









A decade of invasion: distribution patterns and temperature influence on *Kellicottia bostoniensis* (Rousselet, 1908), in the Upper Uruguay River Basin

Uma década de invasão: padrões de distribuição e influência da temperatura sobre *Kellicottia bostoniensis* (Rousselet, 1908), na bacia do Alto Rio Uruguai

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Abstract: Aim: This study reports the spread dynamics of the non-native species *Kellicottia bostoniensis* across all reservoirs in the Upper Uruguay River Basin, a decade after its initial recorded occurrence. Additionally, it assesses the role of temperature in shaping its distribution within this subtropical system. **Methods:** Spatial and temporal variations in *K. bostoniensis* density and environmental parameters were analyzed over a 12-month period. Generalized Linear Models (GLMs) were applied to evaluate the relationship between environmental parameters and species density, providing insights into the key drivers of its distribution. **Results:** The connectivity among reservoirs within the cascade system of the Upper Uruguay River has facilitated the continued spread of the non-native species *K. bostoniensis*. The detection of this species in all reservoirs a decade after its first recorded occurrence suggests its successful establishment and widespread distribution within the system. The observed high densities were likely influenced by the consistently low temperatures characteristic of subtropical regions, particularly those associated with the Serra Geral Mountains, with a more pronounced effect during colder months. **Conclusions:** The widespread distribution of *K. bostoniensis* across the Upper Uruguay River Basin underscores its potential for further expansion into similar environments, driven by a combination of environmental and anthropogenic influences. The species' ability to disperse and establish in diverse habitats highlights the critical need for continuous monitoring and management strategies to mitigate its spread and prevent additional ecological invasions.

Keywords: bioinvasion; non-native species; rotifer; subtropical reservoirs.



Resumo: Objetivo: Este estudo relata a dinâmica de propagação da espécie não nativa *K. bostoniensis* em todos os reservatórios da Bacia do Alto Rio Uruguai, uma década após sua ocorrência inicial registrada. Além disso, avalia o papel da temperatura na formação de sua distribuição dentro deste sistema subtropical. **Métodos:** Variações espaço-temporais na densidade de *K. bostoniensis* e parâmetros ambientais foram analisados ao longo de um período de 12 meses. Modelos Lineares Generalizados (GLMs) foram aplicados para avaliar a relação entre fatores ambientais e densidade de espécies, fornecendo insights sobre os principais impulsionadores de sua distribuição. **Resultados:** A conectividade entre reservatórios dentro do sistema de cascata do Alto Rio Uruguai facilitou a propagação contínua da espécie não nativa *K. bostoniensis*. A detecção desta espécie em todos os reservatórios uma década após sua primeira ocorrência registrada, sugere seu estabelecimento bem-sucedido e ampla distribuição dentro do sistema. As altas densidades observadas foram provavelmente influenciadas pelas temperaturas consistentemente baixas características de regiões subtropicais, particularmente aquelas associadas às Montanhas da Serra Geral, com um efeito mais pronunciado durante os meses mais frios. **Conclusões:** A ampla distribuição de *K. bostoniensis* pela Bacia do Alto Rio Uruguai ressalta seu potencial para expansão em ambientes semelhantes, impulsionado por uma combinação de influências ambientais e antropogênicas. A capacidade da espécie de se dispersar e se estabelecer em habitats diversos destaca a necessidade crítica de estratégias contínuas de monitoramento e gerenciamento para mitigar sua disseminação e prevenir invasões ecológicas adicionais.

Palavras-chave: bioinvasão; espécies não nativas; rotífero; reservatórios subtropicais.

1. Introduction

The primary filter for preventing the spread of non-native species is typically geographic isolation (Etherington, 2015). However, anthropogenic activities have the potential to disrupt this natural barrier (Parkes & Duggan, 2012), facilitating the dispersion of non-native species (Buckley & Catford, 2016). Biological invasion is one of the most common causes of biodiversity loss, as it can significantly alter the structure of native communities, thereby affecting many ecosystem functions (Oliveira et al., 2019; Macêdo et al., 2020). In recent decades, biological invasions within zooplankton communities have been reported in temperate and tropical regions, spanning environments with diverse environmental characteristics (Lopes et al., 1997; Serafim-Júnior et al., 2003; Simões et al., 2009; Bomfim et al., 2016).

The non-native species *Kellicottia bostoniensis* (Rousselet, 1908) is a rotifer from North America that is widely distributed in reservoirs, lakes and rivers across Asia and Europe (Balvay, 1994; Pejler, 1998; Segers, 2007; Lazareva et al., 2013). In South America, the species was recorded in the La Plata basin of Argentina, including the Middle and Lower Uruguay River basins, as well as the Middle Paraná River basin (José de Paggi, 2002; Martins et al., 2020). The introduction of *K. bostoniensis* in South America is an example of a biological invasion within freshwater ecosystems linked to the transport

of ballast water from North America to Brazil (Gray et al., 2007; Latini et al., 2016).

The first occurrence of *K. bostoniensis* in Brazil was recorded in 1997 in the Segredo reservoir, located in the state of Paraná (Lopes et al., 1997). Over the course of two decades, the species has been observed in various regions across Brazil, including the midwestern, southeastern, southern, and northeastern areas (Garraffoni & Lourenço, 2012; Bomfim et al., 2016; Picapedra et al., 2016; De-Carli et al., 2017; Macêdo et al., 2020; Gomes et al., 2022; Ferreira-Junior et al., 2023).

The distribution of *K. bostoniensis* in various regions worldwide may reflect the adaptation of this species to different climates (Bomfim et al., 2016; Mantovano et al., 2021; Zhdanova et al., 2019).

Several studies have demonstrated the capacity of this species to colonize aquatic environments characterized by a wide range of environmental conditions, such as water temperature, pH, dissolved oxygen concentration, and differing trophic states (Bezerra-Neto et al., 2004; Zhdanova & Dobrynin, 2011; Zhdanova et al., 2016; Macêdo et al., 2020; Gomes et al., 2022).

The dispersal potential of this species seems to be associated with multiple mechanisms, including environmental and anthropogenic vectors, such as passive transport by waterfowl, attachment to fish gills, and boat traffic (Rocha et al., 2011; Lazareva & Zhdanova 2014; Zhdanova et al., 2016; Syarki, 2019). In addition, a set of biological characteristics,

including small body size, the presence of dormant eggs, the development of long spines to avoid fish predation, and broad tolerance to varying trophic conditions, are considered key life history traits that likely contribute to its spread and potential establishment (Macêdo et al., 2020).

In the State of Santa Catarina, the first occurrence of *K. bostoniensis* was recorded in the Itajaí-Açu River in 2003 (Serafim-Júnior et al., 2006). Two years later, the invasion of this exotic species was also documented in two reservoirs of the Upper Uruguay River Basin: Itá (Hermes-Silva et al., 2008) and Machadinho (Guereschi et al., 2012; Martins et al., 2020). Given *K. bostoniensis*' dispersal ability and the characteristics of the cascading reservoir system in the Upper Uruguay River Basin, its spread throughout the system seems inevitable. This study reports the occurrence of *K. bostoniensis* in the Upper Uruguay River Basin, emphasizing the role of absent physical barriers in its dispersal and evaluating the influence of environmental parameters on its distribution.

2. Methods

The Upper Uruguay River Basin (27° 38' 22.2" S, 51° 01' 07.1" W) is located entirely in Brazilian territory, in the "Serra Geral", bordering the states of Santa Catarina and Rio Grande do Sul, where the climate is humid subtropical Cfa (Peel et al., 2007). It has a drainage area of 76,209 km² and rugged relief (Zaniboni-Filho & Schulz, 2003).

Five reservoirs installed in the cascade system were studied in this basin (Figure 1), namely Campos Novos (CN), Barra Grande (BG), Machadinho (MA), Itá (ITA) and Foz do Chapecó (FC).

Sampling was conducted monthly between December 2018 and November 2019 at five sites in each reservoir, totaling 300 samples. Water temperature ($\pm 0.2^{\circ}\text{C}$ accuracy and 0.1°C resolution), electrical conductivity ($\pm 0.2 \mu\text{S cm}^{-1}$ accuracy and $0.1 \mu\text{S cm}^{-1}$ resolution), dissolved oxygen ($\pm 0.2 \text{ mg l}^{-1}$ accuracy and 0.1 mg l^{-1} resolution) and pH (± 0.004 accuracy and 0.001 resolution) were measured *in situ* using a multiparameter meter (YSI Model 85).

Zooplankton samples were collected by horizontal trawls using a 68 μm mesh plankton net. Samples were collected from submerged trawls at 1 m depth for 2 min at each sampling location (Guevara et al., 2009). A calibrated flowmeter was attached between the center and the rim of the mouth of the trawl net to estimate the volume of water filtered (water filtered mean = 1.95 m^3). Carbonated water was added to reduce the shrinkage of the organisms' bodies, and the samples were immediately preserved in buffered formaldehyde solution (final concentration 4%). Samples were analyzed using a Sedgewick-Rafter chamber on a light microscope at 100x magnification (Leica MZ6 model) with an attached digital camera. The density of *K. bostoniensis* was estimated by analyzing at least 10% of each sample (100 ml) (Bottrell et al., 1976),

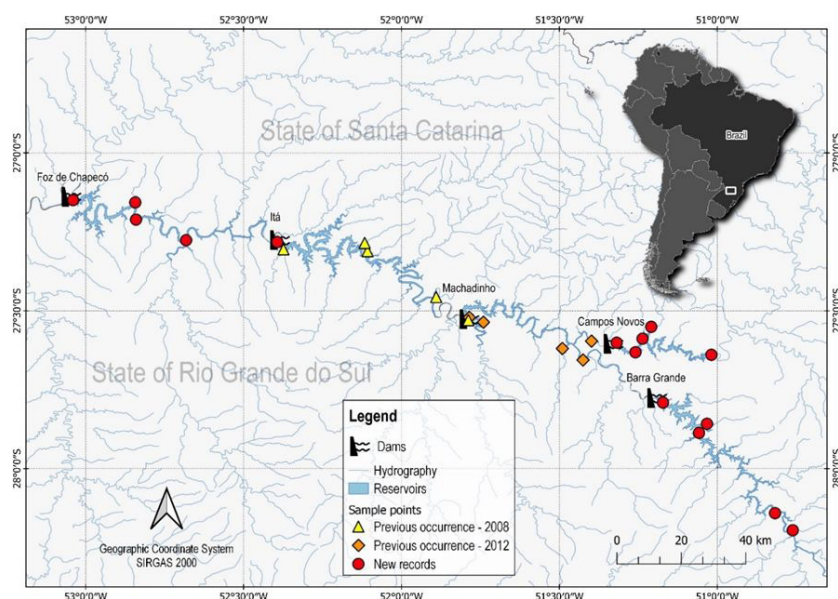


Figure 1. Map of the Upper Uruguay River Basin with the *Kellicottia bostoniensis* register. Previous record: Itá Reservoir in 2008 - yellow triangles, and Machadinho Reservoir in 2012 - orange diamonds. New record: Campos Novos, Barra Grande and Foz do Chapecó reservoirs - red circles.

and the density was expressed in individuals per cubic meter (org. m⁻³). Species identification was done according to Koste (1978) and their taxonomy and distribution according to Segers (2007).

To determine the frequency of occurrence of the species, a constancy index (CI) was used, which considers the number of samples in which the species were present in relation to the total number of samples. This was calculated according to the formula $CI = p \times 100 / P$, where p is the number of samples in which the species were present, and P represents the total number of samples. Species were then classified as constant ($CI > 80\%$), abundant ($50\% < CI < 80\%$), common ($20\% < CI < 50\%$), or rare ($CI < 20\%$) (Dajoz, 2005).

Differences in *K. bostoniensis* densities between reservoirs and months were assessed using the non-parametric Kruskal-Wallis test. A pairwise test for multiple comparisons of ranked data (Dunn's post hoc test) with a Bonferroni correction was performed when a significant difference ($p \leq 0,05$) was detected using the R package PMCMRplus (Dinno, 2017). A Spearman correlation analysis was performed to assess the magnitude and direction of the relationship between environmental parameters and *K. bostoniensis* density. Additionally, generalized linear models (GLMs) were used to examine causal relationship between environmental parameters and *K. bostoniensis* density using grouped data from all reservoirs. We applied the Gaussian probability distribution model with a link identity function, using the mass-based AIC model selection approach (Venables & Ripley 2002). Model simplification was considered for models with the lowest AIC values if $\Delta AIC < 4$ (Bolker, 2008). For all statistical analyses, R ver. 4.2.1 (R Core Team, 2022) was used.

3. Results

Three out of the five reservoirs evaluated in the Upper Uruguay River Basin recorded new occurrences of *K. bostoniensis*: Barra Grande (28° 11' 43,0" S, 50° 45' 39,8" W), Campos Novos (27° 38' 26,8" S, 51° 01' 14,0" W), and Foz do Chapecó (27° 16' 48,7" S, 52° 41' 08,4" W) reservoirs. The specimens were deposited in the scientific collections of the Laboratório de Peixes de Água Doce (LAPAD) at the Universidade Federal de Santa Catarina (Figure 2).

Although *K. bostoniensis* was reported for the first time in three reservoirs sampled in this study (Barra Grande, Campos Novos and Foz do Chapecó reservoirs), the non-native species was found in the samples from all five reservoirs in the Upper

Uruguay River Basin. *K. bostoniensis* was found in 53.72% of the total samples ($n = 300$). The species' occurrence was classified as frequent (50-80% occurrence) in Barra Grande, Foz do Chapecó, Machadinho and Itá, and as common (20-50% occurrence) in Campos Novos (Table 1).

Barra Grande exhibited the highest density, with a mean of 2,041.9 org.m⁻³, followed by Itá and Machadinho (Table 1; Figure 3). The lowest densities were recorded in Foz do Chapecó and Campos Novos reservoirs, with a mean of 249.5 and 232.8 org.m⁻³, respectively (Table 1; Figure 3). Significant differences in *K. bostoniensis* densities were observed between the studied reservoirs ($H = 10.8$, $df = 4$, $p = 0.03$), particularly in Barra Grande, which differed from all other reservoirs:



Figure 2. *Kellicottia bostoniensis* (Rousselet, 1908), a non-native rotifer, sampled in the Barra Grande (BG) reservoir located in the Upper Uruguay River Basin in Santa Catarina state. The image was taken with a light microscope (10x).

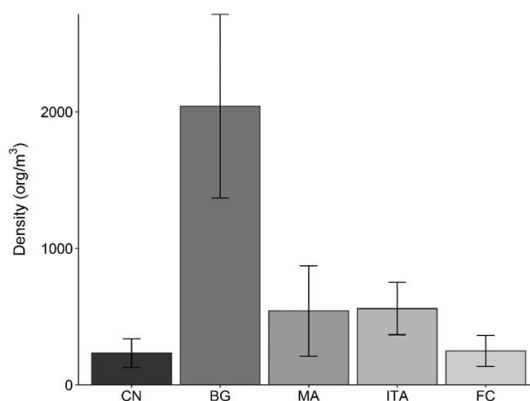


Figure 3. Log-transformed density of *Kellicottia bostoniensis* recorded in five reservoirs of the Upper Uruguay River Basin: CN = Campos Novos, BG = Barra Grande, ITA = Itá, MA = Machadinho and FC = Foz do Chapecó.

Campos Novos ($H = 3.00$, $p = 0.003$), Foz do Chapecó ($H = 2.52$; $p = 0.01$) and Machadinho ($H = 1.99$; $p = 0.04$).

In addition, the reservoirs showed significant differences in environmental parameters (Table 2), with the exception of water temperature (WT; $H = 8.3$, $p = 0.08$). Spearman's correlation coefficient revealed significant relationships between *K. bostoniensis* density and environmental parameters ($p < 0.05$), with WT being the only parameter that showed a moderate ($r > 0.5$) negative correlation with species density ($r = -0.6$, $p < 0.001$; Table 2).

Kellicottia bostoniensis density exhibited temporal variation throughout the study period ($H = 120.23$, $df = 11$, $p < 0.001$), with significant differences in density observed between all months ($p < 0.01$; Data A – available in https://docs.google.com/document/d/1nv3z0LesNlyjj_vY5KtweSolaEZO4OAN/edit?usp=drive_link&ouid=116420406885365764999&rtfpof=true&sd=true). A notable increase in mean density was recorded during the winter months, particularly in June ($1,474.8 \text{ org. m}^{-3}$), July ($1,854.8 \text{ org. m}^{-3}$) and August ($2,474.6 \text{ org. m}^{-3}$)

(Figure 4). The best GLM model, which included WT, DO and EC, had a ΔAIC of 1.75. Of these variables, only water temperature significantly influenced species density, exhibiting a negative effect on density increase ($df = 294$, $p = 0.003$).

4. Discussion

The connectivity among reservoirs within the Upper Uruguay River's cascade system has facilitated the continued spread of the non-native species *K. bostoniensis*. This expansion was likely driven by a combination of environmental and anthropogenic factors, as indicated by the spatial distribution of reservoirs previously reported to harbor the species (Hermes-Silva et al., 2008; Guereschi et al., 2012; Martins et al., 2020).

Reservoirs organized in a cascade system are particularly vulnerable to non-native species invasion and have been extensively studied for their role in facilitating the spread of invasive species (Rocha et al., 2011; Pessoto & Nogueira, 2018). In the Upper Uruguay River Basin, the connectivity

Table 1. Frequency of occurrence (FO%) along with the corresponding classification and descriptive statistic of *Kellicottia bostoniensis* density (org/m^3) in the reservoirs of the upper Uruguay River Basin (Mean, SD = standard deviation, Min = minimum and Max = maximum).

Analysis	Barra Grande	Campos Novos	Machadinho	Itá	Foz do Chapecó
FO	65.5	43.3	55.9	53.3	50.8
Class	Frequent	Common	Frequent	Frequent	Frequent
Density					
Mean	2041.9	232.8	541.5	559.0	249.5
±SD	± 5090.7	± 807.87	± 2518.9	± 14736.2	± 864.9
Min-max	0–22390	0–5410	0–18990	0–9800	0–4910

Table 2. Descriptive statistic (Mean, Sd = standard deviation, Min = minimum and Max = maximum) of physical and chemical parameters and statistical test results (Kruskal-Wallis and Spearman correlation with p-value) in the studied reservoirs in the Upper Uruguay River Basin.

Variables	Statistics	Reservoirs					Kruskal-test (p-value)	Spearman correlation with densitie
		Campos Novos	Barra Grande	Machadinho	Itá	Foz do Chapecó		
WT (°C)	mean ± SD	21.6± 3.8	21.6± 3.9	22.8±4.0	23.2± 4.2	22.8± 3.4	H=8.3	r=-0.6
	min - max	14.0-27.3	15.2 - 31.0	15.4 – 30.6	16.4 - 31.9	17.3 - 30.7	p =0.08	p<0.001
DO (mg. L ⁻¹)	mean ± SD	7.4±1.2	7.19±0.9	7.45±1.1	7.3±1.5	6.71±1.1	H= 15.6	r=0.2
	min - max	4.6-9.9	4.7 - 9.6	5.2 – 9.4	4.2 - 13.1	4.1 - 9.5	p =0.003	p <0.001
EC (µS. cm ⁻¹)	mean ± SD	40.7±7.7	29.6±5.8	42.4±12.1	70.9±52.1	50.5±4.2	H= 142.6	r=-0.3
	min - max	28.6-58.7	15.8– 59.3	22.9- 75.0	4.0- 306.8	41.2- 58.1	p<0.001	p<0.001
pH	mean ± SD	7.2±0.7	7.1±0.9	7.4±0.7	7.3±0.6	6.9±0.4	H= 33.37	r=-0.15
	min - max	6.3-10.4	6.4- 11.4	6.3– 9.5	6.13- 9.0	6.2- 8.1	p<0.001	p=0.01
Secchi transp. (cm)	mean ± SD	1.7±0.7	2.0±0.8	1.9±0.6	1.5±0.6	1.5±0.6	H= 29.92	r=-0.21
	min - max	0.7-3.7	0-3.5	0.6-3.6	0.3-3.0	0-3.8	p<0.001	p<0.001

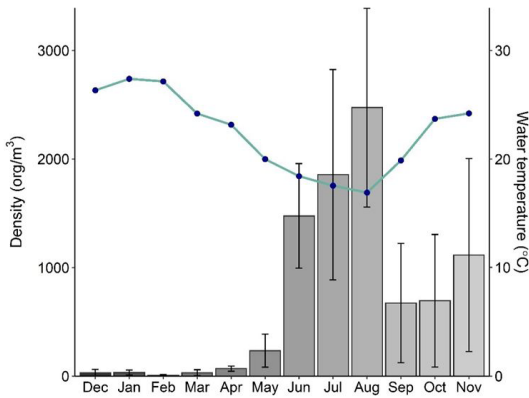


Figure 4. Mean density (grey bars) and standard deviation of *Kellicottia bostoniensis*, along with water temperature (blue dotted line) during the study period (December 2018 to November 2019) in the Upper Uruguay River Basin.

between these reservoirs was a key factor driving the dispersal and distribution of *K. bostoniensis* in the cascading system.

The presence of this non-native species in three reservoirs, a decade after its first recorded occurrence in the Upper Uruguay River cascade system (Hermes-Silva et al., 2008), can be attributed to both the absence of monitoring studies during that period and the influence of dispersal vectors such as waterfowl, fish, and recreational boating activities. While waterfowl and other animal vectors may contribute to dispersal (Zhdanova et al., 2016; Hessen et al., 2019), their impact is limited compared to human-mediated activities, like boat movements, which provide a means for the long-distance dispersal of zooplankton (Syarki, 2019; Havel & Stelzleni-Schwent, 2000).

Furthermore, the Cascading Reservoir Continuity Concept (include the reference here) highlights changes in water quality and composition, as well as in the structure of the original biodiversity along the river continuum (Barbosa et al., 1999). These changes facilitate biological invasions (Havel et al., 2005) and could be associated with the spread of the non-native species along the studied system.

The high frequency of *K. bostoniensis* occurrence across all reservoirs in the Upper Uruguay River Basin indicates that the species is both common and widespread within this system. This distribution pattern further underscores its broad ecological adaptability to varying environmental conditions, a characteristic already reported in other studies (Zhdanova et al., 2019; Macêdo et al., 2020; Martins et al., 2020; Mantovano et al., 2021).

Both the intrinsic traits of the invading species and the ecological characteristics of the invaded environment contribute to its successful establishment and expansion (Espínola & Júlio Junior, 2007). In this context, the frequency of occurrence serves as an important ecological indicator of the successful establishment of a non-native species in certain environments, even at low densities, such as those registered in the Campos Novos and Foz do Chapecó reservoirs, where *K. bostoniensis* was classified as a common species.

Our findings revealed the presence of the non-native species across all reservoirs within the system, with highly variable densities. However, significant differences were also detected in the environmental parameters among the sites, except for water temperature, highlighting the system's heterogeneity. The environmental heterogeneity of the cascading system in the Upper Uruguay River Basin, previously reported by Lopes et al. (2024) and further corroborated by this study, underscores the species' broad ecological tolerance and successful establishment throughout the system.

Several studies have shown that *K. bostoniensis* exhibits a broad tolerance to diverse limnological and climatic conditions, which facilitates its persistence and expansion in various environments (Macêdo et al., 2020; Mantovano et al., 2021). A scientometric analysis conducted across various regions worldwide revealed that Europe had the highest average abundance of *K. bostoniensis*, with 73,376.3 ind./m³, followed by South America with 64.69 ind./m³, and North America with 10.97 ind./m³ (Bomfim et al., 2016). However, studies conducted in tropical regions of South America have recorded even higher averages than those reported in the aforementioned study. The highest abundances were 1779 ind./m³ and 940 ind./m³, as reported by De Carli et al. (2017) and Macêdo et al. (2020), respectively.

Although water temperature did not differ significantly among reservoirs, lower temperatures were associated with an increase in *K. bostoniensis* density, suggesting that water temperature may play a role in regulating its population dynamics within the Upper Uruguay River Basin system. Some studies have also suggested that low temperature is a key factor influencing the development and global distribution patterns of *K. bostoniensis* (Krainev et al., 2018; Mantovano et al., 2021).

The elevated density found in this study aligns with those of Serafim Junior et al. (2010), who similarly observed higher abundances during colder

months, particularly in August. This correlation is likely due to the low temperatures typical of subtropical regions, particularly in the Serra Geral Mountains, which are most prominent during June, July, and August.

The detection of this non-native species in all the reservoirs of the system, a decade after its first record, suggests a broad distribution of *K. bostoniensis* across the Upper Uruguay River Basin and specifically in this subtropical region, highlighting its potential for expansion to similar environments.

The ability of *K. bostoniensis* to disperse and establish in diverse environments highlights the urgent need for continuous monitoring and management strategies to prevent further invasions. Its spread poses a significant threat to biodiversity, as it can disrupt reservoir ecosystems by outcompeting native species and altering trophic interactions, which could lead to ecological imbalances. Addressing this invasion requires proactive measures to mitigate its ecological impact and preserve the integrity of aquatic ecosystems.

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Data availability

Data are freely available with the Z and p values of the post hoc test “DunnTest” for the analysis of variance of the density of *Kellicottia bostoniensis* each month. Data is available at: https://docs.google.com/document/d/1nv3z0LesNLyjj_vY5KtweSolaEZo4OAN/edit?usp=drive_link&ouid=116420406885365764999&rtfpof=true&sd=true

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