

RESEARCH ARTICLE

Timing of hydrologic anomalies direct impacts on migration traits in a flood pulse fishery system

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Abstract

1. Understanding adaptive reservoir management strategies that balance ecological outcomes with other objectives necessitates properly articulated environmental objectives. Aside from flood pulse extent related metrics, residual-based descriptors provide robust descriptions of fish assemblage structure and harvest.
2. We proposed a model framework based on spectral analysis of hydrologic variation and the Multivariate AutoRegressive State Space (MARSS) model to statistically quantify the effect sizes of hydrologic variation impacts on total fish catch and functional group (migration types) fish harvest and applied it to 17 years of fish harvest data from the Lower Mekong River Basin (LMB).
3. Our findings suggest that duration and timing of hydrologic anomalies matter as much as their magnitude. Anomaly droughts coupled with strong pulse can benefit species if timed correctly. Longitudinal migrators were more sensitive to anomalous floods and droughts than other migratory species. Fish catch projections using effect sizes derived from historical data revealed that a well-timed and protracted drought followed by a powerful flood pulse would be advantageous to the fishery, but a flood delay could negate such benefits.
4. *Synthesis and applications:* We designed a spectral analysis framework to quantify hydrological variation and linked it with fishery harvest records. Quantified effect sizes of hydrologic anomalous events demonstrated one designed hydrograph for fishery benefits: properly timed prolong drought followed by a strong flood pulse. Our results add to a growing body of research that suggests ecological flows can be engineered. For most dams, the rule curve describing reservoir releases and resulting downstream hydrograph are designed in an ecological vacuum in which the objectives are to maximize human services—power production, flood control or navigation. Our work demonstrates that hydrograph can be designed to manage aspects of functional biodiversity directly. Though the exact shape of our hydrograph may not apply to other engineered river systems, we suggest that the approach can be applied generally, and globally both to developed and developing river basins. Specifically, a functional biodiversity rule curve could be optimized as an additional objective function in

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a multi-objective optimization framework. Our methodology provides a quantitative method for deriving an ecological flow for this larger tradeoff analysis.

KEYWORDS

environmental flow, fish migration, food security, hydrologic variation, MARSS, reservoir management, spectral analysis

1 | INTRODUCTION

Rivers are vital for clean energy and food production worldwide (Chang, 2013; Sabo et al., 2017). In tropical basins of the developing world, freshwater fishes provide significant majority of the animal protein to millions of people (Belton & Thilsted, 2014; McIntyre et al., 2016). Fish comprises more than 20% of the animal protein consumed in Asia (FAO, 2022). Unfortunately, the security of this food source is challenged by other demands on rivers for energy and irrigation (rice and vegetables), their watersheds for timber and their growing urban centers (Taylor et al., 2007). Among competing anthropogenic demands, dam construction has been considered a pivotal agent of change and threat to food security and biodiversity due to flow regime (Koponen et al., 2007; Lytle & Poff, 2004; Poff et al., 1997), blockage of fish migration routes (Englund & Malmqvist, 1996), and impacts on nutrient transport (Kummu & Varis, 2007). In contrast to the developing world where hydropower is being built, removal of large dams to restore natural flow regimes has gained scientific support and traction on the ground in the developed world (Bednarek, 2001; Orr et al., 2012). Both contexts—dam construction with optimal operations and dam removal—provide contexts for understanding the relationship between managed flow regimes and production and diversity of key riverine taxa (Brown & Ford, 2002; Dugan et al., 2006; Stanley & Doyle, 2003).

Understanding tradeoffs and adaptive management strategies that balance ecological outcomes with hydropower, flood control, irrigation, and other development use have become a focus in river management and conservation (Acreman et al., 2014; Poff et al., 2016). A first step towards such an optimization framework is a clearly articulated operation curve towards optimized environmental objectives, such as abundance of key species and species composition (Arthington et al., 2006; Davis et al., 2015; Sabo et al., 2017), fisheries productivity (Arthington et al., 2003), and sediment transport (Chang et al., 2003; Yin et al., 2014). Recent studies have suggested several promising solutions such as: a scenario-based module that linked flood patterns and habitat quality (Arthington et al., 2003), a neural network model for minimum maintenance flow estimation (Alcázar et al., 2008), a functional regression model for optimizing multiple water use objectives (Chen & Olden, 2017) and a time series modelling framework to design hydrographs that preserve fish harvest (Sabo et al., 2017).

Quantitative flow-ecology relationships are paramount in any approach to optimize ecological and human objectives in a decision-making context. The flood pulse extent (= duration × magnitude) has

a long history and strong support as a key driver of fishery production in various fishery systems (Alford & Walker, 2013; Graaf, 2003; Welcomme, 1979). Flood pulse extent, magnitude and duration are first moment (mean level) descriptors of flow variation and they capture a summary of the observations in a given year (min, max, mean, total). Recent research reveals that second moment (variance) regime descriptors based on residual ("flow anomalies"; Sabo et al., 2017; Sabo & Post, 2008) rather than reported discharge regime shift based on changes in mean trend offer robust descriptors of fish assemblage structure and catch in flood pulse fisheries (Marengo & Espinoza, 2016; Ruhí et al., 2015). Here, we adopt the second moment approach.

Previous work suggests difficult tradeoffs between energy production and fish biodiversity. The substantial impacts of dam closure on river connectivity and blockage of fish migration pathways have been examined in multiple river basins including Paraná River (Antonio et al., 2007), Yangtze River and Dongting Lake system (Yi et al., 2010). Specifically, Ziv et al. (2012) used a network-based migration model combined with optimization of fish and hydropower and found that tributary dams (78 in Mekong River Basin) would be more detrimental to fish passage, survival and biodiversity than the upper cascade (6 dams in China). Since the publication of this paper, 15 mainstem dams have become operational, the most recent one in 2019 (Xayaburi in Lao PDR). Given an ongoing trend of dam construction in many regions, the prospect of utilizing present reservoirs to mitigate the impact of dam closure on fish migration has been raised (Dugan et al., 2010). Sabo et al. (2017) showed using dam reoperations to create flows that maximize variation and capture essential low- and high-flow characteristics for total fish catch could be an effective method for maximizing fish harvest in the presence of hydropower constraints. Yet, positive (or negative) anomalies timed differently on the hydrograph remain undistinguished in Sabo et al. (2017). This seasonal-scale timing and phase shifts of flow regime have been shown to be crucial for migratory fish recruitment in the flood pulse fishery of the Parana River (Agostinho et al., 2001). Here, we attempted to fill this gap and explore how individual species—or groups of species with similar traits—respond to different components of hydrologic variation. Although design flows may improve total harvest under current conditions, future dam closures—especially lower in the basin—may have disproportionately negative effects on migratory fish. Hence, it is important to examine the effects of design flows and how they vary with traits like migratory behaviour.

In this paper, we followed the approach of the Sabo et al. (2017), with two important distinctions that (1) positive (or negative) anomalies with varying timing were differentiated; (2) fish species with different migratory behaviours were classified and modelled as

discrete trajectories. Here, we quantified flow-ecology relationships for 18 of the most common fish species (by biomass) in the Dai bag net fishery of the Tonle Sap River in the Lower Mekong River Basin, a dataset used in both Ziv et al. (2012) and Sabo et al. (2017) analyses. We aimed to test the key hypothesis that timing of negative and positive anomalies could direct their consequences on fish species and formulate three predictions:

1. Negative/positive anomalies in the wet/dry season (respectively) are historically less expected and hence would have a more negative influence on fish catch.
2. A well-timed pair of negative anomalies and a strong flood pulse might aid in fish harvesting.
3. Hydrologic variation impacts on fish catch vary among migration trait groups. Among longitudinal migrators, long distance migration fish catch are less correlated with downstream hydrologic variation as river connectivity reduction would dominate the impacts.

2 | MATERIALS AND METHODS

2.1 | Fish harvest data

The Mekong River basin of Southeast Asia supports almost 900 fish species (18% of which are endemic), and similarly extraordinary diversity of aquatic snails, clams, snakes, turtles and frogs (Baran et al., 2007). Mekong is a flood pulse ecosystem (Welcomme, 1979) in which monsoon rains from the highlands of Viet Nam, Lao PDR and other regions in Lower Mekong Basin cause an inland river to reverse flow direction thereby flooding an inland lake, Tonle Sap River and Lake (TSRL). The Tonle Sap is a nursery and breeding grounds for the extraordinary biodiversity of the Mekong River basin, providing the food base and habitat for larvae from both resident and migratory fishes. Currently, there are 15 mainstem dams on the Mekong, with an equal number of proposed structures not yet built. The hydropower cascade has and will continue to alter the connection between the lake's rearing grounds and the spawning grounds of migratory species higher in the drainage network.

Fishery data were derived via sampling from fishing activity for 141 species in 14 Dai rows, a set of units where fisherman place bagnet to haul fish, collected by Inland Fisheries Research and Development Institute of Cambodia and maintained by the Mekong River Commission (Figure 1). Thus, no field work were involved and no ethical approval required. Our data preprocessing protocol generally followed Ngor, McCann, et al. (2018), except that stratified Dais were pulled together in our analysis. Fish harvest (in kilograms) sampling were conducted across (1) fishing days; (2) Dai units; (3) lunar periods: Peak period were categorized as 7 days till full moon and rest of each month as low period; (4) fish species. Sampling took place daily during peak period while every second or third day during low period. Then catch data with effort data (number of fishing days) were coupled to calculate catch per unit effort (CPUE) via weighed

average of harvest per fishing day, per Dai, per species where peak period and low period fractions were the weights. We used 20 years of daily stage records from the Stung Treng gage station on the Mekong River mainstem, spanning 1 January 1994 to 31 December 2013. To quantify the relative effect size of hydrological impacts on fish catch, we coupled annual catch per unit effort (CPUE) time series from 1996 to 2013 from the Dai, with hydrological features series extracted from the daily stage time series.

2.2 | Hydrologic variation

We applied the discrete fast Fourier transform (DFFT) and associated methods (Sabo & Post, 2008) to quantify recent hydrologic variability. These methods produced six metrics that characterize departures from the long-term seasonal signal (Figure 2). DFFT quantifies periodic, stochastic and catastrophic components of temporal variation in hydrology. First, spectral analysis was used to identify characteristic signals and to estimate signal frequencies, amplitudes and phases. Second, the long-term signal was estimated from the characteristic signals. Third, daily residuals (i.e. anomalies, A_t) were estimated as the difference between the long-term trend (S_t) and observed daily discharge (D_t). The time series of anomalies provides a graphical interpretation of the structure of variance in the discharge time series. The shape of this time series of anomalies provides one high level and several component metrics of variance (Sabo et al., 2017).

Besides adopting two metrics intel-flood-interval (IFI) and inter-drought-interval (IDI) from Sabo et al. (2017), we expanded the concept of net annual anomaly (NAA) and examine positive and negative seasonal anomalies: Positive anomaly in high-flow-period (PAH), negative anomaly in high-flow-period (NAH), positive anomaly in low-flow-period (PAL), and negative anomaly in low-flow-period (NAL), which were derived by sum over positive (or negative) anomalies in corresponding flow condition period. Detailed derivation were included in Supporting Information. By this definition, NAL and PAH were both "in-timing" drivers, meaning anomalous events happening at the appropriate phase according to the long-term signal (anomalous drought in low flow period and anomalous flood in high flow period; Figure 2). On the contrary, PAL and NAH were both "out-of-timing" drivers, meaning anomalous events happening at shifted phase according to the long-term hydrograph (anomalous flood in low flow period and anomalous drought in high flow period).

2.3 | Total catch model: Discharge effects on total fish catch

We determined the relative effect size for each of six hydrologic metrics (NAL, NAH, PAL, PAH, IFI and IDI) using a multivariate autoregressive state-space (MARSS) model. Multivariate autoregressive (MAR) models have been widely used to study different drivers of community structure and resilience in ecology

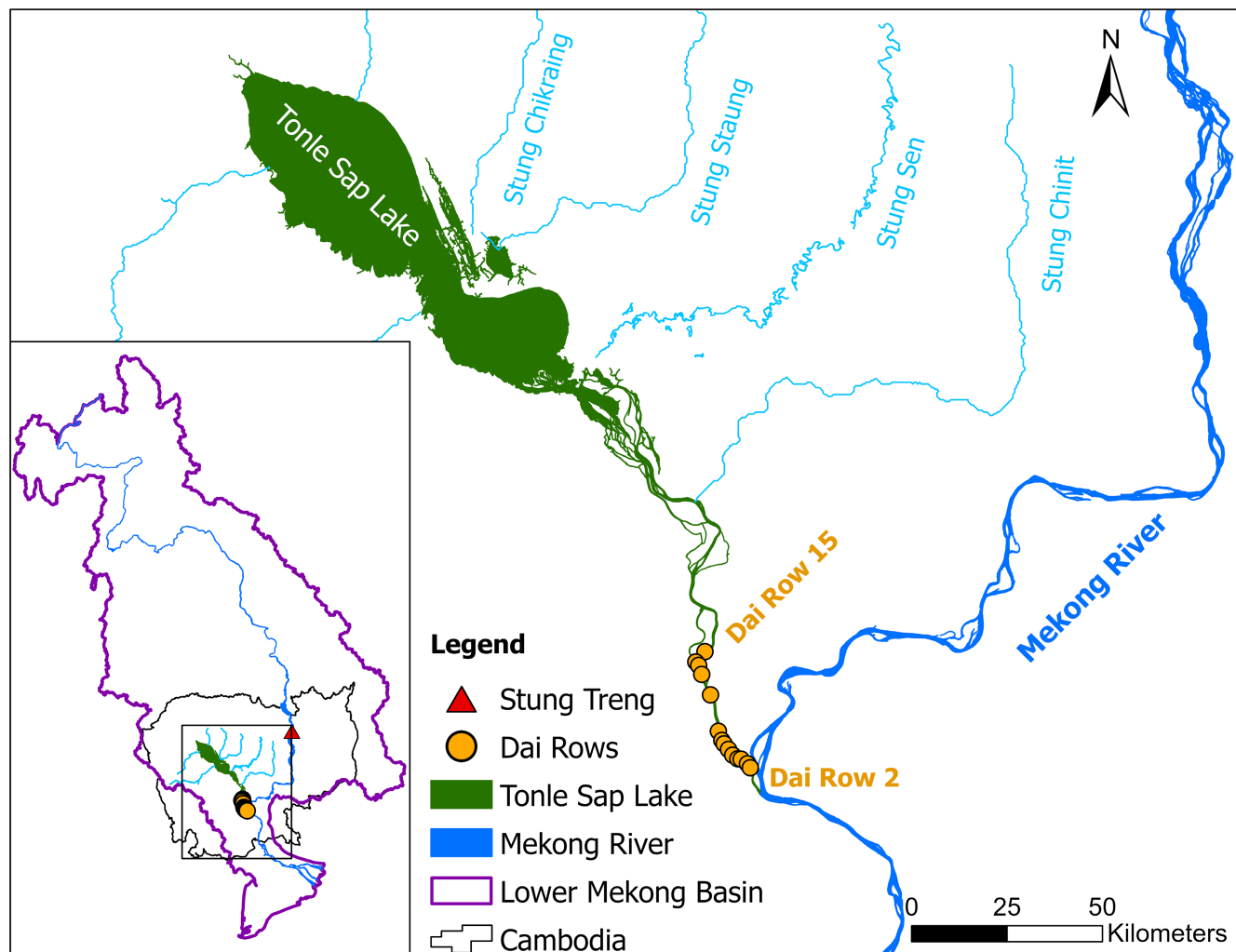


FIGURE 1 Location of fishing Dai rows and Stung Treng station.

(Hampton et al., 2013; Ives et al., 2003). Compared to mechanism-based models, MARSS models can be more parameter efficient. Instead of measuring and validating eco-physical parameters, MARSS models directly estimate relevant parameters from abundance time series data, such as population growth rate, environmental variation impacts and biotic interactions (Ives et al., 2003). Moreover, MARSS is a state space model capable of differentiating observation error from the underlying processes. This state space feature provides more robust estimation of environmental variation and reduces bias in estimation of the effect sizes of drivers (covariates representing hydrology in this analysis; Ruhí et al., 2015). The “MARSS” R-package was used to fit our MARSS model (Holmes et al., 2012). Here, we fitted covariates, that is, annual anomaly metrics with annual fish catch time series data to MARSS. Generally, a MARSS model can be specified as state process and observation process:

$$\mathbf{x}_t = \mathbf{B}\mathbf{x}_{t-1} + \mathbf{C}\mathbf{c}_t + \mathbf{w}_t, \text{ where } \mathbf{w}_t \sim \text{MVN}(\mathbf{0}, \mathbf{Q}), \quad (1)$$

$$\mathbf{y}_t = \mathbf{Z}\mathbf{x}_t + \mathbf{v}_t, \text{ where } \mathbf{v}_t \sim \text{MVN}(\mathbf{0}, \mathbf{R}), \quad (2)$$

where $\mathbf{y}_t$ is observed fish catch (data were log transformed for fish catch), which is modelled as linear combination of $\mathbf{x}_t$ (called states), the actual underlying true fish catch and the observation error $\mathbf{v}_t$ in the observation process. For the state process, $\mathbf{B}$ matrix defines biological factors such as density dependence and interaction between species, like species abundances effects on each other. $\mathbf{c}_t$ is the covariate series (hydrologic anomalies in our case), and $\mathbf{C}$ measures the effect sizes of those anomalies. $\mathbf{w}_t$ is the process error with multivariate normal distribution.

To quantify the effects of hydrologic anomalies on total fish catch, catch data were aggregated across all species for a given Dai row and year, ending up with 14 series, each for one Dai row. Thus, $\mathbf{y}_t = 1 \text{ biomass series} \times 14 \text{ Dai rows} \times 18 \text{ years}$, while $\mathbf{x}_t = 1 \text{ biomass series} \times 18 \text{ years}$ as in Equation (3), representing one hidden process for this fish community. Due to limitations in the dataset and consistency with the migration traits model, $\mathbf{B}$ was set to identity matrix, representing modelling density independence. $\mathbf{R}$ was set to model site-specific observation error, that is, one observation error variance for each Dai row on the diagonal and zero on off-diagonal. For a robust estimation of effect sizes, we estimated quantiles and

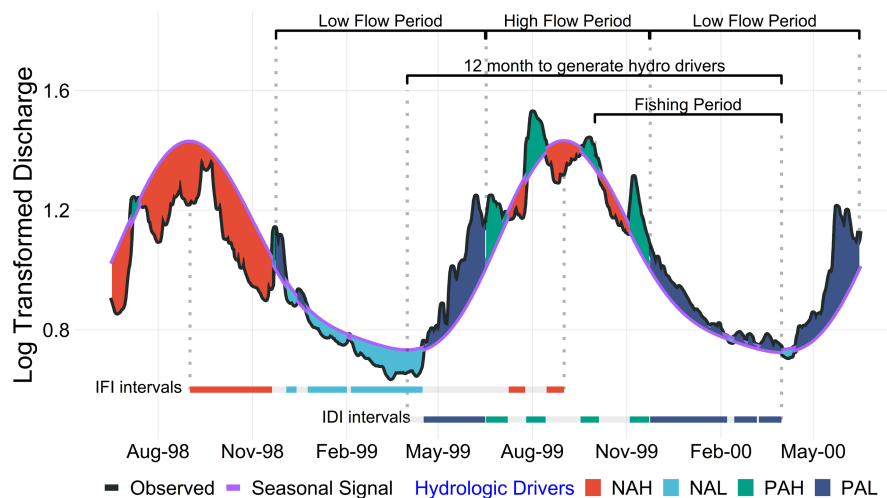


FIGURE 2 Anomalies illustration in a hydrograph. Purple line was observation records from 1999-11-23 to 2000-6-17, blue line was the seasonal signal, that is, characteristic signal as an output of DFFT. High flow/low flow season was determined by the average level of the seasonal signal. NAH, sum of negative anomalies in high-flow-period; NAL, sum of negative anomalies in low-flow-period; PAH, sum of positive anomalies in high-flow-period; PAL, sum of positive anomalies in low-flow-period; IFI is the average contiguous days of negative anomalies between two consecutive peaks, while IDI is average contiguous days of positive anomalies between two consecutive droughts.

frequentist confidence intervals using a bootstrapped multimodel inference (MMI) procedure. Separate MARSS model was fitted to every combination of six anomalies and estimated effect sizes were weight-averaged by model importance

$$x_t = x_{t-1} + [C_1 \dots C_6] \times \begin{bmatrix} c_1 \\ \vdots \\ c_6 \end{bmatrix} + w_t, \quad (3)$$

$$\begin{bmatrix} y_1 \\ \vdots \\ y_{14} \end{bmatrix}_t = \begin{bmatrix} 1 \\ \vdots \\ 1 \end{bmatrix} \times x_t + \begin{bmatrix} v_1 \\ \vdots \\ v_{14} \end{bmatrix}_t. \quad (4)$$

$$\begin{bmatrix} y_{1,1} \\ \vdots \\ y_{1,14} \\ y_{2,1} \\ \vdots \\ y_{2,14} \\ \vdots \\ y_{18,1} \\ \vdots \\ y_{18,14} \end{bmatrix}_t = \begin{bmatrix} 1 & 0 & 0 & \dots & 0 \\ & \vdots & & & \\ & 1 & 0 & 0 & \dots & 0 \\ 0 & 1 & 0 & \dots & 0 \\ & \vdots & & & \\ 0 & 1 & 0 & \dots & 0 \\ & \vdots & & & \\ 0 & \dots & 0 & 0 & 1 \\ & \vdots & & & \\ 0 & \dots & 0 & 0 & 1 \end{bmatrix} \times \begin{bmatrix} x_1 \\ \vdots \\ x_6 \\ x_7 \\ \vdots \\ x_{12} \\ x_{13} \\ \vdots \\ x_{18} \end{bmatrix}_t + \begin{bmatrix} v_1 \\ \vdots \\ v_{14} \\ v_1 \\ \vdots \\ v_{14} \\ \vdots \\ v_1 \\ \vdots \\ v_{14} \end{bmatrix}_t. \quad (6)$$

2.4 | Trait Model: Mitigation effects of migration strategy

$$\begin{bmatrix} x_1 \\ \vdots \\ x_6 \\ x_7 \\ \vdots \\ x_{12} \\ x_{13} \\ \vdots \\ x_{18} \end{bmatrix}_t = I_{18} \times \begin{bmatrix} x_1 \\ \vdots \\ x_6 \\ x_7 \\ \vdots \\ x_{12} \\ x_{13} \\ \vdots \\ x_{18} \end{bmatrix}_{t-1} + \begin{bmatrix} C_{1,1} & \dots & C_{1,6} \\ \vdots & & \vdots \\ C_{1,1} & \dots & C_{1,6} \\ C_{2,1} & \dots & C_{2,6} \\ \vdots & & \vdots \\ C_{2,1} & \dots & C_{2,6} \\ C_{3,1} & \dots & C_{3,6} \\ \vdots & & \vdots \\ C_{3,1} & \dots & C_{3,6} \end{bmatrix} \times \begin{bmatrix} c_1 \\ \vdots \\ c_6 \end{bmatrix}_t + \begin{bmatrix} w_1 \\ \vdots \\ w_{18} \end{bmatrix}_t, \quad (5)$$

In addition to the “Total Catch” model, we developed a “Migration Trait” model to estimate effect sizes for hydrology on groups of fishes with three distinct sets of migration traits: floodplain, longitudinal and lateral (Supporting Information, Table S2). “Floodplain” species often referred as “black fish” migrate occasionally in floodplains adjacent to rivers and stay in floodplain/wetland. During dry seasons, they stay in pools/ponds/swamps in floodplain or rivers. Examples of this strategy include snake-heads (*Channa striata*, *Channa micropeltes*), climbing perch (*Channa micropeltes*) and *Rasbora tornieri*. “Lateral” species, or “grey fish” make limited migrations from the river to the floodplain during the high flow season and migrate to local tributaries as the flood pulse recedes such as *Osteochilus lini*. “Longitudinal” species usually take long distance longitudinal migration especially between Mekong mainstream and lower flood plains, like *Henicorhynchus lobatus* and small-sized mud carp *Labiobarbus leptochelus*.

First, from each migration group, we selected the six most abundant species as determined by occurrence and biomass which accounted for 61% of annual total fish biomass. Second, the 18 species were modelled as 18 individual hidden processes, that is, $\mathbf{y}_t = 18 \text{ species} \times 14 \text{ Dai rows} \times 18 \text{ years}$ and $\mathbf{x}_t = 18 \text{ species} \times 18 \text{ years}$ as in Equation (6). The $\mathbf{C}$ matrix structure was designed so that species with the same migration strategy share one effect size of a hydrology anomaly, but different migration strategy species respond differently to hydrologic anomaly, as indicated by the colour groups of $\mathbf{C}$ in Equation (5). Additionally, $\mathbf{Q}$ was set to represent one single process variance and one single process covariance, that is, one value on diagonal and one value on off-diagonal. The same model selection procedure as in the “Total Catch” model was used to address covariates correlation issue and to find suitable fitting model candidates. Furthermore, to compare effect sizes across different migration strategy groups, we used the bootstrapped multi-model inference (MMI) procedure with between group comparison. The group differences were calculated at each bootstrap step and 2.5% and 97.5% quantiles after 1000 steps were used to construct the frequentist confidence intervals.

2.5 | Alternative trait model: Effects of migration distance

“Longitudinal” species make up 72%–95% of the total biomass in the Dai fishery (Supporting Information, Table S1), and many of the floodplain species captured in this gear type are considered incidental. As a result, we amended our trait-based approach to include an analysis of the 18 most common longitudinal species categorized by migratory distance (long, medium, and short; Supporting Information, Table S4), and analysed the impacts of hydrology on these different groups of migratory fishes using the same structure as the migration strategy model, except that the 18 fish species were selected and categorized into three groups based on migration distance. Here, long-distance migrators include fish like *Henicorhynchus lobatus*, which travel more than 500 km between nursery and reproductive habitats, medium distance migrators include fish like *Henicorhynchus siamensis*, which may swim 300 km as far as Khone Falls (near the Lao-Cambodia border) or the delta in Vietnam, and short distance migrators include fish species like *Osteochilus lini* migrates into flooded forest when water rises.

2.6 | Future fisheries catch forecast by design flows

Finally, we compared future fishery yields by MARSS forecasts using flow simulations (Figure 3) and hydrological anomaly effect size in our result in the same stochastic framework proposed in Sabo et al. (2017). Designed flows were created by Fourier series so that

mean annual flow would not exceed the historical levels. Good design was characterized by a prolonged low flow period followed by a strong pulse, while bad design had a dampened flood peak and shortened low flow period. Both the good and bad design was right shifted 30 days to include a delayed flood scenario.

3 | RESULTS

3.1 | Total catch model

We discovered that hydrologic anomaly magnitudes and duration matter as much as their relative timing when estimating total catch of all species combined. For “in-timing” anomalies, the effect size of low-flow-period drought (NAL) and high-flow-period flood (PAH) were both significant and positive (Figure 4, $\alpha = 0.05$, bootstrap 95% CI above 0) but PAH showed stronger impact. “Out-of-timing” anomalies, low-flow-period flood (PAL) and high-flow-period drought (NAH) were both significant but negative (Figure 4, $\alpha = 0.05$, bootstrap 95% CI below 0) and their effect sizes were similar. It is noteworthy that effects of “out-of-timing” anomalies (around -0.5 for PAL and NAH) were stronger than “in-timing” anomalies (around 0.06 for NAL and 0.23 for PAH). Given relative effect sizes, anomalous droughts (NAL) are less important than flood pulse (PAH) in the hydrograph. Effect sizes of both IDI and IFI were significant positive and of close magnitude.

3.2 | Migration traits model

When differentiating between distinct migratory traits of fish, impacts of hydrological anomalies were generally comparable to those of the total catch model for all hydrologic metrics (Figure 5), since all effect size directions were the same as in (Figure 4). “In-timing” anomalies NAL and PAH proved to be advantageous to all migrators; however, the degree of benefit differed among migrators (Figure 5, NAL, PAH column). NAL favoured longitudinal migrators the most while PAH benefited floodplain migrators the most. All migrators were significantly and negatively impacted by “out-of-timing” anomalies, PAL, and NAH, with longitudinal migrators suffering the most from such depressive hydrological variation (Figure 5, PAL, NAH column). Duration measures, IDI and IFI both had significant positive impacts on all migrators, but anomalous flood duration (IDI) was more influential considering effect sizes (Figure 5, IDI, IFI column).

3.3 | Alternative trait model (migration distance)

When we examined longitudinal migrators in terms of their migratory distance (categorized into three groups), we found that effect sizes of hydrologic drivers were consistent with those

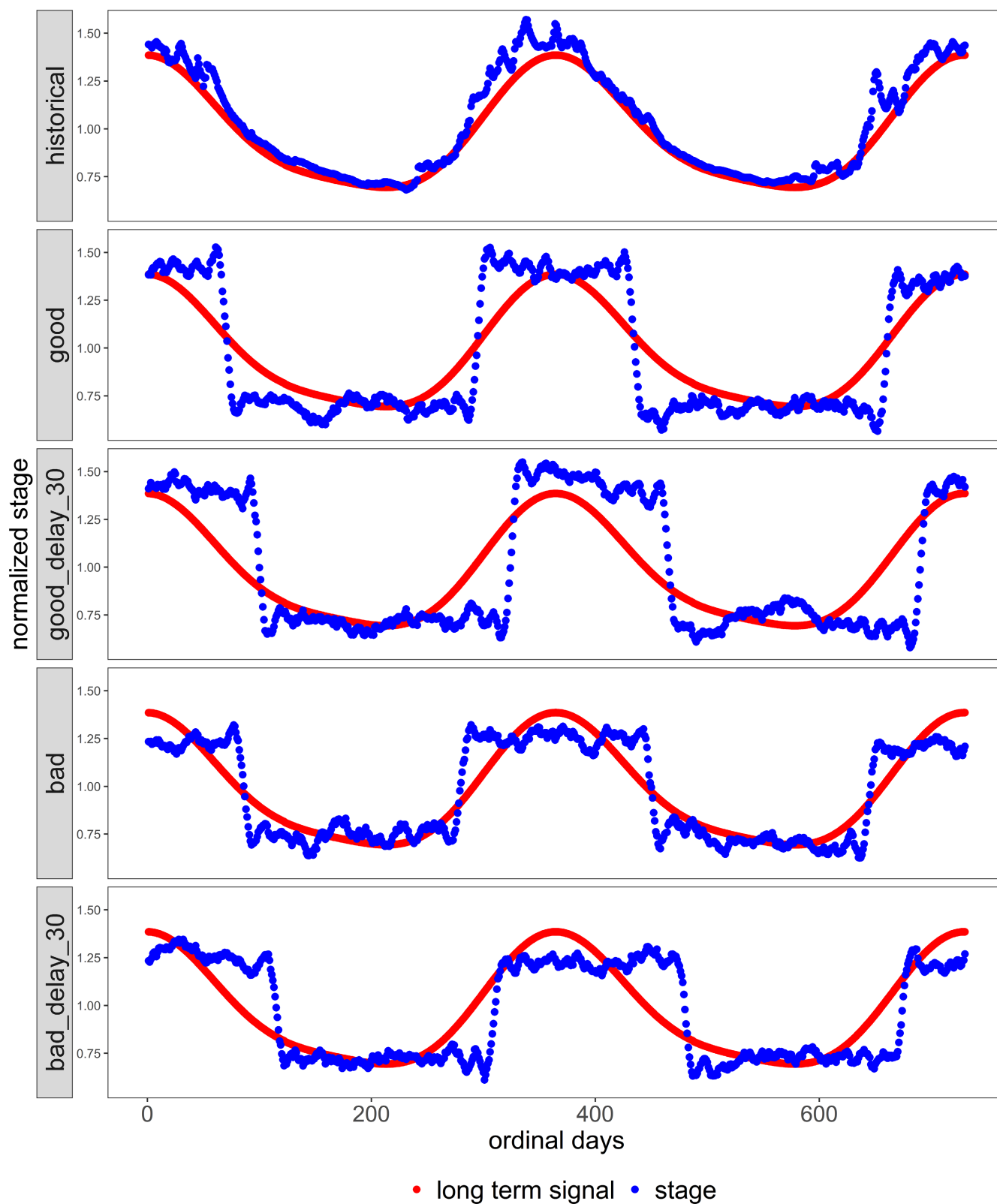


FIGURE 3 Design flow hydrographs. Red points are long term signal extracted via DFFT from historical data. Blue points are designed flow generated via Fourier series.

observed in the previous two models both in terms of direction and magnitude (Figure 6). All hydrologic drivers elicited the same directional reaction from the three migration distance groups.

Interestingly, all drivers except for PAH showed larger effect sizes for medium distance migrators (compared to the other two trait groups).

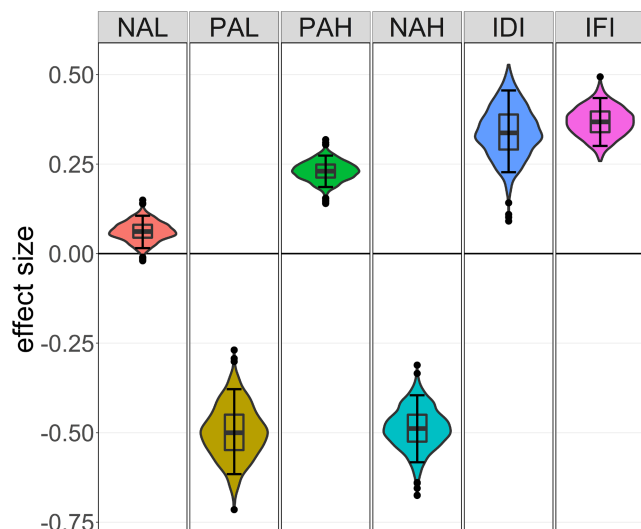


FIGURE 4 Total catch model: Effect size of hydrologic anomalies on total fish catch. Effect sizes were weighted sum across all important model candidates by relative model importance. Violin plot shows the bootstrapped effect sizes distribution. Boxplot shows 5%, 25%, 50%, 75%, and 95% quantiles. Five percent and 95% quantile intervals excluding zero mean significant effect.

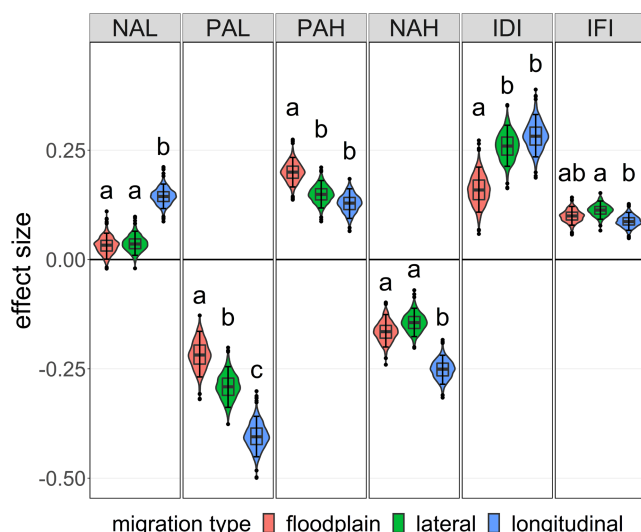


FIGURE 5 Migration traits model: Between migration strategy group comparison for hydrologic anomaly effect size. For each hydrologic anomaly, effect sizes were weighted summed across all important model candidates by relative model importance. Violin plot shows the bootstrapped effect sizes distribution. Boxplot shows 5%, 25%, 50%, 75%, and 95% quantiles. Five percent and 95% quantile intervals excluding zero mean significant effect. Letters above violin plot indicates difference of effect size by between-group comparison.

3.4 | Future fishery catch forecast

In the comparison of different design flow scenarios (Figure 7), good designs were generally beneficial (positive slopes in first two rows)

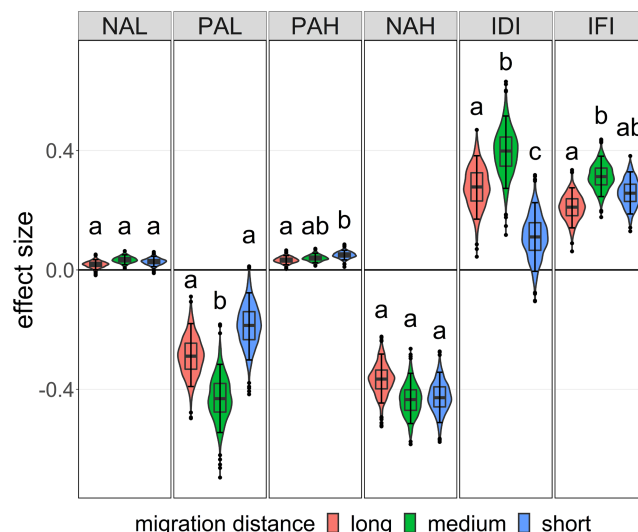


FIGURE 6 Migration distance model: Between migration distance group comparison for hydrologic anomaly effect size. For each hydrologic anomaly, effect sizes were weighted summed across all important model candidates by relative model importance. Violin plot shows the bootstrapped effect sizes distribution. Boxplot shows 5%, 25%, 50%, 75% and 95% quantiles. Five percent and 95% quantile intervals excluding zero mean significant effect. Letters above violin plot indicates difference of effect size by between-group comparison.

while bad designs were harmful (negative slopes in last two rows), and the continuous delayed flood hydrograph led to a deterioration in fishery catches (decreased slope from good/bad design to their delayed flood version). Across migration groups, longitudinal migrators catch increased most in good design scenarios (largest positive slope of 0.52 and 0.08) while declined most in bad design scenarios (smallest negative slope of -0.31 and -0.55). Delayed flood appears to be most detrimental for longitudinal migrators in good designs as the slope decreased 85% from 0.52 to 0.08.

4 | DISCUSSION

4.1 | Timing and relative magnitude of anomalies

Our first significant finding is that the timing of anomalous events matters as much as their magnitude. According to Sabo et al. (2017), flood anomaly extent (sum of positive anomalies), dry period (inter-flood-interval) and drought anomaly magnitude were positively correlated with total fish catch, which is consistent with our observation in the total catch model demonstrated by positive effect sizes of high-flow-period flood (PAH), dry period (IFI), and low-flow-period drought (NAL). With timing encoded anomaly drivers, we were able to distinguish timing effects from magnitude effects. Two “in-timing” anomalies, NAL and PAH both were shown to be positively correlated with fish catch, while two “out-of-timing” anomalies, high-flow-period drought (NAH) and low-flow-period flood (PAL) were found to be significantly and negatively correlated with

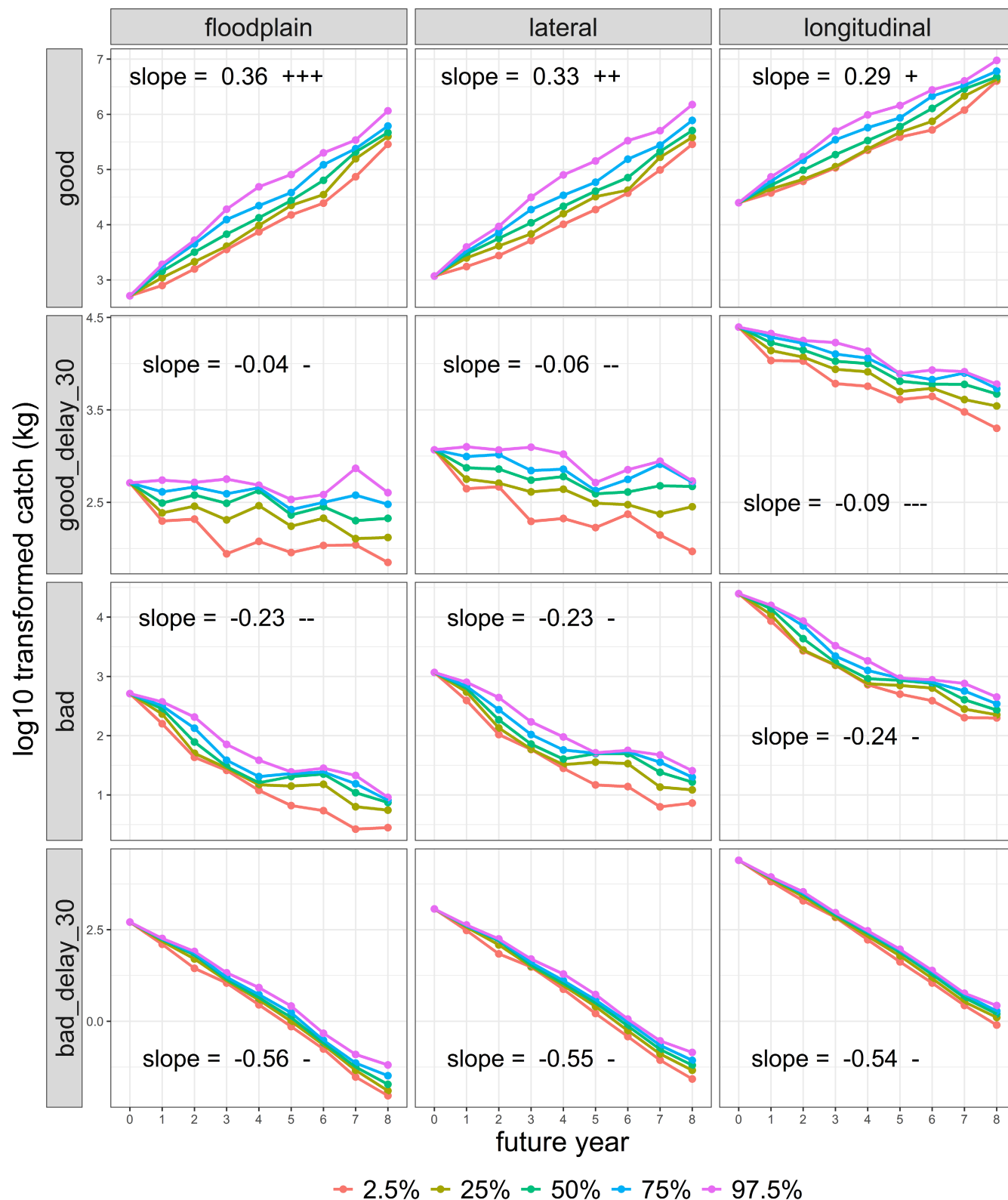


FIGURE 7 Future fishery catch forecast in four design flow scenarios via stochastic simulation. In each plot, points are quantiles of 100,000 simulations. Slope values are the mean values of linear regression slopes fitted in each simulation and the signs in the parenthesis show significance and differences of slopes across migration groups (columns) according to their confidence intervals.

fish catch, with stronger negative effect sizes compared to two “in-timing” anomalies (greater in magnitude but negative). Timing of flow events have been recognized as an important driver for fish life

history patterns (Dudgeon et al., 2006; Ellis et al., 2013). Flood timing directly influences migration as the rising flow level is an crucial trigger for migration start (Baran, 2006) and determines recruitment

success via ensuring gonadal maturation and providing access to early development sites (Oliveira et al., 2015). The importance of low flow timing has been documented as providing recruitment habitats from scouring water for subtropical fishes (Humphries & Lake, 2000; Pusey et al., 2001) and utilizing zooplankton egg banks for fish early life stages (Wedderburn et al., 2013). It is notable that the synchronization between flow events timing, temperature and photoperiod would be more important for fish migration, spawning and growth than just hydrologic conditions (Healy et al., 2020; Tonkin et al., 2011), which requires further investigation than presented work.

Furthermore, our migration model revealed that low-flow-period drought (NAL) had significant favourable impacts on longitudinal migrators, while floodplain species did not show a significant response and lateral migrators showed minimal response (average bootstrapped effect size: 0.036) compared to longitudinal migrators (average bootstrapped effect size: 0.144). Drought (prolonged negative anomalies) can have clear detrimental effects on biota because of increased salinity, decreased available oxygen due to increased biochemical oxygen demand by microbes, and decreased dissolved organic carbon (Dahm et al., 2003; Vliet & Zwolsman, 2008). We hypothesized that negative anomalies—if properly timed and coupled with a strong flood pulse (PAH) and prolonged flood duration (IDI) created variability in hydrologic conditions that allowed for accumulation of nutrients (through deposition or fertilizer applications), proper conditions that enhanced redox processes, and nutrient availability, and hence, augmented nutrient flux from terrestrial to aquatic compartments (Eimers et al., 2007; Mosley, 2015). Post-drought increases in planktivore and detritivore abundance in the Amazon River Basin suggests that this “fertilizer hypothesis” (Freitas et al., 2013) can further stimulate secondary productivity. Alternatively, anomalous droughts concentrate prey and create habitats with higher temperatures, both of which can promote growth rates (Dahm et al., 2003; Freitas et al., 2013). One possible confounding factor could be that fish tend to congregate in deeper water bodies during droughts and can be easily exploited by fishers, resulting in a bigger harvest. Another unaddressed but related factor is the lag effects of hydrology anomaly which should be investigated in future studies, as a large proportion of stocks including brood stocks were taken during the drought period, affecting subsequent years recruitment, and a massive amount to Young-of-Year (YoY) benefited from flood pulse was not captured in current year Dai catch. Finally, our results imply that the duration of anomalous events also matters since IDI and IFI had identical positive effects on three migratory groups. IDI had significant sizeable positive impacts (average effect size of 0.25), particularly on two groups that migrate, “floodplain” and “longitudinal” species. According to Agostinho et al. (2004), annual floods lasting more than 75 days were beneficial to migratory species. Oliveira et al. (2015) also confirmed flood duration as a crucial predictor for YoY abundances. Hence, our findings in the Mekong were consistent with records from other flood pulse fisheries.

4.2 | Migration traits filtered by hydrological variation

The interaction between environmental variation and functional traits filtering has been investigated in various studies (Mims & Olden, 2013). Fish assemblages of traits corresponding to the longitudinal migration strategy were also markedly impacted by flow regime changes (Zhong & Power, 1996) and increasing average water temperature (Rand et al., 2006). Our first observation is that PAH had positive and substantial effect sizes for fishes with all three forms of migratory behaviour, with NAH having a countering negative influence, as expected from a large body of literature on flood plain ecosystems (Welcomme, 1979). The flood pulse concept (Junk et al., 1989) has been widely examined and the importance of flood pulse in shaping fish assemblages has been reported in various studies. Graaf (2003) showed a positive relationship between flood pulse and growth rate of floodplain fishes in Bangladesh. Bénech and Peñáz (1995) described a strong correlation between flood and lateral fish migration. Ngor, Grenouillet, et al. (2018) reported spatiotemporal variation of fish assemblages and abundances shaped by inflow and outflow of the flood pulse in TSRL. In our analysis, longitudinal migrators exhibited the strongest response (smallest negative effect size) to “out-of-timing” drivers, NAH and PAL, which is expected as changing flow level is a critical trigger for migration behaviour (Baran, 2006; Poulsen & Valbo-Jørgensen, 2001; Smith, 2012). As documented in Poulsen and Valbo-Jørgensen (2001), below the Khone Falls, longitudinal migrators such as *Henicorhynchus lobatus*, *Henicorhynchus siamensis*, and *Probarbus jullieni* migrate upstream from October to February as water level is declining and migrate downstream from May to October after the onset of rising water level. Such pattern could explain the strongest suppression effects of NAH and PAL, which are disruptions to the migration trigger of rising water level in flood season and falling water level in dry season, respectively.

Extensive flooding over floodplain provides favourable accommodation for young-of-the-year (YoY) fish (Górski et al., 2011). Fauna species richness was also reported to be greatest in flooded forests, shrub lands and grasslands under long seasonal inundation (Arias et al., 2012). For floodplain species, intensified flooding enriches growth and biomass by providing richer nutrient/organic matter cycle and higher prey species density. This amplifying effect is even more conspicuous when flooding is synchronous with proper temperature conditions (Vilizzi, 2012). Spawning and growth of lateral migration species juvenile also benefit from a fertile floodplain in this circumstance. When the water level falls, lateral species, such as *Phalacrodon micronevus*, migrates back from flood plain to the river channel for their declining flow condition refuge (Poulsen & Valbo-Jørgensen, 2001; Welcomme, 2000). Given that the majority of Dai biomass is comprised of longitudinal migrators, we fine-tuned our trait-based analysis to quantify relative impacts of hydrologic drivers on longitudinal species that migrate different distances (short, medium, and long). We hypothesized that downstream hydrology would have lower effect sizes for long distance relative to short distance migrators, as a result of overriding impacts of recent dam closures and

reduced river connectivity upstream (Ziv et al., 2012). Interestingly, our model showed significant effect sizes for both short and long-distance migrators for most hydrologic drivers except NAL. Also, the greatest effect sizes of every driver were found in medium distance migrators rather than long distance migrators, which could lead credence to our hypothesis 3. On the other hand, our future projections showed that design flows could enhance Dai fishery, even for long distance migratory species. The last year in our fisheries dataset is 2012 and since then many more dams have been closed on both tributaries and the mainstem. Future work should more systematically address the potential effects of strategic operations of tributary and mainstem dams on fish production and biodiversity using a combination of approaches that more effectively link upstream connectivity and downstream flow variation perspectives.

4.3 | Future fishery catch in design flow scenarios

A quantitative and explicit expression of ecosystem flow demands has been the bottleneck of designing flow for environment (Davis et al., 2015; Tickner et al., 2017). Our improved DFFT-MARSS framework offers a quantitative approach to expressing flow demands of fishery yield of specific functional groups using six flow variation metrics based on long term records. In the design flow scenarios test, we showed the effectiveness of good design flows (lengthy low flow period with following strong pulse) preserving fishery catch for different migration groups. Moreover, the importance of timing in hydrological anomalies were validated as the effectiveness of good design was largely diminished by delayed flood. Among the migrators, longitudinal migrators showed more dramatic response in favourable or harmful scenario (largest increasing slope of 0.52 and declining slope of -0.55). The detrimental influence of flood delay was also evidenced in Oliveira et al. (2015), where YOY abundance of migrators decreased exponentially with flood delayed days. Delayed flood could break the synchronization of reproductive behaviour and photoperiod and temperature, which are indicators for initial growth and gonadal development (Oliveira et al., 2020). Thus, properly timed asymmetric pulse train design might serve as guiding concept for other designer environmental flow. It's noteworthy that the good design was not a mathematically optimized answer to protect fishery yield, but a feasible hydrograph created based on our analysis results. Future study into comprehensive optimization with extra objective functions for sustainability, hydropower, rice yields and flood control are necessary.

The tool kit for adaptive management of regulated rivers is evolving (Acreman et al., 2014; Arthington et al., 2003; Poff et al., 2016; Poff & Olden, 2017) and design flows are among the most innovative tools to emerge (Acreman et al., 2014; Chen & Olden, 2017; Sabo et al., 2017). The design flow concept acknowledges dams as tools to deliver a myriad of social benefits with associated costs. Trade-offs can be measured in terms of different objective functions—optimization for sectors like hydropower, flood control or biodiversity. A critical and often missing ingredient to maximizing ecological and societal benefits of dams is a set of quantitative design principles for delivering ecologically relevant flows. Quantified

effect sizes based on long term data could fuel optimizing reservoir operation to deliver flow for fishery at functional group level. The consistency of our migration traits model and total catch model might be explained by overlap in species composition. For the most abundant 85 species modelled in our total catch model, longitudinal migrators accounted for 69%–94% of total fishery harvest each year. Hence, the total catch model and our initial trait model were likely both driven by impacts on longitudinal migrators. Our further investigation into migration distance showed that all three migration distance groups were linked with hydrologic drivers in similar ways.

AUTHOR CONTRIBUTIONS

Qi Deng and John L. Sabo conceived the idea and designed the methodology; John L. Sabo acquired the data; Peng Bun Ngor helped organizing and pre-processing data. Qi Deng, John L. Sabo, and Gordon W. Holtgrieve analysed data; Qi Deng and John L. Sabo led and Joseph Holway contributed in the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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- Our study was initiated with the goal to make contribution to improve local water resources management potential when facing future hydrologic change under the sponsor grant. Collaboration with local authorities and scientists started at day one of this project. Scientists from the study region not only helped in providing data, but also actively participated in the analysis with their expertise and local experience. Literature published by scientists from the study region was cited whenever relevant.
- Apart from including authorships from different countries, efforts were made to expand local research capacity during this study. We organized and held training workshops for local college students and professionals regarding related scientific methods and skills.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are originally provided by Mekong River Commission and the Inland Fisheries Research and Development Institute (IFReDI) of

Cambodia and are available in raw form via request to the Mekong River Commission by writing to S.N. (sonam@mrcmekong.org). After removing attributes that would lead to sensitive personal information, all data used in analysis are archived via the Dryad Digital Repository and are available at <https://doi.org/10.5061/dryad.kwh70rz7j> (Deng et al., 2022).

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REFERENCES

- Acreman, M., Arthington, A. H., Colloff, M. J., Couch, C., Crossman, N. D., Dyer, F., Overton, I., Pollino, C. A., Stewardson, M. J., & Young, W. (2014). Environmental flows for natural, hybrid, and novel riverine ecosystems in a changing world. *Frontiers in Ecology and the Environment*, 12, 466–473.
- Agostinho, A., Gomes, L., & Zalewski, M. (2001). The importance of floodplains for the dynamics of fish communities of the upper river Paraná. *Ecohydrology and Hydrobiology*, 1, 209–217.
- Agostinho, A. A., Gomes, L. C., Veredissimo, S., & Okada, E. K. (2004). Flood regime, dam regulation and fish in the Upper Paraná River: Effects on assemblage attributes, reproduction and recruitment. *Reviews in Fish Biology and Fisheries*, 14, 11–19.
- Alcázar, J., Palau, A., & Vega-García, C. (2008). A neural net model for environmental flow estimation at the Ebro River Basin, Spain. *Journal of Hydrology*, 349, 44–55.
- Alford, J. B., & Walker, M. R. (2013). Managing the flood pulse for optimal fisheries production in the Atchafalaya River Basin, Louisiana (USA). *River Research and Applications*, 29, 279–296.
- Antonio, R. R., Agostinho, A. A., Pelicice, F. M., Bailly, D., Okada, E. K., & Dias, J. H. P. (2007). Blockage of migration routes by dam construction: Can migratory fish find alternative routes? *Neotropical Ichthyology*, 5, 177–184.
- Arias, M. E., Cochrane, T. A., Piman, T., Kumm, M., Caruso, B. S., & Killeen, T. J. (2012). Quantifying changes in flooding and habitats in the Tonle Sap lake (Cambodia) caused by water infrastructure development and climate change in the Mekong basin. *Journal of Environmental Management*, 112, 53–66.
- Arthington, A. H., Bunn, S. E., Poff, N. L., & Naiman, R. J. (2006). The challenge of providing environmental flow rules to sustain river ecosystems. *Ecological Applications*, 16, 1311–1318.
- Arthington, A. H., Rall, J. L., Kennard, M. J., & Pusey, B. J. (2003). Environmental flow requirements of fish in Lesotho rivers using the DRIFT methodology. *River Research and Applications*, 19, 641–666.
- Baran, E. (2006). Fish migration triggers in the lower Mekong basin and other tropical freshwater systems. *MRC Technical paper*, 14, 55.
- Baran, E., Jantunen, T., & Chong, C. K. (2007). *Values of inland fisheries in the Mekong River Basin*. No. 1812. WorldFish.
- Bednarek, A. T. (2001). Undamming rivers: A review of the ecological impacts of dam removal. *Environmental Management*, 27, 803–814.
- Belton, B., & Thilsted, S. H. (2014). Fisheries in transition: Food and nutrition security implications for the global south. *Global Food Security*, 3, 59–66.
- Bénech, V., & Peñáz, M. (1995). An outline on lateral fish migrations within the Central Delta of The Niger River, Mali. *Hydrobiologia*, 303, 149–157.
- Brown, L. R., & Ford, T. (2002). Effects of flow on the fish communities of a regulated California river: Implications for managing native fishes. *River Research and Applications*, 18, 331–342.
- Chang, F., Lai, J., & Kao, L. (2003). Optimization of operation rule curves and flushing schedule in a reservoir. *Hydrological Processes*, 17, 1623–1640.
- Chang, F. K. (2013). The lower Mekong initiative & us foreign policy in southeast Asia: Energy, environment & power. *Orbis*, 57, 282–299.
- Chen, W., & Olden, J. D. (2017). Designing flows to resolve human and environmental water needs in a dam-regulated river. *Nature Communications*, 8, 2158.
- Dahm, C. N., Baker, M. A., Moore, D. I., & Thibault, J. R. (2003). Coupled biogeochemical and hydrological responses of streams and rivers to drought. *Freshwater Biology*, 48, 1219–1231.
- Davis, J., O'Grady, A. P., Dale, A., Arthington, A. H., Gell, P. A., Driver, P. D., Bond, N., Casanova, M., Finlayson, M., Watts, R. J., Capon, S. J., Nagelkerken, I., Tingley, R., Fry, B., Page, T. J., & Specht, A. (2015). When trends intersect: The challenge of protecting freshwater ecosystems under multiple land use and hydrological intensification scenarios. *Science of the Total Environment*, 534, 65–78.
- Deng, Q., Sabo, J. L., Holtgrieve, G. W., Ngor, P. B., & Holway, J. (2022). Data from: Timing of hydrologic anomalies direct impacts on migration traits in a flood pulse fishery system. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.kwh70rz7j>
- Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z.-I., Knowler, D. J., Lévêque, C., Naiman, R. J., Prieur-Richard, A.-H., Soto, D., Stiassny, M. L., & Sullivan, C. A. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, 81, 163–182.
- Dugan, P., Dey, M. M., & Sugunan, V. (2006). Fisheries and water productivity in tropical river basins: Enhancing food security and livelihoods by managing water for fish. *Agricultural Water Management*, 80, 262–275.
- Dugan, P. J., Barlow, C., Agostinho, A. A., Baran, E., Cada, G. F., Chen, D., Cowx, I. G., Ferguson, J. W., Jutagate, T., Mallen-Cooper, M., Marmulla, G., Nestler, J., Petrere, M., Welcomme, R. L., & Winemiller, K. O. (2010). Fish migration, dams, and loss of ecosystem services in the Mekong Basin. *Ambio*, 39, 344–348.
- Eimers, M. C., Watmough, S. A., Buttle, J. M., & Dillon, P. J. (2007). Drought-induced sulphate release from a wetland in south-central Ontario. *Environmental Monitoring and Assessment*, 127, 399–407.
- Ellis, I. M., Stoessel, D., Hammer, M. P., Wedderburn, S. D., Sutor, L., & Hall, A. (2013). Conservation of an inauspicious endangered freshwater fish, Murray hardyhead (*Craterocephalus fluviatilis*), during drought and competing water demands in the Murray-darling basin, Australia. *Marine and Freshwater Research*, 64, 792–806.
- Englund, G., & Malmqvist, B. (1996). Effects of flow regulation, habitat area and isolation on the macroinvertebrate fauna of rapids in north Swedish rivers. *Regulated Rivers: Research & Management*, 12, 433–445.
- FAO. (2022). *The State of World Fisheries and Aquaculture 2022. Towards Blue Transformation*. Rome: FAO.
- Freitas, C. E. C., Siqueira-Souza, F. K., Humston, R., & Hurd, L. E. (2013). An initial assessment of drought sensitivity in Amazonian fish communities. *Hydrobiologia*, 705, 159–171.
- Górski, K., Leeuw, J. J. D., Winter, H. V., Vekhov, D. A., Minin, A. E., Buijse, A. D., & Nagelkerke, L. A. J. (2011). Fish recruitment in a large, temperate floodplain: The importance of annual flooding, temperature and habitat complexity. *Freshwater Biology*, 56, 2210–2225.
- Graaf, G. (2003). The flood pulse and growth of floodplain fish in Bangladesh. *Fisheries Management and Ecology*, 10, 241–247.
- Hampton, S. E., Holmes, E. E., Scheef, L. P., Scheuerell, M. D., Katz, S. L., Pendleton, D. E., & Ward, E. J. (2013). Quantifying effects of abiotic and biotic drivers on community dynamics with multivariate autoregressive (MAR) models. *Ecology*, 94, 2663–2669.
- Healy, B. D., Schelly, R. C., Yackulic, C. B., Smith, E. C. O., & Budy, P. (2020). Remarkable response of native fishes to invasive trout suppression varies with trout density, temperature, and annual hydrology. *Canadian Journal of Fisheries and Aquatic Sciences*, 77, 1446–1462.
- Holmes, E. E., Ward, E. J., & Wills, K. (2012). Marss: Multivariate autoregressive state-space models for analyzing time-series data. *R Journal*, 4(1), 11.
- Humphries, P., & Lake, P. S. (2000). Fish larvae and the management of regulated rivers. *Regulated Rivers: Research & Management: An International Journal Devoted to River Research and Management*, 16, 421–432.
- Ives, A. R., Dennis, B., Cottingham, K. L., & Carpenter, S. R. (2003). Estimating community stability and ecological interactions from time-series data. *Ecological Monographs*, 73, 301–330.

- Junk, W. J., Bayley, P. B., & Sparks, R. E. (1989). The flood pulse concept in river-floodplain systems. *Canadian Special Publication of Fisheries and Aquatic Sciences*, 106, 110–127.
- Koponen, J., Tes, S., & Mykkanen, J. (2007). Influence of built structures on Tonle Sap hydrology and related parameters. In *Technical assistance to the Kingdom of Cambodia for the study of the influence of built structures on the fisheries of the Tonle Sap*. Environmental Impact Assessment Center of Finland Ltd.
- Kummu, M., & Varis, O. (2007). Sediment-related impacts due to upstream reservoir trapping, the lower Mekong River. *Geomorphology*, 85, 275–293.
- Lytle, D. A., & Poff, N. (2004). Adaptation to natural flow regimes. *Trends in Ecology & Evolution*, 19, 94–100.
- Marengo, J. A., & Espinoza, J. C. (2016). Extreme seasonal droughts and floods in Amazonia: Causes, trends and impacts. *International Journal of Climatology*, 36, 1033–1050.
- McIntyre, P. B., Liermann, C. A. R., & Revenga, C. (2016). Linking freshwater fishery management to global food security and biodiversity conservation. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 12880–12885.
- Mims, M. C., & Olden, J. D. (2013). Fish assemblages respond to altered flow regimes via ecological filtering of life history strategies. *Freshwater Biology*, 58, 50–62.
- Mosley, L. M. (2015). Drought impacts on the water quality of freshwater systems; review and integration. *Earth-Science Reviews*, 140, 203–214.
- Ngor, P. B., Grenouillet, G., Phem, S., So, N., & Lek, S. (2018). Spatial and temporal variation in fish community structure and diversity in the largest tropical flood-pulse system of South-East Asia. *Ecology of Freshwater Fish*, 27, 1087–1100.
- Ngor, P. B., McCann, K. S., Grenouillet, G., So, N., McMeans, B. C., Fraser, E., & Lek, S. (2018). Evidence of indiscriminate fishing effects in one of the world's largest inland fisheries. *Scientific Reports*, 8, 8947.
- Oliveira, A. G. D., Lopes, T. M., Angulo-Valencia, M. A., Dias, R. M., Suzuki, H. I., Costa, I. C. B., & Agostinho, A. A. (2020). Relationship of freshwater fish recruitment with distinct reproductive strategies and flood attributes: A long-term view in the Upper Paraná River floodplain. *Frontiers in Environmental Science*, 8, 577181.
- Oliveira, A. G., Suzuki, H. I., Gomes, L. C., & Agostinho, A. A. (2015). Interspecific variation in migratory fish recruitment in the Upper Paraná River: Effects of the duration and timing of floods. *Environmental Biology of Fishes*, 98, 1327–1337.
- Orr, S., Pittock, J., Chapagain, A., & Dumaresq, D. (2012). Dams on the Mekong River: Lost fish protein and the implications for land and water resources. *Global Environmental Change*, 22, 925–932.
- Poff, N. L., Allan, J. D., Bain, M. B., Karr, J. R., Prestegard, K. L., Richter, B. D., Sparks, R. E., & Stromberg, J. C. (1997). The natural flow regime. *Bioscience*, 47, 769–784.
- Poff, N. L., Brown, C. M., Grantham, T. E., Matthews, J. H., Palmer, M. A., Spence, C. M., Wilby, R. L., Haasnoot, M., Mendoza, G. F., Dominique, K. C., & Baeza, A. (2016). Sustainable water management under future uncertainty with eco-engineering decision scaling. *Nature Climate Change*, 6, 25–34.
- Poff, N. L., & Olden, J. D. (2017). Can dams be designed for sustainability? *Science*, 358, 1252–1253.
- Poulsen, A., & Valbo-Jørgensen, J. (2001). *Fish migrations and spawning habits in the Mekong mainstream: A survey using local knowledge*. Cultivate Understanding Multimedia DeKalb.
- Pusey, B., Arthington, A., Bird, J., & Close, P. (2001). Reproduction in three species of rainbowfish (melanotaeniidae) from rainforest streams in northern Queensland, Australia. *Ecology of Freshwater Fish*, 10, 75–87.
- Rand, P. S., Hinch, S. G., Morrison, J., Foreman, M. G. G., MacNutt, M. J., Macdonald, J. S., Healey, M. C., Farrell, A. P., & Higgs, D. A. (2006). Effects of river discharge, temperature, and future climates on energetics and mortality of adult migrating Fraser River Sockeye Salmon. *Transactions of the American Fisheries Society*, 135, 655–667.
- Ruhí, A., Holmes, E. E., Rinne, J. N., & Sabo, J. L. (2015). Anomalous droughts, not invasion, decrease persistence of native fishes in a desert river. *Global Change Biology*, 21, 1482–1496.
- Sabo, J. L., & Post, D. M. (2008). Quantifying periodic, stochastic, and catastrophic environmental variation. *Ecological Monographs*, 78, 19–40.
- Sabo, J. L., Ruhí, A., Holtgrieve, G. W., Elliott, V., Arias, M. E., Ngor, P. B., Räsänen, T. A., & Nam, S. (2017). Designing river flows to improve food security futures in the lower Mekong Basin. *Science*, 358, eaao1053.
- Smith, R. J. F. (2012). The control of fish migration. *Zoophysiology*, 17, 119–151.
- Stanley, E. H., & Doyle, M. W. (2003). Trading off: The ecological effects of dam removal. *Frontiers in Ecology and the Environment*, 1, 15–22.
- Taylor, W. W., Leonard, N. J., Kratzer, J. F., Goddard, C., & Stewart, P. (2007). Globalization: Implications for fish, fisheries and their management. In W. W. Taylor, M. G. Schechter, & L. G. Wolfson (Eds.), *Globalization: Effects on fisheries resources* (pp. 21–46). Cambridge, UK: Cambridge University Press.
- Tickner, D., Parker, H., Moncrieff, C. R., Oates, N. E. M., Ludi, E., & Acreman, M. (2017). Managing rivers for multiple benefits—a coherent approach to research, policy and planning. *Frontiers in Environmental Science*, 5, 4.
- Tonkin, Z. D., King, A. J., Robertson, A. I., & Ramsey, D. S. (2011). Early fish growth varies in response to components of the flow regime in a temperate floodplain river. *Freshwater Biology*, 56, 1769–1782.
- Vilizzi, L. (2012). Abundance trends in floodplain fish larvae: The role of annual flow characteristics in the absence of overbank flooding. *Fundamental and Applied Limnology/Archiv für Hydrobiologie*, 181, 215–227.
- Vliet, M. V., & Zwolsman, J. (2008). Impact of summer droughts on the water quality of the Meuse river. *Journal of Hydrology*, 353, 1–17.
- Wedderburn, S. D., Hillyard, K. A., & Shiel, R. J. (2013). Zooplankton response to flooding of a drought refuge and implications for the endangered fish species *craterocephalus fluviatilis* cohabiting with alien *gambusia holbrooki*. *Aquatic Ecology*, 47, 263–275.
- Welcomme, R. (1979). *Fisheries ecology of floodplain Rivers*. Longman <https://books.google.com/books?id=6AwNAQAIAAJ>
- Welcomme, R. (2000). Principles and approaches for river fisheries management. In *Management and ecology of river fisheries* (pp. 331–345).
- Yi, Y., Yang, Z., & Zhang, S. (2010). Ecological influence of dam construction and river-lake connectivity on migration fish habitat in the yangtze river basin, China. *Procedia Environmental Sciences*, 2, 1942–1954.
- Yin, X.-A., Yang, Z.-F., Petts, G. E., & Kondolf, G. M. (2014). A reservoir operating method for riverine ecosystem protection, reservoir sedimentation control and water supply. *Journal of Hydrology*, 512, 379–387.
- Zhong, Y., & Power, G. (1996). Environmental impacts of hydroelectric projects on fish resources in China. *Regulated Rivers: Research & Management*, 12, 81–98.
- Ziv, G., Baran, E., Nam, S., Rodríguez-Iturbe, I., & Levin, S. A. (2012). Trading-off fish biodiversity, food security, and hydropower in the Mekong River Basin. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 5609–5614.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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