

Article

Responses of Rotifer Community to Microhabitat Changes Caused by Summer-Concentrated Rainfall in a Shallow Reservoir, South Korea

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Received: 8 March 2020; Accepted: 19 March 2020; Published: 21 March 2020



Abstract: Empirical studies suggest that the structural heterogeneity of aquatic ecosystem microhabitat is determined by the diversity and abundance of macrophytes. However, excessive accumulation of free-floating macrophytes on the water surface can reduce the biomass of submerged macrophytes, resulting in a relatively simplified habitat structure. We hypothesized that heavy summer rainfall disrupts the growth of free-floating macrophytes covering much of the Jangcheok Reservoir's water surface, thereby resulting in a more complex habitat structure by allowing development of a more diverse of macrophytic community. We divided long-term (2008–2017) monitoring data (rainfall, macrophytes, and rotifers) into two groups: Rainy and Dry years, corresponding to years with annual rainfall higher and lower than the total annual average, respectively. We found that summer densities of rotifers fell sharply in Rainy years, but increased continuously in Dry years. This trend resulted in greater autumn densities in Rainy relative to Dry years, which we attributed to changes in habitat related to differential macrophyte development. Moderate disturbance of the water surface caused by high summer rainfall can promote growth of submerged macrophytes by creating large areas of open water and therefore a more complex autumnal microhabitat structure, resulting in seasonal variations in rotifer community structures and populations. Moreover, a highly complex microhabitat structure restricts foraging activity of fish (i.e., *Lepomis macrochirus*) that prey on rotifers. Based on these findings, we suggest that summer-concentrated rainfall plays an important role in supporting the density and species diversity of rotifers.

Keywords: habitat structure; submerged macrophyte; open water area; seasonality; species diversity

1. Introduction

Rainfall in eastern Asia is concentrated in the summer months as a result of the monsoonal climate and typhoon events (mainly June–August; [1,2]). Such a pattern frequently promotes dynamic changes in the spatial and temporal distribution of plankton communities [3,4]. Rainfall can substantially disturb freshwater ecosystems, causing changes in biological community structure through the suppression or loss of taxa, as well as by delaying, arresting, or diverting seasonal succession from its typical pattern [5,6]. Several studies have examined spatio-temporal community variability in environments subjected to hydrological disturbances (e.g., [7,8]), and the role of hydrological disturbance in initiating succession in plankton communities (e.g., [9,10]). Summer rainfall can have negative effects on the spatial and temporal distribution of zooplankton communities in freshwater ecosystems by increasing water discharge and velocity [11–13]. Among zooplankton groups, rotifers are especially affected by physical disturbances such as increased discharge [14,15]. Given the relatively small body size and poor swimming ability of rotifers, they are vulnerable to increases in water discharge caused by summer rainfall [16]. These increases are often sufficient to alter rotifer community structures in freshwater

environments and cause seasonal shifts in rotifer ecology. Therefore, the seasonal distribution of South Korean rotifers, particularly in rivers and streams, would be difficult to explain without considering the influence of summer rainfall.

Aquatic macrophytes act as primary habitat to supporting an abundance of rotifer communities in freshwater ecosystems [17–19]. Therefore, understanding the interaction between aquatic macrophytes and rotifers has become crucial to limnological research, especially in systems abundant in macrophytes. The leaves and stems of submerged macrophytes in particular are more heterogeneous in structure than those of other macrophyte forms (e.g., emergent, free-floating, and floating-leaved), and therefore increase the physical habitat complexity of the aquatic environment [20,21]. Previous studies have indicated that rotifer communities utilize aquatic macrophytes as refuges to avoid physical disturbance such as summer rainfall events. Choi et al. [22] found that aquatic macrophytes in wetlands or shallow reservoirs provide a high level of coverage that can protect rotifer communities from marked changes in water levels and turbulence caused by summer rainfall. Epiphytic rotifers occur in particularly high densities in ecosystems where macrophytes are extensively developed, utilizing the abundant surfaces for attachment [23,24]. Pelagic species also benefit from the presence of macrophytes, which help to minimize disturbance pressures such as predation [25,26].

The summer and autumn dynamics of South Korean freshwater environments are governed by rainfall. South Korea experiences concentrated summer rainfall due to a monsoonal climate and typhoons [1]. Rainfall not only increases water levels in the reservoir, but also is also associated with temporarily low vegetative productivity owing to the persistence of cloudy days. This is in contrast to the spring growing season (between March and June), which is characterized by relatively low rainfall and is therefore the only season during which rotifers can grow. Given the impacts of seasonal weather variations on aquatic community dynamics, we believe that an understanding of changes in freshwater ecosystems in South Korea can be gained by analyzing seasonally changing patterns of rainfall and their associated characteristics (e.g., water level).

To date, comparatively few studies have specifically focused on rotifers, particularly epiphytic species, despite their ecological importance. Consequently, only limited information is available regarding their adaptations to hydrological disturbances. Moreover, rotifer dynamics in eastern Asian regions have not been intensively examined with respect to summer-concentrated rainfall patterns. We speculate that rotifers respond differently to interannual variations in hydrological characteristics (e.g., from summer-concentrated rainfall) and hypothesize that the diversity of rotifer species in shallow reservoirs characterized by a well-developed macrophyte flora may respond to hydrological fluctuations differently than those in other freshwater ecosystems (e.g., river, stream, and lake).

In this study, we sought to elucidate the responses of rotifer communities to changes in microhabitat structure caused by summer-concentrated rainfall, with the aim of advancing our current understanding of the seasonality of rotifers in freshwater ecosystems. In shallow-water ecosystems, where macrophytes are frequently abundant, these species are important in determining biodiversity [27]. The aim of this study was to elucidate (1) changes in rotifer community structure and density in relation to environmental variations, (2) the responses of rotifer predators (i.e., fish), and (3) seasonal changes in microhabitat structure, in relation to summer-concentrated rainfall. We predicted that macrophyte-related changes to microhabitat structure in autumn would affect fish predation as well as rotifer community composition and density. To test this hypothesis, we surveyed the Jangcheok Reservoir in South Korea, which supports a diverse range of macrophyte species. During this long-term study (2008–2017), we investigated the response patterns of rotifers, macrophyte biomass, and fish to seasonal and interannual hydrological fluctuations. We found that summer-concentrated rainfall determines autumn habitat structure (e.g., autumn growth of submerged macrophytes), and strongly influences the seasonality of rotifer communities.

2. Materials and Methods

2.1. Description of Study Site

South Korean freshwater ecosystems are temperate with four distinct seasons, which leads to dynamic succession in biological communities. South Korea annually experiences concentrated summer rainfall due to a monsoonal climate and several typhoons; about 60% of annual rainfall occurs from June to early September [28]. Therefore, summer rainfall plays a key role in determining aquatic organism community structures in freshwater ecosystems. Rainfall increases water levels, either from tributary inputs or occasionally from main river-channel countercurrents. The persistence of cloudy days associated with high levels of summer rainfall can temporarily lower the productivity of the system and lead to a large shift in the community structure that had developed during spring. Therefore, changes in South Korean biological communities can be understood by examining their responses to seasonally changing patterns of rainfall and its derived characters (e.g., water level). The study site (Jangcheok Reservoir; Figure 1) is a riverine reservoir which responds dynamically to changes in rainfall.

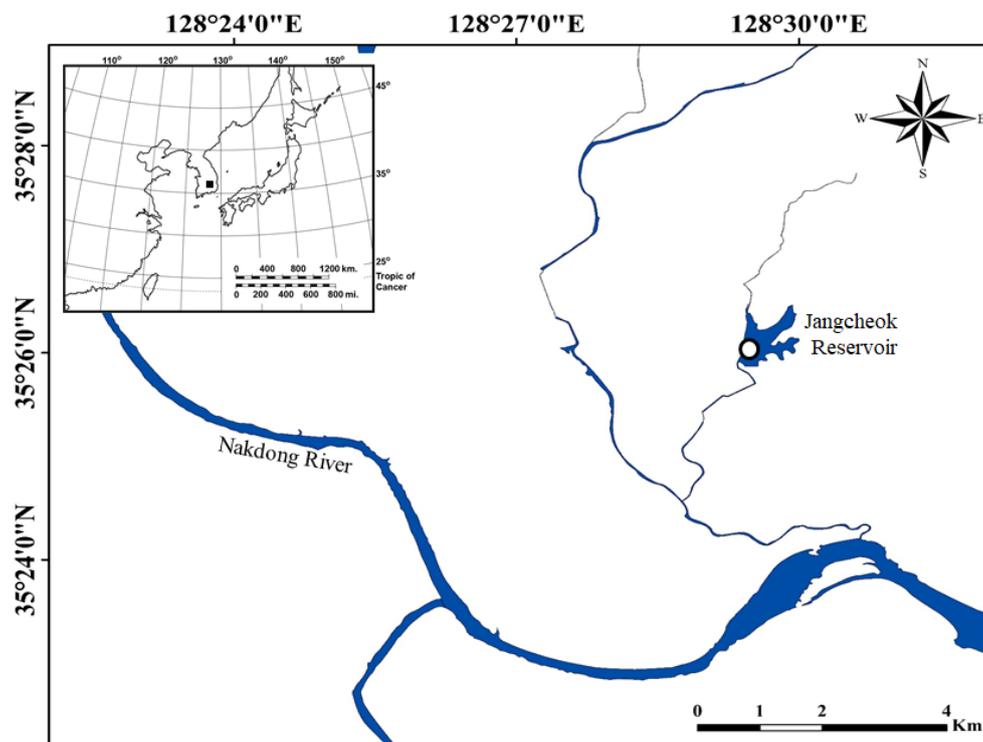


Figure 1. Map of the study sites. The study sites located in southeast South Korea are indicated by solid squares (■). The small map in the upper left-hand corner shows the Korean Peninsula. The map in the upper right-hand corner shows the Jangcheok Reservoir. The sampling points are indicated by open circle (○).

Jangcheok Reservoir is located in southeastern South Korea near the mid to lower reaches of the Nakdong River. The surface water area is 0.5 km², and depth differs between the shoreline and the center of the reservoir. During dry season (winter and spring), the water depth ranges between 0.6 m and 1.2 m (shoreline and center, respectively); depth increases to 0.8 m and 1.4 m at the shoreline and center, respectively, during summer and autumn. The study site is almost completely covered by aquatic macrophytes from spring (May) to autumn (November). In this area, we identified the following eight species of macrophyte: *Phragmites australis*, *Paspalum distichum*, *Zizania latifolia*, *Spirodela polyrhiza*, *Salvinia natans*, *Trapa japonica*, *Ceratophyllum demersum*, and *Hydrilla verticillata*.

2.2. Monitoring Strategy

We conducted monthly monitoring at the study site over a 10-year period from 2008 to 2017. Prior to monitoring, we searched for candidate locations within the reservoir characterized by similar plant species compositions. At the study location, six quadrats (size: 1 m × 1 m) were established for monitoring. Three quadrats were used to monitor environmental variables, rotifers, open water area, and submerged macrophytes. The remaining three quadrats were used to collect fish species (mainly *Lepomis macrochirus*). The quadrats were established at similar depths (average: 0.6–0.7 m).

Environmental variables (water temperature, percent saturation of dissolved oxygen (DO), pH, conductivity, and turbidity) were measured, and rotifers were enumerated using water samples collected from the quadrats. A DO meter (YSI Model 58; Yellow Springs, OH, USA) was used to measure water temperature and DO; conductivity and pH were measured using a conductivity meter (YSI model 152; Yellow Springs, OH, USA) and pH meter (Orion Model 250 A; Orion Research, Beverly, MA, USA), respectively. The water samples were conveyed to the laboratory after sampling to measure turbidity using a turbidimeter (Model 100B; HF Scientific Inc., Ft. Myers, FL, USA).

For rotifer enumeration, we collected 5 L water samples from each quadrat using a 10 L column water sampler (length, 20 cm; width, 30 cm; height 70 cm). The sampler was placed vertically into the water to collect rotifers from the entire water column of the quadrat. The sampled water was filtered through a plankton net (32-mm mesh), and the filtrate was preserved in sugar formalin (final concentration: 4% for formaldehyde; [29]). Rotifer enumeration and identification at the genus level were performed using a microscope (ZEISS, Model Axioskop 40; ×200 magnification), with identification based on the classification key published by Mizuno and Takahachi [30]. The identified rotifers were distinguished as either epiphytic or pelagic species, in accordance with Sakuma et al. [31] and Gyllström et al. [32].

After rotifer collection, we investigated the open water area and submerged macrophyte biomass from each quadrat. We established a virtual grid (20 cm²) over each of the quadrats. The open water area not covered by aquatic macrophytes in each quadrat was measured (m²). The open water area is 1 m². Submerged macrophytes within each quadrat were collected at each sampling time using a core sampler (20 × 20 × 30 cm). Sampling was based on randomly generated numbers in order to avoid bias. The collected macrophytes were dried in the laboratory at 60 °C for 2 days and dry plant weight was estimated for each quadrat.

In order to understand the effect of microhabitat changes resulting from summer-concentrated rainfall on fish predation, we collected fish using a cast net (7 mm × 7 mm) and scoop net (5 mm × 5 mm) in the remaining three quadrats during autumn only (i.e., September–November). The cast net and the scoop net were deployed for 20 min and 10 min, respectively. Each of the collected fish was identified to the species level according to Kim and Park [33], and the classification system of Nelson [34]. The fish assemblage collected from the study site was dominated by *Lepomis macrochirus* (approximately 96%), with other fish species low in density and frequency. Thus, we only used information about *L. macrochirus* for analysis in this study.

2.3. Data Analysis

In order to compare the seasonal and yearly dynamics of rotifers in the reservoir, we obtained rainfall data from the Korea Meteorological Administration (KMA, <http://www.kma.go.kr>), which is collected from Uiryeong Station, the gauging station located closest to the study site. Daily rainfall from the months of June to August was summed (i.e., summer rainfall), and average values were used for comparisons of seasonal and interannual variability. Based on the total summer rainfall, we divided the ten monitored years (2008–2017) into two groups: Rainy years, in which the total rainfall higher than the average; and Dry years, in which total rainfall was less than the average. As the summer rainfall in 2009 was similar to the average rainfall during the study period, we excluded the data for that year from our analysis. Rotifer community structure (i.e., epiphytic and pelagic) data were also divided into two groups corresponding to Dry and Rainy years, and community structural distribution

was assessed. Variations (environmental variables, rotifer community, open water area, submerged macrophytes, and fish) between the two groups were statistically analyzed via one-way ANOVA. Regression analysis was used to examine the following relationships: (i) summer rainfall and area of open water in summer, (ii) area of open water in summer and biomass of submerged macrophytes in autumn, and (iii) autumn biomass of submerged macrophytes and characteristics (density, weight, and body size) of fish species. We assessed linear, exponential, inverse, power, and logistic functions in order to determine an equation generating the curve of best fit. Furthermore, we calculated species diversity (H') of epiphytic and pelagic rotifer according to the following equation [35]: $H' = -\sum P_i \log_2 P_i$ ($P_i = N_i/N$), where N_i is the number of individual organisms of the species, N is the total number of individuals.

We then used non-metric multidimensional scaling (NMDS) to examine seasonal rotifer distribution patterns according to variations (environmental variables, open water area, and submerged macrophytes). The NMDS ordination plots were generated based on Euclidean distance, and goodness of fit was assessed in terms of loss of stress. Each variation was log-transformed after being assessed for normality with the Shapiro–Wilk test. Rare rotifer species showed densities of less than 100 ind. L^{-1} per year; these were excluded from the ordination analysis, leaving 14 species for final analysis. The stress value for the two-dimensional solution was 0.132, which is lower than the generally accepted maximum stress value of < 0.2 [36]. The significance of the fitted vectors was assessed using 3000 permutations, with $p < 0.05$ considered significant. NMDS ordination was conducted with the R package ‘vegan’ (version 2.5–3; [37]).

3. Results

3.1. Rainfall, Environmental Variables, and Rotifer Distribution

Clear interannual variability was observed due to annual rainfall changes (Figure 2). Rainfall was concentrated in the summer (June–August; ca 44% of annual average rainfall), with an average of 589 mm. Rainfall in the other three seasons was much lower. The largest summer rainfall quantity was recorded in 2011 (771 mm), whereas the year 2017 (172 mm) was relatively dry. Based on the total summer rainfall, the years 2008, 2013, 2015, and 2017 were designated as Dry years, with the remaining years (2010, 2011, 2012, 2014, and 2016) designated as Rainy years.

Most of the environmental variables (water temperature, DO, pH, conductivity, and turbidity) showed interannual fluctuations in response to changes in rainfall. Water temperatures were high in summer and low in winter (November–February), while DO, pH, and conductivity showed a contrasting pattern (low in summer and high in winter). Interannual turbidity patterns were relatively irregular. The biomass of submerged macrophytes was the highest in the spring and decreased in the summer each year. Autumnal macrophyte biomass showed interannual variation which was affected by summer rainfall. During the survey period, *C. demersum* and *H. verticillate* were the predominant macrophytic species in study area. The area of open water was high in winter and summer, but relatively low in spring due to the development of aquatic macrophytes. The area of open water also varied with summer rainfall.

Rotifer density exhibited seasonality during the study period, with moderate abundance in spring (March–June), followed by frequent peaks in the summer. Autumn (September–November) rotifer density was generally similar to that of spring; however, in some years autumn density was higher. A total of 21 rotifer species were identified; *Lepadella oblonga*, *Lecane bulla*, and *Philodina roseola* frequently dominated the study site. The rotifer species *L. bulla*, *Lecane hamata*, *Lecane ludwigii*, *Lepadella oblonga*, *Monostyla cornuta*, *P. roseola*, *Testudinella patina*, and *Trichocerca gracilis* were classified as epiphytic, in accordance with Sakuma et al. [31] and Gyllström et al. [32]. The remaining species were classified as pelagic. Throughout the study, the density of epiphytic species was higher than that of pelagic species; however, the two types displayed similar seasonal distribution.

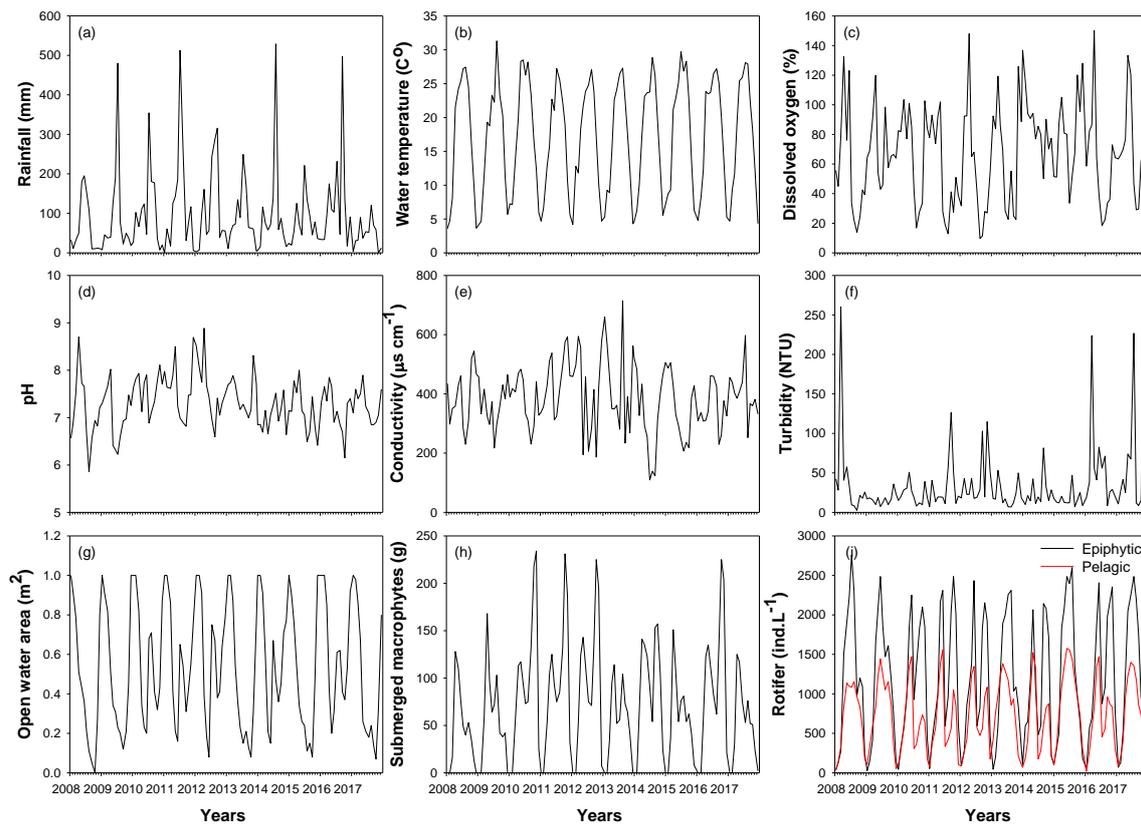


Figure 2. Time-series fluctuations in environmental variables (rainfall, physicochemical factors, open water area, and submerged macrophytes) and rotifers for the study sites in the Jangcheok Reservoirs from 2008-2017. (a) Rainfall, (b) Water temperature, (c) Dissolved oxygen, (d) pH, (e) Conductivity, (f) Turbidity, (g) Open water area, (h) Submerged macrophytes, and (i) Rotifer (epiphytic and pelagic)

We fitted the fourteen dominant rotifer species to NMDS ordination axes and selected four environmental variables that were significantly correlated with those axes ($p < 0.05$; Figure 3). *Brachionus angularis* (Ba), *L. bulla* (Lb), *L. hamata* (Lh), *L. oblonga* (Lo), and *T. patina* (Tp) were frequently found in the autumn of Rainy years, and were associated with higher submerged macrophyte biomass. Rainy years were associated with a high area of open water (OW), summer rainfall (Rainfall), and turbidity (Tur.). A high density of *Mytilina ventalis* (Mv), *Anuraeopsis fissa* (Af), *Euchlanis dilatata* (Ed), *Ploesoma hudsoni* (Ph), *Polyarthra remata* (Por), and *P. roseola* (Pr) were observed in autumn, winter, and spring of Dry years, and were not related to environmental variables. Distributions of *Colurella obtusa* (Co), *Keratella cochlearis* (Kc), and *T. gracilis* (Tg) were relatively irregular.

3.2. Rotifers, Area of Open Water, and Submerged Macrophyte between Dry and Rainy Years

Density and species diversity of both epiphytic and pelagic rotifers showed similar seasonal patterns (Figure 4), with moderately abundant populations in spring (March–May), followed by a tendency to peak in the summer and autumn. Summer (June–August; One-way ANOVA, $df = 1$, $F = 7.735$, $p < 0.01$) and autumn (September–November; One-way ANOVA, $df = 1$, $F = 8.626$, $p < 0.01$) densities of epiphytic rotifers were significantly different in Dry versus Rainy years (Figure 4a and Table 1). Summer density of epiphytic rotifers was higher in Dry years (Dry years: 2502 ind/L; Rainy years: 893 ind/L); however, it declined in the autumn of Dry years to approximately half that of summer. The opposite pattern was observed for epiphytic rotifers in Rainy years, with lower density in the summer and an increase in autumn. A comparison of epiphytic rotifer density between spring and autumn, which are characterized by similar water temperatures, revealed significant differences in Rainy years (one-way ANOVA, $df = 1$, $F = 9.564$, $p < 0.01$), but not in Dry years. Distribution

characteristics of pelagic rotifers were similar to the interannual and seasonal patterns found in epiphytic rotifers; however, the autumn density showed few differences between Dry and Rainy years. Seasonal significant differences for epiphytic and pelagic rotifer were also found in species diversity.

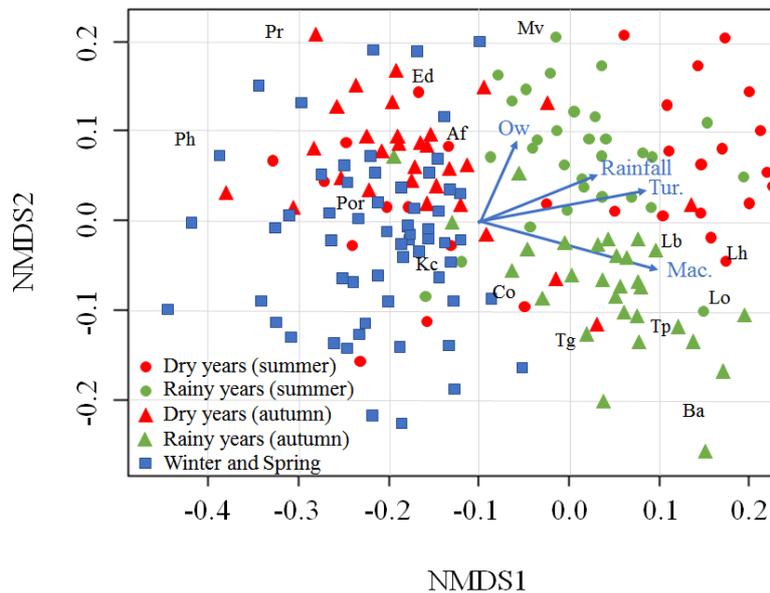


Figure 3. None-metric multidimensional scaling (NMDS) of 14 dominant rotifer species (letters) and 120 sampling time (dots). The blue arrows represent the associations with environmental variables. The sampling times are divided into five time (Dry years in summer, Rainy years in summer, and Dry years in autumn, Rainy years in autumn, and winter and spring). OW, open water area; Rainfall, summer rainfall; Tur. Turbidity; Mac., submerged macrophytes; Af, *Anuraeopsis fissa*; Ba, *Brachionus angularis*; Co, *Colurella obtusa*; Ed, *Euchlanis dilatata*; Kc, *Keratella cochlearis*; Lb, *Lecane bulla*; Lh, *Lecane hamata*; Lo, *Lepadella oblonga*; Mv, *Mytilina ventalis*; Ph, *Ploesoma hudsoni*; Por, *Polyarthra remata*; Pr, *Philodina roseola*; Tg, *Trichocerca gracilis*; Tp, *Testudinella patina*.

Table 1. The results of One-way ANOVA comparing seasonal density and species diversity of epiphytic and pelagic rotifer in Dry versus Rainy years.

Rotifer types	Variables	Seasons	df	F	p
Epiphytic	Density	Spring	1	1.543	0.098
		Summer	1	7.735	<0.01
		Autumn	1	8.626	<0.01
		Winter	1	1.035	0.433
	Diversity	Spring	1	0.865	0.589
		Summer	1	6.642	<0.05
		Autumn	1	8.392	<0.01
		Winter	1	1.322	0.234
Pelagic	Density	Spring	1	1.243	0.267
		Summer	1	8.461	<0.01
		Autumn	1	1.611	0.064
		Winter	1	0.942	0.518
	Diversity	Spring	1	1.043	0.412
		Summer	1	6.822	<0.05
		Autumn	1	1.254	0.251
		Winter	1	1.127	0.343

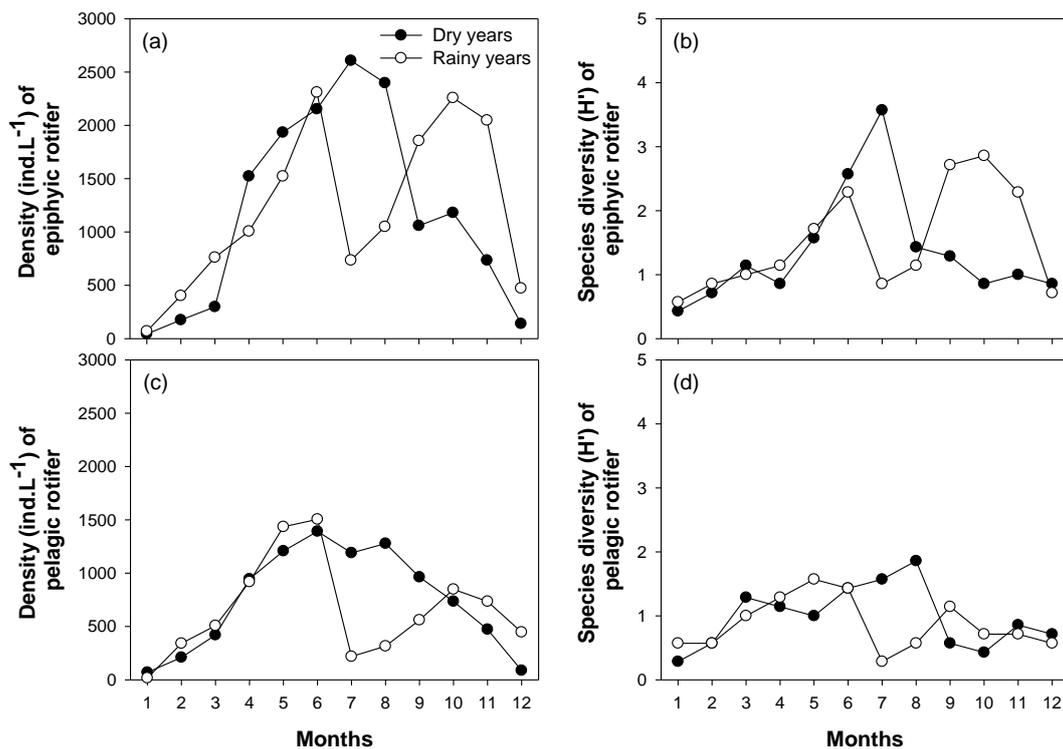


Figure 4. Changes in the monthly means and species diversity of rotifer community following dry years (closed circles) and rainy years (open circles) at the study site. Density (a) and species diversity (b) of epiphytic rotifer, and density (c) and species diversity (d) of pelagic rotifer.

Regression analysis revealed possible relationships among the factors of rainfall, area of open water, and submerged macrophyte biomass (Figure 5). From this, we can draw a plausible sequence of events that contribute to the impact of summer rainfall on open water, submerged macrophytes, and therefore rotifer habitat. Summer rainfall results in a significant increase of open water area ($F = 69.248$, $r^2 = 0.92$, $n = 9$; Figure 5a), which is greater in Rainy years than in Dry years (Figure 5b). In contrast, the months from January to June showed similar rainfall patterns and open water area in both Dry and Rainy years. The increased area of open water in summer correlated with greater biomass of submerged macrophytes in autumn ($F = 40.845$, $r^2 = 0.85$, $n = 9$; Figure 5c), particularly in Rainy years (Figure 5d). Submerged macrophyte biomass in autumn did not appear to influence autumn rotifer density ($F = 3.547$, $r^2 = 0.31$, $n = 9$); however, rotifer populations (both epiphytic and pelagic) are considered unlikely to increase during autumn.

3.3. Influence of Autumn Biomass of Submerged Macrophytes on Fish

Density, weight, and body size of *L. macrochirus* were responsive to changes in summer rainfall (Figure 6). Density and weight were higher in Rainy years than in Dry years (one-way ANOVA, $p < 0.01$); however, body size was similar. As previously mentioned, the autumn biomass of submerged macrophytes was higher in Rainy years than in Dry years (see Figure 5d); these changes clearly influenced *L. macrochirus*. The correlation value between autumn biomass of submerged macrophytes and density of *L. macrochirus* was very strong and showed a positive relationship (Figure 6b). Therefore, density of *L. macrochirus* varies throughout the study site. The weight of *L. macrochirus* decreased with an increase in autumn biomass of submerged macrophytes; however, body size was largely independent.

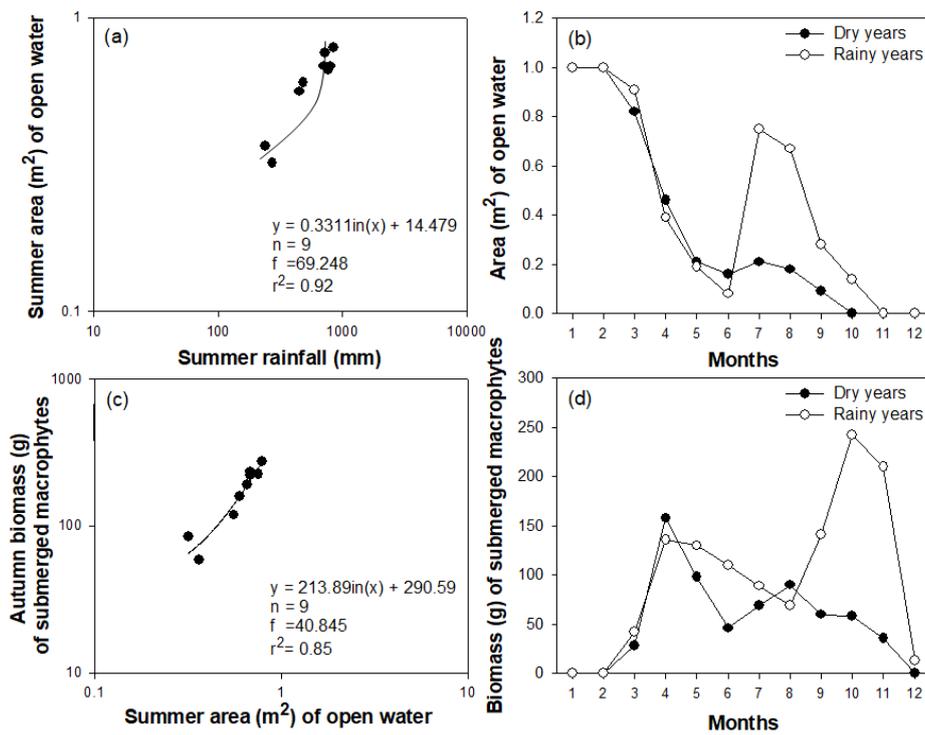


Figure 5. The influence of summer rainfall on the area of open water and submerged macrophyte biomass during the study period (2008–2017). Effect of summer rainfall on (a) the area (m²) of open water in summer in summer rainfall (mm), (b) monthly area (m²) of open water between Dry and Rainy years, (c) autumn biomass (g) of submerged macrophytes in areas (m²) of open water in summer, and (d) monthly biomass of submerged macrophytes between Dry and Rainy years.

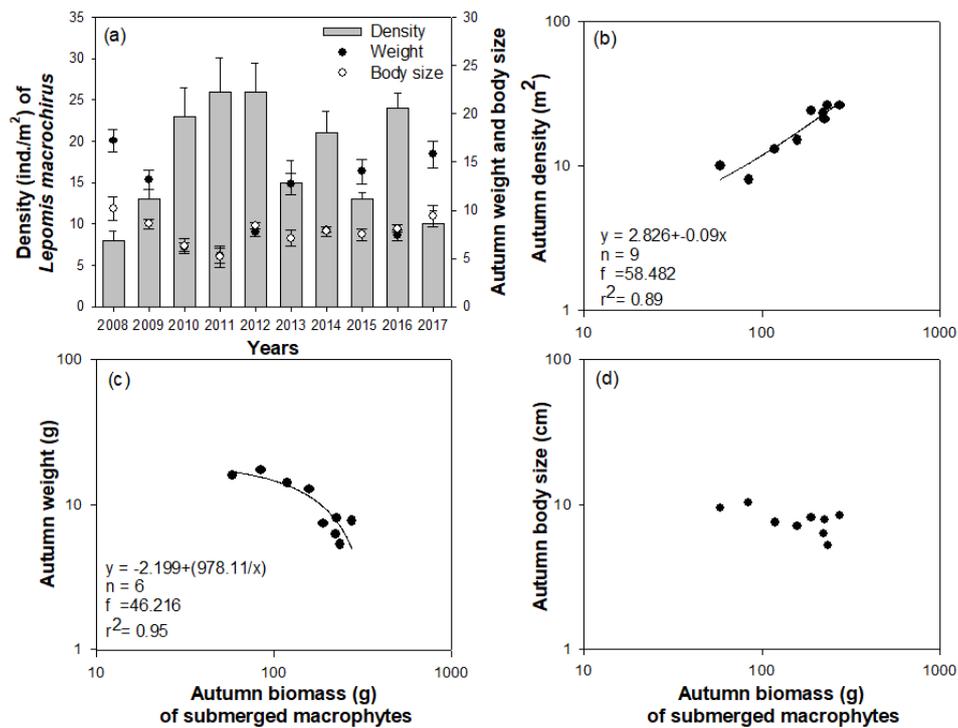


Figure 6. Annual autumn density of *Lepomis macrochirus* and relationship with macrophytes biomass. (a) Annual autumn density, (b) relationship between density and macrophytes biomass, (c) relationship between weight and macrophytes biomass, and (d) relationship between body size and macrophytes biomass.

4. Discussion

4.1. Impact of Summer Rainfall on Rotifer Groups

Hydrological characteristics can induce negative impacts on freshwater ecosystem dynamics. Concentrated rainfall during the summer results in the dilution of organismal density (especially for microbial entities) in ecosystems by augmenting water levels or discharge. In this study, interannual variations in summer rainfall patterns were very influential on rotifer communities. During Rainy years, which were characterized by particularly high rainfall in July, rotifer density was markedly lower (735 ind/L) than in June (2310 ind/L). This pattern was found likewise when considering the species diversity of rotifer communities. During Dry years, however, rotifer density and diversity increased continuously from spring to summer (July). We can therefore conclude that summer rainfall represents a major factor in suppressing rotifer populations, particularly from spring to summer.

Previously, Jeong et al. [28] and Choi et al. [12] reported that summer-concentrated rainfall results in a significant increase in discharge from weirs sited in nearby tributaries and main streams, thereby leading to decreases in the density of zooplankton communities, including rotifers. Thus, burgeoning spring zooplankton populations are disrupted by rainfall events. Given that lotic ecosystems, such as rivers and streams, are directly affected by physical disturbances such as increased discharge and rapid water flow, rainfall events can have pronounced effects on the distribution of animals, including zooplankton [11,38]. Due to the rainfall pattern in East Asia, which tends to be concentrated in summer, zooplankton communities in rivers and streams typically show a dual successional pattern during spring and autumn [12,39]. As wetlands and reservoirs are characterized by lower flow rates than rivers and streams, they tend to be less directly influenced by rainfall; however, zooplankton communities are influenced by substantial changes in both water level and turbulence [40]. Large-bodied zooplankton (e.g., copepods) can migrate to safer spaces (e.g., the benthic boundary layer) to avoid the impact of rainfall [41,42], while rotifers have difficulty migrating or resisting water current. Although the small body size of rotifer is believed to be an effective adaptation that enables higher densities and diversity, it can be a liability in the face of a rapidly changing habitat.

Previous studies suggest that the effects of summer rainfall on rotifer communities differ depending on whether rotifers are epiphytic or pelagic [22]. In our study, epiphytic rotifer density was positively correlated with an increase in rainfall, while pelagic species were vulnerable to rainfall. Epiphytic rotifer species, such as those in the genera *Lecane*, *Lepadella*, and *Monostyla*, can maintain high densities despite physical disturbances caused by summer-concentrated rainfall [22]. In this study, however, we observed that the densities of both types of rotifer decreased in the summers of Rainy years. We attributed this to a difference in habitat structure within the survey area. In areas replete with submerged macrophytes, abundant surfaces are available for attachment by epiphytic species. Further, these areas are resistant to physical disturbance such as summer rainfall. In contrast, environments in which free-floating macrophytes predominate, such as this study area, do not provide habitat appropriate to epiphytic species. From this finding, we suggest that the diversity or seasonal abundance of aquatic macrophytes is an important factor in determining the effect of rainfall on rotifer communities. In particular, a prevalence of submerged macrophytes lessens the likelihood of dispersion or flushing caused by changing water levels or turbulence [43].

4.2. Seasonality of Microhabitat Structures that Support Rotifer Communities

In our study, we found that habitat structure can vary depending on the seasonal abundance and species composition of aquatic macrophytes. Most of the reservoir located in East Asia, including South Korea, tend to receive a constant influx of nitrogen and phosphorus from surrounding agricultural or urban areas [44], which can promote excessive growth of aquatic macrophytes. Thus, free-floating macrophytes such as *Spirodela polyrhiza* and *Salvinia natans* tend to cover large areas on the surfaces of water bodies [45]. This blocks the penetration of light into the water column and thereby prevents the germination and growth of other floating-leaved or submerged macrophytes. However, during early

spring, the growth of free-floating macrophytes tends to be less prolific, which allows light to penetrate the water surface and stimulate various forms of aquatic macrophytic growth. Springtime conditions are therefore conducive to the development of a complex and diverse range of microhabitats, whereas summertime habitat structures are comparatively less diverse [46,47].

In the present study, we observed that free-floating macrophytes covered much of the water surface during summer, whereas the middle and bottom layers of the water column were essentially devoid of aquatic macrophytes. Habitats that are relatively simple in structure not only intensify competitive interactions between rotifer communities [48], but also favor the foraging activities of potential predators such as fish [49]. Both of these factors contribute to decreases in rotifer density. Considering the relatively simple structures of leaves and stems of free-floating macrophytes, Choi et al. [19] have suggested that the habitat space covered by free-floating macrophytes is mainly utilized by small-sized rotifers rather than large-sized cladocerans or copepods. However, in the present study, we assumed that free-floating macrophytes are unsuitable as refuges for evading rainfall-induced disturbances, as these macrophytes—unlike floating-leaved and submerged macrophytes—are susceptible to displacement in response to marked changes in water level or turbulence.

Summer rainfall can lead to changes in the spatial distribution of free-floating macrophytes that result in larger areas of open water; these can lead successional shifts in autumn. Submerged macrophytes showed the most notable differences between Dry and Rainy years, with biomass gradually decreasing from summer to autumn in Dry years and increasing during Rainy years. We surmised that an increase in the area of open water in summer would serve to promote the autumnal growth and development of submerged macrophytes by increasing the penetration of light to lower levels in the water column. In the present study, we accordingly found that the average biomass of submerged macrophytes in the autumn of Rainy years was 226 g, which was two to three times higher than the average autumnal biomass (94 g) in Dry years. Additionally, the autumnal biomass in Rainy years was twice that recorded in spring.

Some studies have indicated that the leaves and stems of submerged macrophytes are more suitable as rotifer habitats than those of other aquatic macrophytes because they are relatively more complex [50–52]. Therefore, the area occupied by submerged macrophytes not only provides a range of microhabitats, but can also contribute to the survival and sustainable population growth of rotifer communities by reducing the foraging efficacy of predators such as fish [21,53]. Based on these findings, we speculate that the development of submerged macrophytes in the autumn of Rainy years generates a more complex habitat structure, and therefore a more diverse community of animals, than that in Dry years. This implies that greater microhabitat complexity should promote higher density in the reservoirs of South Korea. We surmise that summer-concentrated rainfall enables the simultaneous development of different types of macrophytes, which form complex aquatic microhabitats that promote high rotifer species diversity and density. Consequently, we suggest that the moderate disturbance caused by summer rainfall can promote higher rotifer diversity by favoring the development of submerged macrophytes, which may contribute to the emergence of more ecologically sound food-web structures in reservoirs.

4.3. Association between Macrophytes and Fish Predation

The autumn change in submerged macrophyte biomass appeared to affect the characteristics and possibly even the foraging behavior of the fish. High autumn biomass of submerged macrophytes was correlated with high density and low weight in *Lepomis macrochirus*. Previous studies have indicated that foraging activities of fish are limited in areas dominated by aquatic macrophytes [20,54]; however, *L. macrochirus* actively forage in areas of moderate or sub-moderate aquatic macrophyte cover [55]. Choi et al. [56] also suggested that *L. macrochirus* with body size of less than 10 cm are mainly distributed in areas of high aquatic macrophyte cover to avoid larger piscivorous fish (e.g., *Micropterus salmoides*), and that they preferentially consume invertebrates such as branchipoda. In this study, however, the foraging activity of *L. macrochirus* was restricted in the complex habitat structure created

by submerged macrophytes. We found that the body weight of *L. macrochirus* declined as the autumn biomass of submerged macrophytes increased, which indicates limited foraging activity despite the high density of zooplankton such as rotifers. Previous studies have similarly suggested that the presence of submerged macrophytes significantly increases aquatic habitat complexity and contributes to a reduction in foraging activity of *L. macrochirus* [57,58]. In contrast, the body weight of *L. macrochirus* was relatively high in the autumn, when fewer submerged macrophytes were present. Low submerged macrophyte biomass correlates with relatively simple habitat structure, which appears to increase feeding activity in *L. macrochirus*. A high density of *L. macrochirus* may also account for reduced foraging efficiency. Our findings suggest that a high density of submerged macrophytes restricts the movement of *L. macrochirus* and promotes a high density of these fish in certain areas. We can therefore conclude that high autumn biomass of submerged macrophytes provides a “refuge” effect which increases the autumn density of rotifers and is an important factor in sustaining rotifer communities, as well as in providing a continuous food source for *L. macrochirus*. In contrast, in freshwater ecosystems that lack aquatic macrophytes, such as lakes and rivers, the unrestricted foraging activity of predators easily causes depletion of prey items, including zooplankton, which in turn leads to the extinction of predators. Because of the importance of abundant macrophytes to the ongoing sustainability of freshwater trophic webs, we suggest that they act as intermediate regulators of freshwater trophic dynamics and play a critical role in the population growth and fecundity of *L. macrochirus*.

4.4. Effect of Summer Rainfall on Rotifer Diversity

Summer-concentrated rainfall is an important factor in determining the seasonal diversity and density of rotifer communities. Summer rainfall increases physical disturbance, which has a “resetting” effect on rotifer community structure [12,28]. Therefore, the high diversity and density of springtime rotifer communities is disrupted by summer rainfall events. However, this summer rainfall effect can also promote the species diversity of rotifer communities. During Dry years, in which rotifer populations expand from spring to autumn without interruption by summer rainfall, certain species will inevitably dominate the autumnal community structure [59]. Numerous empirical studies have reported such a dominance pattern among zooplankton species whose dynamics are characterized by a variety of predator avoidance techniques and high interspecies competition [60–62]. Thus, under the successional process of zooplankton communities over a long-term period, the density increases but species diversity generally decreases. Summer rainfall, however, disrupts the spring growth of rotifer communities and initiates a new successional progression in autumn. For example, a study on the Nakdong River reported the presence of zooplankton of the *Daphnia* genus earlier in the year, but then showed autumn dominance by *Bosmina longirostris* and *Bosminopsis deitersi* [63]. In this study, we found a differential pattern of diversity in autumn relative to spring in Rainy years, with the former dominated by *Lecane Bulla*, *Lepadella oblonga*, and *Testudinella patina*; this is in contrast to the predominance of *Anuraeopsis fissa* and *Brachionus angularis* in spring. In addition to differences in community composition, the overall autumn species diversity of rotifers was higher than that of spring in Rainy years. Conversely, in Dry years, species diversity peaked in July and decreased throughout autumn and winter. Low biomass of submerged macrophytes may also contribute to this pattern due to simple habitat structure. We believe that the low rotifer density in autumn of Dry years may be driven by heightened interspecies competition within the narrow spaces between the roots of free-floating macrophytes.

Based on the results of this study, we conclude that summer rainfall plays an important role in supporting rotifer diversity. Although summer rainfall negatively affects rotifer density, we found positive effects in terms of species diversity. We suggest that the high autumn rotifer species diversity of Rainy years can be attributed to the effects of submerged macrophytes and therefore reduced predation; however, the differences in species composition are largely influenced by summer rainfall. Thus, a stable environment free of disturbances such as rainfall has a negative effect on the species diversity of rotifer communities.

This study was partly limited in quantifying microhabitat complexity caused by differential summer rainfall. We recommend the development of a relevant methodology for future studies. Based on our results, we further recommend moderated controlling of surface—particularly free-floating—aquatic macrophytes in managed or restored shallow reservoirs and wetlands in order to increase biodiversity and therefore ecologically healthy food webs. Our results show that rotifer density is strongly related to submerged macrophyte biomass; this relationship is also true of other animals (e.g., fish and invertebrate; [64,65]). The convergence of rotifer species diversity with density implies the potential utility of these metrics in determining an optimal level of aquatic macrophyte diversity. Such a measure would help reduce the cost-benefit trade-off in reservoir restoration and management.

Author Contributions: The design of this research is equally shared between the authors. All three authors contributed towards conceptualisation, methodology, investigation. J.-Y.C. contributed towards the development of the software and resources, and wrote the original draft. S.-K.K. contributed significantly in reviewing and editing the draft manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: This research was supported by the Basic Science Research Program through the National Research Foundation of Korea (NRF) funded by the Ministry of Education (grant number: NRF-2012-R1A6A3A04040793).

Conflicts of Interest: The authors declare no conflict of interest.

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