Impact of river-reservoir hybrid system on zooplankton community and river connectivity

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Abstract

Semi-permanent anthropogenic connectivity regulation in rivers, such as via weirs and dams, affects the plankton community. We hypothesised that the longitudinal similarity of the zooplankton community in a river could change in a river-reservoir hybrid system (RRHS). The impact of weir construction on zooplankton communities in terms of species diversity, abundance, and community structure was examined biweekly at six sites on the Nakdong River main channel for 14 years (before construction: 2002–2008; after construction: 2012–2018). We checked time series alignment using dynamic time warping between longitudinal survey sites, regardless of RRHS. Before and after RRHS, the zooplankton community showed an increasing number of species. RRHS decreased the longitudinal connectivity in terms of zooplankton species number and population density. Our study demonstrates that longitudinal zooplankton community trends can be used to study the connectivity of rivers and that longitudinal characteristics are disrupted in RRHSs.

Introduction

Globally, rivers are being transformed from free-flowing reaches into continuous reservoir clusters as lateral barriers are constructed to meet the demand for increasing water consumption. These clusters are known as river-reservoir hybrid systems (RRHSs) (Chang et al., 2003). These changes are part of the efforts to sustain a stable water supply and aquatic ecosystem for growing populations (Chen & Olden, 2017). In addition, RRHSs reduce periodic hydrological disturbances in streams (Takahashi and Nakamura et al., 2011). As RRHSs increase the stability of water bodies, from a human perspective, there is substantial incentive to construct them (Dyson et al., 2003; Tickner et al., 2017).

Discontinuity impacts on rivers by weir construction and damming have been determined. Biological effects from discontinuity of river have focused on both the pre- and post-construction period (Im et al., 2020; Jo et al., 2019). For fish with strong mobility, discontinuity of the river can be overcome via ecological fish pathways (Rourke et al., 2019). Dispersal of aquatic organisms along the continuum of rivers has also been studied (Liu et al., 2013, 2016) and fish, benthic macroinvertebrates, diatoms, and macrophytes, regardless of their mobility, have been used as biotic indices in aquatic ecosystems (Pantle et al., 1955; Woodwis 1964; Gómez et al., 2001; Miller et al., 2006). Recently, zooplankton metacommunities along with spatiotemporal factors of rivers have been studied (Zhao et al., 2017). In the case of run-of-river damming in tropical regions, spatial differences were not observed in the zooplankton community (Souza et al., 2018). Previous studies of the connectivity of rivers using zooplankton have several disadvantages, such as a short investigation periods or a small number of investigations. Due to the characteristics of zooplankton showing an unpatched distribution (Folt and Burns 1999), data interpretation could be biased. Most previous studies analysed the differences in the cluster structure by time between groups, however it can be more reliable to check the connectivity of rivers to determine whether the time series patterns between longitudinal sites are similar. Despite proving a link between zooplankton and environmental factors, there have been few attempts to understand the

state of the aquatic environment with zooplankton itself, similar to other taxonomic groups. In our study, we focused on the characteristics of zooplankton communities.

Zooplankton populations can be maintained in rivers despite them being unable to counteract unidirectional water flow. This is what is known as the drift paradox (Pachepsky et al., 2005). Zooplankton communities in biological gradients are spatiotemporally constructed (Souza et al., 2019). However, RRHSs have properties similar to lakes in terms of periodicity (Chang et al., 2003), and the gradients of the zooplankton community could be disrupted. In other studies, before and after weir construction, native fishes were more sensitive to disturbance than exotic species in RRHSs (Jo et al., 2019), and riverine wetlands used as habitats and refuge for zooplankton also decreased (Im et al., 2020). A cyanobacteria community, a phytoplankton community, was also shown to be affected by weir construction (Malazarte et al., 2017).

Recently, to explain the response of organisms to environmental changes, approaches based on functional groups have been used, rather than based on existing taxon (Kim et al., 2020; Shen et al., 2021). Functionally similar groups respond similarly to environmental changes (Blondel 2003; Violle et al., 2007). South Korea carried out four large national river projects (4LRPs) from 2009 to 2011 (Jo et al., 2019; Im et al., 2020). Although the responses of fish communities and habitats caused by 4LRPs were consistent (Jo et al., 2019; Im et al., 2020), the classical biotic index based on simple population density and species composition, such as Shannon diversity, except for the evenness index, was not suitable for real-population responses (Jo et al., 2019). In plankton communities, species diversity, interactions between species, and surrounding physicochemical factors can cause complicated temporal dynamics (Kim et al., 2020). Therefore, functional grouping using functional traits should also utilise specific traits suitable for environmental changes.

South Korea is in Northeast Asia; it has a distinct summer monsoon and an average annual rainfall of 1,300 mm from 1990 to 2019. However, 54% of the rainfall is concentrated from June to August (<https://www.index.go.kr>; Statistics Korea Government Official Work Conference). Accordingly, over 18,000 reservoirs have been built nationwide to facilitate water use (Kim et al., 2001), and the weirs in large rivers are particularly important for water use in the dry season. Weirs are lateral structures installed on rivers that change the running water ecosystem into a lentic ecosystem (becoming an RRHS) and hinder water flow, which is a core process of the river ecosystem, thus changing the structure of the food webs (Jo et al., 2019). Environmental changes and community changes induced by 4LRPs have been investigated in many studies (Malazarte et al., 2017; Jo et al., 2019; Im et al., 2020). However, there are few studies on the deterioration of the connection between zooplankton communities induced by 4LRPs.

4LRPs widened the width of the target river, increased the water depth, and slowed the flow rate. The predation pressure of the upper predator limited the length of zooplankton individuals and induced them to take refuge (Werner and Hall, 1974; Manatunge et al., 2000). The transformed littoral zone, dredged sediment, and increased water volume can change habitat characteristics (Ko et al., 2020). Various factors need to be considered to understand the changes in zooplankton communities due to RRHS (Kim

et al., 2012; Braun et al., 2021), but understanding all these factors can be challenging. Therefore, considered only two factors: first, the size of plankton, which simultaneously reflects the bottom-up effect leading to water quality-phytoplankton-zooplankton and the top-down effect leading to fish-zooplankton. The main cause of shifts in zooplankton size distribution is the presence or absence of planktivorous fish (Hrbáček et al., 1961; Brooks and Dodson, 1965; Iglesias et al., 2008). To overcome predation pressure, zooplankton use refuges (Choi et al., 2013). Representative refuges are substrates of the littoral zone. Therefore, the second factor was the swimming type (planktonic and epiphytic) that represents these habitat characteristics (Choi et al., 2013; Ko et al., 2020). In addition, the swimming type is suitable for analysing disturbances accompanying changes in flow rates and habitats, such as via RRHS.

This study investigated the changes in zooplankton communities through surveys conducted upstream and downstream of weirs on the Nakdong River, the longest river with the highest density of RRHSs in South Korea. The sites selected had all been monitored since before RRHS construction, rendering them useful for understanding the changes in zooplankton communities caused by RRHS. Specifically, we aimed to 1) confirm how the zooplankton community structure and composition changed before and after RRHS and 2) identify the characteristics that persisted between survey sites despite changes due to RRHS. Through this, we aim to confirm the changes in the zooplankton community ecosystem caused by the semi-controlled aquatic ecosystem represented by RRHS.

Results

Time-series fluctuations of zooplankton

In total, 165 species (SP) were identified, comprising 119 rotifers, 33 cladocerans, and 12 copepods. The average population density (PD) at the six sites was 751.1 ind./L. The SP number and PD fluctuated every year (Figure 1). The continuing river had lower SP number and PD values than the RRHS river (Figure 1). The average SP number collected before (9.5 ± 0.6) and after (10.2 ± 0.4) the RRHS construction was similar; however, the average PD increased by more than four times. Specifically, PD increased by 3.9 times for rotifers, 8.7 times for cladocerans, and 10.2 times for copepods. RRHS impacted zooplankton community composition. In the lotic Nakdong River, 137 SP were identified. In the RRHS Nakdong River, 104 SP were identified. In detail, there were 22 new species of zooplankton; overall, the SP number decreased by 33. The most common species were *Polyarthra vulgaris*, *Keratella cochlearis*, and *Synchaeta* sp..

As a result of the elbow method to determine the optimal number of clusters, zooplankton species were classified into three groups according to their length and swimming type (Table 1). Cluster 1 consisted of large planktonic species. Cluster 2 consisted of small and epiphytic species. Cluster 3 consisted of small and planktonic species.

Table 1
Characteristics of zooplankton community classified according to
length and swimming-type using Elbow method

Category		Cluster 1	Cluster 2	Cluster 3
Species	Rotifers	3	63	53
	Cladocerans	12	10	11
	Copepods	8	2	3
Swimming-type	Planktonic	19	0	67
	Mixing	3	23	0
	Epiphytic	1	52	0
Length(μm)	Minimum	733	50	70
	Maximum	2000	810	700

Although rotifers had the largest proportion of species regardless of RRHS, the SP number and PD ratios of cladocerans and copepods increased after RRHS (Figure 2). Average SP did not show a significant difference ($p = 0.409$), whereas total PD showed a significant difference ($p < 0.001$). Rotifer SP did not show a significant difference ($p = 0.470$). PD of the three taxonomic groups and the SP number of both cladocerans and copepods showed significant differences between pre- and post-4LRPs ($p < 0.001$). After construction, the population density of cladocerans increased relative to that of other taxa (2012–2014), but at the end of the survey, rotifers again dominated. Clusters 2 and 3 occupied most of both SP and PD in a similar proportion (Figure 3). In detail, the SP of Cluster 1 showed a significant difference ($p < 0.001$). The PD of the three clusters showed significant differences between pre- and post-4LRPs ($p < 0.001$). Overall, rotifer-dominant clusters (cluster 1 and cluster 2) did not show significant differences in SP.

Each group showed an increasing trend during both periods. (Table 2). The zooplankton community showed a tendency in the Nakdong River before the disturbance. The SP of large cladocerans showed a significant increase (cladoceran: $p = 0.002$, $Z = 3.050$; cluster 1: $p = 0.041$, $Z = 2.044$). There was also an increase in overall PD (total: $p = 0.048$, $Z = 1.978$), which was affected by small cladocerans and epiphytic species (cladoceran: $p < 0.001$, $Z = 3.506$; cluster 2: $p = 0.023$, $Z = 2.275$). The Nakdong River after RRHS showed more clearly the increase/decrease direction of the zooplankton community compared to the natural state. Overall SP number and PD increased (SP: $p = 0.003$, $Z = 2.989$; PD: $p < 0.001$, $Z = 5.322$). The main groups that affected this were Rotifer (SP: $p < 0.001$, $Z = 4.119$; PD: $p < 0.001$, $Z = 6.710$), cluster 2 (SP: $p < 0.001$, $Z = 4.020$; PD: $p < 0.001$, $Z = 5.430$), and cluster 3 (SP: $p = 0.002$, $Z = 3.106$; PD: $p < 0.001$, $Z = 5.198$).

Table 2
Results of Mann-Kendall trend test

Category		Before RRHS		After RRHS	
		P	Z value	P	Z value
Species	Total	0.259	1.130	0.003	2.989
	Rotifers	0.365	0.905	0.000	4.119
	Cladocerans	0.002	3.050	0.398	-0.845
	Copepods	0.363	0.909	0.061	-1.873
	Cluster 1	0.041	2.044	0.147	-1.450
	Cluster 2	0.509	0.661	0.000	4.020
	Cluster 3	0.196	1.294	0.002	3.106
Population density	Total	0.048	1.978	0.000	5.322
	Rotifers	0.078	1.762	0.000	6.710
	Cladocerans	0.000	3.506	0.267	-1.109
	Copepods	0.445	0.764	0.517	0.648
	Cluster 1	0.122	1.547	0.143	1.467
	Cluster 2	0.023	2.275	0.000	5.430
	Cluster 3	0.062	1.866	0.000	5.198

Time-series Trends And Longitudinal Patterns

The similarity of time series changes of zooplankton communities appearing at the six survey points showed differences before and after RRHS (Figure 4). In the Nakdong River, which has a natural flow, the change in SP according to the flow of water was similar (except for Mulgeum), but after controlling the flow of the water body, the upstream and downstream similarities disappeared. Similarly, PD was randomly arranged with time-series similarities between the longitudinal points from upstream to downstream.

Prior to RRHS, connectivity was evident in SP number and PD of the rotifers as the dominant group. However, after RRHS, all connectivity was disrupted in the taxonomic groups (Figure 5). The functional groups showed different patterns. Regardless of RRHS, SP number was the highest in cluster 3, and PD was the highest in cluster 2. These were the dominant factors in SP (cluster 3) and PD (cluster 2), respectively. In the connected river, the height of cluster 2 with the highest PD showed connectivity for

both SP and PD, but the height of cluster 3 with the highest SP number showed a dendrogram order similar to the upstream and downstream order of only SP.

Discussion

Researchers have conducted many studies to identify and predict changes in ecosystems (Kim et al., 2011; Ko et al., 2020) and used experimental data from the field or laboratory to support their findings. Ecosystem changes are inevitable considering the anthropogenic disturbance of constructing RRHSs. However, if there are insufficient data from before the disturbance, the environmental change cannot be determined. Long-term data are useful for these situations. Our results confirmed that the zooplankton population increased regardless of RRHS. Long-term data of existing uncontrolled ecosystems can be used to evaluate the current natural or anthropogenic ecosystem or predict future ecosystems (Planque et al., 1998). In addition, long-term monitoring is important for the development of empirical academic and management policies because ecosystem changes can be quantified as ecological responses (Lindenmayer and Likens 2009; Lindenmayer et al., 2012; Lovett et al., 2007).

Although long-term data are valuable for identifying ecosystem transitions, it is important to consider which parameters to monitor (Lindenmayer and Likens 2009). To overcome resource and time constraints, using indicator species or groups has been proposed. However, there are many taxa that can be indicators (Lindenmayer and Burgman 2005). Combining taxa into functional groups suitable for the purpose of the specific study has advantages in data interpretation (Ko et al., 2020). In our results, habitat alteration and partial waterflow discontinuity by 4LRPs changed the composition and structure of zooplankton according to the characteristics of each species. If traits corresponding to each species or genus within a taxon suitable for the purpose of the study can be extracted, it may be easy to use an indicator species as a target for long-term monitoring.

A short life cycle and adaptation ability from disturbance are advantages of using zooplankton as indicator species (Gurav and Pejaver 2013; Gutkowska 2013). Assembling zooplankton into functional groups effectively represents the biological components and disturbances of ecology (Krztoń and Kosiba 2020; Ko et al., 2020). In our results, the two selected zooplankton traits were adequate to represent the before-and-after comparison of the 4LRPs. Species-specific functions were as important as taxonomic characteristics in response to environmental changes.

RRHSs reduce periodic hydrological disturbances in streams (Takahashi and Nakamura et al., 2011). RRHS has properties similar to those of lakes in terms of periodicity and plankton dynamics (Chang et al., 2003). Due to the 4LRPs, the Nakdong River had stagnant and volumetrically increased waterbodies. As a result, the suitability of the Nakdong River for zooplankton habitats increased. The overall PD of zooplankton in the Nakdong River showed a stronger trend after the RRHS. In the case of SP, the average SP number had an increasing trend despite decreased accumulated SP, indicating that the connectivity between longitudinal points of the river weakened, meaning that the frequency of occurrence of certain species gradually increased. In conclusion, partially opening a sluice gate or artificial sluice gate control

cannot ensure connectivity between weir sections. A better environment for zooplankton only provides a proliferation opportunity for species that have adapted to it, leading to their dominance.

Zooplankton cannot counteract unidirectional water flow, but populations are still maintained. This is known as the drift paradox (Pachepsky et al., 2005). Our longitudinal survey sites showed similar patterns for both SP number and PD in the natural state of the Nakdong River because of DTW. This may contribute to the similarity of the zooplankton community trend with water flow between the upper and lower rivers. In detail, clusters (taxonomic and functional groups) that dominate at least one of SP and PD represent this connectivity well (Figure 5). This is because, even for long-term sampling, the ecosystem can only be represented by a few generalists among a few generalists and specialists. Naturally, groups with a high PD are more likely to contain have a higher SP number, but this is not guaranteed, which is reflected in the results of time-series similarity between our survey points. The long-term PD and SP trends of Hanam and Namji were the most similar to the average of the Nakdong River. Therefore, the more downstream area, the more useful is the general trend of the zooplankton community in the river. However, Mulgeum, the lowest survey point, could not represent the zooplankton dynamics of the Nakdong River. This is because the area is continuously anthropogenically managed as a water intake source that supplies water to Busan Metropolitan City inhabited by more than 3 million people. Considering such activities in rivers, representative points of river monitoring should be established.

Materials And Methods

Study sites

The Nakdong River is the longest river in South Korea, located in the south-eastern part of the Korean Peninsula in Northeast Asia (length: 525 km; river basin: 23,716.7 km²). The population of the main stream and tributary basin is approximately 10 million (Figure 6). The annual rainfall is 1,200 mm, and it has typical monsoon characteristics, with more than 60% of rainfall concentrated between June and September (Kim et al., 2002). There are two dams, eight weirs, and one estuary bank in the main stream of the Nakdong River, which is equivalent to a large reservoir every 58 km on average. The structure of rivers also changed around 4LRPs. At the most upstream survey point (Waegwan), the average water depth increased from 1.2 to 5.4 m and the river width expanded from 247 to 472 m. At the midpoint of the survey sites (Jukpo), the average water depth increased from 2.5 to 8.1 m, and the river width expanded from 202 to 231 m. At the most downstream point (Mulgeum), the average water depth increased from 5.4 to 8.7 m, and the river width expanded from 251 to 445 m (Jo et al., 2019).

There were six sites in this study (Figure 6). Five sites were points that could be compared up and down the weir (Waegwan-Goryeong, Goryeong-Jukpo, and Namji-Hanam), and four sites were points that can be compared between two consecutive points that exist between RRHS weirs (Jukpo-Namji and Hanam-Mulgeum). The survey was conducted on a bi-weekly basis ($n = 761, 356, 372, 416, 386,$ and 417 , respectively) from 2002 to 2008 (82 months) and 2012 to 2018 (80 months), and the survey data were converted into monthly averages.

Field Survey

Zooplankton samples were collected in 4 or 8 L water samples at 0.5 m depth. The samples were filtered through a 32 µm nylon mesh and preserved in sugar formalin (4% for formaldehyde; Haney and Hall 1973). The zooplankton samples were counted using an optical microscope (Zeiss Axiolab re; Carl Zeiss, Inc.) at x 40–100 magnification in a Sedgwick-Rafter chamber. Zooplankton taxa were identified at the genus or species level, except for nauplii and copepodites (Mizuno and Takahashi 1991; NIER 2016). The zooplankton were categorised by taxon (rotifers, cladocerans, and copepods).

Data analysis

A t-test in SPSS (version 26.0 for Windows; SPSS Inc.) was used to compare the mean of zooplankton community before and after 4LRPs. To examine zooplankton species to the actual ecological status, we performed k-means clustering using both length (µm) and swimming-type (planktonic, epiphytic, and mixing type) data via the elbow method for optimal numbers of clustering using the 'NbClust' package in R 4.1.0. (<http://cran.r-project.org>) (Charrad et al., 2014). For this, nominal data were assigned a number (planktonic: -1, epiphytic: 1, and mixing type: 0), and both factors were standardised and analysed. Mann-Kendall (MK) test was applied to assess the significance of zooplankton community composition trends in average of monthly values of survey sites using the 'trend' package in R (Pohlert et al., 2018). As zooplankton communities are not uniformly distributed (Folt and Burns 1999), a simple and robust MK test is appropriate for analysing our non-parametric data (Gavrilov et al., 2016). Dynamic time warping (DTW) was used to confirm similar pattern changes in the zooplankton community using monthly data from each site in the six sites of the Nakdong River. DTW is a technique of time series alignment that was first applied for spoken word recognition (Sakoe and Chiba 1978). Hierarchical clustering analysis was used to examine the relationship among survey sites along with the RRHS period using Ward's method and Euclidean distance. These analyses were performed using the 'dtwclust' package (Sardá-Espinosa 2017). All analyses were performed using R 4.1.0. software (<http://cran.r-project.org>).

Conclusions

Long-term zooplankton sampling was suitable for confirming that zooplankton communities respond to changes in rivers, even if physicochemical factors are not considered. Large-scale environmental disturbances in rivers, such as 4LRPs, should be thoroughly evaluated before and after construction and managed with constant advice from experts in various fields. Nevertheless, the biodiversity of rivers will be impacted. Although minimising disturbances should be the primary goal, zooplankton can be a useful indicator of river connectivity.

Declarations

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Author contributions

K. E. J.: Conceptualisation, Methodology, Writing – original draft, Writing – review, and editing. J. E.: Formal analysis, investigation, and writing – original draft. D. Y.: Software, Validation, and Methodology. J. G. J.: Conceptualisation and project administration. K. H. W.: Resources, Project administration, Supervision. J. H.: Investigation, Validation, Writing – original draft.

Competing interests statement

The authors declare no competing interests.

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Figures

Figure 1

Monthly variation of zooplankton community before and after the construction of the river-reservoir hybrid system

Figure 2

Taxonomic zooplankton community before and after the construction of the river-reservoir hybrid system

Figure 3

Functional zooplankton community before and after the construction of the river-reservoir hybrid system

Figure 4

Dendrograms of number of species (SP) and population density (PD) in Nakdong River using dynamic time warping. The analysis was performed using the Ward's method and Euclidean distance as the measure of similarity. (Total: overall zooplankton community; 1: average of 6 sites, 2: Mulgeum, 3: Hanam, 4: Namji, 5: Jukpo, 6: Goryeong, and 7: Waegwan).

Figure 5

Detailed dendrograms of the number of species (SP) and population density (PD) in Nakdong River using dynamic time warping. Analysis was performed using the Ward's method and Euclidean distance as the measure of similarity. (1: average of 6 sites, 2: Mulgeum, 3: Hanam, 4: Namji, 5: Jukpo, 6: Goryeong, and 7: Waegwan).

Figure 6

Description of study sites in the Nakdong River. The yellow dots are the study sites, and the red rectangles are the constructed weirs.

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