



COMPARISON OF BIOMETRIC FACTORS OF THE INVASIVE SPECIES *PLAGIOSCION SQUAMOSISSIMUS* (HECKEL, 1840) IN FOUR RESERVOIRS OF THE PARANAPANEMA RIVER, UPPER PARANÁ, BRAZIL

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ABSTRACT

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The Paranapanema River, a major tributary of the upper Paraná basin, has been heavily altered by eleven hydroelectric dams. As a result, the basin is highly fragmented and further impacted by the presence of more than sixty invasive fish species. We analyzed standard length (Ls), total weight (Wt) and relative condition factor (Kn) of *Plagioscion squamosissimus*—one of the impactful invasive species in the basin—across four different reservoirs. While the length and/or weight of individual croakers varied significantly among reservoirs, the relative condition factor remained statistically consistent, with mean values above 1. These findings indicate that *P. squamosissimus* responds differently to the specific characteristics of each reservoir, while maintaining robust health and exhibiting remarkable plasticity in adaptation to diverse environments.

Keywords: Silver croaker. Biological invasions. Invasion ecology. Alien fish condition.

STATEMENT OF SIGNIFICANCE

The silver croaker (*Plagioscion squamosissimus*) is among the most impactful invasive freshwater fish worldwide. Yet, despite its ecological importance, studies examining morphometric variation between populations in invaded environments remain scarce. In this study, we detected measurable differences between populations of silver croaker across different reservoirs, and correlated these variations with environmental characteristics that may have exerted selective pressure. By highlighting population-level responses to local conditions, our work provides a new perspective on the invasion dynamics of *P. squamosissimus* and offers a foundation for more targeted management and mitigation strategies tailored to each location where this species poses significant ecological challenges.

1 Introduction

The Neotropical region, encompassing much of the Americas, is recognized as a biodiversity hotspot for virtually all living taxa (Voss & Emmons, 1996; Slik et al., 2015; Albert et al., 2021; Pelicice et al., 2021). The river basins in this region harbor the greatest diversity of freshwater fish in the world (Langeani et al., 2007), with Brazil hosting the highest number of introduced exotic fish (Agostinho & Julio-Junior, 1996). The Paraná River basin, the second largest in the Neotropical region (Reis et al., 2016), includes the Paranapanema River—its principal left bank tributary—whose course is widely exploited for hydroelectric power generation, with eleven dams constructed along its length (Jarduli et al., 2019).

The Paranapanema River basin supports 226 fish species, of which 165 are native and 61 are exotic or invasive (Jarduli et al., 2019; Ferraz et al., 2024). Introduction pathways for non-native species are diverse, including intentional release for sport fishing, escape from fish farms, and basin simplification associated with dam construction (Dechoum et al., 2024). Such modifications have facilitated contact between species that have been isolated for millions of years in the upper and lower parts of the Paraná River basin. For example, the Itaipu dam led to the upstream invasion of 33 species into the upper Paraná River (Julio Junior et al., 2009).

Plagioscion squamosissimus (Heckel, 1840), commonly known as South America silver croaker or whitefish, is a freshwater species native to the Amazon Basin, where it inhabits lakes and rivers (Soares, 1978). Today, *P. squamosissimus* is widespread across numerous Brazilian reservoirs and is recognized as a voracious predator, with considerable potential to disrupt native fish diversity (Agostinho et al., 2007; Buckup et al., 2007). In the late 1960s and early 1970s, the São Paulo Energy Company (CESP) translocated silver croaker specimens from northeastern dams to the State of São Paulo (Barros et al., 2012), after which the species successfully colonized the Paraná River (Panarari-Antunes et al., 2015).

As a result, *P. squamosissimus* is regarded as a prime example of an introduced species that became invasive in the Paraná River basin, particularly in reservoirs (Bennemann et al., 2006; Agostinho et al., 2008). Invasive alien species are responsible for billions of dollars in annual losses worldwide (Dechoum et al., 2024), underscoring the need to understand their dynamics in Neotropical river basins. Such knowledge is essential for developing scientifically grounded management and mitigation strategies.

This study investigates morphometric differences among populations of *Plagioscion squamosissimus* in four anthropogenically modified environments of the Paranapanema River: the reservoirs created by the Capivara, Rosana, Taquaruçu, and Canoas II hydroelectric dams. Our objective was to identify these differences and evaluate the environmental conditions most likely driving them.

2 Materials and methods

Morphometric and abundance data were obtained from *Plagioscion squamosissimus* individuals collected in the main stem of the Paranapanema River during projects conducted in the Capivara, Canoas, Rosana, and Taquaruçu reservoirs. Sampling periods varied significantly: samples from the Capivara reservoir were collected in 2009 and 2010, those from Canoas in 2010, and those from the Rosana and Taquaruçu reservoirs between 2018 and 2021. This temporal variation represents a limitation of the study and is addressed in the Discussion section. Despite differences in the objectives of each project, samplings and methodology were standardized across projects. Gillnets with mesh sizes ranging from 20 to 140 millimeters (20, 30, 40, 50, 60, 70, 80, 90, 100, 120, 140 mm, measured between opposite nodes) were installed for 16 hours, from 7.00 pm to 11:00 am, covering a total area of 9,500 m². Fieldwork was conducted seasonally, with two expeditions per station during each project, ensuring balanced sampling across sites. The morphometric variables analyzed were standard length (Ls), total weight (Wt), and relative condition factor (Kn).

The spatial layout of the reservoirs is shown in Figure 1. The Canoas reservoir system comprises the contiguous Canoas I and Canoas II reservoirs, connected by an ichthyofauna passage system known as ladders (Britto, 2009). Although some studies treat Canoas I and II as a single environment (Lopes et al., 2007), our analysis focused exclusively on individuals collected from the Canoas II reservoir bed. Capivara HPP contains the largest reservoir along the Paranapanema, with a flood area of nearly 600 km², and is the only reservoir in this study with an accumulation-based water storage system (Ferreira et al., 2023).

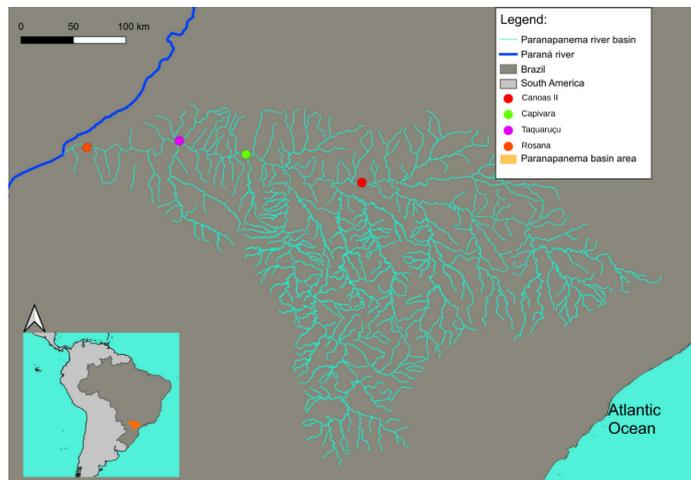


Figure 1. Map showing the location of the reservoirs analyzed in this study.

Canoas, Rosana and Taquaruçu are reservoirs that operate under a “run-of-river” system, in which the floodgates of the plant remain permanently open, allowing continuous water flow and theoretically reducing environmental impacts (Kuriqi et al., 2021). The Taquaruçu reservoir, however, is located in the lower Paranapanema, where its banks are among the most environmentally degraded areas of the basin (Garcia et al., 2015). By contrast, the Rosana reservoir lies closer to the mouth of the Paranapanema River, bordered by Morro do Diabo State Park on the right bank and the Caiuá Ecological Station on its left. However, the areas around it are largely occupied by pastures (Kipper et al., 2011).

The collected individuals were anesthetized with clove oil and euthanized by hypoxia. Biological material was fixed in 10% formalin and subsequently processed at the Laboratory of Fish Ecology and Biological Invasions (LEPIB) at the State University of Londrina. Standard length (Ls) was measured with an ichthyometer, defined as the distance in centimeters from the terminal portion of the mouth to the base of the caudal fin. Biomass was determined using a Marte AL 500-millimeter precision scale.

The sample size (N) for each reservoir was 30 individuals for Canoas II, 223 for Rosana, 186 for Capivara and 266 individuals for Taquaruçu. The small sample size for Canoas II (N=30) is a limitation that should be considered when interpreting the results for this reservoir. The data were tabulated in Excel, where a power series trend line was fitted to define the equation estimating the expected weight for each *P. squamosissimus* population based on its standard length (Ls), and thereby the condition factor (Kn) of each individual. Kn was calculated as the ratio between the total weight (Wt) and the expected weight (We) derived from the equation created for each reservoir (Ferraz et al., 2021).

After tabulating the values of Ls, Wt and Kn for each individual, the samples were subjected to the Shapiro-Wilk test to determine the normality of the data distribution. The test results indicated non-normal distributions for all three morphometric measurements, with p-values significantly below 0.05.

Given the non-normal distribution of the samples, the Kruskal-Wallis test was applied to detect possible differences between the data sets. For Ls and Wt, the low p-value indicated significant differences between reservoirs. For Kn, however, the test indicated a non-significant p-value, showing no statistical differences in the relative condition factors of the individuals across the four reservoirs (Table 1).

Table 1. Results of the Kruskal-Wallis test showing significant differences in Ls and Wt and statistical similarity of Kn between the reservoirs.

Variable	H Statistic	p-value
Standard length (Ls)	182.412	2.66e-39*
Total weight (Wt)	262.049	1.62e-56*
Relative condition factor (Kn)	4.807	1.86e-01

* Significant at p < 0.05

Finally, Dunn’s test with Bonferroni’s correction was conducted to compare the reservoirs pairwise, identifying which reservoirs had significant differences between them in terms of populations. All statistical analyses were performed in R, using the FSA, gt, and gridExtra packages (Auguie et al., 2017; Iannone et al., 2024; Ogle et al., 2025).

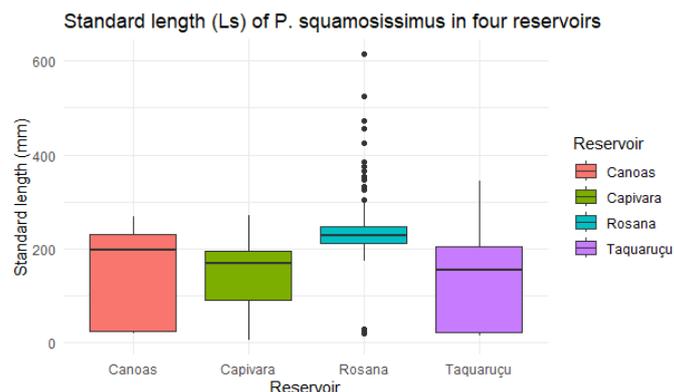


Figure 2. Boxplots showing the distribution of standard length (Ls) for individuals across the four reservoirs.

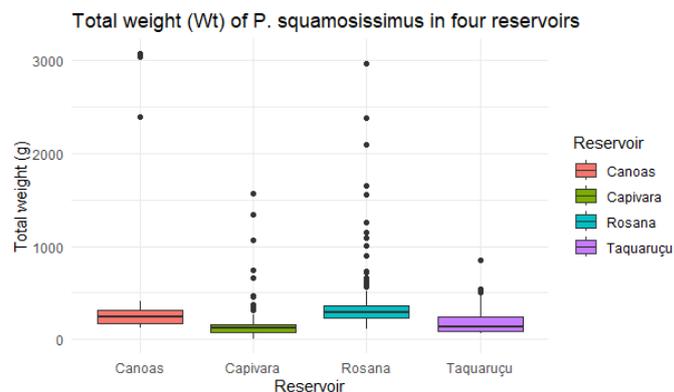


Figure 3. Boxplots showing the distribution of total weight (Wt) for individuals across the four reservoirs. To facilitate visualization and avoid distortion of the boxplots, the three heaviest individuals from the Rosana reservoir were excluded from the graph.

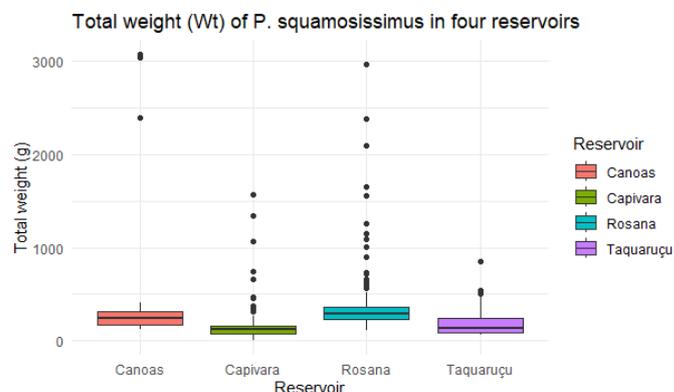


Figure 4. Boxplots showing the distribution of condition factor (Kn) for individuals across the four reservoirs. For better visualization, the three heaviest individuals were excluded.

Figures 2, 3 and 4 show the distribution of Ls, Wt, and Kn, respectively, in boxplot format. For the Wt distribution graph, the three heaviest individuals from Rosana were excluded to improve visualization, as their inclusion flattened the plot and obscured the overall data distribution. Nevertheless, all the statistical analyses were conducted using the complete dataset of specimens. The boxplots illustrate the variability among individuals across reservoirs, and highlight that despite variations in size and weight of the croakers across environments, Kn remains constant, indicating good health throughout the studied stretch of the Paranapanema River.

3 Results and Discussion

Pairwise analyses revealed significant differences in length, or weight, or both measurements, between nearly all reservoir comparisons (Tables 2 and 3). These findings suggest that environmental conditions across reservoirs influence the morphometric characteristics of *P. squamosissimus*, demonstrating the capacity of this species to adapt to varying environmental conditions. In contrast, comparisons of Kn did not indicate any significant differences between reservoirs (Table 4), indicating that despite the size variation, the populations maintain similar relative conditions.

Table 2. Dunn's test results for Ls in pairwise analyses. Bold values with a superscript asterisk are significant at $p < 0.05$.

Comparison	Z Statistic	p-value*
Canoas - Capivara	2.644	4.92e-02*
Canoas - Rosana	-3.043	1.41e-02*
Capivara - Rosana	-11.197	5.54e-28*
Canoas - Taquaruçu	2.625	5.19e02
Capivara - Taquaruçu	-0.152	1.00e00
Rosana - Taquaruçu	12.085	7.57e-33*

*Significant at $p < 0.05$ (Bonferroni correction)

Table 3. Dunn's test results for Wt in pairwise analyses. Bold values with a superscript asterisk are significant at $p < 0.05$.

Comparison	Z Statistic	p-value*
Canoas - Capivara	5.193	1.24e-06*
Canoas - Rosana	-2.284	1.34e-01
Capivara - Rosana	-14.761	1.58e-48*
Canoas - Taquaruçu	3.713	1.23e-03*
Capivara - Taquaruçu	-3.207	8.06e-03*
Rosana - Taquaruçu	12.768	1.49e-36*

*Significant at $p < 0.05$ (Bonferroni correction)

Table 4. Dunn's test results for Kn in pairwise analyses. No significant values > 0.05 were found.

Comparison	Z Statistic	p-value*
Canoas - Capivara	-0.235	1.00e+00
Canoas - Rosana	-1.081	1.00e+00
Capivara - Rosana	-1.652	5.91e-01
Canoas - Taquaruçu	-1.160	1.00e+00
Capivara - Taquaruçu	-1.855	3.81e-01
Rosana - Taquaruçu	-0.146	1.00e+00

*Significant at $p < 0.05$ (Bonferroni correction)

The results indicate that the Rosana reservoir is an environment that supports *Plagioscion squamosissimus* individuals with the greatest median and mean values for both weight and length values (Tables 5 and 6). This pattern can be attributed to ecological and geographic factors. As the final reservoir before the Paranapanema River meets the Paraná river, the Rosana benefits from increased connectivity with the latter, which likely enhances species diversity and the presence of competitors and large predators (Hoeinghaus et al., 2009; Ganassin et al., 2021). Following the concept of river continuity, we can infer that the Rosana reservoir will exhibit greater environmental complexity, favoring the presence of larger predators such as the silver croaker (Vannote et al., 1980). Ecological pressures associated with these factors may have favored the selection of larger individuals (Agostinho et al., 2016). The proximity of the Morro do Diabo State Park, one of

the largest Atlantic Forest reserves in Brazil, located upstream, on the banks of the Paranapanema River, may also contribute to this increased environmental complexity, by providing shelter and diverse ecological niches that support larger organisms (Casatti et al., 2001). Rosana was also the only reservoir to present outlier individuals with much greater weight and length, a factor that influenced the construction of the data distribution boxplots, and which provides further evidence of the reservoir's greater capacity to shelter large individuals of a predatory species such as *P. squamosissimus*.

The consistently high Kn values (above 1 in all reservoirs) indicate that *P. squamosissimus* is in better-than-expected condition throughout the studied stretch of the Paranapanema River. This relatively high condition, even in anthropogenically modified environments, reinforces its status as a successful invasive species (Agostinho et al., 2008). Despite differences in sampling periods, the statistical similarity of Kn values suggests that the species' relative condition has remained stable over time in the basin, reflecting persistent success in adapting to different environments.

Table 5. Mean values of Ls and Wt in the four reservoirs.

Reservoir	Mean LS (mm)	Mean Wt (g)
Canoas	221.0	240.67
Rosana	243.2	413.07
Capivara	175.6	122.7
Taquaruçu	192.8	173.44

Table 6. Medians values of Ls and Wt in the four reservoirs

Reservoir	Mean LS (mm)	Mean Wt (g)
Canoas	223.5	237
Rosana	233.0	300
Capivara	180.0	115
Taquaruçu	187.0	135

Figures 6 and 7 confirm that Kn values did not differ statistically across the four reservoirs. The fact that the average Kn values exceeded 1 in all reservoirs indicates that *P. squamosissimus* individuals are well established and in better-than-expected conditions throughout the Paranapanema River, demonstrating high adaptability. This pattern also highlights the impacts of environmental degradation in the basin, facilitating the establishment of invasive species (Didham et al., 2005; Britto & Carvalho, 2006; Simberloff et al., 2013; Garcia et al., 2015). This degradation reduces ecological complexity, creating conditions that favor colonization and growth of the species (Pelicice & Agostinho 2009). *P. squamosissimus* has proven resilient both in environments with greater ecological diversity and in more degraded areas, reinforcing its potential as an invasive species under altered ecological conditions.

The Canoas reservoir system, interconnected by fish ladders that enable migration and exchange of organisms between reservoirs, presented great environmental similarity. This connectivity reduces ecological barriers, creating a uniform ecotone for the silver croaker that allows us to treat Canoas I and II as a single ecological unit for analysis purposes (Lopes et al., 2007; Ferraz et al., 2022).

At Capivara HPP, water storage practices often produce large periodic variations in depth due to the control of hydroelectric turbines (Luo et al., 2023). These fluctuations in water levels appear to directly affect specimen size, resulting in smaller individuals in the reservoir because of uneven food distribution and abiotic factors such as water transparency, temperature, and oxygenation (De Barcelos et al., 2024). To confirm this hypothesis, further studies are needed to compare the size and weight of other species from the Paranapanema River across multiple reservoirs, as was done here for *P. squamosissimus*.

The Taquaruçu reservoir lies in one of the most environmentally degraded areas of the basin (Garcia et al., 2015). This degradation likely reduces availability or increases physiological stress, producing a different growth trajectory compared to other reservoirs. However, the similarity of Kn values suggests that, despite this altered growth pattern, surviving individuals maintain relatively good condition.

4 Conclusion

The statistical analyses conducted in this study demonstrate that the distinct environmental conditions of each reservoir influence the length and total weight of *P. squamosissimus* individuals along the Paranapanema River basin. Despite these size differences, the similarity of Kn values among reservoirs, with averages consistently greater than 1, indicates that the species is in better-than-expected condition throughout the basin. These findings highlight both the adaptability of *P. squamosissimus* in invaded environments, and the considerable challenges involved in proposing effective management actions for the species.

The results of our work provided a clearer understanding of how environmental variation affects the size of the silver croaker across different habitats, while also contributing to the broader discussion on the need for multifaceted strategies to control its distribution in invaded areas, given its ability to adapt to diverse conditions. We considered several ecological variables that may explain this variation in morphometric traits among populations, but further research is needed, to determine whether abiotic factors also play a role. There is an urgent need for new studies to deepen knowledge of the physical and physiological characteristics of *P. squamosissimus* that enable this species to successfully invade neotropical environments, so that more effective mitigation and control measures can be developed.

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