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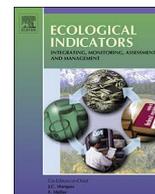
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## Research paper

# Factors determining zooplankton assemblage difference among a man-made lake, connecting canals, and the water-origin river



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## ABSTRACT

Zooplankton play an important role in the pelagic food web as a mediator of nutrient and energy fluxes. Understanding factors determining zooplankton abundance, composition, and dispersal provides information needed for improving plankton dynamic predictions and enhancing effective water resource management and biodiversity conservation. We studied zooplankton dispersal and identified factors influence zooplankton composition and abundance under a unique *in situ* environment with four connected water types from the natural river to a man-made main canal, then interior canal-web, and finally lake that have different flow regimes. We found that, after seven years creation of the water system and zooplankton community development, the main canal, interior canal-web, and lake had 53%–64% zooplankton taxa similar to their water origin river but that each water type was represented and dominated by different zooplankton taxa. Our optimal model identified three key local factors that affected the difference in zooplankton abundance and composition among the four water types: Chlorophyll *a* concentration, turbidity, and salinity. We concluded that both zooplankton dispersal through watercourse and species sorting by local factors were important for structuring communities in our study system. Since most studies on dispersal and influence of local factors on zooplankton assemblages in new environment have been done largely in temporal ponds, our findings provide unique insights on how zooplankton communities are jointly regulated by their species dispersal origins and local environmental factors in newly created canals and lakes.

## 1. Introduction

Zooplankton communities play an important role in the function of aquatic ecosystems by providing linkages in food webs through consuming primary and small secondary production and providing food to higher trophic consumers (Capriulo et al., 2002; Sotton et al., 2014; Turner, 2004). Zooplankton are sensitive to changes in aquatic environment and have been suggested to be good biological indicators for water quality, lake trophic state, and types of water mass (Bays and Crisman, 1983; Gannon and Stemberger, 1978; Pagès et al., 2001). The effects of environmental variation can be detected through changes in species composition and abundance.

It is well recognized in ecology that biological assemblages,

including zooplankton, can be explained by a traditional niche-based paradigm (Drake, 1990) that predicts the match between species and their environment or species responses to both abiotic physicochemical factors and biotic competition and predation (Amarasekare, 2002; Cottenie and De Meester, 2004; Louette et al., 2008; Shurin and Allen, 2001). This combination of processes can be seen as initial exclusion of species that are unable to tolerate the abiotic environment (e.g., environmental filtering), followed by the operation of assembly rules (e.g., biotic filtering; Goberna et al., 2014; Keddy, 1992). For example, Cottenie et al. (2003) reported that local environmental constraints could be strong enough to structure local zooplankton communities among highly interconnected ponds. Zhao et al. (2017) found that zooplankton community structure was correlated to both local

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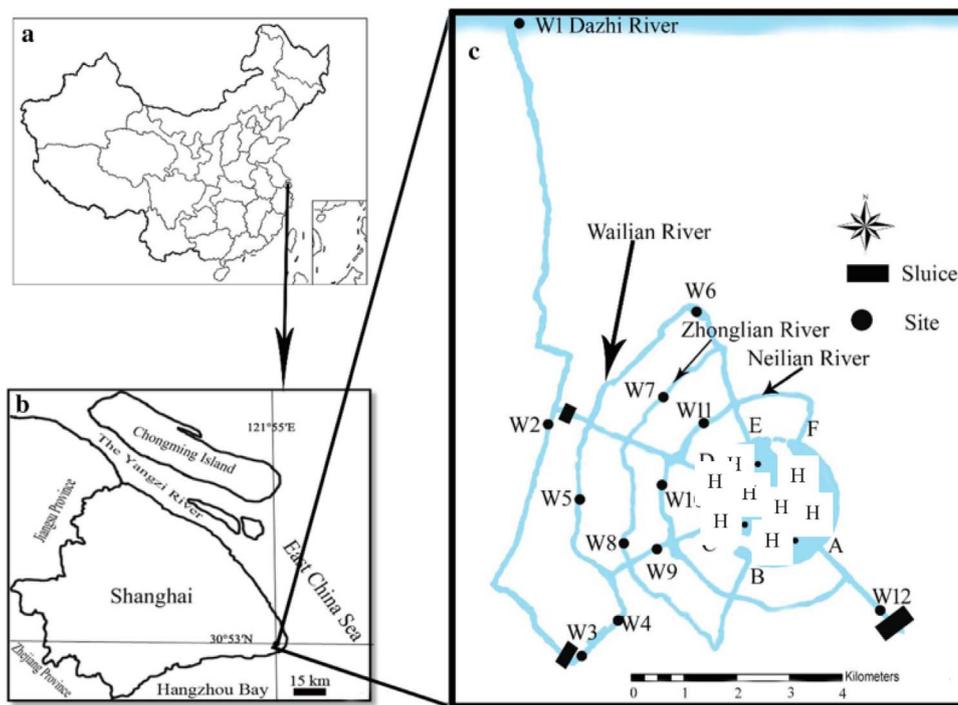


Fig. 1. Map of China showing the location of Lake Dishui (a); Lake Dishui and its surroundings (b); and locations of the sampling sites in Lake Dishui and connecting canals (c).

environmental factors and spatial process, of which zooplankton community variation was best explained by local environment in the dry season while spatial factors were significant in the wet season. These findings imply that zooplankton assemblages are influenced by both temporal variation of local conditions and spatial gradients of environment among different types of waters, resulting in a set of dominant species best suited to thrive in the selective forces of environment. Hence, understanding how zooplankton assemblages vary according to temporal and spatial variations of environmental conditions will improve the prediction of zooplankton population dynamics and detection of environmental degradation or improvement (Jeppesen et al., 2011).

Effects of abiotic and biotic factors on zooplankton communities have been well documented. Abiotic factors driving variation in zooplankton communities among rivers and lakes include water chemistry (e.g., nutrient concentration, pH, conductivity, salinity, and turbidity; Jeppesen et al., 2003; Peck et al., 2015), hydrodynamics (e.g., current, waves, water turnover; Chen and Chen, 2017; Lacroix and Lescher-Moutoué, 1995; Li et al., 2017), thermal regime (e.g., temperature fluctuation and duration; Havens et al., 2015; Šorf et al., 2015), and water body type (e.g., lentic, lotic, semi-lotic; Basu and Pick, 1996; Walks and Cyr, 2004). Biotic driving forces can be both bottom-up factors involving natural productivity and resource limitation and top-down factors including resource competition and predator-prey interactions (Carpenter et al., 1985; Hulot et al., 2014; McQueen et al., 1989).

These abiotic and biotic drivers are often distinctive between lentic and lotic systems, which makes it relatively easy to identify key factors influencing zooplankton community structure between lakes and rivers. Studies have shown that current velocity and water residence time is of greater importance to planktonic community development in rivers than in lakes (Basu and Pick, 1996; Pace et al., 1992). Mean river zooplankton biomass was low compared to lakes of similar chlorophyll *a* concentration (Basu and Pick, 1996). It is generally considered that zooplankton dynamics in lentic systems are predictable and driven predominantly by biological process (Sommer et al., 1986), whereas zooplankton dynamics in lotic systems are largely driven by physical processes dictated by hydrological conditions (Lair, 2006).

In contrast, these abiotic and biotic drivers for semi-lotic systems are less well understood. Because hydrological characteristics of semi-

lotic systems are between lentic and lotic environments, it can be assumed that the abiotic and biotic drivers are less variable and indistinctive than between lentic and lotic systems, which makes it challenging to clearly define the difference in their effects on zooplankton. It is even more challenging to generalize the driving forces determining zooplankton communities for river-lake connecting canals because their hydrological settings could vary anywhere along the gradient between rivers and lakes.

Biological colonization theory suggests that successful zooplankton colonization in a new habitat depends on both the arrival of the species and subsequent successful settlement in the habitat (Caley and Schluter, 1997; Louette et al., 2008). Studies testing this theory are largely carried out under the condition of newly created temporal ponds (e.g., Frisch et al., 2012; Frisch and Green, 2007; Louette et al., 2008). For example, successful colonization depended on newly arrived species interactions with local abiotic and biotic conditions (Louette et al., 2008; Shurin and Allen, 2001). Studies of zooplankton colonization and controlling factors under the conditions of newly created canals and lakes are rare.

Lake Dishui, located in the vicinity of Shanghai, China, is a man-made shallow coastal lake fed by water from the Dazhi River through a nest of connecting canals that were created and connected with water origin in October 2003. Such a man-made lake and surrounding canals provide an ideal environment to test the biological colonization theory. Answering the question of how zooplankton communities have colonized in such a lake and its connecting canals after seven years of their creation not only improves our understanding of the biological colonization processes, but also provides insights on zooplankton dispersal capacity and controlling mechanisms for the development of strategies and measures for conserving species diversity under environmental change (e.g., human disturbance and climate change).

The objectives of this study were to: (1) compare the difference in zooplankton communities along a gradient of conditions from lotic to lentic and from natural to man-made (from dispersal origin natural river, man-made connecting canals, to man-made shallow lake) seven years after creation of the canal-lake water system, and (2) identify the main factors that contributed to the differences in zooplankton community composition and dispersal mechanisms among the different types of connected water bodies.

## 2. Methods

### 2.1. Study area

Lake Dishui (30°53'N, 121°55'E) and its connecting canals are a man-made water system located in the southeast of Shanghai, China (Fig. 1), developed for flood control and tourist attraction. The lake and its connecting canals were constructed and filled with water from the Dazhi River in October of 2003. The water originates from the Dazhi River, a tributary of the Huangpu River, then flows to the main canal and through a system of radiated and parallel canals to the lake. The lake was constructed on an inning beach with the bottom covered by clay. The middle part of the water system consists of three semi-circular canals that are parallel to each other and to one side of the circular lake. The parallel canals are connected to the lake by five connecting canals radiating out from the lake to the outermost parallel canal to form an interior canal-web. The outermost parallel canal is connected to an 18-km long and 25-m wide main canal through two (each with a discharge control structure) of the five radiating canals. The lake water, linked to the middle parallel connecting canal, flows out through a flow control structure directly to the East China Sea (Fig. 1). The sea water level change has no effect on the Lake Dishui system because of its water control structure at the outlet. The circular Lake Dishui has a surface area of 5.66 km<sup>2</sup>, mean depth of 3.7 m, and maximum depth 6.2 m.

The Lake Dishui system is located in a subtropical region with a humid and semi-humid monsoon climate. For this region, the annual average air temperature is 15.6 °C with the lowest temperature about –5 °C in January and highest temperature about 37 °C in July. Mean annual precipitation is 1061 mm, with 70% of annual precipitation occurring from May to September. For descriptive purpose, we divided the Lake Dishui system into the lake itself (Fig. 1, H1-H8), the interior system including the five radiating canals, the three parallel canals (Fig. 1, W3-W11) and outlet (Fig. 1, W12), the exterior system including the main canal (Fig. 1, W2), and finally water origin—the Dazhi River (Fig. 1, W1).

### 2.2. Sampling and measurement procedures

We sampled 8 sites in Lake Dishui and 12 sites in the surrounding canals and the river (Fig. 1). Sampling was carried out monthly on calm days (wind < 5 km/h) from January 2010 to December 2012. Zooplankton were collected from 0.5-m depth below surface at each site. A 5-L water sample was taken from each site and immediately preserved with 1.5% Lugol's iodine solution in the field and then concentrated to 50 ml after sedimentation for 48 h in laboratory. After mixing completely, zooplankton identification was conducted from 1 ml of the sample counting chamber. This process was repeated 3–5 times. Zooplankton were counted under a light microscope (Nikon ECLIPSE 50i) at 100× magnification. Most samples were identified to species or lowest taxa possible following the keys by Bayly (1992), Koste (1978), Koste and Shiel (1987), and Smirnov and Timms (1983).

To assess the relationship between zooplankton assemblages and environmental variables, we measured *in situ* water quality variables from April to December in 2012 in conjunction with the zooplankton sampling. The measured variables included water temperature, pH, dissolved oxygen, turbidity, salinity, conductivity, total dissolved solids (TDS), total suspended solids (TSS), chlorophyll *a*, chlorides (Cl<sup>–</sup>), sodium (Na<sup>+</sup>), potassium (K<sup>+</sup>), and calcium (Ca<sup>2+</sup>) using a portable multi-parameter probe (SEBAMPS-CHECKER, Germany). At each site, water samples for chemistry analysis were also collected at 0.5-m depth below surface and then sent to laboratory within 24 h for laboratory determination of total phosphorus (TP), total nitrogen (TN), and chemical oxygen demand (COD). The surface current velocity was measured during one sampling event using the floating object method (Gierke, 2002) and was presented (Table 1) to help characterize the flow at each site in the river and canals.

### 2.3. Statistical analysis

To describe zooplankton-environmental relationships, we divided zooplankton community into three broad taxonomic groups: Rotifera, Copepoda and Cladocera (Kruk et al., 2010). Zooplankton community data were square-root transformed to improve their normality before analysis. A combination of hierarchical agglomerative cluster method with an average link was used to identify relatively homogeneous site groups using the Bray–Curtis dissimilarity index (Bray and Curtis, 1957) for detecting zooplankton assemblages along the gradient of environmental factors. The zooplankton community in each group was further characterized using an indicator species analysis to identify species that characterize a site or group of sites (Dufrene and Legendre, 1997). Indicator species were defined as the taxa with  $P < 0.05$ .  $P$  values for all taxa were determined using Monte Carlo permutation tests (1000 times).

Local species diversity pattern is important to explore if it is maintained by spatial process or local environment. We compared taxa similarities among cluster groups on a species-by-species basis. We expressed taxa similarities among cluster groups as percentages of species in common: taxa similarity =  $(n/N) \times 100\%$ , where  $n$  is the number of zooplankton species in common between the pair-wise groups and  $N$  is the total accumulative taxa richness of each pair of groups.

Classification and regression trees (CART) are ideally suited for analysis of complex ecological data. We used CART (Breiman et al., 1984) to identify the most probable factors affecting zooplankton community distribution from the aforementioned environmental variables. The CART algorithm is a binary recursive tree structure that asks only the yes/no questions, so the parent nodes are always divided into two child nodes with searches for all possible variables and all possible values in order to find the best split. The splitting criterion used was the Gini index, a commonly used measure of node purity, with a small value indicates that all records in the node belong to the same category, or else that each record in the node belongs to a different category. The splitting process is continued until the criteria of minimum reduction in Gini index and/or minimum size of a node are satisfied.

All analyses were carried out in R environment (R Development Core Team, 2014), using the packages VEGAN, LABDSV, CARET, E1071, RATTLE, RPART, and RPART.PLOT.

## 3. Results

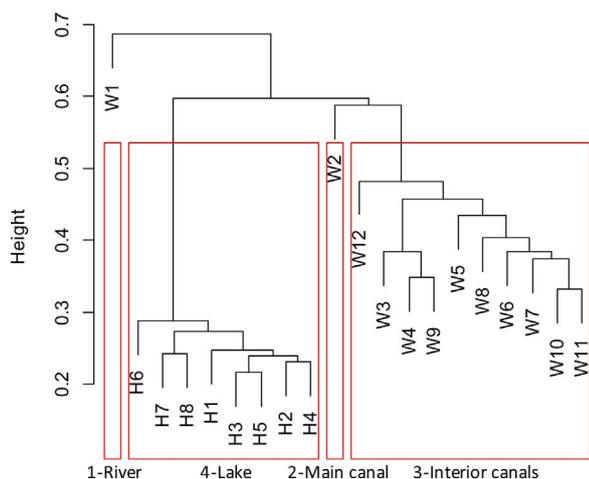
A total of 74 zooplankton taxa were identified, including 60 Rotifera, 7 Copepoda, and 7 Cladocera. The overall mean zooplankton taxa richness was 6 with a range from 0 taxa/site in the lake to 17 taxa/site in interior canals. The overall mean zooplankton abundance was 1652 ind./L with a range from 0 ind./L in the lake to 38,375 ind./L in interior canals. Rotifera abundance accounted for more than 90% of the overall mean of zooplankton abundance. The monthly mean zooplankton taxa richness was highest in June, followed by August, and lowest in December. The monthly mean zooplankton abundance was found highest in May (3204 ind./L), followed by August (2715 ind./L), and least in November (597 ind./L).

### 3.1. Difference in zooplankton assemblages among the lake and connecting canals

Our cluster analysis of zooplankton abundance divided the 20 sampling sites into four site-type groups according to zooplankton community composition (Fig. 2). The first site-type group (1-River) included the site on water origin of the Dazhi River (W1). The second site-type group (2-Main canal) included the site on main canal (W2) that connects river water and the interior water system. The third site-type group (3-Interior canals) included all sites on the interior canals around the lake and outlet of the lake (W3-W12). The last site-type

**Table 1**  
Current velocity at each site in the river and canals from one sampling event.

Site	W1	W2	W3	W4	W5	W6	W7	W8	W9	W10	W11	W12
Velocity (m/s)	0.30	0.14	0.036	0.06	0.05	0.09	0.026	0.01	0.025	0.015	0.016	0.09



**Fig. 2.** Cluster dendrogram of sampling sites based on zooplankton communities of Lake Dishui and surrounding canals (Shanghai, China) from January, 2010 to December, 2012.

group (4-Lake) included all sites on the lake itself (H1–H8). These four groups represent four different sampling site types (hereafter refers to as water types) with a decreasing trend in flow velocity from the river, main canal, interior canals, to the lake (Table 1).

The overall zooplankton abundance, composition and taxa richness varied considerably among the four water types across all sampling years (Fig. 3). The interior canals had the highest and the lake had the lowest zooplankton abundance (Fig. 3a). Three-year site average zooplankton taxa richness was the highest for the river, followed by the interior canals, and lowest for the main canal and lake (Fig. 3b). The zooplankton community was dominated by Rotifera for all four cluster groups (Fig. 3c), and Rotifera abundance accounted for over 87%–99% of zooplankton composition, with lowest value found in the water origin river and highest in the interior canals. In contrast, Copepoda and Cladocera abundances were much lower (2%–13%) and represented a decreasing trend from the river, to the main canal, interior canals, and the lake. The abundances of Copepoda and Cladocera for the site on the river were more than 4 times higher than those for the other sites.

Seasonal variation of Rotifera, Copepoda, and Cladocera abundances also varied considerably among the four water-type groups (Fig. 4). The seasonal and annual abundances of all three zooplankton groups was most variable at the river site, followed by that of main canal site, while those for interior canals and the lake sites varied the least. The differences in abundance between Rotifera and Copepoda or

Cladocera groups were much smaller for river and main canal, but the differences between Rotifera and Copepoda or Cladocera were much larger for interior canals and the lake sites.

Different abundance patterns in zooplankton swim ability were observed among the four water types (Table 2). The relative abundances of stronger swimmers were highest in the river and main canal, followed by interior canals, and lowest in the lake, while the relative abundance of spiraling motion taxa showed an opposite trend. The total accumulative zooplankton taxa richness was highest in interior canals, followed by the lake, and lowest in the river and the main canal.

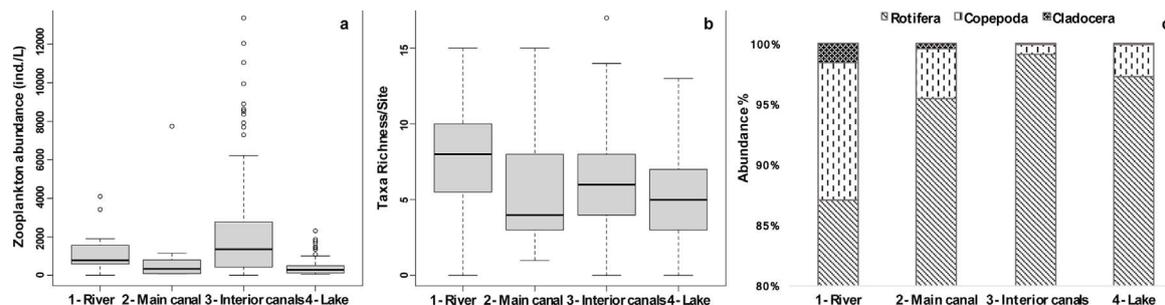
The four water-type groups had different zooplankton indicator taxa (Table 2). Our indicator taxa analysis indicated that the river with relatively fast flow velocity was characterized by *Synchaeta* sp.; the main canal with slower but visible current was characterized by *Brachionus calyciflorus*; the interior canals with unnoticeable current was characterized by *Brachionus urceolaris* and *Enclanlis dilatata*; and the lake was represented by *Brachionus calyciflorus* and *Asplanchna* sp.

The four water-type groups were also dominated by different zooplankton taxa (Table 2). Among the nine dominant taxa identified by our dominant taxa analysis, *Polyarthra trigla* and *Synchaeta* sp. were the only dominant taxa for all the four water-type groups. The relative abundance of *Polyarthra trigla*, a euryhaline taxa, showed a clear decreasing trend from river to lake water types (40.3%–12.7%). In contrast, the relative abundance of *Synchaeta* sp., a good indicator of mesohaline conditions, presented a reverse pattern with the highest relative abundance in the lake water type and lowest in the river (6.9%–27.9%). *Brachionus angularis*, *Brachionus calyciflorus*, and *Filinia longiseta*, good indicators of eutrophic conditions, were dominated in the river, while *Anuraeopsis fissa* and *Trichocerca pusilla*, two oligosaprobic species, were dominant in the main canal, interior canals, and lake.

Taxa similarities were substantially different among the four water-type groups based on pair-wise comparison (Table 3). Taxa in the river and main canal were most similar with 63.5% taxa occurred in both groups. The interior canals were least similar to the river and main canal with about 53% taxa in common with both groups. The zooplankton taxa in the lake were intermediately similar to those in the river, main canal, and interior canals with 59% taxa in common with river, 57% in common with main canal, and 58% in common with interior canals.

### 3.2. Influence of environmental factors on zooplankton

Several environmental factors varied substantially among the four water-type groups during the study period (Fig. 5). Salinity and its



**Fig. 3.** Zooplankton abundance (a), taxa richness (b), and Relative abundance (c) in each cluster group of Lake Dishui and surrounding canals (Shanghai, China) from January, 2010 to December, 2012.

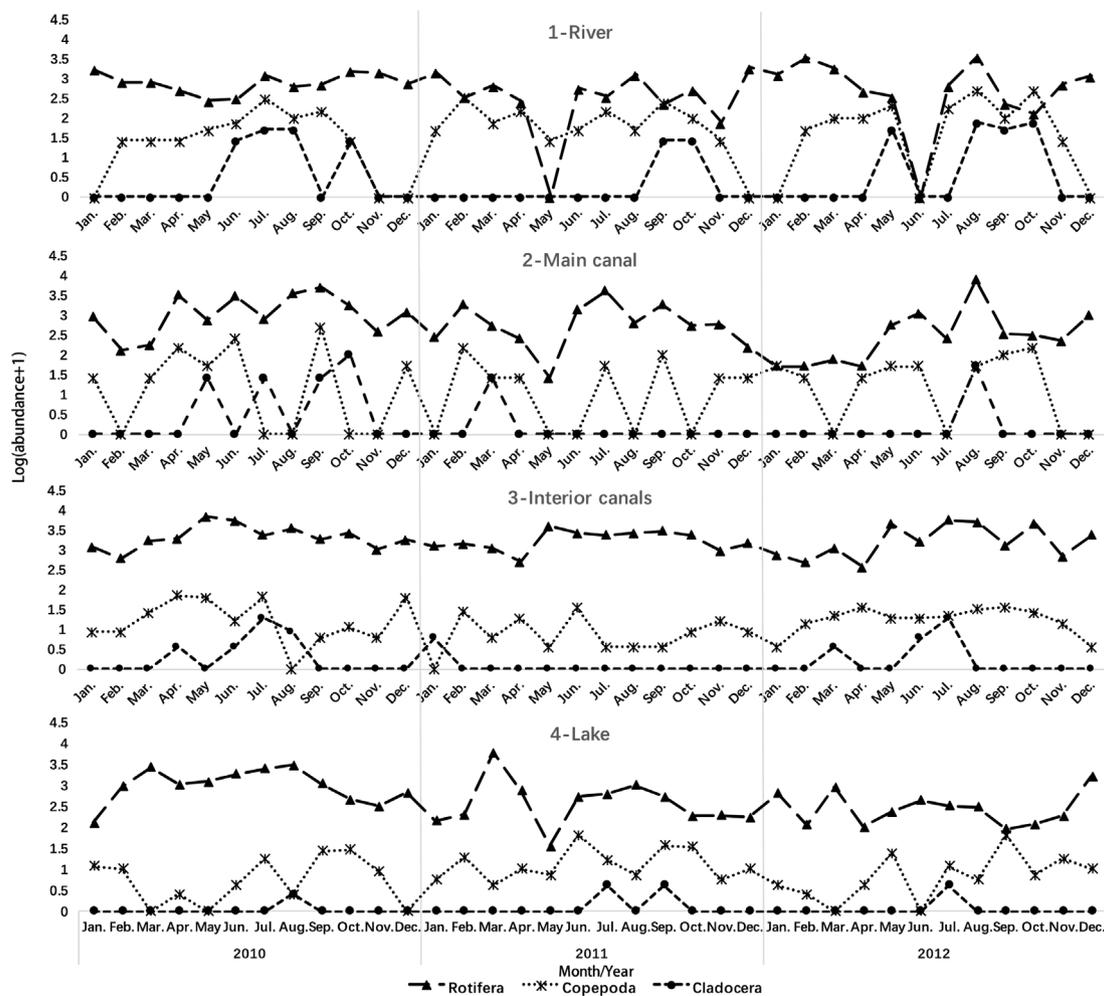


Fig. 4. Seasonal variation of Rotifera, Copepoda, and Cladocera abundances among the four water-type groups.

related measures, such as  $\text{Na}^+$ ,  $\text{Cl}^-$ ,  $\text{K}^+$ , TDS and conductivity, showed an increasing trend from the river, to main canal, interior canals, and the lake. All sampling sites presented alkaline condition with  $\text{pH} > 8$ . pH values and dissolved oxygen in the lake and interior canals were higher than those in the river and main canal, while  $\text{Ca}^{2+}$  concentration showed a reversed trend. The concentrations of TN, TP, COD, TSS, and turbidity in the river were much higher than those in other water-type groups. Chlorophyll *a* concentration was the highest in the interior canals.

The distribution patterns of zooplankton community seemed associated with several key environmental factors (Fig. 6). Our optimal classification tree (*i.e.*, lowest misclassification error rate [0.1379], highest percentage of communities identified) identified key environmental factors influencing zooplankton distribution among the four water-type groups using all environmental variables in Fig. 5 as predictors. The optimal CART model partitioned groups first by chlorophyll *a*, then by turbidity, and finally by salinity. Chlorophyll *a* was the best single predictor and the most important discriminatory variable (first binary partition) in the optimal CART model. This partition separated interior canals that had the most abundant zooplankton from the lake that had the lowest zooplankton abundance. Turbidity split the river where the site had the lowest Rotifera and highest Copepoda abundances from interior canals where the sites had the highest Rotifera and lowest Copepoda abundances (Fig. 6). Salinity partitioned the main canal from the lake with the most abundant mesohaline indicated taxa.

#### 4. Discussion

We studied biological community dispersal and colonization patterns by comparing zooplankton community abundance, composition, and taxa similarity among four connected water types with descending flow velocity from the water origin river through a series of canals to the lake. The newly created main canal, interior canals, and lake had 53%–64% zooplankton taxa similar to their water origin river, although each water type was represented and dominated by different zooplankton taxa after seven years creation of the water system and zooplankton community development. These results imply that both zooplankton dispersal through watercourse and species sorting by local factors were important in structuring zooplankton communities in our study system. Our results corroborate previous findings that species sorting is very efficient in a system with high dispersal rates (Cottenie and De Meester, 2004) and establishment success of inoculated species from the regional species pool is relatively low in established communities (Shurin, 2000; Vanschoenwinkel et al., 2008).

Our results indicate that relatively active dispersal zooplankton (able to jump) are more dominant in flowing water environments (*i.e.*, the river and main canal), while more passively dispersing zooplankton (*e.g.*, spiral motion) dominate in slower moving and lentic water conditions (*i.e.*, the interior canals and lake). Our results also imply that flowing water supports relatively more abundant Copepoda and Cladocera than lentic condition. These findings support the hypothesis that zooplankton community composition and species dominance in lotic-lentic connected waters are largely shaped by local species sorting processes such that local conditions may favor certain species due to

**Table 2**

Overall average of zooplankton relative abundance in swim ability, dominant taxa, and indicator taxa in each water-type group. Taxa richness: total accumulative zooplankton taxa richness of all sites in the group; #: dominant taxa in the group; \* & \*\*: indicator taxa, \* $p < 0.05$ , \*\* $p < 0.01$ ; -: not detected in the group.

Item	Category	1-River	2-Main canal	3-Interior canals	4-Lake
Motion type(%)	Spiral	42.26	48.03	70.60	80.56
	Jump	45.89	47.28	26.20	17.96
	Stroke	1.26	0.54	2.48	0.03
	Combine jump with others	10.60	4.15	0.72	1.44
Taxa richness		43	42	73	49
Dominant taxa and Indicator taxa (%)	<i>Polyarthra trigla</i>	40.31 <sup>#</sup>	45.98 <sup>#</sup>	22.32 <sup>#</sup>	12.71 <sup>#</sup>
	<i>Synchaeta</i> sp.	6.90 <sup>##</sup>	9.43 <sup>#</sup>	13.54 <sup>#</sup>	27.88 <sup>#</sup>
	<i>Brachionus angularis</i>	7.74 <sup>#</sup>	6.47	1.21	1.17
	<i>Brachionus calyciflorus</i>	6.49 <sup>#</sup>	1.08 <sup>*</sup>	1.71	0.52 <sup>*</sup>
	<i>Filinia longiseta</i>	4.11 <sup>#</sup>	0.7	0.41	1.32
	Copepoda Nauplii	8.79 <sup>#</sup>	2.91	0.54	0.88
	<i>Anuraeopsis fissa</i>	2.65	13.42 <sup>#</sup>	13.30 <sup>#</sup>	7.67 <sup>#</sup>
	<i>Trichocerca pusilla</i>	3.00	7.87 <sup>#</sup>	24.19 <sup>#</sup>	11.67 <sup>#</sup>
	<i>Rhinoglena frontalis</i>	1.05	0.75	4.46	19.10 <sup>#</sup>
	<i>Brachionus urceolaris</i>	1.12	0.49	0.34 <sup>**</sup>	0.14
	<i>Enchlanis dilatata</i>	0.07	0.05	0.11 <sup>*</sup>	–
	<i>Diaphanosoma leuchtenbergianum</i>	0.14	–	0.04 <sup>*</sup>	0.02
	<i>Asplanchna</i> sp.	0.70	0.92	0.47	0.48 <sup>*</sup>

**Table 3**

Zooplankton taxa comparison among the four water-type groups. Values are percent similarities in taxa composition between the paired water-type groups.

	1-River	2-Main canal	3-Interior canals	4-Lake
1-River	1	64%	53%	59%
2-Main canal		1	53%	57%
3-Interior canals			1	58%
4-Lake				1

responses of individual species to environmental heterogeneity (Louette and De Meester, 2005). This finding is consistent with previous studies that suggest zooplankton communities and population in systems with high dispersal rates would be more strongly regulated by local selection processes (De Meester et al., 2002; Havel and Shurin, 2004).

Our findings that zooplankton abundance and taxa richness varied among connected waters with descending flow velocity gradient from the river, to the main canal, interior canals, and lake indicates that flow velocity is a local filter determining zooplankton composition. This finding is consistent with previous studies that flow velocity or water residence time is a driving force determining zooplankton difference among lotic, semi-lotic, and lentic systems. For example, Basu and Pick (1996) studied zooplankton biomass, nutrient concentrations, and water residence time in 31 rivers in Canada and found that water residence time rather than resources limited zooplankton biomass in rivers, while in lakes zooplankton biomass was more related to measures of productivity. Reckendorfer et al. (1999) reported that zooplankton abundance in River Danube, Austria, was strongly associated with water residence time with low flushing rates of inshore habitats acting as storage zones for zooplankton. Baranyi et al. (2002) also found that Danube River floodplain zooplankton abundance was significantly positively related to water residence time.

Our finding that flowing water (i.e., river and main canal) supported relatively more abundance of large-bodied Copepoda and Cladocera than Rotifera is different from previous findings that high water residence time supported more large-bodied zooplankton than Rotifera.

For example, Baranyi et al. (2002) reported that along a water storage gradient in a riverine floodplain system rotifers dominated the zooplankton community during more river-like conditions, while crustaceans dominated the community during more lentic-like conditions. Thorp and Mantovani (2005) compared zooplankton communities from Ohio and St Lawrence Rivers (USA) and reported that crustacean abundances were positively related to the degree of hydrological retention (negatively to current velocities), but rotifer abundance was depressed by current velocities only when river discharge was high. Havel et al. (2009) studied zooplankton communities of Missouri River (USA) and found that Crustacean zooplankton were dominant in the inter-reservoir zone of the river, and their taxonomic composition was similar to regional lakes and reservoirs but Rotifers dominated in the channelized zone of the river.

The difference between these previous findings and ours could be partially due to our slow flowing system where different zooplankton taxa groups can adapt to the limited velocity gradient to some extent, and partially due to potentially prey-predator interactions (Lair, 2006). Our study lake was stocked with high density of filtering feeding carps (personal communication with Lake Dishui administrator) that are known to selectively feed on large zooplankton (Li et al., 2017; Lin et al., 2014). Water clarity is relatively higher in the interior canals and lake than the river, which may have enhanced the predation on large-bodied zooplankton since increased water clarity favors activity of predator fish (Abrahams and Kattenfeld, 1997). The river site had higher turbidity and TSS than the interior canals and lake, which may have reduced predation risk of large zooplankton in the river. Our results suggest that our study system is primarily governed by abiotic factors, primarily flow regime, and secondarily by biological control. The phenomenon of predation effect in reducing relative abundance of large-bodied zooplankton of our interior canals and lake has also been broadly found in many other lentic systems (e.g., Brooks and Dodson, 1965; Chen and Chen, 2017; Christoffersen et al., 1993; O'Brien, 1979; Persson et al., 1996).

Our findings support studies that found zooplankton community composition in lotic-lentic connected waters were largely shaped by the responses of individual species to environmental heterogeneity, such that local conditions may favor specific species (Louette and De Meester, 2005). Our findings are also consistent with studies that showed local selection processes are most important for shaping populations and communities of organisms with high dispersal rates (De Meester et al., 2002; Havel and Shurin, 2004).

Our models identified three key local factors (chlorophyll *a*, turbidity, salinity) that clearly distinguished zooplankton communities among the four study water types, which have also been shown to impact zooplankton composition and abundance in other waters (e.g., Basu and Pick, 1997; Basu and Pick, 1996; Chen and Chen, 2017; Peck et al., 2015). In our study, there was a strong correspondence between phytoplankton (chlorophyll *a*) and zooplankton abundances, but no strong correlation between phytoplankton abundance and TP or TN concentrations. This could be largely due to the higher levels of TSS and turbidity in the river than the other water types. Although the river had high concentrations of TP, TN, and COD, the high TSS and turbidity concentrations could have inhibited the growth of phytoplankton by reducing light penetration at this location. Water clarity and macrophyte abundance increased and water velocity decreased gradually as the water flowed from the river to the main canal, which corresponded to increased abundance of both phytoplankton and zooplankton in the interior canals than the other water types.

Turbidity and salinity were also important factors influencing zooplankton composition and abundance. Salinity has been shown to be one of the important factors driving the heterogeneity of habitats and zooplankton communities (Lucena-Moya and Duggan, 2017; Biancalana et al., 2014; Arora and Mehra, 2009; Heneash et al., 2015). Turbidity has also been shown to affect zooplankton community structure through effects on competition, feeding, growth, age of

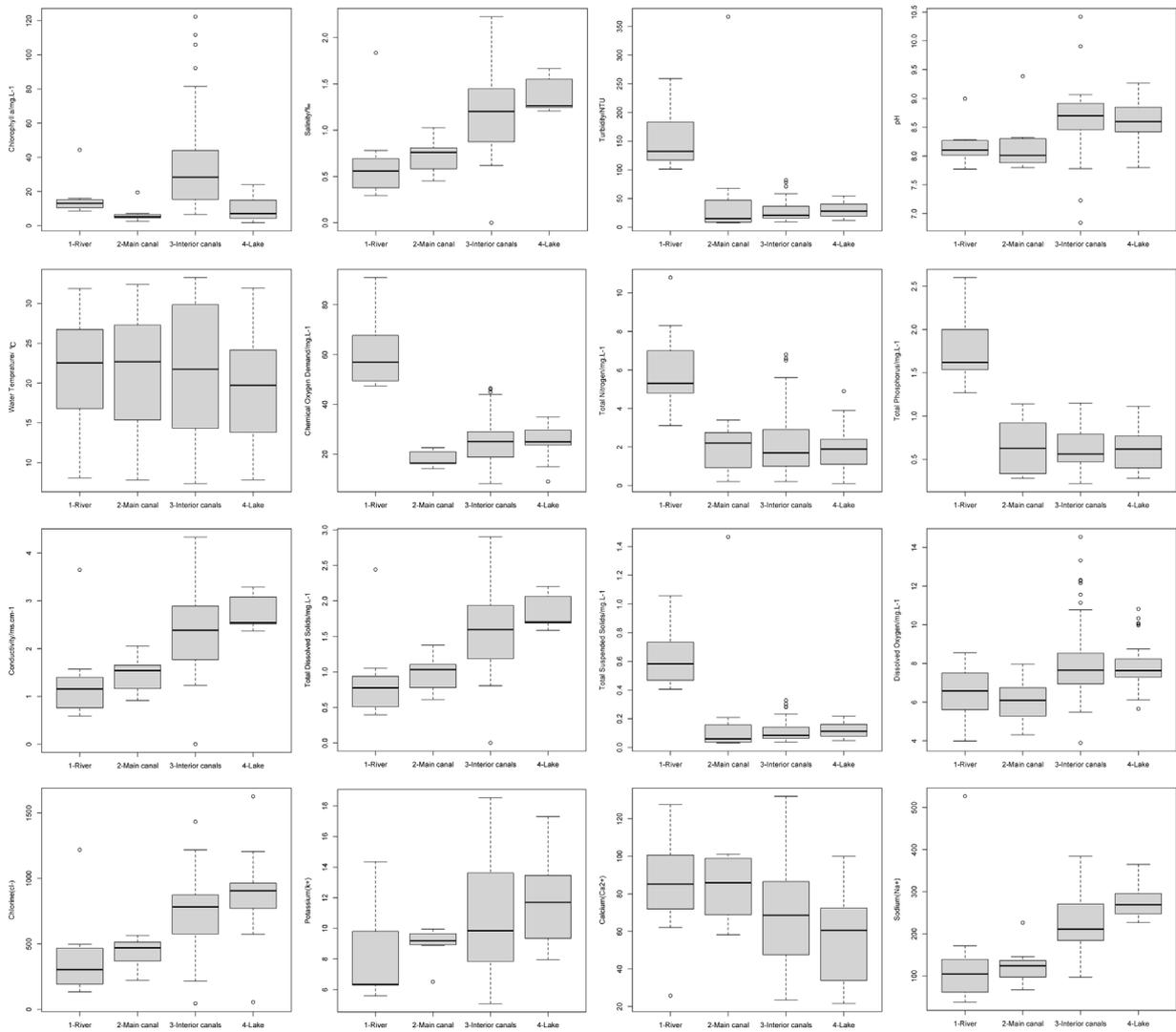


Fig. 5. Boxplot of environmental variables for identifying trends among the four water-type groups.

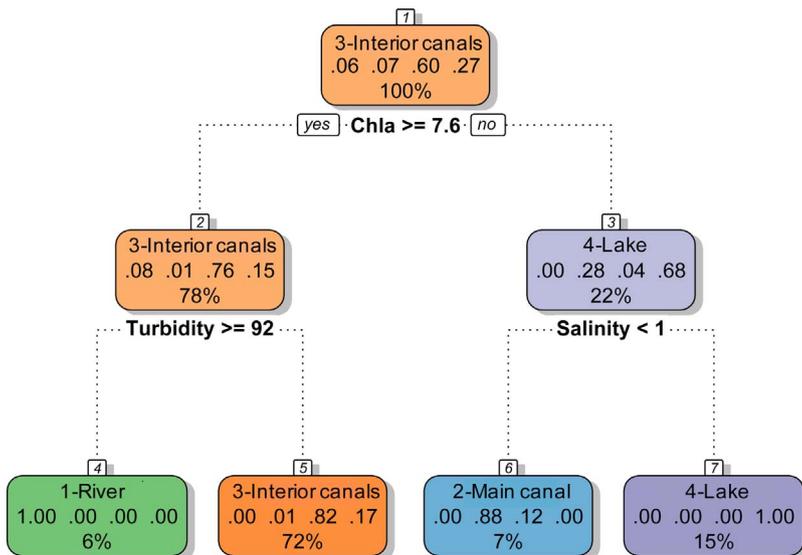


Fig. 6. Classification tree solution for a model identifying key environmental factors influencing zooplankton distribution among the four water-type groups using all environmental variables in Fig. 5. The water-type group in each node indicates the “predicted class”. The numbers below the predicted class are the probabilities of class counts (sum of class counts equal to all observations in this node). The percentage at the bottom of each box presents the proportion of observations accounted for by that node.

maturity, and fecundity (Hart, 1992; Kirk, 1991; Levine et al., 2005). In our study, salinity separated zooplankton communities between the lake and main canal, and turbidity split the river from interior canals. This separation of non-adjacent waters could be a result of that the four studying water types belong to a continuous water flowing system, and the measures of turbidity and salinity change gradually from the river to lake in an opposite direction without clear water boundary separation. Hence, turbidity and salinity can only distinguish water types that are not adjacent to each other.

For our study system, the salinity of the water origin river is near the edge of the range of freshwater (about 0.05%), but salinity increases gradually from the river to the lake with the value up to the lower range of brackish water (0.05–0.2%). One potential reason that may have contributed such salinity change is the study system was constructed on an innig beach. Although there is no tidal sea water influence on the lake, the soil in the beach area may contain high level salt that would raise the salinity content. The lake salinity decrease from 0.32% in 2006 to 0.16% in 2011 (Zhu et al., 2015) supports this speculation. Another potential reason for the high salinity level in our study system is evaporation. The original water from the Dazhi River with the lowest salinity slowly flows through a large area of the main canal (18-km long and 25-m wide), interior canals (total 34-km long and 24-m wide), and lake (5.7 km<sup>2</sup>) ending up with the highest salinity, which would increasingly expose the river water to greater surface area for evaporation.

## 5. Conclusion

We studied zooplankton dispersal and identified factors influencing zooplankton composition and abundance under a unique *in situ* environment with four connected water types in descending flow velocity from the zooplankton-origin river through a system of man-made main canal, and interior canal web, and finally a receiving shallow lake. Our study reveals that zooplankton abundance and community composition are substantially different among the four connected water types after seven years construction of the water system. Zooplankton taxa originated from the source river consist of near half of the taxa in the man-made canals and lake implying direct dispersal from water origin plays a predominant role in establishing zooplankton communities in a new environment. However, the difference in indicator and dominant taxa among study water types indicates that local physicochemical (e.g., turbidity, salinity, nutrients) and biological conditions (e.g., phytoplankton abundance, fish predation) play vital roles in determining zooplankton communities. It is worth mentioning that our study system is in an urban setting and factors not included in our study, such as urban runoff and tourism impacts, may also have influenced the zooplankton community structure.

We concluded that both zooplankton dispersal through watercourse and species sorting by local factors were important for structuring communities in our study system. Since most studies on dispersal and influence of local factors on zooplankton in new environments have been done largely in temporary ponds, our findings provide unique insights on how zooplankton communities are jointly regulated by their species dispersal origins and local environmental factors in newly created canals and lakes.

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