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Article

The Response Patterns of Non-Native Rotifer Species *Kellicottia bostoniensis* (Rousselet, 1908) to Environmental Factors and Its Relationship with Potential Competitors and Predators

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Abstract: *Kellicottia bostoniensis* is a rotifer species originating from North America, with numerous reports documenting its spread to Europe and South America. Meanwhile, in Asia, the occurrence of this non-native species has been scarcely documented, but its presence was recently reported in Korea in 2020. In Korea, the close geographic proximity of artificial reservoirs within a small area is expected to make the region vulnerable to the spread of *K. bostoniensis*. Therefore, it is deemed necessary to study the spatio-temporal distribution of *K. bostoniensis*, which appears to have extensively proliferated across the region, and its relationship with environmental factors. We analyzed the response of *K. bostoniensis* occurrence to environmental factors and aimed to compare its response patterns with those of potential competitor and predator groups, which were classified based on a functional group approach. This study, conducted on 12 small lakes located under similar climatic conditions, revealed that the response of *K. bostoniensis* to variables representing the trophic state of the lakes differed from those of the potential competitor and predator groups. The study sites, encompassing a wide range of trophic states from oligotrophic to hypereutrophic, across various lakes and survey periods, were well-suited for examining these relationships. Furthermore, when TSI was calculated to compare the abundance of *K. bostoniensis* and potential competitors across trophic conditions, the abundance of potential competitors was proportional to TSI. In contrast, *K. bostoniensis* exhibited higher abundances in mesotrophic and lower eutrophic environments, which distinguished it from its competitors. Our results indicate that the impact of introduced *K. bostoniensis* on native communities is minimal, while the resistance of native communities through the biological filter based on biological interactions is ineffective against this non-native rotifer species. This provides key evidence for explaining the widespread distribution of *K. bostoniensis* across continents.

Keywords: plankton invasion; trophic status; functional groups; competitor; predator

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1. Introduction

Non-native species are important at the community level because they directly or in-directly influence native species through biological interactions [1]. In invasive species studies, it is essential to observe their spreading across the new regions and to investigate the biotic and abiotic interactions that occur in these new environments. It is most of all necessary to monitor the abundance and distribution of such species and its dynamics, and to compare it with native species to see if the potentially invasive species causes extinction of local groups of organisms, especially taxonomically close ones [2–4]. Furthermore, information on the interactions between non-native species and the biotic and abiotic factors of their habitats provides valuable insights for predicting the likelihood of further introductions into new habitats and assessing potential changes to existing ecosystems [5].

Kellicottia bostoniensis (Rousselet, 1908) belongs to a freshwater zooplankton species (Rotifera, Monogononta, Ploima, Brachionidae), originating from North America. Since 1943, its presence has been reported in many European countries [6,7], and subsequently, its dispersion was also noted in South America during the 1990s [8]. In Asia, the occurrence of the genus *Kellicottia* was historically reported to be restricted to *K. longispina* until relatively recently [9]. In East Asia, although environmental conditions appear suitable for the establishment of *K. bostoniensis*, it is presumed that its population has not yet stably established itself [10]. In the East Asia in Palearctic realm, the occurrence of *K. bostoniensis* was first reported as a rare species in Japan in 1999 [11]. However, no further occurrences of *K. bostoniensis* have been recorded since then, and research on *K. bostoniensis* as a non-native species in Asia remains limited compared to studies conducted in North America, Europe, and South America.

The second recorded occurrence of *K. bostoniensis* in Asia was recently confirmed in Korea [12]. In Korea, artificial reservoirs constructed for agricultural and drinking water supply purposes are distributed nationwide, with many located in geographical proximity. This geographic arrangement suggests that human activities may continuously facilitate the spread of non-native species. Furthermore, many reservoirs are eutrophicated [13], and the lack of significant variation in geographical and climatic factors may result in low spatiotemporal heterogeneity of environmental factors within and between habitats. This can facilitate the spread of introduced non-native species [14]. Considering the temporal gaps between studies on the occurrence of *K. bostoniensis* in Asia and the limited information which increases the potential for misidentification with the morphologically similar *K. longispina*, there appears to be a significant lack of data regarding the distribution of *K. bostoniensis* and its interactions with other species within zooplankton communities in Asia, including Korea. Therefore, research on the spatio-temporal distribution of this species at the community level and its response patterns to environmental factors is considered necessary.

From the perspective of biological interactions, *K. bostoniensis* has a relatively long body length, including its spines (250–450 µm). It possesses long anterior and posterior spines, which lengthen in response to predation pressure, serving as a defensive mechanism against predators [15–17]. Thus, it is known to effectively respond to predation pressure from macro-invertebrate predators (e.g., Chaoborus larvae) and predatory rotifer, *Asplanchna* spp. [15,18]. Additionally, bacteria, nanoflagellates, and nano- and picophytoplankton have been studied as its primary food sources [19–21]. From the perspective of interactions with environmental factors, variables such as water temperature, dissolved oxygen concentration, and the trophic state index (TSI) of lakes have been identified as related to *K. bostoniensis* [14,15,17,22]. However, *K. bostoniensis* appears to respond differently to environmental factors depending on the study. For instance, Branco [15] described a strong negative correlation with water temperature, whereas Shurganova [23] reported a positive correlation with the same factor. Similarly, conflicting findings exist regarding the relationship between the trophic state of lakes and this species [14,17], suggesting that its responses vary depending on the complex environments and the range of environmental factors in the studied habitats. Based on current research findings, it is evident that further studies are needed to validate the relationships of *K. bostoniensis* with various biotic and abiotic factors across diverse environments. Moreover, studies interpreting population dynamics as the result of the combined effects of these factors remain insufficient.

In this study, a functional group-based approach was used to understand the population relationships between *K. bostoniensis* and other zooplankton species with which it interacts within the food web. Species with similar feeding characteristics within the functional group were identified as potential competitors, while species known as general predators of rotifers, including *K. bostoniensis*, were identified as potential predators. The response patterns of these groups to environmental factors were compared with those of *K. bostoniensis*. Additionally, the spatial distribution of *K. bostoniensis* within the Geumgang River basin in Korea, part of the East Asian region where regional studies on *K. bostoniensis* are limited, was investigated. This study aimed to elucidate the relationships between *K. bostoniensis* and environmental factors in a new environment, examine its fluctuations with potential competitor and predator groups, and explore the potential impact of this non-native rotifer species on native zooplankton communities.

2. Materials and Methods

2.1. Study Site and Data Collection

To investigate the spatial distribution of *Kellicottia bostoniensis* and its relationships with environmental factors and zooplankton community composition, a study was conducted on 12 small lakes (maximum surface area < 3 km^2) located in close geographic proximity. These lakes, within a 50 km radius, belong to the same watershed (Geumgang River) and share similar physical characteristics and climatic conditions (Figure 1, Table A1). Surveys of zooplankton and measurements of environmental parameters were carried out in May, June, September, and November of 2023.

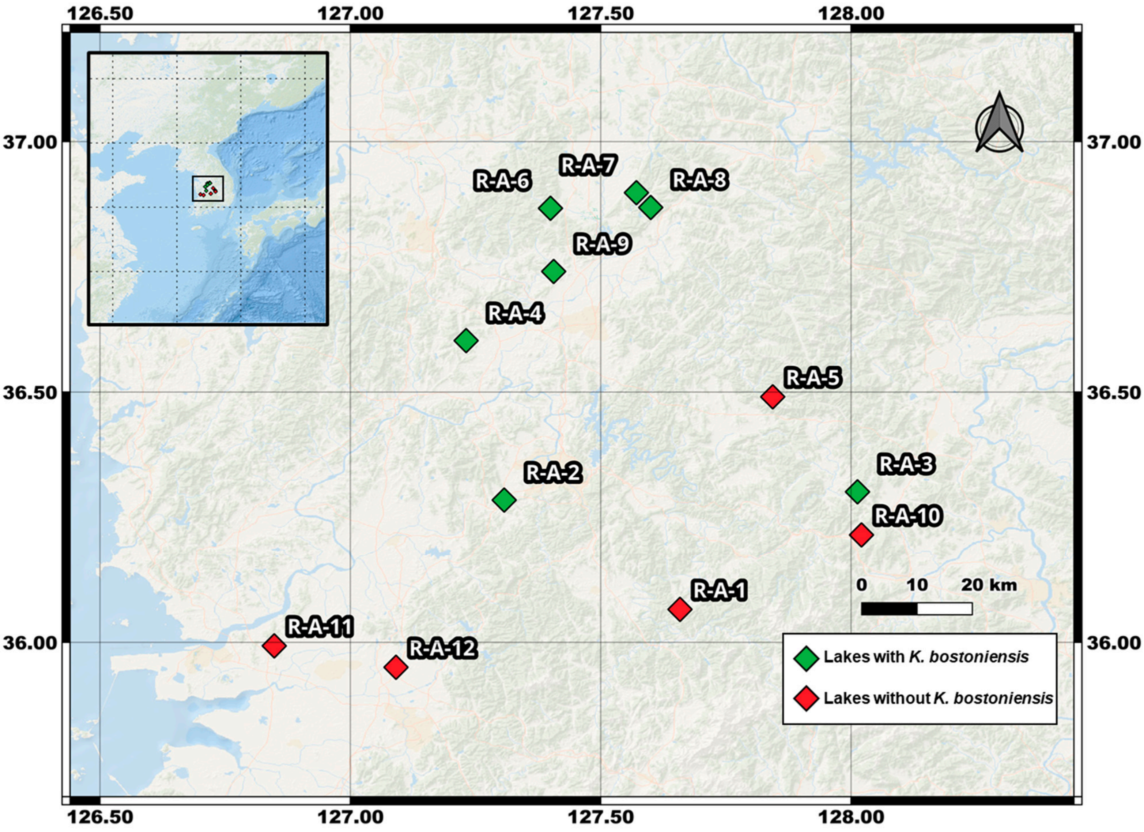

Figure 1. Geographic distribution of the lakes in this study. The green diamonds represent the lakes where *Kellicottia bostoniensis* appeared in our study, while the red diamonds indicate lakes where it did not appear.

2.2. Data Collection

Zooplankton samples were collected using a plankton net (30 cm diameter, 60 µm mesh) at the center of each lake. Considering the vertical distribution of the zooplankton community, sampling was performed as follows: in lakes with depths more than 5 m, vertical towing covering the entire water column; and in lakes with depths less than 5 m, oblique towing was conducted from 5 m (towing speed: 1 m/s). The collected zooplankton samples were preserved with formalin (final concentration 5%), and a 1 to 5 mL subsample was extracted and examined in an S-R chamber under a microscope (Olympus BX51, Tokyo, Japan for identification to genus and species levels. Zooplankton abundance (density) was calculated by determining the volume of water filtered based on the net area and towing depth and was expressed as individuals per liter (ind./L).

Environmental factors that could influence zooplankton community were selected: water temperature (WT, °C), dissolved oxygen (DO, mg/L), suspended solids (SS, mg/L), total nitrogen (TN, mg/L), total phosphorus (TP, mg/L), total organic carbon (TOC, mg/L), chemical oxygen demand (COD, mg/L), pH, and chlorophyll-*a* concentration (Chl-a, mg/m^3). Environmental factor data were obtained from publicly available datasets of Rural Agricultural Water Resource Information System (https://rawris.ekr.or.kr (accessed on 10 December 2024)), corresponding to the survey period of each lake (Table A2).

2.3. Classification of Functional Groups of Zooplankton

To distinguish species that directly interact with *K. bostoniensis*, potential competitor and predator species among the observed zooplankton were classified based on functional traits (Tables 1 and A3). The phylum Rotifera (referred to as rotifers), to which *K. bostoniensis* belongs, exhibits variations in feeding tendencies and consequent environmental responses depending on the structure of their mastax, specifically the trophi [24]. Species with malleate trophi, such as *K. bostoniensis*, feed by cutting and chewing their food. Rotifers can also be categorized by their habitat preferences into planktonic species (which live suspended in the water column) and littoral and periphytic species (which attach to substrates like aquatic plants or rocks) [25,26]. Accordingly, species which could compete with *K. bostoniensis* for food sources due to their malleate trophi and preference for planktonic habitat were classified as the potential competitor group. Meanwhile, the genus *Asplanchna*, which is a predatory rotifer, *Asplanchna* spp., and cyclopoid copepods, known as primary predators of rotifers [27–29], were classified as the potential predator group.

Table 1. Classification of functional groups of rotifers that appeared in the studied lake (at genus level).

Functional Group		**Habitat Type**	
		Planktonic	**Littoral, Periphytic**
trophi	Malleate type	*Anuraeopsis*, *Brachionus*, *Kellicottia*, *Keratella*	*Euchlanis*, *Lecane*, *Lepadella*, *Mytilina*, *Platyias*, *Trichotria*
	Virgate type	*Ascomorpha*, *Cephalodella*, *Ploesoma*, *Polyarthra*, *Synchaeta*, *Trichocerca*	-
	Incudate type	*Asplachna*	-
	Ramate type	*Rotaria*	*Philodina*
	Malleoramate type	*Conochilus*, *Filinia*, *Hexarthra*, *Pompholyx*	*Testudinella*, *Tetramastix*

2.4. Statistical Methods

Differences in each environmental factors (environmental and biological factors) in the presence or absence of *K. bostoniensis* were analyzed using a permutation test (The R package “coin”) [30]. This method, a type of non-parametric statistical approach, mitigates issues related to sample size disparities and non-normality arising from differences in frequency between the presence and absence of *K. bostoniensis*. This analysis was conducted on nine environmental factors, zooplankton abundance by taxonomic group (rotifers, cladocerans, and copepods), and the abundance of potential competitor and predator groups.

Detrended Correspondence Analysis (DCA) was performed to analyze the response of *K. bostoniensis* to multivariate environmental factors and to compare these responses with those of potential competitor and predator groups (The R package “Vegan”) [31]. DCA was chosen to address non-linearities among variables caused by the absence data for *K. bostoniensis* (presence count: 0) [32].

3. Results

3.1. Seasonal Variation in the Abundance of Kellicottia bostoniensis, Zooplankton Factors, and Environmental Factors

Kellicottia bostoniensis was found in 7 out of 12 lakes, while it was absent in 5 lakes (Figure 1). For *K. bostoniensis*, the monthly average abundance was the lowest in May, with no occurrences recorded across all lakes.

Among the lakes where *K. bostoniensis* appeared, R-A-2, R-A-4, and R-A-8 exhibited very low abundance during most survey periods except for November, when the abundance of *K. bostoniensis* increased, showing similar seasonal appearance patterns (Figure 2(a1,a3,a6)). On the other hand, lakes R-A-3 and R-A-9 demonstrated the highest abundance in July, with lower occurrences during other survey periods (Figure 2(a2,a7)). Meanwhile, lakes R-A-6 and R-A-7 differed from other lakes by showing the highest abundance of *K. bostoniensis* in September, distinguishing seasonal appearance patterns by lake.

Potential competitors and predators also exhibited distinct seasonal occurrence patterns depending on the lake. For potential competitors, some lakes showed a pattern of increasing in July and then gradually decreasing (Figure 2(b2,b4,b6,b7)), while other lakes did not display a common seasonal pattern. In lakes R-A-2 and R-A-3, potential predators showed patterns similar to those of potential competitors’ patterns in many lakes, with high occurrences in July followed by gradual decreases (Figure 2(c1,c2)). Other patterns were further categorized into rapidly changing fluctuation patterns, with the lowest abundance in July (Figure 2(c3,c4)) and those with the highest abundance in July (Figure 2(c6,c7)). When summarized, the lakes where the fluctuation patterns of *K. bostoniensis* were similarly grouped differed from the lakes where the fluctuation patterns of potential competitors or predators were similarly grouped.

When examining the fluctuation patterns of environmental factors across the seven lakes where *K. bostoniensis* appeared (Figure 3), water temperature and DO exhibited similar patterns across lakes, indicating that they were the factors most influenced by seasonality. In contrast, other variables showed differing fluctuation trends depending on the lake. Similar to zooplankton factors, there were no factors in which the fluctuation trends of specific environmental factors grouped similarly across lakes that also grouped similarly for the fluctuation trends of *K. bostoniensis*.

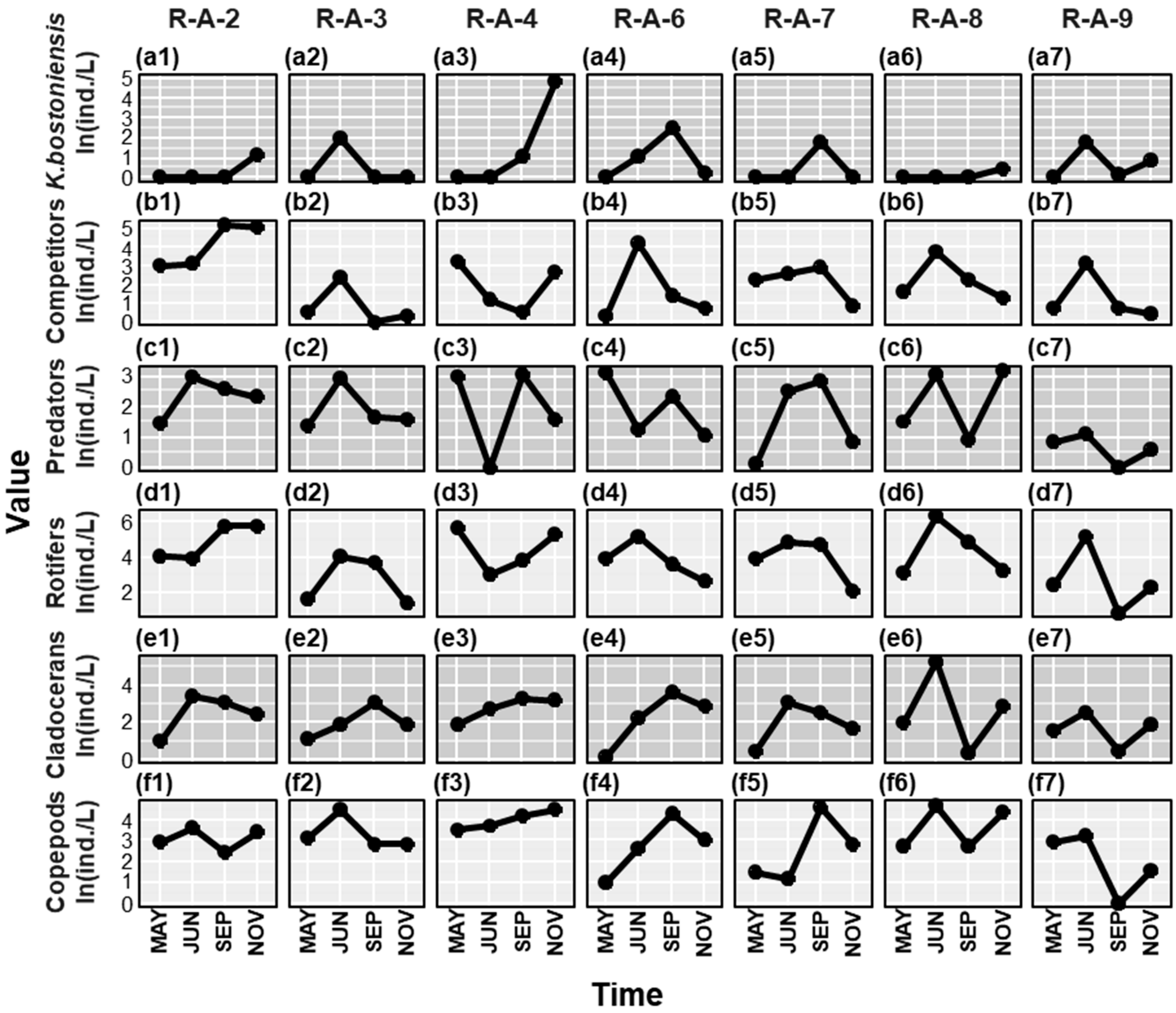

Figure 2. The fluctuation trends of zooplankton factors (abundance of potential competitors (Competitors, **b**); abundance of potential predator (Predator, **c**); abundance of total rotifers (Rotifers, **d**); Abundance of total cladocerans (Cladocerans, **e**); abundance of total copepods (Copepods, **f**)), including *Kellicottia bostoniensis*, in the seven lakes where *K. bostoniensis* appeared are represented, with variables arranged in rows and lakes in columns (**a**). Abundance has been converted to a log scale. The numbers **1**–**7** in the subfigures refer to lakes R-A-2, R-A-3, R-A-4, R-A-6, R-A-7, R-A-8, and R-A-9, in that order.

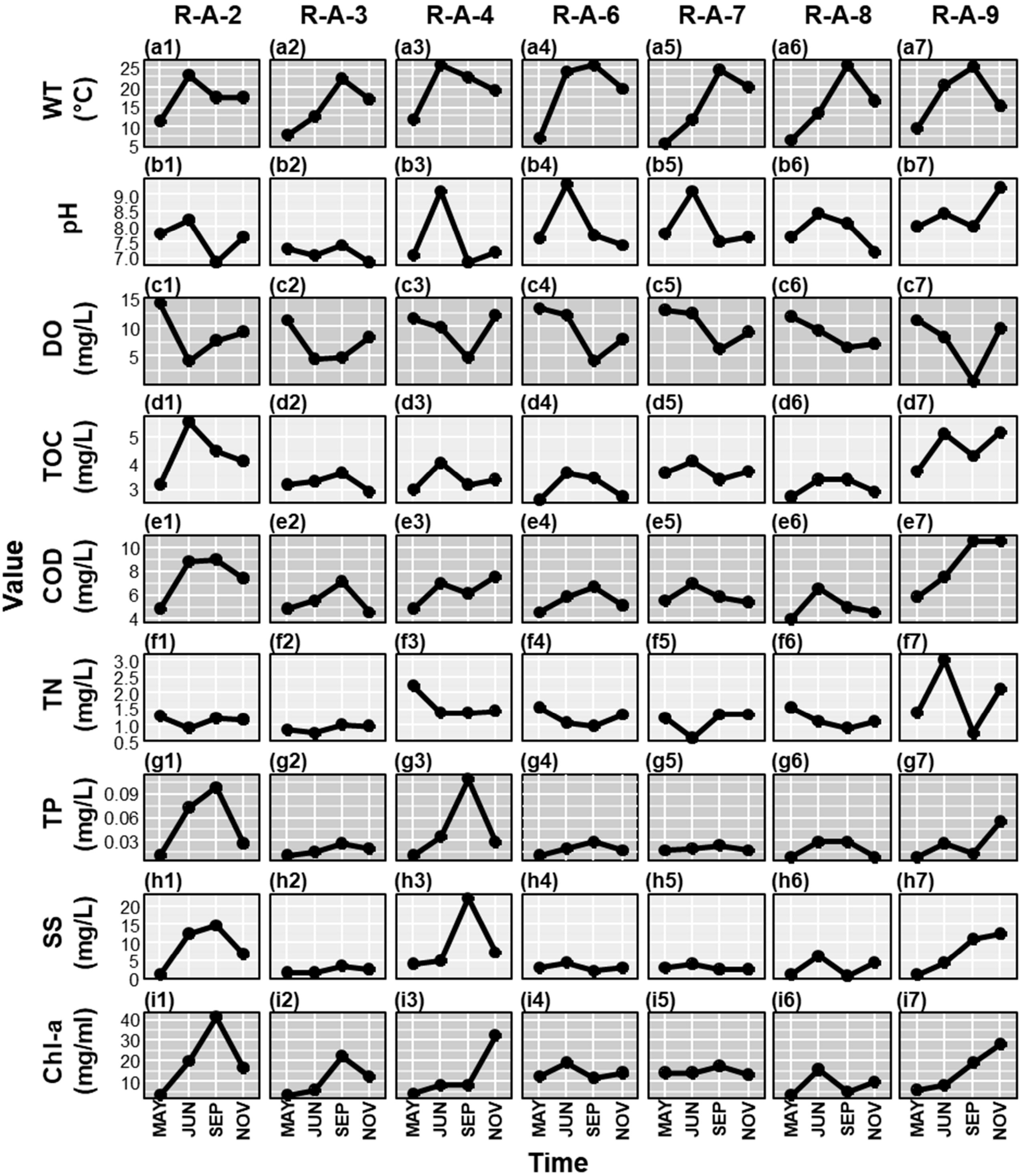

Figure 3. The seasonal dynamics of environmental factors in the seven lakes where *Kellicottia bostoniensis* appeared are represented, with variables arranged in rows and lakes in columns. From the top: water temperature (WT, °C; **a**), hydrogen ion concentration (pH; **b**), dissolved oxygen concentration (DO, mg/L; **c**), total organic carbon concentration (TOC, mg/L; **d**), chemical oxygen demand (COD, mg/L; **e**), total nitrogen concentration (TN, mg/L; **f**), total phosphorus concentration (TP, mg/L; **g**), suspended solids concentration (SS, mg/L; **h**), and chlorophyll a concentration (mg/mL; **i**). The numbers **1**–**7** in the subfigures refer to lakes R-A-2, R-A-3, R-A-4, R-A-6, R-A-7, R-A-8, and R-A-9, in that order.

3.2. Comparison of Differences in Environmental Factors Between Lakes with the Presence and Absence of Kellicottia bostoniensis

The results of the permutation test indicated that the environmental factors showing significant differences between lakes with and without the presence of *K. bostoniensis* were TOC and TP (Figure 4D,G). For TOC, lakes where *K. bosotoniensis* was present, TOC reached an average value of 3.94 mg/L, while in the ones where *K. bosotoniensis* was not present, it had an average value of 5.30 mg/L. Similarly, for TP, lakes with *K. bostoniensis* showed an average value of 0.03 mg/L, compared to 0.11 mg/L in lakes without its presence. This indicates that lakes where *K. bostoniensis* was absent had statistically significantly higher concentrations of TOC and TP compared to those where it was present (p < 0.01). In the case of R-A-5, a lake where *K. longispina* was observed among the non-occurrence lakes of *K. bostoniensis*, differences were observed in TOC, COD, TN, SS, and Chl-a when compared to lakes where *K. bostoniensis* was present (Figure 4D–F,H,I). TOC showed a significant difference, with 3.94 mg/L in lakes with *K. bostoniensis* and 2.00 mg/L in the lake with *K. longispina* (Figure 4D) (p < 0.01). COD also differed from 6.38 mg/L in lakes with *K. bostoniensis* and 3.15 mg/L in the lake with *K. longispina* (Figure 4E) (p < 0.001). Similarly, TN was 1.29 mg/L in lakes with *K. bostoniensis* and 0.83 mg/L in the lake with *K. longispina* (Figure 4F) (p < 0.05). SS was 5.38 mg/L in lakes with *K. bostoniensis* and 1.30 mg/L in the lake with *K. longispina* (Figure 4H) (p < 0.05). Chl-a showed a statistically significant difference between lakes with the presence of *K. bostoniensis* (13.95 mg/m^3) and the lake with the presence of *K. longispina* (4.80 mg/m^3) (Figure 4I) (p < 0.05).

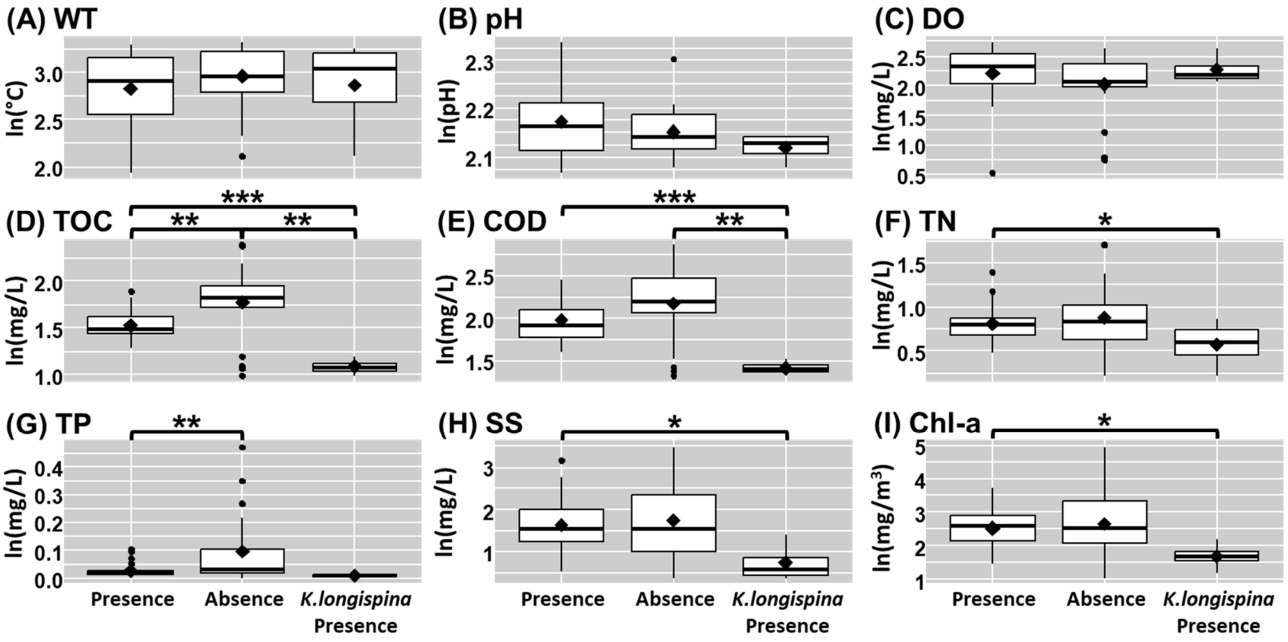

Figure 4. Results of the permutation test for differences in environmental factors (water temperature (WT, °C; **A**), hydrogen ion concentration (pH; **B**), dissolved oxygen concentration (DO, mg/L; **C**), total organic carbon concentration (TOC, mg/L; **D**), chemical oxygen demand (COD, mg/L; **E**), total nitrogen concentration (TN, mg/L; **F**), total phosphorus concentration (TP, mg/L; **G**), suspended solids concentration (SS, mg/L; **H**), and chlorophyll a concentration, mg/mL, **I**) among the lakes with the presence of *K. bostoniensis*, the lakes without its presence, and the lakes with the presence of *K. longispina* (Permutation test: $p < 0.05$ *, $p < 0.01$ **, $p < 0.001$ ***).

Among the zooplankton abundances, there were no statistically significant differences between the lakes with the presence of *K. bostoniensis* and those without its presence (p > 0.05) (Figure 5). Additionally, there were no statistically significant differences in zooplankton abundances between the lakes with the presence of *K. bostoniensis* and those with the presence of *K. longispina*.

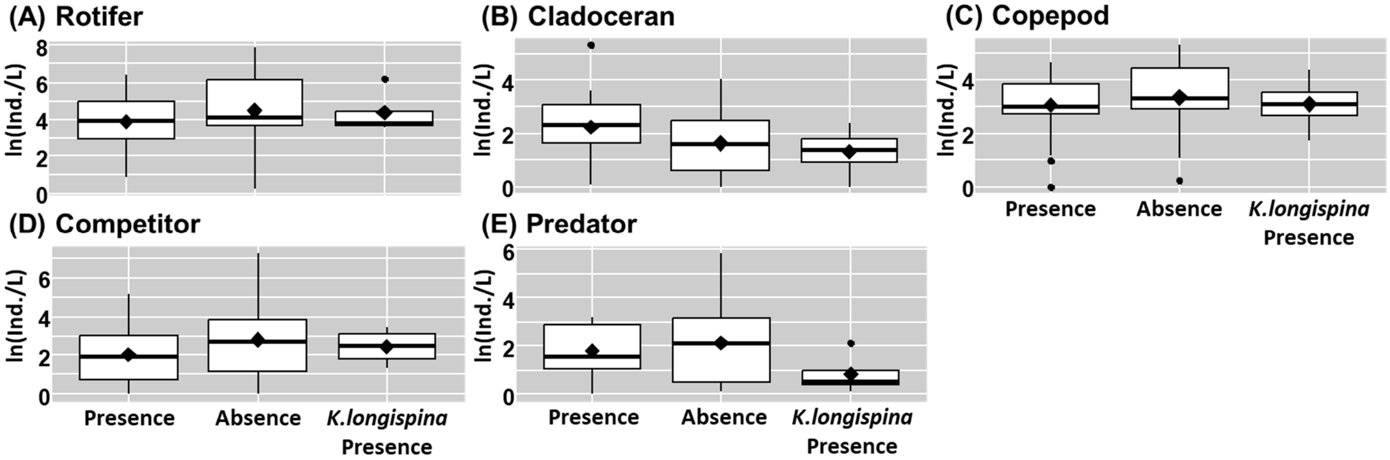

Figure 5. Results of the permutation test for differences in zooplankton factors (abundance of potential competitors (Competitors; **D**); abundance of potential predator (Predator; **E**); abundance of Total Rotifers (Rotifers; **A**); abundance of total cladocerans (Cladocerans; **B**); abundance of total copepods (Copepods; **C**)) among the lakes with the presence of *K. bostoniensis*, the lakes without its presence, and the lakes with the presence of *K. longispina* (permutation test: $p < 0.05$ *, $p < 0.01$ **, $p < 0.001$ ***).

3.3. Comparison of the Responses of Kellicottia bostoniensis, and Its Potential Competitor/Predator Groups to Environmental Factors

In the DCA, COD, which was identified to exhibit multicollinearity, was excluded, and the analysis was conducted using the remaining eight variables. The analysis results showed that 7 out of the 8 environmental factors, excluding pH, had a significant influence on the formation of the first and second axes in the DCA dimensionality reduction ($p < 0.05$).

The first axis was primarily explained by DO and water temperature, while the second axis was explained by TOC, TN, TP, SS, and Chl-a, indicating that the explanatory contributions of the seven variables were generally distinct across the two axes (Figure 6). For the first axis, DO showed a positive relationship, whereas water temperature exhibited a negative relationship, indicating an inverse relationship between these two variables. On the second axis, TOC, TN, TP, SS, and Chl-a all displayed negative relationships, suggesting that the patterns among these variables were partially similar.

K. bostoniensis was positioned in the second quadrant of the DCA plot (Figure 6). Thus, its abundance showed a negative relationship with DO and a positive relationship with water temperature. On the other hand, *K. bostoniensis* exhibited negative relationships with TOC, SS, TP, TN, and Chl-a. These variables, which reflect the trophic state of the lakes, were found to negatively influence the abundance of *K. bostoniensis*.

When only species classified as potential competitors with *K. bostoniensis*, due to their similar feeding and habitat characteristics, were plotted on the DCA plane, most species exhibited response patterns to environmental factors that differed from those of *K. bostoniensis* (Figure 6A). Among the 13 potential competitor species observed, the response patterns to the first axis varied by species. However, all species showed similar responses to the second axis, with the exception of *K. longispina*. For DO and water temperature, each species displayed distinct response patterns. In contrast, the environmental factors representing the trophic state of the lakes (TOC, TN, TP, SS, and Chl-a) were found to exert a uniformly positive influence across species. Meanwhile, *K. longispina*, like *K. bostoniensis*, exhibited response patterns to environmental factors that were distinct from those of *K. bostoniensis* and its other potential competitors.

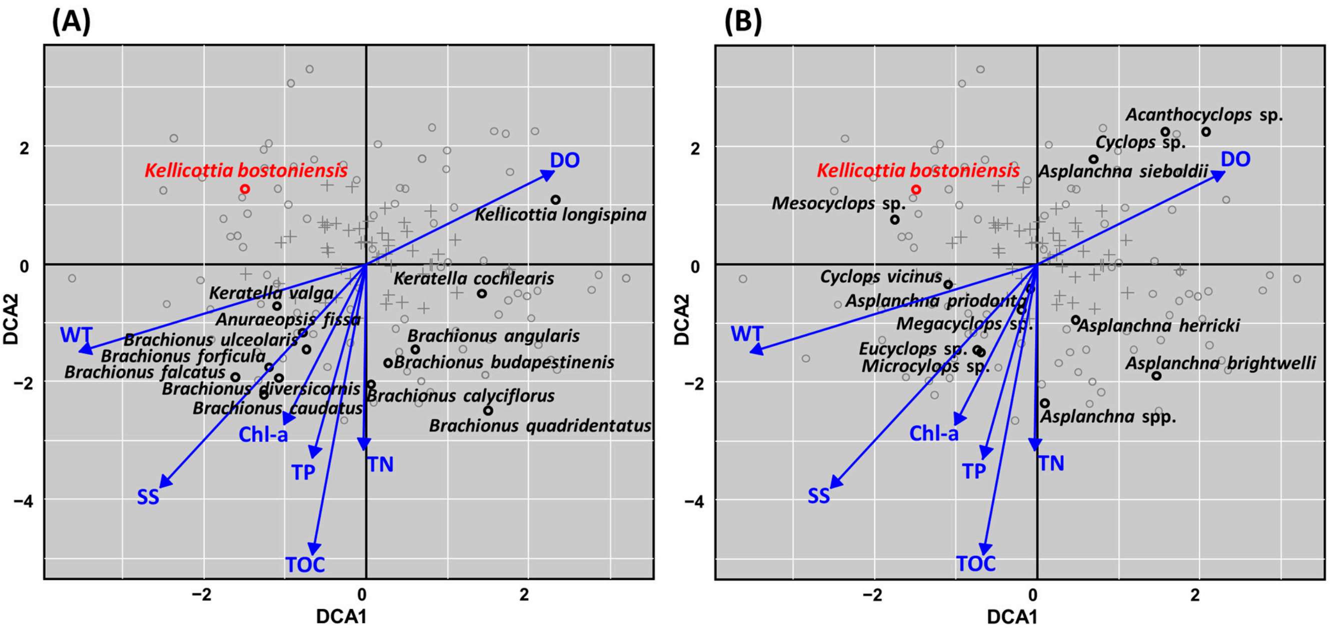

Figure 6. Detrended Correspondence Analysis (DCA) of *K. bostoniensis* abundance, zooplankton community, and their responses to environmental factors. (**A**) Graph showing only the potential competitor group. (**B**) Graph showing only the potential predator group. Environmental factors with $p < 0.05$ are represented. Red circle indicate *K. bostoniensis* and, black circles indicate the target species that assumed to potentially have a biological interaction with *K. bostoniensis* ((**A**) potential competitor, (**B**) potential predator). Grey circles indicate remaining observed species, and plus signs indicate sampling sites.

Cyclopoid copepods (*Cyclopoidae*) and rotifers of the genus *Asplanchna*, known predators of *K. bostoniensis* and other rotifers, were classified as potential predators and were plotted on the DCA plane (Figure 6B). Among the 12 predator species observed, the DCA plane showed that most species were primarily differentiated along the second axis. Excluding certain species, the majority exhibited a negative relationship with the second axis, indicating a positive influence from environmental factors representing the trophic state of the lakes. However, *Acantocyclops* sp., *Cyclops* sp., *Mesocyclops* sp., and *Asplanchna sieboldii* displayed negative relationships with these variables, differing from other potential predators. Among them, *Mesocyclops* sp. was positioned on the same plane as *K. bostoniensis*, showing a negative response to DO and a positive response to water temperature.

To compare the response patterns of *K. bostoniensis* and its potential competitor group to lake trophic states, TSI(TP) was calculated based on TP concentrations, and their abundances (log scale) were plotted (Figure 7). *K. bostoniensis* exhibited relatively high abundances in mesotrophic and lower-level eutrophic environments according to TSI(TP) but showed low abundances in oligotrophic and hypereutrophic environments. In contrast, the potential competitor group exhibited very high abundance in hypereutrophic environments. Despite showing substantial variability due to high residuals, the group displayed a pattern proportional to TSI(TP).

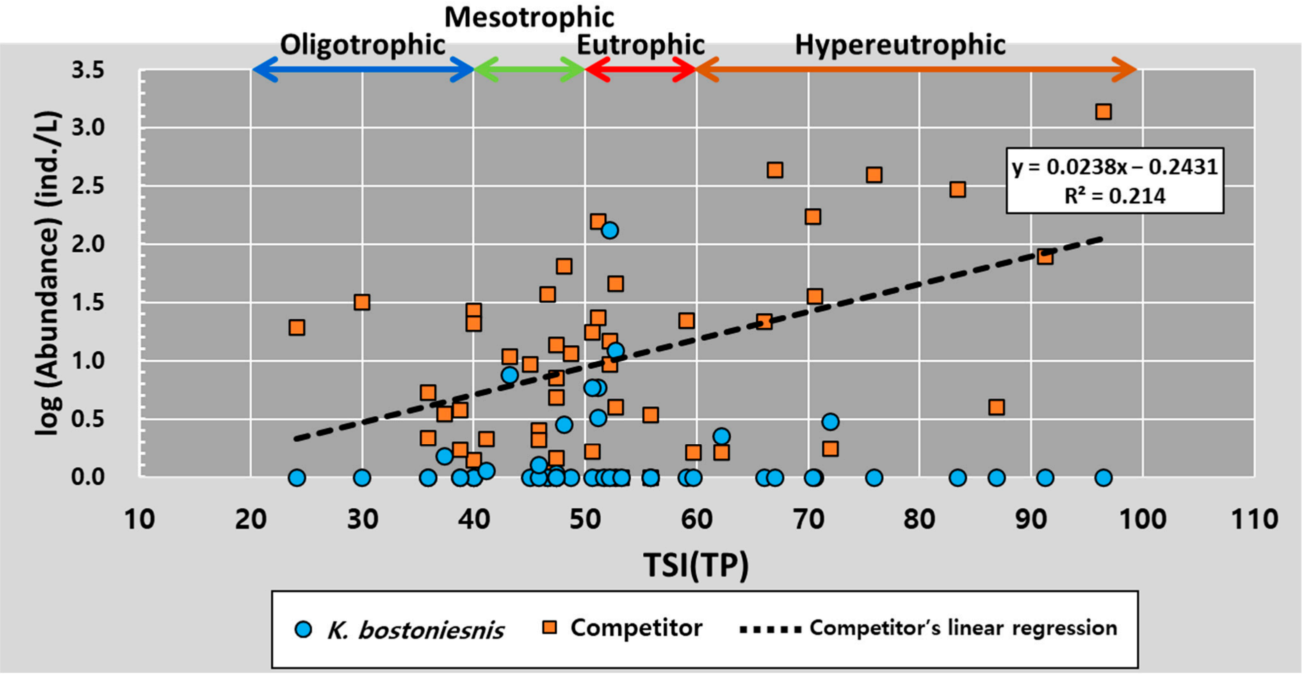

Figure 7. Responses of *K. bostoniensis* and the potential competitor group to TSI (TP). The dotted line represents the regression line for the potential competitor group in relation to TSI (TP). Oligotrophic: 20 < TSI < 40; Mesotrophic: 40 < TSI < 50; Eutrophic: 50 < TSI < 60; Hypereutrophic: 60 < TSI.

4. Discussion

The trophic state of a lake is a key variable determining the occurrence of *K. bostoniensis* [23,33–37]. In this study, TOC and TP were also analyzed to be closely associated with the presence/absence of *K. bostoniensis* (Figure 2). Furthermore, the multivariate analysis conducted to examine relationships with environmental factors revealed that the abundance of *K. bostoniensis* showed inverse correlation with variables representing the trophic state of the lakes (TOC, TN, TP, Chl-a) (Figure 6). However, when visualizing the univariate relationship between TSI(TP) and the abundance of *K. bostoniensis*, the species showed relatively low abundance or was absent in oligotrophic and hypereutrophic environments, while exhibiting high abundance in meso-eutrophic trophic conditions. Looking at past studies on the occurrence of *K. bostoniensis* along the TSI gradient, Macêdo, who studied lakes ranging from oligotrophic to eutrophic (TSI: 30–60), reported an inverse relationship between the calculated trophic state index (TSI) values of the lakes and the average abundance of *K. bostoniensis* [17]. However, Palazzo's study, conducted in oligotrophic environments with Chl-a concentrations below 2 μg/L, also found an inverse relationship between lake trophic status and the abundance of *K. bostoniensis* [14]. When summarizing the contrasting findings from previous studies, it suggests that *K. bostoniensis* and trophic status do not exhibit a linear relationship but rather a bell-shaped relationship, with the highest abundance occurring within a specific range. Our study, which analyzed a broad range of trophic states from oligotrophic to hypereutrophic environments (TSI: 24.1–96.4), provided meaningful insights by identifying the specific range of trophic conditions suitable for the habitation of *K. bostoniensis*. Considering numerous studies that reported the occurrence of *K. bostoniensis* within the mesotrophic to eutrophic range [22,23,36,37], the trophic state suitable for its habitation and population growth is determined to be within the meso-eutrophic range based on the results of this analysis. This finding is significant, as it differentiates the response patterns of *K. bostoniensis* from those of its potential competitors and predators within the community.

The response of potential competitors, categorized based on trophic state and habitat characteristics, to environmental factors revealed a consistent positive relationship with trophic state variables (TOC, TN, TP, Chl-a) along the second axis of the DCA, excluding *K. longispina* (Figure 6A). Additionally, the total abundance of species within the potential competitor group was found to be proportional to the TSI values in the surveyed lakes. This indicates that the difference in preferred environments between potential competitors and *K. bostoniensis* is related to the trophic state of the lakes. Many species within the potential competitor group were from the genus *Keratella* and *Brachionus*, which are known to dominate in eutrophic lakes [38,39]. Additionally, species with malleate trophi, including most rotifers and species of the potential competitor group, tend to increase in abundance as eutrophication indicators rise [24,40,41]. Although their abundance trends did not exhibit a strong linear relationship ($R^2 = 0.21$), most species showed high abundances in hypereutrophic lakes. This pattern of occurrence based on trophic state contrasts with the distribution of *K. bostoniensis*, which showed peak abundances in meso-eutrophic environments. These differences suggest that *K. bostoniensis* may prefer different habitat conditions compared to species within the potential competitor group, despite their functional similarities.

Rotifers exhibit different feeding characteristics depending on the structure of their trophi [42]. *K. bostoniensis* possesses malleate trophi, and species within this trophi group are known to gather food using their corona and then chew or cut it with their trophi for ingestion [43,44]. Representative genera with malleate trophi *Kellicottia*, *Brachionus*, and *Keratella* are all classified as polyphagous, known to commonly feed on fine detritus/organic aggregates, picoplankton, and nanoplankton [19–21]. However, their clearance rates for these food sources varied significantly. Bogdan's study comparing the clearance rates of *Keratella cochlearis* and *Kellicottia bostoniensis* revealed that *Keratella cochlearis* exhibited higher clearance rates than *Kellicottia bostoniensis* across all tracer cell types [45]. Similarly, Starkweather's research showed that *K. cochlearis* had higher clearance rates than *K. bostoniensis* for both live algae and heat-killed algae [46]. In another study by Starkweather, which extended the comparison to species within the genera *Brachionus*, it was found that species from the *Brachionus* genus also exhibited higher clearance rates than *K. bostoniensis* [47]. The physiological differences underlying the variation in feeding rates between *K. bostoniensis* and other species in the competitor group remain unknown. Factors such as differences in swimming speed [43] and the size range of ingestible food particles [20] may influence these differences. However, the specific reasons why *K. bostoniensis* exhibits uniquely lower feeding rates and efficiency compared to other species have yet to be elucidated. The low clearance rate of *K. bostoniensis* limits the maximum food concentration it can effectively utilize. Consequently, beyond a certain threshold food concentration (meso-eutrophic levels, according to the findings of this study), the population size of *K. bostoniensis* is expected to decrease.

In this study, rotifer predators from the genus *Asplanchna* and the order *Cyclopoida* were classified as the potential predator group for *K. bostoniensis* and analyzed (Figure 6B). However, most species within the predator group, similar to the potential competitor group, exhibited higher abundances in high-nutrient environments, demonstrating response patterns to environmental factors distinct from those of *K. bostoniensis*. Therefore, it is inferred that a tight predator–prey interaction between *K. bostoniensis* and its predators was not observed. *K. bostoniensis* has long spines, which it elongates further in environments with high predation pressure, serving as an effective defense mechanism against predators. This indicates that the population of *K. bostoniensis* is relatively independent of predation pressure compared to other rotifer species that serve as prey for the same predators. The results of this study suggest that there is no connection between the abundance of *K. bostoniensis* and the abundance of potential predators, and this disconnection can be inferred to result from its effective defensive adaptations. Some previous studies have shown that this independence from predation pressure can confer an advantage in apparent competition (a form of competition mediated by shared predators), resulting in a positive correlation between *K. bostoniensis* populations and predation pressure [22,23]. However, such a trend was not observed in this study. Meanwhile, an abundance of *Asplanchna* species and *Cyclopoida* is generally known to have a positive correlation with the trophic state of lakes [48–50]. This phenomenon occurs because, in addition to the general rotifers, including potential competitors, appearing in large numbers in high-nutrient lakes, alternative food sources such as phytoplankton are also present at high densities. In other words, the increase in prey density leads to a corresponding rise in the abundance of predators. Therefore, these predators' abundance increases or decreases in response to the total biomass of prey, rather than specifically following changes in that of *K. bostoniensis*.

In conclusion, this study indicates that the population size of *K. bostoniensis* is more strongly influenced by environmental factors than by the population size of potential competitors or predators. As *K. bostoniensis* overlaps in functional groups with potential competitors, the species identified as competitors generally exhibited environmental responses characteristic of general rotifer species. However, this non-native species displayed preferences for different habitat conditions. The unique responses of *K. bostoniensis* to environmental factors have been noted in some previous studies, and our results highlight its distinct reaction to the trophic state of lakes—an indirect indicator of its feeding environment. Whether this difference in habitat preference arises from direct avoidance of competition when *K. bostoniensis* enters established native communities or from an evolutionary process of niche differentiation remains unclear from our study. To elucidate the mechanisms underlying the specificity of *K. bostoniensis*, further research is required that considers vertical distribution within habitats, accumulates data across diverse and broad environmental ranges, and integrates physiological and genetic approaches. What is clear, however, is that its distinctive responses reduce interactions with native communities, implying that the direct impact of *K. bostoniensis* on native communities after establishment may be minimal. At the same time, these traits suggest that the biological filter—a resistance mechanism of native communities—may have little effect in resisting the introduction of *K. bostoniensis*. Therefore, the findings of this study provide significant evidence for explaining the widespread (or ongoing) distribution of *K. bostoniensis* across continents.

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Appendix A

Table A1. Physical properties of the studied lake.

Lake No.	Latitude	Longitude	Basin Area	Total Water Storage	Effective Storage	Height of Dike	Reservoir LENGTH
			(ha)	($\times 10^3$ m^3)	($\times 10^3$ m^3)	(m)	(m)
R-A-1	36.0656	127.6583	510	784	753	15.4	187
R-A-2	36.2845	127.3072	1375	2846	2821	20.0	187
R-A-3	36.3009	128.0128	2200	5773	5679	23.7	276
R-A-4	36.6027	127.2312	1620	5284	4868	17.0	226
R-A-5	36.4906	127.8435	4226	8236	8163	49.0	170
R-A-6	36.8669	127.3996	8479	26,618	26,372	28.7	401
R-A-7	36.8980	127.5712	706	14,329	13,907	33.0	237
R-A-8	36.8685	127.5998	3655	8791	8690	27.2	205
R-A-9	36.7408	127.4060	3310	7590	6390	26.7	202
R-A-10	36.2149	128.0208	1000	2206	2205	21.7	123
R-A-11	35.9930	126.8480	144	254	241	5.5	200
R-A-12	35.9504	127.0911	104	342	342	5.0	150

Appendix B

Table A2. Environmental factors for the study lakes (mean ± standard deviation), (minimum–maximum).

Lake No.	WT	pH	DO	TOC	COD	TN	TP	SS	Chl-a
	°C		mg/L	mg/L	mg/L	mg/L	mg/m^3	mg/L	mg/m^3
R-A-1	18.0 ± 5.0	7.9 ± 0.3	5.2 ± 4.4	5.3 ± 0.5	9.0 ± 1.7	1.5 ± 0.5	26.0 ± 8.4	4.3 ± 2.9	13.2 ± 10.4
	11.4–23.5	7.5–8.1	1.2–10.9	4.9–5.9	7.6–11.2	1.0–2.2	19.0–36.0	0.9–7.0	1.9–27.0
R-A-2	17.4 ± 4.7	7.7 ± 0.5	8.9 ± 4.2	4.4 ± 1.0	7.5 ± 1.9	1.2 ± 0.2	52.5 ± 40.5	8.9 ± 6.1	20.4 ± 15.8
	11.6–23.1	6.9–8.2	4.2–14.4	3.2–5.6	4.8–9.0	0.9–1.3	12.0–99.0	1.3–14.9	3.3–41.4
R-A-3	15.1 ± 6.1	7.2 ± 0.2	7.2 ± 3.3	3.3 ± 0.3	5.6 ± 1.2	0.9 ± 0.1	18.3 ± 6.9	2.4 ± 0.8	11.3 ± 8.5
	8.1–22.3	6.9–7.4	4.4–11.4	2.9–3.6	4.6–7.2	0.8–1.0	11.0–27.0	1.7–3.4	3.4–22.6
R-A-4	20 ± 5.9	7.6 ± 1.0	9.7 ± 3.3	3.4 ± 0.4	6.4 ± 1.2	1.6 ± 0.4	46.5 ± 43.5	9.7 ± 8.5	13.4 ± 13.0
	12.0–25.9	6.9–9.1	4.9–12.1	3.0–4.0	4.8–7.6	1.4–2.2	12.0–110.0	4.0–22.3	4.2–32.6
R-A-5	18.1 ± 8.1	7.3 ± 0.2	8.9 ± 2.8	2.0 ± 0.2	3.2 ± 0.3	0.8 ± 0.5	10.3 ± 7.1	1.3 ± 1.2	4.8 ± 2.4
	7.3–25.0	7.0–7.5	6.9–13.0	1.7–2.3	2.8–3.6	0.3–1.4	4.0–20.0	0.5–3.1	2.3–8.1
R-A-6	19.0 ± 8.5	8.0 ± 0.9	9.4 ± 4.1	3.1 ± 0.5	5.6 ± 0.9	1.2 ± 0.3	20.0 ± 7.1	3.2 ± 0.8	14.1 ± 3.3
	7.0–25.8	7.4–9.4	4.3–13.3	2.6–3.6	4.6–6.7	1.0–1.6	12.0–29.0	2.4–4.4	11.3–18.8
R-A-7	15.5 ± 8.2	8.0 ± 0.7	10.3 ± 3.2	3.7 ± 0.3	6.0 ± 0.7	1.1 ± 0.3	20.0 ± 3.6	3.2 ± 0.7	14.6 ± 1.7
	5.9–24.2	7.5–9.1	6.3–13.2	3.4–4.1	5.4–7.0	0.6–1.3	17.0–25.0	2.7–4.2	13.1–17.1
R-A-8	15.6 ± 8.0	7.9 ± 0.5	8.9 ± 2.4	3.1 ± 0.4	5.1 ± 1.1	1.2 ± 0.3	19.0 ± 11.0	3.2 ± 2.7	8.6 ± 5.4
	6.6–25.8	7.2–8.4	6.6–11.9	2.7–3.4	4.0–6.6	0.9–1.6	9.0–29.0	0.7–6.2	3.5–15.7
R-A-9	17.7 ± 6.7	8.4 ± 0.6	7.5 ± 4.7	4.6 ± 0.7	8.7 ± 2.4	1.8 ± 1.0	26.0 ± 21.3	7.3 ± 5.3	15.3 ± 10.5
	9.7–25.2	8.0–9.2	0.7–11.3	3.7–5.2	5.8–10.6	0.7–3.0	9.0–56.0	1.0–12.4	5.5–28.4

Table A2. *Cont.*

Lake No.	WT	pH	DO	TOC	COD	TN	TP	SS	Chl-a
	°C		mg/L	mg/L	mg/L	mg/L	mg/m^3	mg/L	mg/m^3
R-A-10	18.7 ± 8.0	7.8 ± 0.9	7.9 ± 5.2	5.3 ± 0.6	7.5 ± 0.6	1.1 ± 0.4	34.3 ± 13.7	3.8 ± 3.6	10.8 ± 2.0
	9.2–26.7	7.0–9.0	1.1–13	4.6–5.8	7.0–8.2	0.8–1.7	20.0–47.0	1.0–9.1	8.5–12.9
R-A-11	20.8 ± 5.7	7.6 ± 0.3	7.3 ± 1.6	6.2 ± 2.4	10.5 ± 4.4	1.7 ± 0.9	122.0 ± 95.1	18.9 ± 12.2	20.3 ± 18.3
	14.5–25.7	7.3–7.9	6.2–9.7	4.5–9.7	6.4–16.5	0.7–3.0	22.0–243.0	2.3–31.3	4.3–45.5
R-A-12	20.7 ± 5.0	7.5 ± 0.3	7.6 ± 2.0	7.8 ± 1.5	13.2 ± 3.2	2.6 ± 1.5	357.5 ± 209.6	10.5 ± 6.5	65.6 ± 51.3
	15.1–26.0	7.1–7.8	5.4–9.8	6.5–9.9	10.0–16.1	0.8–4.5	100.0–601.0	4.4–19.7	29.2–141

Appendix C

Table A3. Abundance of zooplankton in the study lakes categorized by taxonomic and functional groups (mean ± standard deviation), (minimum–maximum).

Lake No.	*K. bostoniensis*	*K. longispina*	Competitor	Predator	Rotifer	Cladoceran	Copepod
	ind./L	ind./L	ind./L	ind./L	ind./L	ind./L	ind./L
R-A-1	0.0 ± 0.0	0.0 ± 0.0	9.1 ± 18.1	117.1 ± 162.2	158.9 ± 201.1	11.2 ± 18.1	8.3 ± 12.6
	0.0–0.0	0.0–0.0	0.0–36.3	0.1–344.8	0.3–423.0	0.0–38.2	0.3–27.1
R-A-2	0.6 ± 1.1	0.0 ± 0.0	92.8 ± 83.7	11.0 ± 6.6	183.5 ± 148.5	15.1 ± 11.4	23.4 ± 11.4
	0.0–2.3	0.0–0.0	20.0–172.2	3.4–19.2	53.0–313.9	1.8–28.0	10.8–36.6
R-A-3	1.7 ± 3.3	0.0 ± 0.0	2.8 ± 4.8	7.2 ± 7.3	26.1 ± 26.4	8.5 ± 8.6	35.9 ± 36.2
	0.0–6.6	0.0–0.0	0.0–10.0	2.9–18.2	3.3–55.6	2.0–21.2	15.7–90.1
R-A-4	33.8 ± 66.3	0.0 ± 0.0	10.8 ± 11.7	10.8 ± 10.3	147.4 ± 139	17.5 ± 9.9	57.7 ± 25.4
	0.0–133.2	0.0–0.0	0.8–26.0	0.0–20.4	19.2–309.2	5.2–27.3	34.0–89.0
R-A-5	0.0 ± 0.0	7.7 ± 13.7	14.7 ± 12.8	2.3 ± 3.5	150.6 ± 221.5	4.1 ± 4.2	32.1 ± 33.2
	0.0–0.0	0.0–28.2	2.8–31.0	0.1–7.5	35.4–482.9	0.0–9.9	4.7–80.1
R-A-6	3.3 ± 5.3	0.0 ± 0.0	17.1 ± 31.2	8.8 ± 9.1	69.1 ± 74.4	15.0 ± 15.3	26.9 ± 31.9
	0.0–11.2	0.0–0.0	0.4–63.8	2.0–21.6	13.3–178.4	0.1–35.9	1.6–73.4
R-A-7	1.2 ± 2.4	0.0 ± 0.0	9.8 ± 6.5	7.6 ± 8.2	76.6 ± 59.5	9.5 ± 9.1	30.8 ± 47.5
	0.0–4.9	0.0–0.0	1.5–16.8	0.1–17.0	7.6–137.6	0.6–21.2	2.2–101.4
R-A-8	0.1 ± 0.3	0.0 ± 0.0	15.0 ± 20.1	12.1 ± 11.1	192.6 ± 273.7	56.3 ± 97.1	54.8 ± 47.0
	0.0–0.5	0.0–0.0	2.5–44.9	1.5–23.2	21.8–596.3	0.5–201.6	14.4–105.6
R-A-9	1.6 ± 2.3	0.0 ± 0.0	6.3 ± 10.7	1.0 ± 0.8	51.1 ± 88.4	5.4 ± 4.9	11.8 ± 11.9
	0.0–4.9	0.0–0.0	0.6–22.4	0.0–2.0	1.4–183.7	0.6–12.2	0.0.–25.1
R-A-10	0.0 ± 0.0	0.0 ± 0.0	6.6 ± 10.0	9.6 ± 5.4	64.0 ± 73.8	8.7 ± 5.7	47.8 ± 31.7
	0.0–0.0	0.0–0.0	0.6–21.4	4.5–17.2	9.4–173.1	2.9–14.0	14.7–75.3
R-A-11	0.0 ± 0.0	0.0 ± 0.0	284.8 ± 191.4	49.0 ± 47.9	611.2 ± 423.7	19.4 ± 25.8	108.4 ± 73.6
	0.0–0.0	0.0–0.0	10.6–434.2	0.3–113.7	37.8–943.5	0.7–57.3	19.5–197.4
R-A-12	0.0 ± 0.0	0.0 ± 0.0	377.6 ± 678	7.0 ± 9.1	746.0 ± 1231.4	1.8 ± 2.8	60.7 ± 42.2
	0.0–0.0	0.0–0.0	3.0–1393.6	0.4–19.8	7.6–2583.0	0.0–6.1	22.2–105.7

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