jana, 1998; Chen et al., 2010), which are not good food source for zooplankton. As a result, the proportion of edible algae for zooplankton increased, which was evident from the increase in feeding rate (Figure 4g). The above changes of internal properties led to the changes of dynamic state and trophic cascade: the dynamic state changed from S1 during 1980 and 1984 to S2 and S3 during 1985 and 1999, and had remained in S3 since 2000, and the trophic cascade continuously decreased (Figure 4h). The results were further confirmed by the stochastic simulations (Appendix 3).

Combined measures of composition manipulations on the fish community and pulse-like fish removals should be effective for lake restoration. Schooling omnivorous fish such as Silver Carp and Bighead Carp is effective for controlling blue-

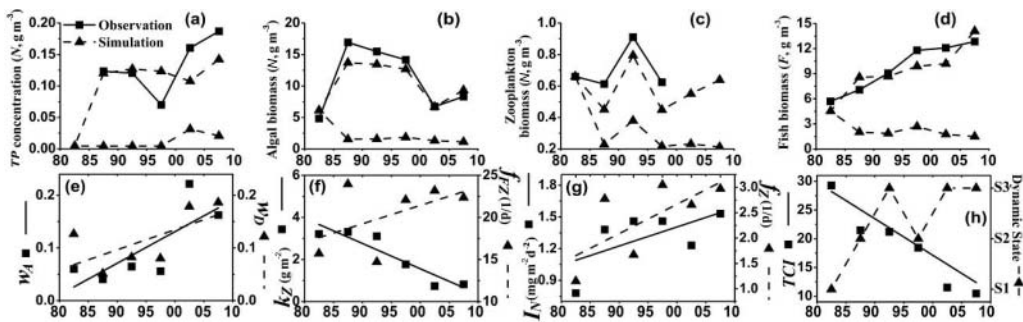


Figure 4. Results of the case study. Upper panels show the comparison between modeling results (triangle) and observation values (square) of (a) TP concentration, (b) algal biomass, (c) zooplankton biomass and (d) fish biomass. Modeling points represent variables in their equilibria. Two modeling points which coexist in the same period are alternative equilibria. Lower panels show the calibrated parameters representing (a) omnivory (w_A , w_D), (b) predation intensity (k_Z , f_{FZ}), (c) loading (I_N) and feeding rate of zooplankton on algae (f_Z) and (d) the calculated results of TCI and dynamic state.

green algae. While an increase in omnivory level used to be regarded as an unfavorable factor for reducing trophic cascade (Lazzaro, 1997; Pace et al., 1999), it is more favorable to drive the system into alternative states (Figures 1a, 4e and h). On the other hand, these fish prey highly on zooplankton (Figure 4f; see also Okun et al., 2008), and are harmful to aquatic vegetation (Miller and Crowl, 2006). Therefore, it is necessary to remove fish to trigger positive regime shifts in the lake (Starling et al., 2002). Here, the mathematical model provides a useful approach to calculate the timing of biomanipulation through evaluating the dynamic state and trophic cascade. Based on the results of Wuhan East Lake, the ecosystem has changed from monostable to bistable, and the lake remained in S3 (alternative states exist in a wide loading range) since 2000 (Figure 4h). This indicated the long-term effects of biomanipulation would become significant. Meanwhile, the fish removal intensity should be sufficiently high, since the strength of trophic cascade has remarkably decreased.

Conclusions

The comprehensive influence of omnivory level and predation intensity on trophic cascade and dynamic state was examined through an ecological model. Biomanipulation strategies of omnivorous fish were discussed based on the model analysis results and a case study. A higher omnivory level increased the occurrence of alternative states and reduced the strength of trophic cascade, while the predation intensity resulted in opposite effects.

The combination of the two factors led to more comprehensive outcomes. The results clearly explained the biomanipulation challenge with omnivorous fish. It is essential to evaluate dynamic state and trophic cascade for implementing biomanipulation. A combinative measure of adjusting dynamic state and pulse-like fish removal should be an effective biomanipulation strategy.

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Supplemental material

Supplemental data for this article can be accessed on the publisher's website.

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