

Impact of a dam on wintering waterbirds' habitat use

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SUMMARY

The degradation, alteration and depletion of riparian habitats caused by river regulation are among critical conservation concerns. Aquatic and riparian habitats support not only river-dwelling biota such as macroinvertebrates and fish, but also waterbirds, the top predators in the aquatic food web. Despite the intimate relationships between fish and waterbirds, the two groups are often investigated separately. Using an integrative approach, we examined the effects of dams on fish and scaly-sided merganser (*Mergus squamatus*), an endangered, iconic riverine species, where the lack of knowledge about habitat preferences greatly hampers long-term conservation efforts. Our analysis quantified three causal links: (1) water depth had direct, comparable, negative effects on both fish and waterbirds, and the path coefficients for fish and birds are -0.31 and -0.46 , respectively; (2) river landscape heterogeneity directly and positively affected fish and waterbirds, and the path coefficients for fish and birds are 0.63 and 0.19 , respectively; and (3) depth and river landscape also exerted indirect effects on waterbirds through their impacts on fish abundance, and the path coefficients for fish and birds are -0.15 and 0.28 , respectively. Our findings could contribute to the rational spatial planning and sustainable operation of dams in that maintaining instream habitat availability and heterogeneity would benefit the whole riverine ecosystem.

Keywords: dam, river ecosystem, waterbird, habitat, scaly-sided merganser

INTRODUCTION

For thousands of years, humans have built millions of dams and impoundments for various purposes, including flood control, water supply, irrigation, recreation, navigation and hydropower (WCD 2000). In the last 60 years, the number and storage capacity of dams and reservoirs have rapidly increased (Lehner *et al.* 2011). Dams have benefitted human

society through mitigating floods, securing water supplies and providing hydropower (WCD 2000; Lehner *et al.* 2011); however, damming is also a dominant form of human impact on riverine ecosystems, as nearly 50% of freshwater ecoregions across the world are affected by large- and medium-sized dams (Liermann *et al.* 2012).

Dams and reservoirs dramatically change river hydrological regimes: they alter the timing, magnitude, frequency, duration and rate of change of flows (Poff *et al.* 1997), they alter channel morphology (Gordon & Meentemeyer 2006), they impede migratory paths and fragment ecological connectivity (Bednarek 2001) and they modify thermal, sediment and nutrient regimes (Ligon *et al.* 1995). Aquatic habitats are closely associated with the hydrological and geomorphological processes of the associated rivers (Wohl 2004). Any changes in these processes could affect organisms through changes in habitats (Graf 2006). For example, the shift from lotic to lentic environments after dam construction often favours generalist over specialist species, and puts endemic species at particular risk of extinction (Poff *et al.* 2007). Numerous studies have demonstrated the adverse impacts of dams on vegetation dynamics, macroinvertebrate habitat and fish abundance and diversity (Liermann *et al.* 2012). Dams constitute a major threat to global freshwater species diversity (Vörösmarty *et al.* 2010) and have wide effects on species distributions among aquatic trophic levels (Pringle *et al.* 2000). This has prompted recent river environment restoration efforts focused on enhancing connectivity through a variety of mechanisms, including dam removal (Stanley & Doyle 2003), adjusting reservoir management to provide more natural flow regimes (e.g. environmental flow), levee breaching (Guida *et al.* 2015), restoring natural morphology to streams disturbed by channelization, agriculture or urbanization (Eekhout *et al.* 2015) and improving fish passage (Kemp & O'Hanley 2010).

As with fish and invertebrate assemblages, the distribution, diversity and abundance of waterbirds have long been recognized as suitable bio-indicators of environmental change in aquatic systems (Caro and O'Doherty 1999), and are often integrated into monitoring programmes for environmental impact assessment and evaluation of ecosystem recovery (Hebert *et al.* 2000). Waterbirds are linked to aquatic food webs in multiple ways, with many species relying on both aquatic and the adjacent terrestrial areas (Steinmetz *et al.* 2003). Thus, waterbirds may be considered as proxies for the ecosystem's biotic health. In addition, as birds function at a larger spatial scale than many other taxa, they are

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highly relevant to understanding the linkages between rivers, riparian habitats and watersheds (Robinson *et al.* 2002). Numerous studies have assessed the effects of river regulation (especially damming and water diversion) on river-dwelling biota, including invertebrates, fish and waterbirds (Ligon *et al.* 1995; Hebert *et al.* 2000). Moreover, many studies have demonstrated the associations between waterbirds, especially piscivores, and fish and/or other invertebrates (Elmberg *et al.* 2010). However, few studies have investigated the effect of river regulation on fish and waterbirds in an integrated way.

Empirical habitat models, such as generalized linear regression, random forests and artificial neural networks, are based on a description of the abiotic variables that affect the distribution of species (Ahmadi-Nedushan *et al.* 2006), which can be generated using methods requiring information on species presence, or species presence and absence (Brotons *et al.* 2004). More recently, structural equation modelling (SEM) is increasingly being used in ecological studies to map these complex relationships and to determine causality (Grace 2006), and it might provide a framework for extricating the direct and indirect effects of damming on river birds and fish.

The wetland complex of the middle and lower Yangtze River watershed is the main wintering area for many endangered migratory waterbirds (e.g. scaly-sided merganser (*Mergus squamatus*) and Siberian cranes (*Grus leucogeranus*)), and a large number of migratory fish (e.g. Chinese sturgeon (*Acipenser sinensis*) and Chinese sucker (*Myxocyprinus asiaticus*)) depend on the Yangtze River for survival. The Yangtze River and its associated lakes are biodiversity hotspots and one of Earth's most biologically valuable eco-regions, harbouring globally important biodiversity and ecological processes. At the same time, the region is also the economic development frontier of China, representing a large number of river regulation projects, including the world's largest dam – the Three Gorges Dam (Dudgeon *et al.* 2006). The environmental and ecological consequences of these developments are still unfolding, and continuous monitoring and assessment are critical in order to avoid catastrophic biodiversity loss (Dudgeon *et al.* 2006).

In this study, we aim to examine the effects of dams on fish and waterbirds within the SEM framework using the scaly-sided merganser (*M. squamatus*) as an example. The scaly-sided merganser is an endangered, iconic fish-eater, wintering primarily in central and southern China. It has a very small population that is suspected to be undergoing a continuing and rapid decline due to dam construction, illegal hunting and logging (EAAFW 2015). In their wintering sites, scaly-sided mergansers prefer to forage in fast-flowing, clear water rivers with riffles, shoals or sand banks in mountainous areas and with low levels of human disturbance (EAAFW 2015). Almost all rivers in southern China have been dammed, and often the distance between dams is short, which leads to the disappearance of optimal river habitats. Based on a previous study, which established the importance of instream habitats for the scaly-sided merganser in the middle Yangtze catchment (Zeng *et al.* 2015b), we test whether or not the

association between the scaly-sided merganser and habitat changes when adding fish (the main food resource) into the equation. The specific objectives of this study are: to compare the instream physical and landscape variables upstream and downstream of the dams; to quantify the contributions of physical and landscape variables on fish abundance and scaly-sided merganser distribution; and to identify the direct and indirect effects of physical and landscape metrics on scaly-sided merganser occurrence.

MATERIALS AND METHODS

Study area

This study was conducted in the lower reach of Yuan River, one of the largest tributaries of the Yangtze River in central China (Fig. 1). It originates in Guizhou Plateau, and flows through the Wuling Mountain region. The studied river section spans 24 km, and a cascade hydropower dam (Lingjintan) is located at the southwest corner, which was constructed in 2000. The dam is 39 m high with a total reservoir capacity of 6.34×10^8 m³. This river section supports a wintering population of approximately 40 scaly-sided mergansers.

Gravel patch data and landscape metrics

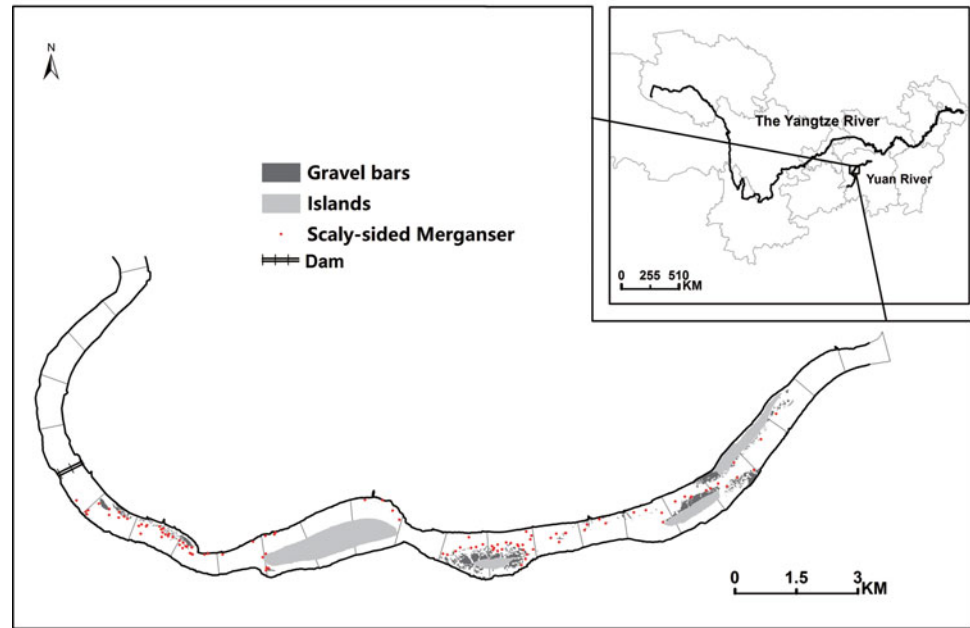
We used the Bing Maps aerial image (2011–2012) with a spatial resolution of 0.6 m to derive the landscape vectors. We then classified all of the habitat patches into three types through visual interpretation: water, islands and gravel bars. Islands are much higher and larger than gravel bars; they normally have human residence or activity, and are seldom used by waterfowl.

Considering that the study is carried out at the river reach scale, we drew a central line through the river, and equally divided the studied river section into 24 segments by drawing 23 lines perpendicular to the central line (Zeng *et al.* 2015b). The 24 river segments were processed in FRAGSTATS 3.3 (McGarigal *et al.* 2002) with landscape-level metrics, namely number of patches (total number of patches in the landscape), edge density (the lengths of all edge segments in the landscape divided by the total landscape area) and Shannon's diversity index.

Scaly-sided merganser occurrence

The distribution data of wintering scaly-sided merganser in the Yuan River were collected through fortnightly surveys from November to February in three winters (2010/2011, 2011/2012 and 2012/2013), resulting in a total of 24 surveys. For each survey, we travelled along the 24-km long river course by boat, using binoculars to identify and locate scaly-sided merganser. The scaly-sided merganser locations were recorded by global positioning system (GPS). As suggested by Zeng *et al.* (2015a), we kept our boat in the middle of the

Figure 1 Study area in the Yangtze River Basin and the distribution of scaly-sided merganser flocks and gravel bar patches in the 22-km river section of the lower Yuan River. The dots indicate 90 scaly-sided merganser flocks recorded over three winters. Areas in dark grey are gravel bars and areas in light grey are islands.



river to minimize disturbance to the birds, and also to ensure a full view was obtained. Distances of less than 10 m between individuals were defined as a flock (i.e. identified as a single occurrence point in mapping; Zeng *et al.* 2015a).

The scaly-sided merganser occurrences from the three winter surveys were then mapped with ArcGIS software (ESRI Inc., Redwood, CA, USA), and the counts were summed for all points within the 24 predefined 1-km river segments. We termed the ratio of this sum and total points as the occurrence frequency, which is the response variable in our model.

Fish density: hydroacoustic survey

Hydroacoustic surveys can produce comparable estimates of abundance to those obtained by trawling when focusing on small fish (Emmrich *et al.* 2010; Ren *et al.* 2012). The hydroacoustic survey was conducted in late November 2011. We used a BioSonics DT-X digital echosounder (BioSonics, Inc., Seattle, WA, USA) equipped with a 200-kHz split-beam circular transducer with a half-power beam width of 6.8°. The echosounder was fixed on the bow of the research vessel, with a draught of 0.58 m. The vessel zigzagged through the river section at a speed of 6 km h⁻¹ on average. Vessel position was measured with a GPS 17x HVS differentially corrected GPS unit (Garmin Inc., Olathe, KS, USA), and this information was embedded in the acoustic data files.

Acoustic signals were collected with BioSonics Visual Acquisition Software (version 6, BioSonics, Inc., Seattle, WA, USA), and output files were stored to a laptop hard drive. The S_V threshold was -65 dB, the pulse length was 0.3 ms and the ping rate was six pulses per second. Thresholds were set to allow detection of all echoes exceeding -75 dB on the acoustic axis.

The recorded data were processed in Visual Analyzer software (version 4.1, BioSonics, Inc., Seattle, WA, USA). The acoustical data were divided into seven depth layers (0–1, 1–2, 2–3, 3–4, 4–5, 5–6 and 6–7 m). Echo integration was used for calculation of the volumetric fish densities.

We divided the hydroacoustic-surveyed river section into the same 24 segments and calculated the fish density in each segment. Two datasets were excluded due to excess noise. Water depth was measured with a Biosonics DT-X sonar system (Biosonics Sound Navigation and Ranging Inc., Seattle, WA, USA), and the depth of each ping was derived by Visual Habitat software (BioSonics, Inc., Seattle, WA, USA).

Structural equation modelling

SEM is a multivariate method that is increasingly being used by researchers in the natural sciences to address questions about complex systems (Grace *et al.* 2012). SEM is designed to disentangle the complicated relationships in observed ecological phenomena and allows explicit testing of these direct and indirect dependencies, providing a framework for learning about causal processes. A simplified general conceptual model provides a basic outline of the hypothesized relationships between different components of the river ecosystem: (1) water depth and river landscape, which are latent variables measured by the number of patches, density of edges and diversity index, are both considered to be important drivers of fish abundance and the occurrence of scaly-sided mergansers (Zeng *et al.* 2015a); (2) the density of fish will influence the distribution of wintering scaly-sided mergansers, as fish is their main food (considering the diving range of the scaly-sided merganser, the average fish density in the top 5 m was specified in the model); and (3) water

depth and river landscape have indirect effects on scaly-sided mergansers through their influence on fish schools.

Spatial and temporal auto-correlations are frequently encountered in ecological data (Lichstein *et al.* 2002). To inspect the potential effects of autoregression in fish abundance and scaly-sided merganser occurrence data, we first included a variable that represented distance from the Lingjintan dam (negative for upstream and positive for downstream sections) in the model structure. The trial run indicated that distance was insignificant for both fish ($p = 0.46$) and waterbirds ($p = 0.68$), and so was excluded in the final model.

We used both absolute fit indices (model χ^2 and root mean square error of approximation) and incremental fit indices (comparative fit index) to evaluate model fit. We reported the means and standard errors of those indices based on 1000 bootstrapping draws. All analyses were conducted using R (version 3.1.1) with the package lavaan (version 0.5.14; Rosseel 2012).

RESULTS

Instream habitat and water depth

The average water depth in the river segments varied from 3.48 to 19.48 m, and the average water depth was 6.11 and 16.88 m below and above the Lingjintan dam, respectively. On average, the water depth at river segments upstream of the dam was 10 m deeper than those located downstream, and the difference was significant (two-tailed t -test, $df = 5.97$, $p < 0.001$).

While gravel bars and instream islands were abundant at the river segments downstream of the dam (number of patches, edge density and Shannon's diversity index were 28, 76 and 0.42, respectively), open water was the main feature upstream, with no other types of habitat patch identified from aerial images. The landscape metrics were significantly greater downstream (two-tailed t -test, $df = 16$, $p = 0.001$, $p < 0.001$ and $p < 0.001$ for the number of patches, edge density and Shannon's diversity index, respectively).

Fish and bird modelling

The number of single echo detections for the total volume was 336; the average target strength was -53.934 dB. Fish density was significantly higher (two-tailed test, $df = 16.07$, $p = 0.04$) downstream than upstream, especially for the 1–5-m stratum (two-tailed test, $df = 16.85$, $p = 0.008$; Fig. 2). During the entire survey period, we counted 427 scaly-sided mergansers, which belonged to 90 flocks, all found downstream of the dam (Fig. 1).

Water depth and river landscape were both included in the final model and had significant effects on fish density and the occurrence of scaly-sided mergansers (Fig. 3). Fish and scaly-sided mergansers were positively affected by landscape ($p = 0.141$ and $p = 0.002$ for waterbird and fish

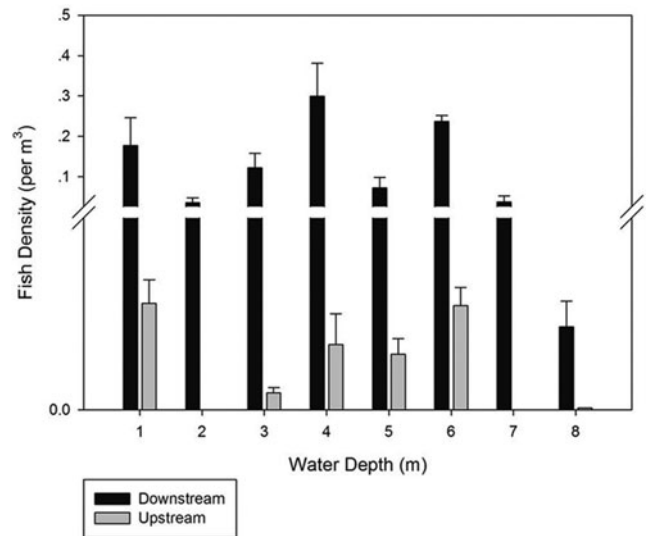


Figure 2 Fish densities at each stratum in river sections below and above the dam.

regressions, respectively) and negatively affected by water depth ($p = 0.028$ and $p = 0.037$ for fish and waterbird regressions, respectively). Density of fish directly influenced the distribution of wintering scaly-sided mergansers, while water depth and river landscape had indirect effects on the bird through their influences on fish abundance (Fig. 3).

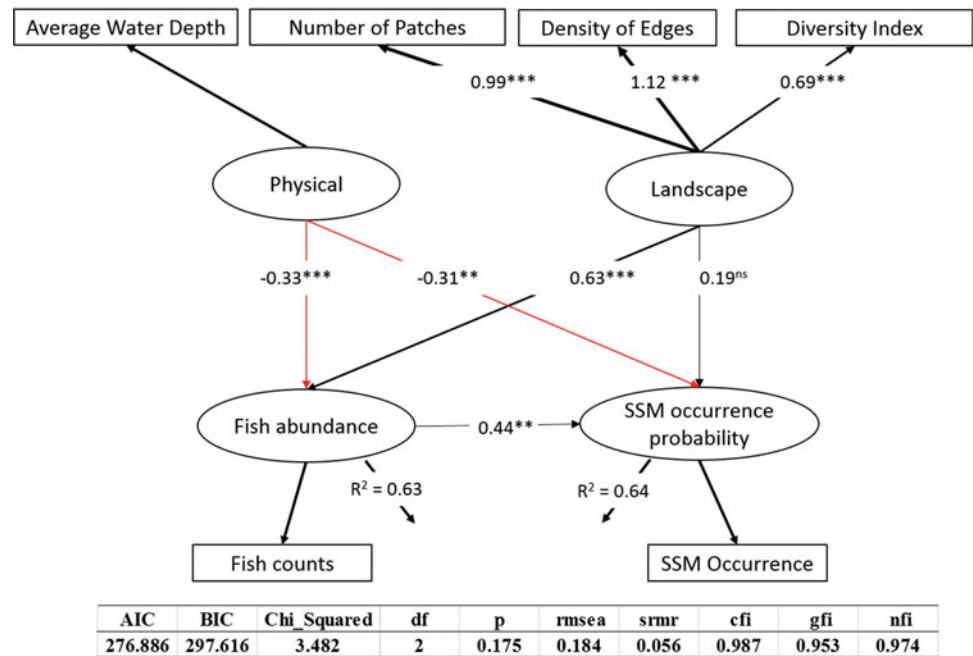
Fish abundance had a direct effect of 0.44 on scaly-sided mergansers; water depth had a total effect of -0.46 on the bird's occurrence – an indirect effect through fish ($-0.33 \times 0.44 = -0.15$) and a direct effect of -0.31 , as well as a direct effect of -0.33 on fish abundance; and landscape had a total effect of 0.47 on the bird's occurrence – an indirect effect through fish ($0.63 \times 0.44 = 0.28$) and a direct effect of 0.19, as well as a direct effect of 0.63 on fish abundance (Fig. 3). The model explained 64% of the variation in scaly-sided merganser occurrence probability and 63% of the variation in fish density.

DISCUSSION

We found that there were significant differences in river landscape and water depth between river segments below and above the Lingjintan dam. In general, the river below the dam is shallower and has a diverse habitat of gravel bars and islands. These differences in physical attributes and habitats influenced the densities of fish and scaly-sided mergansers.

The adverse impacts of river regulation such as dam construction on the distribution and habitat selection of waterbirds has been recognized for decades; 92% of 165 studies reported decreased values for recorded ecological metrics on different organism categories (such as birds, fishes, macroinvertebrates and zooplankton) in response to flow alteration (Poff & Zimmerman 2010). Habitat availability and heterogeneity are pivotal for waterbirds (Zeng *et al.* 2015a), which suggests that food availability might underpin waterbird distribution. This study goes beyond previous work

Figure 3 Structural equation model used to describe the full covariance matrix among habitat condition, fish and scaly-sided mergansers. The strength of the causality is indicated by the size of the link. Black lines indicate positive effects while red lines indicate negative impacts. ** $p < 0.01$; *** $p < 0.001$. AIC = Akaike information criterion; BIC = Bayesian information criterion; rmsea = root mean square error of approximation; srmr = standardized root mean square residual; cfi = comparative fit index; gfi = goodness of fit index; nfi = normed fit index; ns = non-significant.



by including both food resources (fish abundance) and habitat quality (gravel bar and water depth) in an integrated modelling framework. Our findings confirm that spatial heterogeneity (i.e. gravel bar diversity) and physical setting (water depth), in addition to their well-known direct effects on individual populations (fish and waterbirds in this study), might also affect the trophic interactions among species, although we did not find evidence for a causal link from waterbirds to fish.

The effects of prey

Prey size and prey abundance are the two main availability factors of importance to predators (Griffiths 1975). In a captive setting under controlled conditions, prey density outweighed prey behaviour (schooling versus solitary trout), exerting the strongest influence on foraging success of the double-crested cormorant (*Phalacrocorax auritus*), and prey size and light conditions did not measurably affect cormorant prey-capture performance (Enstipp *et al.* 2007). In the wild, common mergansers select their foraging sites based only on density of juvenile salmon, while tide, weather and time of day have no significant effect (Wood & Hand 1985). A merganser's average daily food requirement (*c.* 400 g) can be satisfied at smolt densities of 0.02–0.30 m⁻² (Wood & Hand 1985). In captivity, the average daily food requirement of scaly-sided mergansers is 200–300 g (authors' personal observations). In our study site, the average fish density downstream of the Lingjintan dam is 0.0014–0.1792 m⁻², indicating that some river sections could be satisfactory. We found no literature reporting the effect of prey size on waterfowl foraging site selection and assumed that the size of fish had no significant influence on the distribution of scaly-sided mergansers, because most of

the fish at our study site are small (<10 cm) and easy for the mergansers to handle.

Effects of the dam on fish

The SEM demonstrated two causal paths that linked the dam to fish density. The first path was related to river landscape as defined by three landscape metrics (i.e. number of gravel bar patches, density of edges and diversity index), which had a significant positive effect on fish density. This result is in agreement with studies in North America, in that a diverse landscape (e.g. the mosaic of islands and gravel bars) has greater variability in depth, substrate, cover and current velocity, as well as greater habitat complexity. This increases the number and diversity of foraging positions and shelters, which increases the density of Atlantic salmon (Van Zyll de Jong *et al.* 1997). The second path was related to the physical attributes of the river, which were measured by the average water depth of a river segment. The path coefficient showed that fish density was negatively affected by water depth. Katano *et al.* (2006) also showed that fish diversity and abundance were lower at locations downstream of the dam, which was attributed to the interrupted migration. In most circumstances, shallow and slow-flowing habitats were used by small, young fish of several species, while deep areas were primarily inhabited by larger, older fish (Finger 1982).

Effects of the dam on scaly-sided mergansers

Three direct and indirect effects of the dam on scaly-sided merganser occurrence were identified. The first path was the direct link between river landscape and bird occurrence probability. Including this link greatly increased the model

Akaike information criterion (AIC; $\Delta\text{AIC} = 6.54$), which indicated the importance of the link (Burnham & Anderson 2004). As shelters from disturbance, as well as sites for roosting and feeding, a diversity of gravel bars within a river is vital for the scaly-sided merganser (Zeng *et al.* 2015a).

The second path was the indirect effect of the river landscape through its influence on fish abundance. The explicit realization and quantification of this causality is one of the main contributions of this study. Previous studies documented the importance of habitat diversity for river-dwelling biota, including fish and waterbirds, as well as the association between fish and waterbirds (Zeng *et al.* 2015a). Our results clearly demonstrate the causal path from habitat diversity to fish abundance to waterbird occurrence. We recognize that several meaningful paths are missing (e.g. connections between physical environment and flow rate, nutrients or water temperature) in our relatively simple conceptual model. In addition, the path coefficients and significant levels of the included causal links might differ if we included the distributions of submergent macrophytes (types of substrate for fish) and the disturbance to waterbirds (Klein 1993) in the conceptual SEM. Our intention is neither to illustrate the enormous interconnectivity in nature nor to identify the 'optimal model'. In this study, we simply formulated a model based on our best knowledge of the system, which aims to illuminate the relative impact of the considered causal factors on the occurrence of the scaly-sided merganser in its known wintering area through a reasonable representation of the observed variability.

The third path indicated the negative effect of water depth on the occurrence of scaly-sided mergansers. This might be related to its foraging behaviour. When searching for prey (i.e. salmon), common mergansers and red-breasted mergansers probe the river bottom with their bills, or insert their bills into cavities and potential refuges among stones (Sjöberg 1987). The common mergansers seek their food visually; therefore, they prefer clear or relatively shallow water habitats. The scaly-sided mergansers might use a similar foraging strategy. The longest diving duration of scaly-sided mergansers is 112 seconds, with a diving depth of 2 m and a diving distance of 15 m (Fang *et al.* 2009). Scaly-sided mergansers seldom appeared in the upstream area of the dam (authors' personal observations), which might be related to the water depth limiting their foraging. Similarly, buffleheads (*Bucephala albeola*) normally do not forage in water that is deeper than 3 m and appear to be physiologically constrained in this manner (Erskine 1972). Therefore, food at depths beyond 3 m is not actually available (Schummer *et al.* 2008). Selection and use of foraging patches involve trade-offs between various factors, including food availability, the energy content of available foods, prey handling time, thermoregulatory costs associated with body size and diving ability to greater depths (Krebs & Davies 2009). For piscivore birds such as mergansers, the recorded diving depths of diving ducks are much greater than their foraging depths (Nilsson 1972; Croll *et al.* 1992). The

effect of water depth on the scaly-sided merganser is in need of further study.

CONCLUSION

Dams have direct and indirect negative effects on the density of fish and the distribution of fish-eaters. In fact, dam construction could be one of the most serious threats to the wintering scaly-sided merganser (Barter *et al.* 2014). The cascade of development of hydropower has transformed the Yangtze River into a chain of reservoirs, and this has cumulative effects on the whole ecosystem, which could cause the loss and degradation of critical habitats and affect the distribution and survival of fish, birds and other aquatic organisms. Further research on dam design, location and operation is needed in order to ameliorate ecologically deleterious geomorphic changes (Ligon *et al.* 1995). The sites and sizes of dams need to be carefully studied before construction. Flow and sediment inputs downstream will interact with the river channel, and different flow release policies introduce changes to the hydrological regime. Habitat restoration techniques should be employed in order to increase habitat heterogeneity and the degree of habitat complexity in channelized river sections. For river segments behind the dam, locally based management actions can be successful in restoring biotic integrity, whereas dam removal actions require more integrated measures at a regional scale (Van Looy *et al.* 2014).

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