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Dominant aquatic species and their hydrological niches in freshwater ecosystems in a developing city

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Abstract. Maintenance of appropriate hydrological niches is crucial to aquatic organisms. This study identified keystone species using the Ecopath with Ecosim food web model for hydrological niche analysis in Jinan City, the first pilot city of the Water Ecological Civilisation Project in China. The niche breadth of keystone species was analysed using Levins' breadth model. Results revealed 35 keystone species in the aquatic ecosystems of Jinan City, including 5 phytoplankton, 7 zooplankton, 9 zoobenthos and 14 fish species. Streamflow was the most important hydrological factor affecting the phytoplankton, zooplankton, zoobenthos and fish communities in the study area, and excess variation in streamflow had an adverse effect on the normal evolution of the four biotic communities. We found that: (1) higher trophic levels in the food web contained more keystone species in the corresponding community; (2) carbon is an important element constraining the food web structure, and the magnitude of its effect on energy flow determines the degree of importance of the keystone species in the food web; and (3) changes to the survey season and at the spatiotemporal scale will have strong effects on the results of hydrological niche analysis and, to reduce these effects, it will be important to lengthen the spatial and temporal scales to cover both dry and flood seasons in the future. These results may provide an important basis for decision making regarding ecological scheduling and remediation of rivers in the study area, and potentially regions worldwide, thus facilitating aquatic ecological remediation and sustainable water resource management.

Additional keywords: aquatic ecosystem, hydrology, Jinan City, keystone species.

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Introduction

With increased rates of urbanisation, many rivers have been severely affected by human activities in recent years, reducing available river habitat area and the number of waterbodies connected to rivers (such as wetlands and lakes; Dudgeon 2010; Shannon *et al.* 2016). This can severely degrade river ecological functions by degrading the hydrological buffer, shrinking fish spawning grounds and deteriorating the biotope landscape (Gilvear *et al.* 2002).

Keystone species are defined as species with a structuring role within ecosystems and interconnecting food webs despite a low biomass, and hence food intake (Paine 1969; Power *et al.* 1996). Keystone species affect the communities of which they are a part in a manner disproportionate to their abundance (Power *et al.* 1996), and have strongly effects on the abundance of other species and the ecosystem dynamic (Piraino *et al.* 2002). Generally, there are three types of keystone species, namely flagship species (Western 1987), dominant species (Tilman *et al.* 1994) and keystone species (Power *et al.* 1996). In previous studies keystone species have often been identified on the basis of the field experiments in which the strength of interactions is quantified through effects of changes in the abundance of one species on the abundance of other species in a community (Paine 1969; Wootton 1994; Wootton *et al.* 1996; Berlow 1999; Zhao *et al.* 2017). However, these experiments can only focus on a few species and they require *a priori* assumptions on the importance of the interactions in order to exclude those species that are not species of interest from the experiment, which can bias the identification of keystone species (Wootton 1994; Bustamante *et al.* 1995). The modelling approach allows some of the difficulties associated with the experimental quantification of keystoneness to be overcome. Through a model it is possible to estimate the strength of the interactions between model functional groups. Therefore, the modelling approach provides at least a prescreening analysis and allows for improved planning of subsequent field experiments (Libralato *et al.* 2006). There are previous estimates of keystone species from mathematical models that are based on successive elimination of functional groups from a trophic web and evaluating effects on other functional groups using a graph theoretical method (Jordán *et al.* 1999; Jordán 2001; Solé and Montoya 2001), evaluation of changes in the biomass of an ecosystem with dynamic models (Okey *et al.* 2004) and assessment of the dominance of species (Zhao *et al.* 2012). However, these methods do not consider energy flow and material exchange within ecosystems. The Ecopath and Ecosim (EwE) modelling approach was primarily developed to answer 'what if…' questions about policy that could not be addressed with single-species assessment models (Christensen and Walters 2004). Thus, EwE is suitable for studying aquatic food webs, but has been primarily used to examine marine ecosystems. To date, over the past decade more than 400 ecosystem models using the EwE approach have been published and these are cited more than 700 times per year (Coll *et al.* 2015; Colléter *et al.* 2015).

To be accurate, the EwE model is an ecosystem nutritional balance model based on trophodynamics that is used to describe the flow of energy based on the food web structure of an ecosystem (Guesnet *et al.* 2015). This model quantitatively analyses the structure, trophic flow process and trophodynamic characteristics of ecosystems (Liu *et al.* 2007; Coll *et al.* 2015; Halouani *et al.* 2015; Tecchio *et al.* 2015). The Ecopath model has been widely used to analyse the trophic structure and energy flow of aquatic ecosystems and to predict trends in their development, and is recognised as a core new-generation tool for studying aquatic ecosystems worldwide (Christensen and Walters 2004; Sandberg *et al.* 2007; Parrish *et al.* 2012; Deehr *et al.* 2014; Ortiz *et al.* 2015).

In aquatic ecosystems, each species has an ecological niche. The ecological niche is an objective entity and important means for analysing and evaluating relationships among different species and species population status in communities (Chen and Yin 2008). Ecological niches have been widely used in studies of interspecies relationships, community structures, community succession, biodiversity and species evolution (Zhang *et al.* 2003; Ding *et al.* 2007). For aquatic organisms, hydrological niches are prerequisite for all survival environments, so it is important to analyse hydrological niches when studying these organisms. However, in previous studies, the species used for niche analysis were often selected without accounting for their effects on the ecosystems. This may induce great uncertainties when applied to ecosystem restoration projects. That is, keystone species having a great effect on ecosystem development should be identified objectively and quantitatively before niche analysis.

To restore degraded ecosystems, China's government has proposed a Water Ecological Civilisation Project. As the first pilot city of the project, Jinan City is famous for its numerous springs, which number in the hundreds (Liu *et al.* 2017). However, with the rapid development of the economy and society, human activities such as urbanisation, industrialisation and domestic sewage discharge, have greatly stressed the health of the aquatic ecosystem. As the first city to move towards becoming ecologically sustainable, Jinan City is a model case for other cities (Zhao *et al.* 2015*a*).

The aim of this study was to identify the dominant keystone species and investigate their hydrological niches in freshwater ecosystems in the pilot city, namely Jinan City. Based on synchronous monitoring data related to hydrology and aquatic organisms of Jinan City, we analysed keystone species in the aquatic ecosystem using EwE software (ver. 6.5, Ecopath International Initiative, see http://ecopath.org/) and calculated the niche breadth of keystone species over gradients of hydrological factors using Levins' (1968) breadth model. These results could provide important references not only for the protection and remediation of the aquatic ecosystem and hydrological scheduling in Jinan City, but also the remediation of degraded aquatic ecosystems in developing cities worldwide.

Materials and methods

Study area

The city of Jinan (36.0–37.5°N, 116.2–117.7°E) is a pilot city of China's healthy water communities project, constructed as a 'water ecological civilisation city' in eastern China. Jinan City is bordered by Mount Tai to the south and traversed by the Yellow River, and has a steeper topography in the south than in the north (Fig. 1). Hilly areas, piedmont clinoplain and alluvial plains span the city from south to north. The altitude ranges from −66 to 957 m above sea level, with highly contrasting relief. The semi-humid continental monsoon climate in the city area is characterised by cold, dry winters and hot, wet summers. The average annual precipitation is 636 mm, 75% of which occurs in the autumn during the high-flow periods. The mean annual temperature is 14.3°C and the mean monthly temperature is highest in July, ranging from 26.8 to 27.4°C, and lowest in January, ranging from −3.2 to −1.4°C (Cui *et al.* 2009; Zhao *et al.* 2015*a*).

The city represents a typical developing city in China, with an area of 8227 km^2 and a population of 5.69 million (Zhang *et al.* 2007; Zhao *et al.* 2015*a*). With rapid industrial development and urbanisation in recent decades, the waters in Jinan have become severely polluted and reduced in quantity through extraction. As a result, drinking water, human health and well-being and the ecological community are being increasingly threatened (Hong *et al.* 2010). Therefore, research is urgently needed to identify dominant keystone species so as to determine their proper hydrological niches so that these keystone species can be protected and sustainable ecological functions maintained. Policy makers and stakeholders are aware of this need, and thus 59 monitoring stations have been evenly distributed along typical rivers (Fig. 1).

Data collection

The aquatic hydrological and organism data used in this study were recorded in four hydroecological monitoring surveys

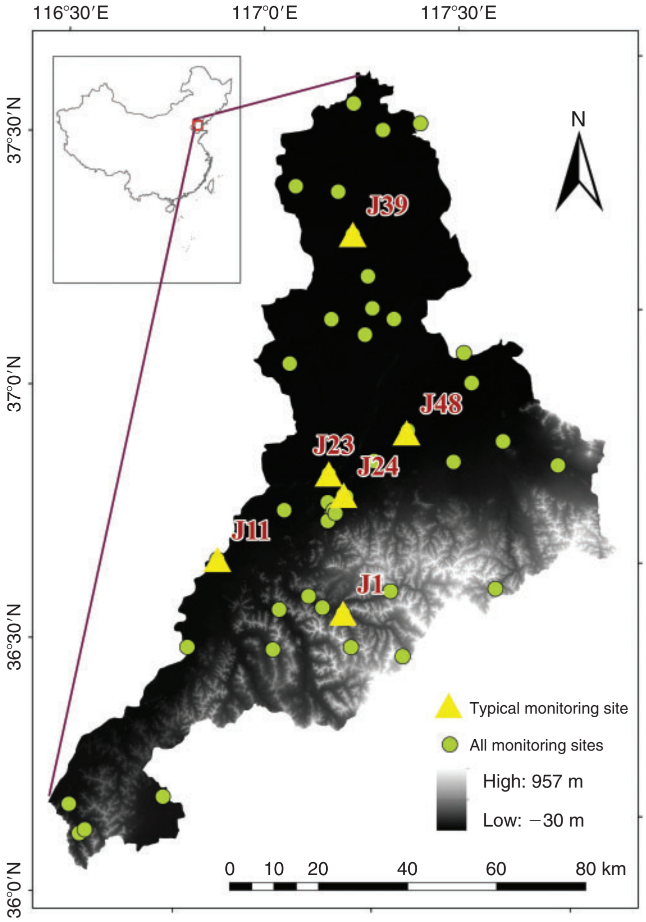

Fig. 1. Map of the study area.

conducted in 2016. Ten representative monitoring stations were selected based on previous studies (Zhao *et al.* 2015*a*, 2015*b*) (shown in Fig. 1), and hydrological parameters, including water depth and flow velocity, were routinely monitored. Flow velocity data were acquired by combining an electric wave current meter (Stalker II SVR V1.0 Applied Concept Inc., see http://stalkersvr.com/) and a traditional current meter (number LS25-1, Nanjing Tiandi Jingye Equipment Co. Ltd, Nanjing, China), thereby guaranteeing the precision of the measured results. Both water depth and river width were measured using tape. Streamflow was calculated using flow velocity and water depth. In addition, phytoplankton, zooplankton, zoobenthos and fish samples were collected at each monitoring station using methods described previously (Zhao *et al.* 2015*b*; Liu *et al.* 2017).

Phytoplankton

For rivers with a depth <2 m, water samples (2 L) were collected at a depth of 0.5 m, and an extra water sample was collected at a deeper layer if the transparency of the water was very low. This water sample was mixed with the superficial water sample to prepare a hybrid sample. For rivers with depths <5 m, five water samples were collected from five water layers (at depths of 10, 20, 40, 80 100%) and a 2-L hybrid water sample was obtained. For rivers with depths >5 m, water samples were collected from the water layers at intervals of 3–6 m, and a smaller volume of water was collected from water layers below the epilimnion. Lugol's solution (30 mL) was added to the water samples in a volumetric proportion of 1.5%.

Zooplankton

A water sampler was used to collect a water sample (20–50 L) from each water layer and a 25-μm plankton net was used to filter the water samples. The organisms collected were stored in a 100-mL plastic bottle. The net was placed in the water with the net mouth exposed above the water, and the net body was then shaken to concentrate the zooplankton to the bottom of the net. The valve on the plastic bottle that was used for collecting organisms was opened to transfer the samples collected into sample bottles; these steps were repeated three to five times. Formaldehyde was added in a volumetric proportion of 5% to fix the collected samples.

Zoobenthos

For mountain streams with depths <30 cm or the shallow zones of rivers, a 60-mesh (0.5 × 0.5 m) Sürber net was used to collect samples. For biotopes with a large depth, a 625 cm^2 Peterson bottom sampler was used to collect samples. A 60-mesh screen was used to rinse the collected bottom mud, and all bottom materials were poured into a white ceramic plate for handpicking until no zoobenthos were observed. All zoobenthos were stored in a 1-L-wide-mouth bottle and 70% alcohol was added to preserve the samples.

Fish

For wadable rivers with depths <1.5 m, an electric fishing apparatus was used to catch fish. During the sampling process, one person held a 20-pipe ultrasonic electric fishing apparatus on their back to catch the fish, whereas another person collected the samples using a dip net. The samples were collected under different conditions in terms of flow velocity and water depth. The sampling time was 30–60 min. For non-wadable rivers with depths >1.5 m, a boat was used to catch the fish by trawling, with a travelling distance not exceeding 100 m between each sampling point. In addition, fish samples were collected from fishermen (if available).

Modelling

This study analysed the hydrological niches of keystone species in the aquatic ecosystem of Jinan City to identify keystone species important for energy flow in the food web of the aquatic ecosystem using the Ecopath food web model EwE software and to determine the optimised hydrological niches for the keystone species in Jinan City using Levins' breadth model.

The Ecopath model is an ecosystem nutritional balance model based on trophodynamics and is used to describe the flow of energy based on the food web structure of an ecosystem (Guesnet *et al.* 2015). This module quantitatively analyses the structure, trophic flow process and trophodynamic characteristics of ecosystems (Liu *et al.* 2007; Coll *et al.* 2015; Halouani *et al.* 2015; Tecchio *et al.* 2015). The Ecopath model has been widely used to analyse the trophic structure and energy flow of aquatic ecosystems and to predict trends in their development, and is recognised as a core new-generation tool for studying aquatic ecosystems worldwide (Christensen and Walters 2004; Sandberg *et al.* 2007; Parrish *et al.* 2012; Deehr *et al.* 2014; Ortiz *et al.* 2015).

The keystone species were identified using the Ecopath model contained in EwE software. The Ecopath-based approach enabled us to use trophic effect and biomass as measurable species traits, and to propose ecosystem-specific thresholds of minimum trophic effect and maximum biomass for a species to be identified as a keystone species (Libralato *et al.* 2006).

The EwE software provides three methods for calculating the degree of significance of the targeted keystone species. The first index (KS_1) was proposed by Libralato *et al.* (2006), the second (KS_2) was adapted from a method proposed by Power *et al.* (1996) and the third (KS_3) was adapted from a method proposed by Valls *et al.* (2015). All indices are estimated based on the same parameters; a measure of trophic impact (ε_i) derived from mixed-trophic impact (MTI) analysis and a measure of biomass (p_i). The ε_i parameter represents the overall effect of Group *i* on all other groups in the food web (without including the effect of the group on itself). According to an analysis of 101 published Ecopath models (Valls *et al.* 2015), the result calculated by KS_3 is more consistent with the definition of keystone species. Therefore, KS_3 was selected in this study to calculate the keystoneness (*KS*) of species by using the following equations (Valls *et al.* 2015):

$$KS = \log(IC \times BC) \tag{1}$$

where *IC* is the impact component and is calculated as follows:

$$IC = \sqrt{\sum_{j \neq i} m_{ij}^2} \tag{2}$$

and *BC* is biomass component and is calculated as follows:

$$BC = drank(B_i) \tag{3}$$

where m_{ij} indicates the MTI of Species *i* versus Species *j* in the food web and can be calculated directly using EwE software, B_i is the biomass of Group *i* and $drank(B_i)$ indicates the descending rank of the biological sequence in terms of biomass.

After identifying keystone species, it is necessary to calculate the ecological niches of aquatic creatures. Many models are available to calculate niche breadth and overlap (Levins 1968; Pianka 1974; Hurlbert 1978; Smith 1982). In this study, we used Levins' (1968) breadth model (Eqn 4) to determine niche breadth.

$$B_i = 1 / \sum_{j=1}^{R} (P_{ij})^2 \tag{4}$$

where B_i is the niche breadth of Species *i*, P_{ij} indicates the ratio of the number of individuals of Species *i* in resource State *j* to the total number of individuals of Species *i* and *R* refers to the total number of resource states (Zhao *et al.* 2012). Resource states stand for gradients along one available resource. Available resources include flow velocity, river width, stream flow and water depth.

Results and discussion

Identification of keystone species

The four hydroecological monitoring surveys in 2016 recorded four ecological communities: (1) 96 species of phytoplankton in 6 phyla, 10 classes, 18 orders, 28 families and 30 genera; (2) 50 species of zooplankton in 4 types, 11 orders, 16 families and 38 genera; (3) 28 species of zoobenthos in 5 classes, 3 orders, 15 families and 19 genera; and (4) 28 species of fishes in 3 phyla, 7 classes, 9 families and 11 genera, as shown in Table 1.

Based on the four community species, and using the method for identifying keystone species by Ecopath (as described above), a set of keystone species in the typical monitoring stations of Jinan City was obtained (Table 2). In all, 35 keystone species were identified. Specifically, there were five keystone taxa of phytoplankton, seven keystone taxa of zooplankton, nine keystone taxa of zoobenthos and fourteen keystone taxa of fishes at the top of the aquatic ecosystem.

With increases in the trophic level, the proportion of keystone species increased; species at a high trophic level in the food web typically have a greater degree of irreplaceability (Peterson. 2011). Among all keystone species, phytoplankton keystone species accounted for 14.29%, zooplankton keystone species accounted for 20.00%, zoobenthos keystone species accounted for 25.71% and fish keystone species accounted for 40.00%. In terms of the food chain relationship, species in the top layer of the food chain play a more important role in the whole food web than species in the bottom layer of the food chain (Krabbenhoft *et al.* 2017), and are closely related to activities, such as the carbon sink, of other species (Kohlbach *et al.* 2017). Therefore, the quantity of keystone species in the corresponding community likely accounts for the higher proportion as the trophic level increases, and carbon is an important factor constraining this structure. Hitchman *et al.* (2018) drew a similar conclusion by studying biotic communities in the Neosho River. Thus, carbon is an important material element that imposes a constraint on the food web structure, and the magnitude of its effect on energy flow determines the degree of importance of keystone species in the food web, which is consistent with other studies. For example, Thorp and Delong (2002) proposed that large river food webs were primarily fuelled by carbon from autochthonous primary production in the main channel and lateral slack waters. Pingram *et al.* (2014) concluded that autochthonous benthic carbon was the major energy source supporting littoral food webs in New Zealand's Waikato River. This is similar to findings of studies from other biomes (for a review, see Pingram *et al.* 2012). Thorp and Bowes (2017) emphasised that sources of carbon influenced animal production rather than overall system metabolism. Above researches are all consistent with our results.

Analysis of hydrological niche

Using Levins' breadth model (Eqn 4), we calculated the niche breadth of the keystone species among the four types of species (phytoplankton, zooplankton, zoobenthos and fish) in

Table 1. Quantities of aquatic organism species

	Class	Number of species		Class	Number of species
Phytoplankton	Bacillariophyta	43	Zoobenthos	Megaloptera	3
	Chlorophyta	29		Odonata	1
	Euglenophyta	7		Gastropoda	8
	Cryptophyta	2		Lamellibranchia	2
	Cyanophyta	14		Oligochaeta	1
	Pyrrophyta	1		Hirudinea	1
Zooplankton	Protozoon	12		Malacostraca	3
	Rotifer	23	Fish	Cyprinidae	19
	Cladocerans	8		Gobiidae	2
	Copepod	7		Cobitidae	3
Zoobenthos	Ephemeroptera	1		Belontiidae	1
	Plicipenna	2		Synbranchidae	1
	Diptera	6		Oryziatidae	1

Table 2. Set of keystone species in typical monitoring stations in Jinan City

Type	Keystone species
Phytoplankton	*Navicula*, *Nitzschia*, *Chroococcus*, *Synedra ulna* and *Scenedesmus quadricauda*
Zooplankton	*Brachionus calyciflorus* (Pallas), *Branchionus leydign*, *Brachionus diversicornis*, *Brachionus urceus*, *Phryganella nidulus*, *Phryganella hemisphaerica* and *Epiphanes senta*
Zoobenthos	*Polypedilum nubifer* (Skuse), *Turritella terebra linnaeus*, *Radix ovata*, Chinese white prawn, *Hippeutis umbilicalis* (Benson), *Assiminea* sp., *Hydrobiidae*, *Radix auricularia* and *Limnodrilus claparedeianus* (Ratzel)
Fish	*Opsariichthys bidens*, crucian carp, *Pseudorasbora parva*, *Hemiculter leucisculus* (Basilewsky), loach, *Mastacembelus aculeatus*, *Abbottina rivularis*, *Cobitis sinensis*, *Ophiocephalus argus* (Cantor), *Paramisgurnus dabryanus*, *Saurogobio dabryi*, *Oryzias latipes*, *Rhodeus lighti* and *Sinibrama wui*

Table 3. Niche breadth of five keystone species of phytoplankton in the gradients of four hydrological factors (flow velocity, river width, stream flow and water depth)

Phylum	Species	Flow velocity	River width	Streamflow	Water depth	Mean niche breadth	Rank
Bacillariophyta	*Navicula*	1.622	1.758	1.167	1.730	1.569	4
	Nitzschia	1.658	2.165	1.466	2.155	1.861	1
	Synedra ulna	2.139	1.668	1.632	1.230	1.667	3
Cyanophyta	*Chroococcus*	2.407	1.237	1.021	1.228	1.473	5
Chlorophyta	*Scenedesmus quadricauda*	1.963	1.419	1.067	2.743	1.798	2
	Mean niche breadth	1.958	1.650	1.271	1.817		
	Rank	1	3	4	2		

the gradients of four hydrological factors (flow velocity, river width, stream flow and water depth), as shown in Tables 2–5.

Phytoplankton

Among the five keystone species of phytoplankton, *Nitzschia* showed the largest mean niche breadth (1.861), indicating strong adaptability. This species showed the maximum niche breadth (2.165) in the gradient of river width and minimum niche breadth (1.466) in the gradient of streamflow. In addition, the rank of its niche breadth in the gradient of water depth was far higher than that in the gradient of flow velocity, indicating that the survival of *Nitzschia* has a more stringent requirement for flow velocity than for water depth (Grüss *et al.* 2015). *Chroococcus* showed the smallest mean niche breadth (1.473), indicating weak adaptability to environmental changes in its habitats. Among the five species of phytoplankton, *Chroococcus* showed the largest niche breadth in the gradient of flow velocity, but the smallest niche breadth in the gradients of river width, stream flow and water depth (Table 3), indicating the strongest adaptability to changes in flow velocity but weak

Table 4. Niche breadth of seven keystone species of zooplankton in the gradients of four hydrological factors (flow velocity, river width, stream flow and water depth)

Species	Flow velocity	River width	Streamflow	Water depth	Mean niche breadth	Rank
Brachionus calyciflorus (Pallas)	1.010	2.311	1.826	1.946	1.774	1
Branchionus leydign	1.009	1.000	1.000	1.302	1.078	6
Brachionus diversicornis	1.471	1.471	1.000	1.471	1.353	4
Brachionus urceus	1.405	1.049	1.000	1.307	1.190	5
Phryganella nidulus	1.240	1.000	1.000	2.552	1.448	3
Phryganella hemisphaerica	2.486	1.220	1.000	1.411	1.529	2
Epiphanes senta	1.000	1.000	1.000	1.000	1.000	7
Mean niche breadth	1.375	1.293	1.118	1.570		
Rank	2	3	4	1		

Table 5. Niche breadth of nine keystone species of zoobenthos in the gradients of four hydrological factors (flow velocity, river width, stream flow and water depth)

Species	Flow velocity	River width	Streamflow	Water depth	Mean niche breadth	Rank
Polypedilum nubifer (Skuse)	1.560	1.000	1.000	1.000	1.140	7
Turritella terebra (Linnaeus)	1.551	1.000	1.000	1.000	1.138	8
Radix ovata	2.172	2.849	2.000	3.336	2.589	1
Chinese white prawn	1.223	1.107	1.114	1.188	1.158	5
Hippeutis umbilicalis (Benson)	1.198	1.198	1.000	1.198	1.149	6
Assiminea sp.	1.194	1.000	1.000	1.925	1.280	4
Hydrobiidae	1.489	1.169	1.106	1.462	1.306	3
Radix auricularia	1.000	1.000	1.000	1.000	1.000	9
Limnodrilus claparedeianus (Ratzel)	1.461	1.318	1.000	1.502	1.320	2
Mean niche breadth	1.428	1.293	1.136	1.512		
Rank	2	3	4	1		

adaptability to changes in river width, stream flow and water depth, similar to findings for algae in north-west Spain (Sanmiguel *et al.* 2016).

At the phylum level, *Navicula*, *Nitzschia* and *S. ulna* belong to the Bacillariophyta, *Chroococcus* belongs to Cyanophyta and *Quadricauda* belongs to Chlorophyta. In the gradient of flow velocity, the niche breadth of Cyanophyta and Chlorophyta was larger than that of Bacillariophyta; this is consistent with the conclusions of Xia *et al.* (2014), who studied the ancient canal of Zhenjiang. However, in the gradients of river width and streamflow, the niche breadth of Cyanophyta and Chlorophyta was fairly small. In the gradient of water depth, the niche breadth of Chlorophyta was the largest, whereas the niche of breadth of Cyanophyta was the smallest. Overall, the five keystone species of phytoplankton showed the largest niche breadth (1.958) in the gradient of flow velocity but the smallest niche breadth (1.271) in the gradient of streamflow, indicating that they have the most stringent requirement for streamflow, but a fairly flexible requirement for flow velocity.

A study in Argentina by Garciá de Emiliani (1993) suggested that stream flow in the flood and drought seasons has a marked effect on phytoplankton species. This is in agreement with the findings of this study in that the five keystone phytoplankton species showed the smallest niche breadth in the gradient of low quantity. In a study of the hydrological niche of riverine phytoplankton, Descy (1993) and Qu *et al.* (2018) obtained similar results to those of the present study, namely that water discharge itself may produce changes in the physiochemical condition, thus affecting phytoplankton communities. A smaller niche breadth of phytoplankton in the gradient of streamflow is associated with weaker adaptability to changes in stream flow, indicating that stream flow variation has amore significant effect on phytoplankton species.

Zooplankton

As shown in Table 4, among the seven keystone species of zooplankton, *B. calyciflorus* (Pallas) has the largest mean niche breadth (1.774), indicating strong adaptability. In the gradients of river width, stream flow and water depth, *B, calyciflorus* (Pallas) showed a large niche width (with a maximum niche breadth (2.311) in the gradient of river width). However, among the seven keystone species of zooplankton, *B. calyciflorus* (Pallas) has a small niche breadth (1.010) in the gradient of flow velocity. This indicates that except for changes in flow velocity, *B. calyciflorus* (Pallas) is strongly adaptable to changes in river width, stream flow and water depth. Among the seven keystone species of zooplankton, *E. senta* has the smallest mean niche breadth (1.000) and always had the smallest niche breadth (1.000) in the gradients of flow velocity, river width, stream flow and water depth, indicating weak adaptability to environmental changes of its habitat. In the gradient of flow velocity, the niche breadth of *P. hemisphaerica* was significantly larger than that of other species, whereas the niche breadth of *P. nidulus* was significantly larger in the gradient of water depth than that of other species. This indicates that these two species have strong adaptability to flow velocity and water depth respectively.

Overall, the seven keystone species of zooplankton have a large niche breadth in the gradients of water depth, flow velocity and river width (mean 1.570, 1.375 and 1.293 respectively), but a small mean niche breadth (1.118) in the gradient of streamflow. This indicates that these species have a stringent requirement for streamflow, but a fairly flexible requirement for water depth, flow velocity and river width.

Within individual rivers, zooplankton biomass has been inversely correlated with discharge (Pace *et al.* 1992; Thorp *et al.* 1994). A study by Zheng *et al.* (2014) showed that water depth is a dominant factor affecting the distribution of zooplankton. However, our study showed that the seven keystone species of zooplankton have a large niche breadth and the strongest adaptability to changes in water depth. This discrepancy may be related to the differences in the geophysical characteristics of the study areas. A study by Bolduc *et al.* (2016) revealed an increase in submerged aquatic vegetation with increased streamflow; the increase in submerged aquatic vegetation significantly affected the community structure and functional diversity of zooplankton in aquatic ecosystems, and thus zooplankton communities are quite sensitive to streamflow. The niche breadth of zooplankton is low in the gradient of streamflow, indicating weak adaptability to changes in streamflow. Therefore, streamflow is an important hydrological factor affecting zooplankton communities.

Zoobenthos

As shown in Table 5,among the nine keystone species of zoobenthos, *R. ovate* has the largest mean niche breadth (2.589) and consistently showed the largest niche breadth in the gradients of four hydrological factors. Specifically, this species showed the maximum niche breadth (3.336) in the gradient of water depth, but the minimum niche breadth (2.000) in the gradient of streamflow, indicating strong adaptability to changes in hydrological factors in its habitat. Among the nine keystone species of zoobenthos, *R. auricularia* showed the smallest mean niche breadth (1.000) and consistently showed the smallest niche breadth (1.000) in the gradients of flow velocity, river width, stream flow and water depth, indicating weak adaptability to environmental changes in its habitats.

Overall, the nine keystone species of zoobenthos had a large mean niche breadth in the gradients of water depth, flow velocity and river width (1.512, 1.428 and 1.293 respectively). In contrast, the nine keystone species of zoobenthos had the smallest niche breadth (mean: 1.136) in the gradient of streamflow, indicating that they have a stringent requirement for streamflow but a fairly flexible requirement for flow velocity, river width and water depth. Similar findings were reported by Zhao *et al.* (2017), who studied zoobenthos in Jinan City. In a study of the hydrological niche of zoobenthos in Rybinsk Reservoir, Skalskaya *et al.* (2008) found that snails have the largest niche breadth and strongest environmental adaptability, which is similar to the results of the present study. Streamflow is an important hydrological factor affecting zoobenthos communities.

Fish

As shown in Table 6, among the 14 keystone species of fish, *H. leucisculus* (Basilewsky) had the largest mean niche breadth (2.182) and consistently showed the largest niche breadth in the gradients of four hydrological factors. Specifically, this species had the maximum niche breadth in the gradient of flow velocity (3.444), but the minimum niche breadth in the gradient of water depth (1.736), indicating strong adaptability to changes in hydrological factors in its habitat. Among the 14 keystone species of fishes, *S. dabryi* showed the smallest mean niche breadth (1.000) and consistently showed the smallest niche breadth (1.000) in the gradients of the four hydrological factors, indicating weak adaptability to environmental changes in its habitats. In the gradient of flow velocity, loach had a larger niche breadth than the 13 other keystone species, indicating strong adaptability to changes in flow velocity.

Overall, the 14 keystone species showed a maximum mean niche breadth in the gradient of flow velocity (2.285), but a minimum mean niche breadth in the gradient of stream flow (1.107). This indicates that these species have a stringent requirement for streamflow, are insensitive to changes in flow velocity and have strong adaptability to variations in flow velocity.

A study by Delong *et al.* (2011) showed that dam construction causes a decline in the peak flow and aggravates seasonal low flow in the river way, leading to a decreased niche breadth of fishes. This demonstrates that fishes have a stringent requirement for stream flow in their habitats. In a morphological analysis of fishes, Wang *et al.* (2015) studied the evolution of the hydrological niche of fishes in Yangtze River and found that flow velocity and streamflow play very important roles in fish morphology. A study by Muir *et al.* (2016) revealed that water depth is very important in fish diversity, which is in agreement with the results of the present study. However, the results of this study showed that fishes are strongly adaptable to changes in flow velocity and that flow velocity is not the most important factor affecting fish. Studies by Karatayev *et al.* (2005), Carpenter *et al.* (2011) and Wenger *et al.* (2011) showed that flow velocity is a dominant factor affecting the structure of the fish community. The differences in results are most likely because our study was conducted when a river was at its normal water level. Compared with the flood season, the flow velocity in the period that river is at normal water level in the study area shows low spatial variation. Our results indicate that flow velocity has little effect on fish. With spatial variation in river width and water depth, streamflow increases spatial variation and becomes the most important hydrological factor affecting fish communities. An excessive amplitude of variation in streamflow adversely affects normal evolution of the four fish communities. This reveals that the survey season and spatiotemporal scale affect the results of hydrological niche analysis. To reduce these effects, it is necessary to conduct larger-scale

Table 6. Niche breadth of 14 keystone species of fishes in the gradients of four hydrological factors (flow velocity, river width, stream flow and water depth)

Species	Flow velocity	River width	Streamflow	Water depth	Mean niche breadth	Rank
Opsariichthys bidens	2.632	1.000	1.000	1.000	1.408	10
Crucian carp	2.078	1.200	1.012	1.526	1.454	8
Pseudorasbora parva	2.264	1.017	1.009	1.072	1.341	11
Hemiculter leucisculus (Basilewsky)	3.444	1.754	1.792	1.736	2.182	1
Loach	3.476	1.365	1.335	1.490	1.917	2
Mastacembelus aculeatus	2.766	1.000	1.000	1.000	1.442	9
Abbottina rivularis	3.376	1.023	1.023	1.047	1.617	3
Cobitis sinensis	1.568	1.000	1.000	1.000	1.142	12
Ophiocephalus argus (Cantor)	3.049	1.000	1.000	1.000	1.512	5
Paramisgurnus dabryanus	1.960	1.324	1.324	1.324	1.483	7
Saurogobio dabryi	1.000	1.000	1.000	1.000	1.000	14
Oryzias latipes	1.807	1.568	1.000	1.723	1.525	4
Rhodeus lighti	1.571	1.682	1.000	1.682	1.484	6
Sinibrama wui	1.000	1.000	1.000	1.153	1.038	13
Mean niche breadth	2.285	1.210	1.107	1.268		
Rank	1	3	4	2		

surveys, specifically by enlarging the spatial scale and using a temporal scale covering both the dry and flood seasons.

Conclusions

In this study, 35 keystone species were identified. Specifically, 5 keystone species of phytoplankton, 7 keystone species of zooplankton, 9 keystone species of zoobenthos and 14 keystone species of fishes at the top of the aquatic ecosystem were identified. Among the keystone species of phytoplankton, Nitzschiaceae had the largest mean niche width, whereas *Chroococcus* had the smallest mean niche breadth. For the keystone species of zooplankton, *B. calyciflorus* (Pallas) and *E. senta* have the largest and smallest mean niche breadths respectively, whereas of the keystone zoobenthos species, *R. ovata* and *R. auricularia* have the largest and smallest mean niche breadths respectively. For keystone fish species, *H. leucisculus* (Basilewsky) and *S. dabryi* have the largest and smallest mean niche breadths respectively. Overall, the keystone species have minimum niche breadths in the gradient of flow velocity, indicating that flow velocity is crucial to the distribution of such species.

Statement of authorship

C. Zhao and S. Yang designed the study; Y. Zhang performed modelling work and analysed output data; X. Wang, Y. Sun, Z. Wang and Y. Zhang collected data; Y. Gai and Z. Wang performed the meta-analysis; C. Zhao, T. Pan, and Y. Zhang wrote and revised the manuscript.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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References

Berlow, E. L. (1999). Strong effects of weak interactions in ecological communities. *Nature* **398**(6725), 330. doi:10.1038/18672

Bolduc, P., Bertolo, A., and Pinel-Alloul, B. (2016). Does submerged aquatic vegetation shape zooplankton community structure and functional diversity? A test with a shallow fluvial lake system. *Hydrobiologia* **778**(1), 151–165. doi:10.1007/S10750-016-2663-4

Bustamante, R. H., Branch, G. M., and Eekhout, S. (1995). Maintenance of an exceptional intertidal grazer biomass in South Africa: subsidy by subtidal kelps. *Ecology* **76**(7), 2314–2329. doi:10.2307/1941704

Carpenter, S. R., Stanley, E. H., and Vander Zanden, M. J. (2011). State of the world's freshwater ecosystems: physical, chemical, and biological changes. *Annual Review of Environment and Resources* **36**, 75–99. doi:10.1146/ANNUREV-ENVIRON-021810-094524

Chen, Y., and Yin, L. (2008). Community composition and niche change characteristics of dominant species in the wind-breaking and sand-fixing forest, Xinjiang, China. *Journal of Plant Ecology* **32**(5), 1126–1133.

Christensen, V., and Walters, C. J. (2004). Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling* **172**(2–4), 109–139. doi:10.1016/J.ECOLMODEL.2003.09.003

Coll, M., Akoglu, E., Arreguin-Sanchez, F., Fulton, E. A., Gascuel, D., Heymans, J. J., Libralato, S., Mackinson, S., Palomera, I., Piroddi, C., Shannon, L. J., Steenbeek, J., Villasante, S., and Christensen, V. (2015). Modelling dynamic ecosystems: venturing beyond boundaries with the Ecopath approach. *Reviews in Fish Biology and Fisheries* **25**(2), 413–424. doi:10.1007/S11160-015-9386-X

Colléter, M., Valls, A., Guitton, J., Gascuel, D., Pauly, D., and Christensen, V. (2015). Global overview of the applications of the Ecopath with Ecosim modeling approach using the EcoBase models repository. *Ecological Modelling* **302**, 42–53. doi:10.1016/J.ECOLMODEL.2015.01.025

Cui, B., Wang, C., Tao, W., and You, Z. (2009). River channel network design for drought and flood control: A case study of Xiaoqinghe River basin, Jinan City, China. *Journal of Environmental Management* **90**(11), 3675–3686. doi:10.1016/J.JENVMAN.2009.07.010

Deehr, R. A., Luczkovich, J. J., Hart, K. J., Clough, L. M., Johnson, B. J., and Johnson, J. C. (2014). Using stable isotope analysis to validate effective trophic levels from Ecopath models of areas closed and open to shrimp trawling in Core Sound, NC, USA. *Ecological Modelling* **282**, 1–17. doi:10.1016/J.ECOLMODEL.2014.03.005

Delong, M. D., Thorp, J. H., Thoms, M. C., and McIntosh, L. M. (2011). Trophic niche dimensions of fish communities as a function of historical hydrological conditions in a Plains river. *River Systems* **19**(3), 177–187. doi:10.1127/1868-5749/2011/019-0036

Descy, J. P. (1993). Ecology of the phytoplankton of the River Moselle: effects of disturbances on community structure and diversity. *Hydrobiologia* **249**(1–3), 111–116. doi:10.1007/BF00008847

Ding, B., Jin, X., Yu, M., Yu, J., Shen, H., and Wang, Y. (2007). Impact to native species by invaded subaqueous plant *Cabomba caroliniana*. *Oceanologia et Limnologia Sinica* **38**(4), 336–342.

Dudgeon, D. (2010). Prospects for sustaining freshwater biodiversity in the 21st century: linking ecosystem structure and function. *Current Opinion in Environmental Sustainability* **2**(5–6), 422–430. doi:10.1016/J.COSUST.2010.09.001

Garciá de Emiliani, M. O. (1993). Seasonal succession of phytoplankton in a lake of the Paraná River floodplain, Argentina. *Hydrobiologia* **264**(2), 101–114. doi:10.1007/BF00014097

Gilvear, D. J., Heal, K. V., and Stephen, A. (2002). Hydrology and the ecological quality of Scottish river ecosystems. *The Science of the Total Environment* **294**(1–3), 131–159. doi:10.1016/S0048-9697(02)00060-8

Grüss, A., Schirripa, M. J., Chagaris, D., Drexler, M., Simons, J., Verley, P., and Ainsworth, C. H. (2015). Evaluation of the trophic structure of the West Florida Shelf in the 2000s using the ecosystem model OSMOSE. *Journal of Marine Systems* **144**, 30–47. doi:10.1016/J.JMARSYS.2014.11.004

Guesnet, V., Lassalle, G., Chaalali, A., Kearney, K., Saint-Béat, B., Karimi, B., and Lobry, J. (2015). Incorporating food-web parameter uncertainty into Ecopath-derived ecological network indicators. *Ecological Modelling* **313**, 29–40. doi:10.1016/J.ECOLMODEL.2015.05.036

Halouani, G., Gascuel, D., Hattab, T., Lasram, F. B. R., Coll, M., Tsagarakis, K., and Le Loc'h, F. (2015). Fishing impact in Mediterranean ecosystems: an EcoTroph modeling approach. *Journal of Marine Systems* **150**, 22–33. doi:10.1016/J.JMARSYS.2015.05.007

Hitchman, S. M., Mather, M. E., Smith, J. M., and Fencl, J. S. (2018). Identifying keystone habitats with a mosaic approach can improve biodiversity conservation in disturbed ecosystems. *Global Change Biology* **24**(1), 308–321. doi:10.1111/GCB.13846

Hong, Q., Meng, Q., Wang, P., Wang, H., and Liu, R. (2010). Regional aquatic ecological security assessment in Jinan, China. *Aquatic Ecosystem Health & Management* **13**(3), 319–327. doi:10.1080/14634988.2010.502819

Hurlbert, S. H. (1978). The measurement of niche overlap and some relatives. *Ecology* **59**(1), 67–77. doi:10.2307/1936632

Jordán, F. (2001). Seasonal changes in the positional importance of components in the trophic flow network of the Chesapeake Bay. *Journal of Marine Systems* **27**(4), 289–300. doi:10.1016/S0924-7963(00)00074-9

Jordán, F., Takács-Sánta, A., and Molnár, I. (1999). A reliability theoretical quest for keystones. *Oikos* **86**, 453–462. doi:10.2307/3546650

Karatayev, A. Y., Burlakova, L. E., and Dodson, S. I. (2005). Community analysis of Belarusian lakes: relationship of species diversity to morphology, hydrology and land use. *Journal of Plankton Research* **27**(10), 1045–1053. doi:10.1093/PLANKT/FBI072

Kohlbach, D., Schaafsma, F. L., Graeve, M., Lebreton, B., Lange, B. A., David, C., and Flores, H. (2017). Strong linkage of polar cod (*Boreogadus saida*) to sea ice algae-produced carbon: evidence from stomach content, fatty acid and stable isotope analyses. *Progress in Oceanography* **152**, 62–74. doi:10.1016/J.POCEAN.2017.02.003

Krabbenhoft, C. A., Burdett, A. S., and Turner, T. F. (2017). Direct and indirect effects of predatory young-of-year fishes in a dryland river food web. *Freshwater Biology* **62**(8), 1410–1421. doi:10.1111/FWB.12954

Levins, R. (1968). 'Evolution in Changing Environments: Some Theoretical Explorations', 2nd edn. (Princeton University Press: Princeton, NJ, USA.)

Libralato, S., Christensen, V., and Pauly, D. (2006). A method for identifying keystone species in food web models. *Ecological Modelling* **195**(3–4), 153–171. doi:10.1016/J.ECOLMODEL.2005.11.029

Liu, Q. G., Chen, Y., Li, J. L., and Chen, L. Q. (2007). The food web structure and ecosystem properties of a filter-feeding carps dominated deep reservoir ecosystem. *Ecological Modelling* **203**(3–4), 279–289. doi:10.1016/J.ECOLMODEL.2006.11.028

Liu, L., Xu, Z., Yin, X., Li, F., and Dou, T. (2017). Development of a multimetric index based on benthic macroinvertebrates for the assessment of urban stream health in Jinan City, China. *Environmental Monitoring and Assessment* **189**(5), 205–217. doi:10.1007/S10661-017-5920-8

Muir, A. M., Hansen, M. J., Bronte, C. R., and Krueger, C. C. (2016). If Arctic charr *Salvelinus alpinus* is 'the most diverse vertebrate', what is the lake charr *Salvelinus namaycush? Fish and Fisheries* **17**(4), 1194–1207. doi:10.1111/FAF.12114

Okey, T. A., Banks, S., Born, A. F., Bustamante, R. H., Calvopiña, M., Edgar, G. J., Espinoza, E., Farina, J. M., Garske, L. E., Reck, G. K., Salazar, S., Shepherd, S., Toral-Granda, V., and Wallem, P. (2004). A trophic model of a Galápagos subtidal rocky reef for evaluating fisheries and conservation strategies. *Ecological Modelling* **172**(2-4), 383–401. doi:10.1016/J.ECOLMODEL.2003.09.019

Ortiz, M., Berrios, F., Campos, L., Uribe, R., Ramirez, A., Hermosillo-Núñez, B., and Rodriguez-Zaragoza, F. (2015). Mass balanced trophic models and short-term dynamical simulations for benthic ecological systems of Mejillones and Antofagasta bays (SE Pacific): comparative network structure and assessment of human impacts. *Ecological Modelling* **309–310**, 153–162. doi:10.1016/J.ECOLMODEL.2015.04.006

Pace, M. L., Findlay, S. E., and Lints, D. (1992). Zooplankton in advective environments: the Hudson River community and a comparative analysis. *Canadian Journal of Fisheries and Aquatic Sciences* **49**(5), 1060–1069. doi:10.1139/F92-117

Paine, R. T. (1969). A note on trophic complexity and community stability. *American Naturalist* **103**(929), 91–93. doi:10.1086/282586

Parrish, F. A., Howell, E. A., Antonelis, G. A., Iverson, S. J., Littnan, C. L., Parrish, J. D., and Polovina, J. J. (2012). Estimating the carrying capacity of French frigate shoals for the endangered Hawaiian monk seal using Ecopath with Ecosim. *Marine Mammal Science* **28**(3), 522–541. doi:10.1111/J.1748-7692.2011.00502.X

Peterson, A. T. (2011). Ecological niche conservatism: a time-structured review of evidence. *Journal of Biogeography* **38**(5), 817–827. doi:10.1111/J.1365-2699.2010.02456.X

Pianka, E. R. (1974). Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences of the United States of America* **71**(5), 2141–2145. doi:10.1073/PNAS.71.5.2141

Pingram, M. A., Collier, K. J., Hamilton, D. P., David, B. O., and Hicks, B. J. (2012). Carbon sources supporting large river food webs: a review of ecological theories and evidence from stable isotopes. *Freshwater Reviews* **5**(2), 85–103. doi:10.1608/FRJ-5.2.476

Pingram, M. A., Collier, K. J., Hamilton, D. P., Hicks, B. J., and David, B. O. (2014). Spatial and temporal patterns of carbon flow in a temperate, large river food web. *Hydrobiologia* **729**(1), 107–131. doi:10.1007/S10750-012-1408-2

Piraino, S., Fanelli, G., and Boero, F. (2002). Variability of species' roles in marine communities: change of paradigms for conservation priorities. *Marine Biology* **140**(5), 1067–1074. doi:10.1007/S00227-001-0769-2

Power, M. E., Tilman, D., Estes, J. A., Menge, B. A., Bond, W. J., Mills, L. S., and Paine, R. T. (1996). Challenges in the quest for keystones. *Bioscience* **46**(8), 609–620. doi:10.2307/1312990

Qu, Y., Wu, N., Guse, B., and Fohrer, N. (2018). Riverine phytoplankton shifting along a lentic–lotic continuum under hydrological, physiochemical conditions and species dispersal. *The Science of the Total Environment* **619-620**, 1628–1636. doi:10.1016/J.SCITOTENV.2017.10.139

Sandberg, J., Kumblad, L., and Kautsky, U. (2007). Can ECOPATH with ECOSIM enhance models of radionuclide flows in food webs? An example for ^{14}C in a coastal food web in the Baltic Sea. *Journal of Environmental Radioactivity* **92**(2), 96–111. doi:10.1016/J.JENVRAD.2006.09.010

Sanmiguel, A., Blanco, S., Álvarez-Blanco, I., Cejudo-Figueiras, C., Escudero, A., Pérez, M. E., and Bécares, E. (2016). Recovery of the algae and macroinvertebrate benthic community after *Didymosphenia geminata* mass growths in Spanish rivers. *Biological Invasions* **18**(5), 1467–1484. doi:10.1007/S10530-016-1095-4

Shannon, G., McKenna, M. F., Angeloni, L. M., Crooks, K. R., Fristrup, K. M., Brown, E., and McFarland, S. (2016). A synthesis of two decades of research documenting the effects of noise on wildlife. *Biological Reviews of the Cambridge Philosophical Society* **91**(4), 982–1005. doi:10.1111/BRV.12207

Skalskaya, I. A., Bakanov, A. I., and Flerov, B. A. (2008). Study on zooperiphyton and zoobenthos of a small river. *Inland Water Biology* **1**(1), 84–92. doi:10.1007/S12212-008-1013-2

Smith, E. (1982). Niche breadth, resource availability, and inference. *Ecology* **63**(6), 1675–1681. doi:10.2307/1940109

Solé, R. V., and Montoya, J. M. (2001). Complexity and fragility in ecological networks. *Proceedings of the Royal Society of London – B. Biological Sciences* **268**(1480), 2039–2045. doi:10.1098/RSPB.2001.1767

Tecchio, S., Rius, A. T., Dauvin, J. C., Lobry, J., Lassalle, G., Morin, J., and Niquil, N. (2015). The mosaic of habitats of the Seine estuary: insights from food-web modelling and network analysis. *Ecological Modelling* **312**, 91–101. doi:10.1016/J.ECOLMODEL.2015.05.026

Thorp, J. H., and Bowes, R. E. (2017). Carbon sources in riverine food webs: new evidence from amino acid isotope techniques. *Ecosystems* **20**(5), 1029–1041. doi:10.1007/S10021-016-0091-Y

Thorp, J. H., and Delong, M. D. (2002). Dominance of autochthonous autotrophic carbon in food webs of heterotrophic rivers. *Oikos* **96**(3), 543–550. doi:10.1034/J.1600-0706.2002.960315.X

Thorp, J. H., Black, A. R., Haag, K. H., and Wehr, J. D. (1994). Zooplankton assemblages in the Ohio River: seasonal, tributary, and navigation dam effects. *Canadian Journal of Fisheries and Aquatic Sciences* **51**(7), 1634–1643. doi:10.1139/F94-164

Tilman, D., May, R. M., Lehman, C. L., and Nowak, M. A. (1994). Habitat destruction and the extinction debt. *Nature* **371**(6492), 65. doi:10.1038/371065A0

Valls, A., Coll, M., and Christensen, V. (2015). Keystone species: toward an operational concept for marine biodiversity conservation. *Ecological Monographs* **85**(1), 29–47. doi:10.1890/14-0306.1

Wang, M., Liu, F., Lin, P., Yang, S., and Liu, H. (2015). Evolutionary dynamics of ecological niche in three *Rhinogobio* fishes from the upper Yangtze River inferred from morphological traits. *Ecology and Evolution* **5**(3), 567–577. doi:10.1002/ECE3.1386

Wenger, S. J., Isaak, D. J., Luce, C. H., Neville, H. M., Fausch, K. D., Dunham, J. B., and Hamlet, A. F. (2011). Flow regime, temperature, and biotic interactions drive differential declines of trout species under climate change. *Proceedings of the National Academy of Sciences of the United States of America* **108**(34), 14175–14180. doi:10.1073/PNAS.1103097108

Western, D. (1987). Africa's elephants and rhinos: flagships in crisis. *Trends in Ecology & Evolution* **2**(11), 343–346. doi:10.1016/0169-5347(87)90112-1

Wootton, J. T. (1994). The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics* **25**(1), 443–466. doi:10.1146/ANNUREV.ES.25.110194.002303

Wootton, J. T., Parker, M. S., and Power, M. E. (1996). Effects of disturbance on river food webs. *Science* **273**(5281), 1558–1561. doi:10.1126/SCIENCE.273.5281.1558

Xia, T., Chen, J., Cao, F. Y., and Gao, J. F. (2014). Niche analysis of phytoplankton in an urban river connected with the Yangtze River, Zhenjiang, China. *Resources & Environment in the Yangtze Basin* **23**(3), 344–350. doi:10.1870/CJLYZYYHJ201403006

Zhang, J., Zhao, H., Zhang, T., and Zhao, X. (2003). Niche dynamics of main populations of plants communities in the restoring succession process in Horqin Sandy Land. *Acta Ecologica Sinica* **23**(12), 2741–2746. doi:10.3321/J.ISSN:1000-0933.2003.12.030

Zhang, W., Zhang, X., Li, L., and Zhang, Z. (2007). Urban forest in Jinan City: distribution, classification and ecological significance. *Catena* **69**(1), 44–50. doi:10.1016/J.CATENA.2006.04.021

Zhao, C., Liu, C., Xia, J., Zhang, Y., Yu, Q., and Eamus, D. (2012). Recognition of key regions for restoration of phytoplankton communities in the Huai River Basin, China. *Journal of Hydrology* **420–421**, 292–300. doi:10.1016/J.JHYDROL.2011.12.016

Zhao, C. S., Yang, S. T., Liu, C. M., Dou, T. W., Yang, Z. L., Yang, Z. Y., and Mitrovic, S. M. (2015*a*). Linking hydrologic, physical and chemical habitat environments for the potential assessment of fish community rehabilitation in a developing city. *Journal of Hydrology* **523**, 384–397. doi:10.1016/J.JHYDROL.2015.01.067

Zhao, C. S., Yang, S. T., Xiang, H., Liu, C. M., Zhang, H. T., Yang, Z. L., and Lim, R. P. (2015*b*). Hydrologic and water-quality rehabilitation of environments for suitable fish habitat. *Journal of Hydrology* **530**, 799–814. doi:10.1016/J.JHYDROL.2015.10.031

Zhao, C. S., Yang, S. T., Zhang, H. T., Liu, C. M., Sun, Y., Yang, Z. L., Zhang, Y., Dong, B. E., and Lim, R. P. (2017). Coupling habitat suitability and ecosystem health with AEHRA to estimate E-flows under intensive human activities. *Journal of Hydrology* **551**, 470–483. doi:10.1016/J.JHYDROL.2017.05.047

Zheng, T., Lin, Y., Cao, W., Zhang, W., Zheng, L., Wang, Y., and Yang, W. (2014). Ecosystem structure and function in northern Beibu Gulf. II. Quantitative distribution and dominant species of zooplankton. *Acta Oceanologica Sinica* **36**(4), 82–90. doi:10.5846/STXB20121119162

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