LETTER

Reservoir ecological operation by quantifying outflow disturbance to aquatic community dynamics

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Keywords: aquatic community, hydrological alteration, flow–ecology, reservoir operation, multi-objectives

Abstract

Reservoir operation causes spatiotemporal variations in outflow, which influence the dynamics of downstream aquatic communities. However, empirical evidence of community responses to hydrological alteration remains limited for dam-regulated rivers. This study focused on quantifying the streamflow disturbance to multi-population dynamics in downstream of the China's Danjiangkou Reservoir. First, the stochastic population dynamics model (PDM) was used to simulate aquatic community dynamics. Then, the flow–ecology relationship was established to identify community response to reservoir outflow. Third, two novel ecological indicators, stable time (ST) and coefficient of variation at stable time (CVST), were proposed to evaluate the resilience and resistance of multi-population systems, respectively. Finally, the reservoir operating rule curves were optimized by considering tradeoffs between socioeconomic and ecological objectives. The coevolution processes of multi-population systems (fish, phytoplankton, zooplankton, zoobenthos, and macrophytes) were simulated by stochastic PDMs. The population densities of stable states showed continuous downward trends with increasing degree of hydrological alteration for multi-population systems, and aquatic community systems could be destroyed when alteration reached its acceptable maximum. The greater the degree of hydrological alteration, the longer the recovery time from an unstable to a stable state, and the weaker resistance for each population system. The resilience and resistance of downstream multi-population systems were enhanced by optimizing reservoir outflow. The optimization results illustrated that the performances of the multiple objectives of water supply, hydropower generation, and ST were improved by 2.37%, 2.40%, and 2.67%, respectively, whereas the performance of CVST was the same as the conventional operation. The flow–ecology relationship provided an approach to quantify the impacts of reservoir outflow on an aquatic community, which is helpful in guiding ecological flow strategies.

1. Introduction

Reservoirs can bring huge socioeconomic benefits by providing flood control, water supply (WS), hydropower generation (HG), navigation, and tourism (Gong et al 2021, Huang et al 2021). However, these have a considerable influence on the spatiotemporal allocation of natural inflows (Tonkin et al 2018, Grill et al 2019, Wang et al 2021). Consequently, hydrological characteristics such as the seasonal and inter-annual streamflow distribution of rivers are greatly changed, and this adversely impacts the function, structure, and dynamics of downstream aquatic communities (Poff et al 2007, Chen and Olden 2017,
Benjankar et al. 2018, Palmer and Ruhi 2019, Sabzi et al. 2019). For example, variations in reservoir outflow may change the composition and quantity of fish populations, which will have inevitable impacts on the structure of the food webs through population interactions including predation, competition, and interdependence (Gao et al. 2019, Lin and Robinson 2019, Fornaroli et al. 2020, Mathers et al. 2020). Given the current situation of ecological degradation for dam-regulated rivers, most restoration practices have focused on improving channel morphology or habitat. For example, reestablishing native riparian, reclaiming farmland to wetland and restoring fish spawning habitat. Unfortunately, these practices proved difficult to restore biodiversity or flow regime (Lorenz et al. 2018). This has motivated researchers to move from morphological to ‘process-based’ studies of the ecological linkage between streamflow and aquatic communities, as well as other physical and ecological processes that focus on flow regime and specific species (Beechie et al. 2010).

Existing studies have discussed the hypothesis that aquatic community dynamics depend largely on flow regime (Robson et al. 2017, Horne et al. 2019). Poff and Ward (1989) showed that intra-annual variation in hydrological conditions played a major role in population dynamics by affecting reproductive success, natural flow, and biotic competition. Ruhi et al. (2015) applied multivariate autoregressive state-space models to long-term flow and fish biomass data, and illustrated that interannual variation in flow anomalies ultimately drive the dynamics of a desert stream fish community. Shuai et al. (2018) found a strong association between the spawning of silver carp larvae and peak flows over a particular magnitude. Hydrological metrics including magnitude, duration, timing, rate of change, and frequency of flow events under different flow conditions are critical driving factors in the diversity of fish traits (Bruckerhoff et al. 2019, Fornaroli et al. 2020). The streamflow regime can be stochastically altered by reservoir operations, which can have profound influence on the ecological functions of aquatic community systems (Zarri et al. 2019).

The restoration of ecologically important flow regimes downstream of a reservoir has prompted a variety of approaches in terms of ecological base flow, natural flow, seasonally variable ecological flow, and biodiversity in recent decades (Chen and Olden 2018). Maintaining natural flow regimes has been long recognized as a water management priority because it is considered to be critical for sustaining freshwater ecosystems (Bruckerhoff et al. 2019). Subsequently, growing interest in improving river ecosystems compelled researchers to consider multiple populations (Aspin et al. 2020), generating a greater understanding of the flow–ecology relationship (Horne et al. 2019, White et al. 2021). Although multiple populations interact, their effects are small compared with the effects of flow regime alteration (Palmer and Ruhi 2019). Thus, it is essential to predict how populations will fluctuate through time when flow regimes are altered. The dynamics of aquatic communities are dominated by deterministic biotic interactions and the stochastic consequence of flow regime alteration (Grossman et al. 1982). Stochasticity is inherent to any ecological system (Thompson et al. 2020). The biological processes (e.g. births, deaths, immigration, and emigration) and environmental conditions (e.g. flow regime alteration) have been demonstrated to be probabilistic, resulting in the stochasticity of community dynamics (Zhao et al. 2018, Shoemaker et al. 2020). This stochasticity has been included in the long history of ecological models via probabilistic draws of the underlying biological processes (Matias et al. 2013, Shoemaker and Melbourne 2016, Fournier et al. 2017). Recent models have been capable of describing the stochastic dynamics of a metacommunity by changing critical parameters such as niche breadth, growth rate, and population interactions, bringing us closer to the goal of understanding the effects of flow regime alteration on an aquatic community. For instance, the population dynamics model (PDM) was widely used to describe the dynamic behaviors of aquatic community systems under stochastic intrinsic growth rate (Zhang et al. 2020), but it was unable to capture the streamflow disturbance to aquatic species in the natural world. Nevertheless, these models only explored stochasticity from a mathematical point of view, but remained an issue that how to quantify the relationship between streamflow regime and its stochastic disturbance to aquatic community systems.

To address the above issue, this study provided a new flow–ecology relationship to quantify the disturbance of reservoir outflow to multi-population dynamics by using stochastic PDMs. It aimed to answer three questions: (a) What is the coevolution mechanism of multi-population systems? (b) How to identify the response relationship between river streamflow and aquatic community? (c) How to formulate ecologically important and socially desirable measures for reservoir operation?

2. Methodology

The methodology consisted of four components (figure S1 available online at stacks.iop.org/ERL/16/074005/mmedia): (a) formulate the stochastic PDM; (b) establish the flow–ecology relationship; (c) propose two novel ecological indicators; and (d) conduct the reservoir optimization operation.

2.1. Stochastic PDM

The logistic growth model is widely used to describe the density dynamics of a single population owing to its efficient performance, but its application is limited
because of the competition, interdependence, and predator–prey relationships among different populations (Golec and Sathananthan 2003, Sun and Wang 2008, Cufaro Petroni et al 2020). Thus, development of the multi-PDM was based on the logistic model by considering interactions among different populations (section S1 and figure S2). The stochastic PDM was established by combining the multi-PDM and stochastic differential equation (SDE). SDE is prominent in various areas of application, including biology, chemistry, epidemiology, mechanics, economics, microelectronics, and finance (Higham 2001, An et al 2021). It can be used to simulate the biomass (e.g. quantity or density) dynamics of populations under external stochastic disturbance (Kampen and Reinhardt 1981, Öttinger 1995, Gardiner 2009).

The stochastic PDM can be written in the form of a differential equation, as in equation (1). Note that the stochastic term is assumed to be added to $N(t)$ because this study concentrates on the stochastic disturbance of the whole population system, although the influence on specific parameters (e.g. environmental carrying capacity) can also be examined (Sun and Wang 2008, Costa et al 2016). In agreement with convention, the stochastic PDM is emphasized in its differential form rather than in an integral form:

$$
\frac{dN(t)}{dt} = r_N N(t) \left( 1 - \frac{N(t)}{K_N} - \sum_{i=1}^{I} \alpha_{NLi} L_i(t) K_i \right) + \sum_{j=1}^{W} \alpha_{NMj} M_j(t) K_{Mj} - \sum_{p=1}^{R} \alpha_{NXp} X_p(t) K_{Xp} + \sum_{q=1}^{Y} \alpha_{NYq} Y_q(t) N K_{Yq} + \sigma_N^{\text{flow}} dW(t)
$$

(1)

where $N(t)$ represents the density of population $N$ at time $t$; $r_N$ represents the intrinsic growth rate of $N$; $K_N$, $K_i$, $K_{Mj}$, $K_{Xp}$, and $K_{Yq}$ represent the environmental carrying capacity of $N_i$, $L_i$ $(i = 1, \ldots, I)$, $M_j$ $(j = 1, \ldots, W)$, $X_p$ $(p = 1, \ldots, R)$, and $Y_q$ $(q = 1, \ldots, Y)$, respectively; $\alpha_{NLi}$, $\alpha_{NMj}$, $\alpha_{NXp}$, and $\alpha_{NYq}$ represent the competitive coefficient between $N$ and $L_i$, $N$ and $M_j$, $N$ and $X_p$, and $N$ and $Y_q$, respectively; $\sigma_N^{\text{flow}}$ represents the noise intensity caused by flow regime alteration for population $N$; and $W(t)$ represents a random variable that is called a scalar standard Brownian motion, which can be regarded as the integral of white noise with time. $W(t)$ meets the following criteria: (a) $W(0) = 0$; (b) the random variable given by the increment $W(t) - W(s)$ is normally distributed with mean zero and variance $t - s$ for $0 \leq s < t \leq T$; and (c) the increments $W(t) - W(s)$ and $W(v) - W(u)$ are independent for $0 \leq s < t < u < v \leq T$.

Population dynamics systems with various noise intensities may have multiple stable states described by multiple peaks of stationary probability distribution functions (PDFs) (figure 1). When the population system is briefly disturbed, the population density variability may be relatively small, and the state variable may fluctuate around the current stable state. When the population system is continuously disturbed within lower and upper thresholds, it can have alternative stable states according to the equilibrium theory (Nolting and Abbott 2016, Feng et al 2019). However, the system will be broken when the noise intensity increases and exceeds a maximum value (May 1977). One or more populations of an aquatic community will be extinct if the noise intensity.

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**Figure 1.** Graphical representation of stable state transfer of a population system. Panel (a) the transfers of a stochastic dynamic population system from a nonstable to a stable state. The three solid lines of different colors represent various stable states of a population system, visualized by their potential functions. The solid balls represent the equilibrium points for stable states, and dashed balls show the variability in population density. Panel (b) the stable states described by stationary probability distribution functions (PDFs) may change in response to environmental drivers (e.g. flow regime alteration). Stationary PDFs of a population dynamics system can have different forms as flow regime changes. Panel (c) the transfer of equilibrium points with increasing noise intensity. Solid balls marked as A, B, C, and D refer to different stable state of a population system under various noise intensities. The lower threshold indicates that noise intensity is zero, and the upper threshold refers to the maximum value of intensity that can destroy the system.
exceeds the maximum value, which seriously reduces the biodiversity and destroys the integrity of a river ecosystem.

### 2.2. Flow–ecology relationship

The ecological integrity of riverine ecosystems is strongly connected to the natural flow regime (Poff et al. 1997), which is altered in terms of the flow magnitude, duration, timing, frequency, and rate of change in dam-regulated rivers. The flow magnitude is a measure of the availability or suitability of the habitat. The occurrence timing of particular flow events is used to indicate whether certain life-cycle requirements are met. The occurrence frequency of droughts or floods, for example, may be tied to reproduction or mortality events for various species. The duration of a flow event may determine whether a particular life-cycle phase can be completed. The rate of change may be tied to the stranding of aquatic organisms (Richter et al. 1998). Thus, the aquatic community can be disturbed by flow regime alteration through linkages among ecosystem structure, environmental conditions, and biotic processes (figure S3).

Richter et al. (1996) proposed an indicators of hydrologic alteration (IHA) method including 32 hydrological parameters (table S1) for assessing the degree of hydrological alteration attributable to human influence within an ecosystem. Richter et al. (1997) proposed the range of variability approach (RVA), based on the IHA method, for totally assessing flow regime alteration and its ecological disturbance.

Although the IHA/RVA method is widely used in river ecological evaluation, it does not take ecosystem dynamics into consideration, and is based on statistical analyses of long-series streamflow data. Nevertheless, the degree of hydrological alteration revealed by the IHA/RVA method can be used to describe reservoir outflow disturbance to an aquatic community. The disturbance represented by noise intensity can be calculated by equation (2):

$$\sigma_{N}^{\text{altered flow}} = \sigma_{N}^{\text{max}} \frac{D_{\text{altered flow}} - D_{\text{natural flow}}}{1 - D_{\text{natural flow}}}$$

where $\sigma_{N}^{\text{max}}$ represents the maximum value of noise intensity of population $N$; $D_{\text{altered flow}}$ is the total hydrological alteration degree of the altered streamflow; and $D_{\text{natural flow}}$ is the total hydrological alteration degree of the natural flow (i.e. reservoir inflow). The method of calculating the degree of hydrological alteration is clarified in section s2.

The hydrological alteration degree is positively correlated with noise intensity. A smaller $D_{\text{natural flow}}$ value may be preferred because it represents less disturbance to a single population system. For an aquatic community comprising multiple populations, the external disturbance to one population can be transferred to others due to multi-population interactions such as predation, competition, and interdependence. It is uncertain whether a smaller $D_{\text{natural flow}}$ will be beneficial to multi-population systems. Thus, the flow–ecology relationship is needed to quantify such disturbance. The flow–ecology relationship (figure S4) can be interpreted as: (a) the noise intensity of the population system under a natural flow regime is zero; (b) the noise intensity is $\sigma_{N}^{\text{max}}$ when the hydrological alteration degree is 1 (i.e. the natural flow regime has been completely altered); and (c) the noise intensity is determined proportionally between 0 and $\sigma_{N}^{\text{max}}$ when the hydrological alteration degree is between $D_{\text{natural flow}}$ and 1. The establishment of the flow–ecology relationship provided an approach for quantifying the impacts of reservoir outflow on an aquatic community.

### 2.3. Ecological indicators

Two novel ecological indicators are proposed based on the analyses of population system stability given in sections 2.1 and 2.2.

Stable time (ST) is defined as the recovery time for a population system with stochastically continuous perturbations from an unstable state to a stable state (figure 2). ST reflects the resilience of population systems. The unit of ST is day. The PDF of population density reaches stationarity and the mean population density reaches a stationary level as the dynamic system reaches a stable state. The L2 norm of the difference between transient and stationary PDFs is calculated to determine the ST value. A stochastic system is generally considered to have reached a stable state when the L2 norm approaches zero. The ST is described in equation (3) as:

$$\text{ST} = t, \text{ when } \| \text{PDF}^{\text{transient}} - \text{PDF}^{\text{stationary}} \|_{2} \approx 0,$$

where $\text{PDF}^{\text{transient}}$ indicates the one-dimensional matrix of transient PDF at $t$ for a stochastic population system; and $\text{PDF}^{\text{stationary}}$ indicates the one-dimensional matrix of stationary PDF at the end of the simulation period for a stochastic population system.

A smaller ST indicates that the population system responds faster to external disturbance, which is a positive signal of a healthy system. ST will change with various noise intensities of the population system.

Coefficient of variation at stable time (CVST) is defined as the variation coefficient of stochastic simulation values at ST. CVST reflects the resistance of population systems, which is presented in equation (4) as:

$$\text{CVST} = \sqrt{\frac{\sum_{i=1}^{P} (N_{ST}^{i} - \overline{N_{ST}})^{2}}{N_{ST}}}$$

where $N_{ST}^{i}$ represents the population size at stable time; $\overline{N_{ST}}$ is the mean population size at stable time; and $P$ is the number of simulation runs.
where $N_{ST}^i$ is the population density of $N$ at ST for the $i$th stochastic path; $\overline{N_{ST}}$ is the mean population density of $N$ at ST; and $P$ is the number of stochastic paths.

A smaller CVST value indicates that the stochastic simulation values at ST are more concentrated near the mean level and that the population system is more resistant.

2.4. Multi-objective optimization

For reservoirs with multiple functions including WS, power generation, and ecological management, the multiple objectives of average annual WS and average annual HG are described as follows (Cheng et al 2021, Xu et al 2021). The minimizations of ST and CVST have been described by equations (3) and (4), respectively.

Equations (5) and (6) describe the maximizations of WS and HG, respectively:

\[
\text{max } \text{WS} = \sum_{i=1}^{S} W_i / S, \tag{5}
\]

\[
\text{max } \text{HG} = \sum_{i=1}^{S} H_i / S, \tag{6}
\]

where $S$ is the total number of operational periods; $W_i$ is the water diversion during period $i$; $S$ is the average water diversion from period 1 to $S$; $H_i$ is the HG during period $i$; and HG is the average HG from period 1 to $S$.

The constraints of multi-objective optimization are listed in section S3. The multi-objective optimization method is clarified in section S4.

3. Materials and data

The Han River in China, which is the longest tributary of the Yangtze River, is rich in aquatic biological resources. Fish, phytoplankton, zooplankton, zoobenthos, and macrophytes were selected as target populations in this study. These five represent the main aquatic biological resources in the middle and lower reaches of the Han River. The stochastic PDMs are shown in section S6, which considers the interaction relationships among the five target populations. The study area was the Danjiangkou Reservoir, which is in the upper and middle reaches of the Han River (figure S5). The reservoir provides comprehensive benefits and has multiple uses including flood control, HG, irrigation, navigation, fishery, and tourism. The operational characteristics of the Danjiangkou Reservoir are summarized in table 1. The water volume in the mid–lower Han River is greatly reduced after withdrawing water from the
Danjiangkou Reservoir, and this has major adverse influences on downstream ecosystems.

Seven hydrological gage stations are located in the mid–lower Han River. The streamflow data observed at Huangjiagang station (6 km downstream of the Danjiangkou dam) is generally used as the outflow of the Danjiangkou Reservoir. The population density data of fish, phytoplankton, zooplankton, zoobenthos, and macrophytes for 2015–2017 near Huangjiagang station were used to establish the stochastic PDMs. Fish biomass is stated in kg d⁻¹, which refers to the daily catch by each fishing vessel at the river section near Huangjiagang station. The daily catch reflects fish biomass under certain catching capacity and certain catching range for each fishing vessel. Thus, the unit of kg d⁻¹ is useful to describe the dynamics of fish population system in this study, although it does not represent the general population densities. Phytoplankton, zooplankton, zoobenthos and macrophytes biomass are stated in cell l⁻¹, mg l⁻¹, mg l⁻¹ and kg m⁻², respectively. The daily inflow data of the Danjiangkou Reservoir in 1975–2013 were used in reservoir operations. The settings for reservoir operation parameters are shown in section S5.

### 4. Results and discussion

#### 4.1. Model validation and sensitivity analysis

The PDM was validated by using the trial-and-error method (section S7.1 and figure S6). A sensitivity analysis of model parameters was conducted (section S7.2 and figure S7).

#### 4.2. Analysis of flow–ecology relationship

The dynamics of multi-population systems with varied noise intensities were stochastically simulated, and showed that the noise intensity had a significant effect on population dynamics. As shown in figure S8, the noise intensity was accumulated by 0.01 increments for each population system. Zoobenthos and macrophytes population densities were more sensitive to changes in noise intensity due to their larger change for each noise increment. The stable densities of multiple populations tended to decline with increasing noise intensity. The noise intensity was taken as the acceptable maximum value when the population density at stable state approached zero. Excessive noise intensity may result in extreme changes of population dynamics and even extinction of a population, thus destroying the normal function and structure of food webs. The maximum noise intensities of target population systems are shown in table 2, whose reasonability can be interpreted as follows. Fish depends largely on the magnitude, frequency, duration, timing and rate of change in flow conditions (Fornaroli et al 2020). Phytoplankton, such as diatoms, may grow rapidly with low water level and slow flow velocity (Baho et al 2020). Zooplankton migrates with streamflow due to its weak swimming ability. A large number of zooplankton can be released from reservoir to downstream with the outflow. The densities of fish, phytoplankton and zooplankton were sensitive to flow regime alteration. In fact, existing studies have shown that flow regime alteration can significantly affect population dynamics (Tonkin et al 2018), but this is not true for every aquatic ecosystem. For example, the dynamics of phytoplankton and macrophytes depend largely on trophic state and population interactions in reservoirs or lakes where, flow regime alteration is negligible (Zhang et al 2018). The habitats of zoobenthos and macrophytes are on the river bottom or bank, and their population dynamics have a close relationship with channel morphology, hydrochemistry, water temperature, and nutrients (Alahuhta et al 2018, Sharapova and Babushkin 2019). Thus, the acceptable maximum noise intensities caused by reservoir outflow variation are higher for zoobenthos and macrophytes than they are for fish, phytoplankton, and zooplankton. More details about multiple populations can be found in section S7 of supplementary materials.

The established flow–ecology relationship can be validated by using the obtained maximum noise intensities of multi-population systems. Several specific values of hydrological alteration degree with increasing trend were set by taking Dnatural flow as the initial value. The noise intensities of multi-population systems were calculated through the flow–ecology relationship. Stochastic simulations were then conducted under these specific noise intensities. As shown in figure 3, the deterministic autonomous nonlinear multi-population systems approached to a stable state (known as equilibrium point) although the initial conditions were different. Nevertheless, the equilibrium point can be transferred if the systems are stochastically disturbed. The equilibrium points showed a continuous downward trend with increasing noise intensities, and approached

| Items                              | Unit       | Value  |
|------------------------------------|------------|--------|
| Total storage                      | Billion m³ | 33.91  |
| Installed capacity                 | MW         | 900    |
| Firm output                        | MW         | 247    |
| Minimum outflow                    | m³ s⁻¹     | 490    |
| Normal water level                 | m          | 170    |
| Dead water level                   | m          | 145    |
| Flood limited water level          | m          | 160    |
| June 21st–August 10th              |            |        |
| Flood limited water level          | m          | 163.5  |
| August 21st–September 20th         |            |        |
| Regulation ability                 | —          | Multi-years |

**Table 1.** Operational characteristics of the Danjiangkou Reservoir, China.
Table 2. The acceptable maximum noise intensities for multi-population systems. A population system will be destructed if the corresponding noise intensity exceeds the maximum value.

| Population system       | Fish | Phytoplankton | Zooplankton | Zoobenthos | Macrophytes |
|-------------------------|------|---------------|-------------|------------|-------------|
| Maximum noise intensity | 0.2  | 0.22          | 0.22        | 0.4        | 0.4         |

Figure 3. Phase portrait of a deterministic multi-population dynamics system and the transfer of equilibrium points with increasing noise intensities. Panel (a) fish, phytoplankton, and zooplankton. Panel (b) fish, zoobenthos, and macrophytes.

their lowest values when the noise intensity reached the acceptable maximum for population systems. Most research has shown that an increasing degree of hydrological alteration will not be conducive to river ecosystem health (Richter et al 1996, 1998, Horne et al 2019, Palmer and Ruhi 2019). It may lead to significant destruction in an aquatic community, or even extinction, when the natural flow regime is completely altered. The noise intensity was encouraged by increasing hydrological alteration degree, and the stable state of multi-population systems suffered a constant transfer to a worse situation until they were destroyed rather than experiencing the reverse trend (e.g. better, or from better to worse) with increasing noise intensity. The effects (i.e. system destruction or population extinction) of increasing hydrological alteration on multi-population systems are consistent with those of increasing noise intensity, which
illustrates that there is a positive correlation between hydrological alteration and noise intensity. Therefore, the established flow–ecology relationship is validated in terms of stable state transfer in aquatic community systems, but there needs to be further research into more detailed structures of flow–ecology models.

4.3. ST with varied noise intensity
The ST and CVST of the fish population system were taken as optimization objectives of reservoir operations. Fish are one of the main decisive factors affecting the dynamics of food web. Fish-based indexes are critical to the measurement of river ecological status (Oberdorff et al. 2002), and fish were listed as a key performance indicator of aquatic ecology by the European Water Framework Directive (EU-WFD) in 2000 (Barth and Fawell 2001, Hering et al. 2010).

The ST of the fish population system with varied noise intensity (figure 4) was calculated. Note that the maximum noise intensity of zoobenthos system equaled to that for macrophytes system. Therefore, the noise intensity of the zoobenthos system derived by the established flow–ecology relationship under a certain flow regime will equal that of the macrophytes system. The noise intensities of the phytoplankton and zooplankton systems can be interpreted in a similar way. Thus, \( \sigma_2 \) and \( \sigma_3 \) were denoted by \( \sigma_2(3) \), and \( \sigma_4 \) and \( \sigma_5 \) were denoted by \( \sigma_4(5) \). The ST of the fish population system was more sensitive to \( \sigma_1 \) than to \( \sigma_2(3) \) and \( \sigma_4(5) \), which indicated that the system recovery time from an unstable state to a stable state was mainly affected by its own noise intensity (figure 4). The performance of ST increased as \( \sigma_1 \) decreased.

From the perspective of dynamical systems, the relationship between ST and hydrological alteration for the fish population system can be explained as follows: (a) when the noise intensity was low (i.e. below 0.07), the variation of population density was constrained by the environmental capacity, intrinsic growth rate, and interactive relationships among populations. Therefore, the change of ST was not obvious as the degree of hydrological alteration increased. (b) When the noise intensity was high (i.e. between 0.15 and 0.2, where 0.2 refers to the acceptable maximum value), the population density was greatly affected by flow regime alteration. ST value remained high and stable. (c) When the noise intensity was at an intermediate level (i.e. between 0.07 and 0.15), the variation of population density was controlled by stochastic disturbance of reservoir outflow. For this case, ST increased as the flow alteration increased. The greater the hydrological alteration, the longer the time from an unstable state to a stable state, and the worse the resilience of the fish population system.

Figure S9 gives more information about the CVST of a fish population system with varied noise intensity. The ST and CVST obtained with varied noise intensity greatly improved the calculation efficiency of multi-objective optimization.

4.4. Optimization results
Pareto solutions were obtained through multi-objective optimization. The preferred solution

![Figure 4](https://example.com/figure4.png)
A representative solution was preferred when multi-objective values were improved compared with that of the conventional operation. Conventional operation was conducted by existing traditional operating rules, which permitted a hydropower reservoir’s decisions (e.g. water release or power output) to be made using currently available information (e.g. inflow or storage level) by leveraging information from historical hydrological processes. The optimized operating rule curves corresponding to the preferred solution were shown in figure S10(b).

The preferred solution had three objective function values—WS, HG, and ST—that were better than those of the conventional operation, while its performance was the same as the conventional operation in terms of CVST (figure 5). The WS and HG of the preferred solution were increased by 2.35% and 2.40%, respectively, compared to the conventional operation. The performance of WS and HG illustrated that HG compete with WS. The ST of the preferred solution was decreased by 2.5% compared with that of the conventional operation, which illustrated that the recovery time of the fish population system with stochastic disturbance under the optimized rules was shorter than under the traditional operating rules.

The coevolution processes of multi-population systems were stochastically simulated with noise intensities under optimized rules (figure 6). The mean of the stochastic trajectories trended to steady, and PDFs approached to stationary, within the simulation period. For population systems, the more concentrated probability density indicated that the system was more resistant. It can be seen from transient PDFs that the resistance of fish, phytoplankton, zoobenthos, and macrophytes population systems was stronger at the beginning of the coevolution processes than in the later period. The resistance of the phytoplankton system clearly decreased with time, whereas the resistance of the zooplankton system remained strong. This can be intercepted as that phytoplankton was sensitive to flow regime alteration, resulting in fast divergence in stochastic trajectories. The optimized operating rule curves and the stochastically simulated population dynamics under an optimized operation strategy can provide a significant reference for different stakeholders.

4.5 Influence of reservoir outflow on an aquatic community

Outflow regimes differ across river types, climate, land use, or human activities. Spatiotemporal variation in reservoir outflow exerts direct and indirect control on the function, structure, and dynamics

![Figure 5. Parallel coordinate plot for the operational profits of Pareto solutions and the conventional operation.](image-url)
of aquatic communities at local to regional scales (Bruckerhoff et al 2019). The following discussion examines the influence of reservoir outflow on a downstream aquatic community, based on the case study of the Danjiangkou Reservoir.

Studies have identified the strong relationships with hydrological, water quality, water temperature, and biomonitoring metrics across flow regimes (Aspin et al 2020, Fornaroli et al 2020). For example, environmental variations will cause changes in the composition and quantity of fish population, which have inevitable impacts on the structure of the food webs through population interactions such as predation, competition, and interdependence. The impacts on biotic processes in turn affect the physical and chemical characteristics of water body. The biotic processes can be disturbed by flow regime alteration, which consequently influence the integrate river ecosystem. These address the question of what a flow–ecology relationship is. This study further revealed the sensitivity of aquatic community systems to reservoir outflow, which has explicated the question of how to quantify the flow–ecology relationship, demonstrating that variation in population dynamics can affect the trend of the whole aquatic community. Different populations have various ecological responses to the same alteration in flow regime, and the same population reacts in various ways to different flow regime patterns. Critical variations in reservoir outflow regime (e.g. recurrent

Figure 6. Stochastic simulations in panels (a), (c), (e), (g), and (i), and transient probability distribution functions (PDFs) in panels (b), (d), (f), (h), and (j) of population densities of fish, phytoplankton, zooplankton, zoobenthos and macrophytes under the optimized operation strategy. The color scale plates illustrate the values of probability density. Note that the color scale is different for each population density.
unpredictable droughts) may drive aquatic community systems into novel stable states (Bogan and Lytle 2011).

The optimized outflow and water level were derived from the optimized operating rule curves. The imbalance of inflow and outflow was caused by water diversion from the Danjiangkou Reservoir. The reservoir inflow was generally regarded as natural flow. The optimized outflow was more consistent with natural flow compared with the overall observed outflow (figure S11). The disturbance to downstream aquatic communities was weakened by optimized operation. For example, practical experience indicated that the optimized outflow in the spawning and breeding (February to April) and growth periods (July to September) can satisfy the water demands of fish in terms of flow magnitude. The optimized outflow, which was obtained by weakening the disturbance of reservoir outflow to an aquatic community, may also promote invasive species while benefiting the fish population. Therefore, ecological flow should be determined from the perspectives of both stability of aquatic community and conservation objectives of native and nonnative species.

The reservoir outflow regime is one of the main factors but not the only one that can influence an aquatic community (Chen and Olden 2018). Predicting the impacts of water quality, water temperature, and other factors is beyond the scope of this study. The flow–ecology relationship may have been influenced by the regional scale (Damiani et al 2019). The methodology of this study can be used in other basins.

5. Conclusions

The coevolution processes of multiple populations showed that multi-populations are inseparable owing to close interactions between them. Alteration in any parameter can affect the trend of the whole multi-population systems, and the dynamics were more sensitive to alterations in flow regime than in parameters. The flow–ecology relationship was used to quantify the disturbance of reservoir outflow to multiple populations downstream, and it helped to demonstrate that the stable states in multi-population systems depend largely on flow regime alteration. The greater the hydrological alteration, the longer the time from an unstable state to a stable state, and the worse the resilience of the fish population system. The preferred operating rule curves of the Danjiangkou Reservoir were obtained by multi-objective optimization. The average annual WS, average annual HG, and ST of the preferred operation were improved by 2.37%, 2.40%, and 2.67%, respectively, compared with the conventional operation.

This work provided an approach to quantify the impacts of streamflow on an aquatic community. The established flow–ecology relationship may help to identify important environmental covariates and motivate the implementation of river ecosystem restoration. Nevertheless, consideration of factors such as the effects of hydrochemistry, water temperature, nutrients, and invasive species is still lacking. Mathematical models based on biomechanical, hydrochemical, and hydrodynamic constraints may help in predicting the effects of environmental fluctuations on aquatic organisms, food webs, and ecosystem processes.

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: 10.6084/m9.figshare.14541099.v1.

Acknowledgments

This study was supported by the National Natural Science Foundation of China (Grant No. 51861125102), the Joint Funds of the National Natural Science Foundation of China (Grant No. U1865201), and the Innovation Team in Key Field of the Ministry of Science and Technology (Grant No. 2018RA4014). Sincere gratitude is extended to the editor and anonymous reviewers for their professional comments and corrections, which greatly improved the quality of the paper.

Conflict of interest

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

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