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The effect of macrophytes on the presence and population structure of the red swamp crayfish *Procambarus clarkii* (Decapoda: Cambaridae) in neotropical ecosystems

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ABSTRACT

Introduction: The red swamp crayfish, *Procambarus clarkii*, is a crustacean species native to Mexico and the United States. It has been introduced around the world, often becoming established as an invasive exotic species. Since its introduction in 1985 in Colombia, no studies have been carried out to determine factors that influence the presence of the species in high mountain ecosystems.

Objective: To evaluate the relationship over time between macrophytes and the different stages of development of *P. clarkii* in a tropical high Andean aquatic ecosystem.

Methods: A new collection method called "macrophyte sweep" was standardized. This method ensured the collection of crayfish of all possible sizes, especially juveniles. Sampling was carried out bimonthly for seven months. The morphometry of *P. clarkii* was evaluated in three macrophytes: *Juncus effusus*, *Ludwigia peruviana*, and *Polygonum punctatum*.

Results: A total of 778 individuals were collected, of which 365 were females, 344 males, and 69 sexually indeterminate. The total population density was 6.48 ind/m^2. Most organisms were found on *P. punctatum* (71.9 %), followed by *L. peruviana* (17.7 %) and *J. effusus* (10.28 %). The largest and heaviest organisms were recorded in September in all three macrophytes, while the smallest were collected in July and May. *P. clarkii* exhibited a greater affinity for *P. punctatum* in its different developmental stages, possibly because it offers greater structural complexity in the submerged zone, providing shelter for juveniles and a food source for adults.

Conclusions: Our results highlight that much of the colonization success of *P. clarkii* is due to the relationship between macrophytes and the development of different life stages in neotropical ecosystems.

Key words: exotic species; invasive; aquatic plants; juvenile; size; high Andean.

RESUMEN

Efecto de las macrófitas sobre la presencia y estructura poblacional del cangrejo rojo americano *Procambarus clarkii* (Decapoda: Cambaridae) en ecosistemas neotropicales.

Introducción: El cangrejo rojo americano, *Procambarus clarkii*, es una especie de crustáceo originaria de México y Estados Unidos. Se ha introducido en todo el mundo, estableciéndose a menudo como especie exótica invasora.

Desde su introducción en 1985 en Colombia, no se han realizado estudios para determinar los factores que influyen en la presencia de la especie en ecosistemas de alta montaña.
Objetivo: Evaluar la relación en el tiempo entre las macrófitas y los diferentes estadios de desarrollo de *P. clarkii* en un ecosistema acuático tropical altoandino.
Métodos: Para ello se estandarizó un nuevo método de recolecta denominado "jameo de macrófitas". Este método aseguró la recolección de cangrejos de río de todos los tamaños posibles, especialmente juveniles. El muestreo se realizó bimensualmente durante siete meses. Se evaluó la morfometría de *P. clarkii* en tres macrófitas: *Juncus effusus*, *Ludwigia peruviana* y *Polygonum punctatum*.
Resultados: Se recolectaron 778 individuos, de los cuales 365 eran hembras, 344 machos y 69 sexualmente indeterminados. La densidad de población total fue de 6.48 ind/m^2. La mayoría de los organismos se encontraron sobre *P. punctatum* (71.9 %), seguido de *L. peruviana* (17.7 %) y *J. effusus* (10.28 %). Los organismos más grandes y pesados se registraron en septiembre en las tres macrófitas, mientras que los más pequeños se recogieron en julio y mayo. *P. clarkii* mostró una mayor afinidad por *P. punctatum* en sus diferentes estadios de desarrollo, posiblemente porque ofrece una mayor complejidad estructural en la zona sumergida, proporcionando refugio a los juveniles y fuente de alimento a los adultos.
Conclusiones: Nuestros resultados ponen de manifiesto que gran parte del éxito de colonización de *P. clarkii* se debe a la relación entre las macrófitas y el desarrollo de las diferentes etapas vitales en los ecosistemas neotropicales.

Palabras clave: especies exóticas; invasivas; plantas acuáticas; juveniles; tamaño; alto andino.

INTRODUCTION

The physical configuration and heterogeneity of microhabitats in aquatic ecosystems are determining factors that affect the distribution, survival, growth and structure of populations (Wang et al., 2018). Macrophytes, which are aquatic plants, play an essential role in the structural complexity of aquatic habitats (Thomaz & Cunha, 2010). Depending on their form, stratum and distribution, these plants provide shelter and food, especially in littoral zones (Choi et al., 2014; Son et al., 2021).

The architectural complexity of macrophytes has been characterized using fractal dimension (FD), a metric that quantifies the rate of increase in the linear distance between two points across various scales (Morse et al., 1985). This measure enables the assessment of the spatial and morphological irregularity of the plants. It allows for a three-dimensional evaluation of the space occupied by the plant within a water body, and how this influences the animals that may potentially colonize the plant for various purposes, such as shelter and food (Gee & Warwick, 1994; Jeffries, 1993; Shorrocks et al., 1991). Plants with more complex architectures have an FD close to 2, while those with simpler structures have an FD close to 0 (McAbendroth et al., 2005). In macrophytes from Andean ecosystems such as *Polygonum, Ludwigia* and *Juncus*, a complexity of 1.44; 1.42 and 1.33, respectively, have been identified (Fernández & Florencia, 2019; McAbendroth et al., 2005; Yofukuji et al., 2021).

Architectural complexity has been correlated with the presence of some crustaceans in their early life stages (Thomaz & Cunha, 2010). Crustaceans, such as the red swamp crayfish, *Procambarus clarkii* (Girard, 1852), can be affected by macrophytes (Madzivanzira et al., 2023), as they are typical inhabitants of littoral zones, where they seek food and shelter, and burrow during part of their reproductive cycle (Gherardi & Barbaresi, 2007; Nyström, 2002; Nyström et al., 1999). For example, it has been described how the presence of the macrophyte *Ludwigia repens* Forst. serves as a refuge for juvenile *P. clarkii* to protect themselves from the cannibalism of adult crayfish, causing the latter to focus more on other prey, such as tadpoles (Cruz & Rebelo, 2005; Jordan et al., 1996).

Although there are studies on the population behavior of *P. clarkii* and its possible areas of occupation and invasion in tropical America (Camacho-Portocarrero et al., 2020; Palaoro et al., 2013; Scalici, & Gherardi, 2007), the relationship between the macrophytes present in these invaded areas and the different stages of the life cycle of the red swamp crayfish is still unclear. We propose that rooted floating and emergent macrophytes, such as *Polygonum* and *Ludwigia*, due to their higher density and architectural complexity, may provide suitable habitats for the early life stages of crayfish. In contrast, emergent macrophytes with simpler structures, such as *Juncus*, could serve as refuges for crayfish in more advanced stages. Therefore, it is essential to identify, through repeated assessments over time, the relationship between macrophyte architecture and the distribution of *Procambarus clarkii* populations in a tropical high Andean aquatic ecosystem.

MATERIALS AND METHODS

Study area: The study was conducted in the cooling lakes of a thermoelectric plant in the municipality of Paipa (5°45'58.94" N & 73°8'34.61" W), Department of Boyacá, Colombia (SMF 1). This artificial body of water originates from the diversion of part of the Chicamocha River to be channeled into a lentic system for industrial use. The climate is cold and very dry, with a bimodal regime of two rainy seasons in March-May and September-November, while there is low rainfall in June-July and December-January. The average total annual precipitation is 881 mm, with an average temperature of 13.7 °C (Instituto de Hidrología Meteorología y Estudios Ambientales, 2022).

Sampling of crayfish in macrophytes and physicochemical parameters of water: The crayfish were collected over seven months, using the "macrophyte sweep" method with hand nets 30 x 30 x 20 cm with a 2 mm pore mesh. This method consists of manually lifting and shaking the macrophytes located in 10-meter-long strips and up to one meter away from the shore. Simultaneously, two people, using hand nets and zig-zag movements, remove the organisms attached to the macrophytes and collect those that become detached from the plants. Subsequently, the plant material is placed in white trays to extract the juvenile crayfish that remain attached.

Sampling was conducted in three coastal strips, each dominated exclusively by one of the three most abundant macrophyte species. To prevent the mixing of influences from these aquatic plants on crayfish, distinct zones were designated for each species, ensuring no overlap between them. This approach facilitated an independent evaluation of the impact of each type of aquatic vegetation on the crayfish population, thereby minimizing potential biases in the results. The species studied included spotted knotweed (*Polygonum punctatum* Elliott), Peruvian primrose (*Ludwigia peruviana* L.), and soft rush (*Juncus effusus* L.) (SMF 1). *P. punctatum*, native to America, inhabits wetlands, floodplains and ecotones in tropical and subtropical regions, forming dense colonies along the banks of water bodies (Quirino et al., 2019). It is commonly used for slope stabilization due to its ability to mitigate erosion (Keddy, 2010). *L. peruviana*, also native to South America, is found along the shores of water bodies and has deep roots that create an ideal habitat for fish egg-laying, underscoring its importance in fisheries management (Gallardo & Aldridge, 2013). Introduced as an ornamental plant on other continents, it has become invasive due to its rapid growth and adaptability (Jacobs et al., 1994). *J. effusus* is a cosmopolitan species that thrives in humid environments and on steep slopes, demonstrating remarkable tolerance to drought and fluctuating water levels, thanks to its aerenchymatous tissues (Visser & Bögemann, 2006). It is widely used in bioremediation projects to improve water quality in acidic and polluted wetlands by adsorbing pollutants (Fyson, 2000; Syranidou et al., 2017).

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In each sampling strip, oxygen concentration was measured using a WTW 3205, conductivity with a WTW 3110, and both pH and temperature with a WTW 3110. The collected organisms were refrigerated and transported to the Integrated Ecosystem and Biodiversity Management Laboratory (XIUÂ) at the Universidad Pedagógica y Tecnológica de Colombia, where they were euthanized by freezing at -20 °C.

Morphometry and size analysis: In the laboratory, using a Mitutoyo digital calibrator of 0.1 mm precision, the following measurements were taken from the crayfish: Total length (TL), which was measured from the tip of the rostrum to the end of the telson; carapace length (CL), which was taken from the tip of the rostrum to the end of the cephalothorax; post orbital length (POCL), which was taken from the posterior end of the eye to the end of the cephalothorax (Anastácio & Marques, 1995) (SMF 1).

Each organism was weighed without the claws, using a 0.1 g digital scale. The claws were not included because some individuals had lost or were at different stages of the regeneration of these structures. Organisms with a total length of less than 60 mm were considered juveniles, and those larger than this size were considered adults, according to Cano and Ocete (2000). Length intervals were obtained using the post-orbital carapace length (POCL), as described by Anastácio et al. (2009) and Hamasaki et al. (2020), with each interval representing a 5 mm size range (Rodríguez-Almaraz, 2001).

Data analysis: Environmental variables were compared using Spearman's rank correlation analysis to evaluate the influence of variables on organisms by season and by plant species. Biological data were evaluated using Shapiro-Wilks normality tests and a three-way analysis of variance to make comparisons between months, macrophytes and sex (excluding data from sexually indeterminate individuals). Multiple comparisons were conducted with Tukey's post hoc to determine which variables were different. Finally, to observe the contribution of variables to the dissimilarity between macrophytes, a SIMPER similarity percentage analysis was applied with Euclidean and Bray Curtis distance indices. Statistical analyses were performed using Primer 7 and SigmaPlot 14.

RESULTS

Physicochemical parameters of water: Environmental variables showed that the body of water was, on average, warm, at 19.3 °C (15.6-20.9), with high conductivity 152.2 µS/cm (130.1-164.4) and low oxygenation at 3.7 mg/L (1.44-9.1). There was an inverse correlation between dissolved oxygen and conductivity ($R = -0.93$, $p < 0.05$) and between the latter and pH ($R = -0.52$, $p < 0.05$). In microhabitats containing *P. punctatum*, a lower temperature was observed compared to those dominated by *L. peruviana* and *J. effusus*. Among the environmental variables, pH exhibited the highest percentage of similarity between *P. punctatum* and *L. peruviana*, accounting for 49.14 % of the similarity between these two habitats. Dissolved oxygen was the second most significant variable, demonstrating a 28.8 % similarity between *P. punctatum* and *J. effusus*. Lastly, conductivity emerged as the variable that contributed most to the similarity between *J. effusus* and *L. peruviana*, with a contribution of 25.8 %. Regarding the sampling periods, the highest dissolved oxygen and pH were observed in May, while July was the month with the lowest temperature (17 °C) compared to the other months. As for the substrate, in the area of *P. punctatum* it was muddy, for *J. effusus* it was clayey and for *L. peruviana* it was rocky (SMT 1).

Red swamp crayfish: During the study, 778 individual crayfish were collected from the three macrophytes evaluated. Of the individuals collected, 365 were females, 344 were males and 69 individuals could not be sexually identified. The total population density averaged 6.48 ind/m^2, with the macrophyte *P. punctatum* having the highest population density with 14 ind/m^2, followed by *L. peruviana* with 3.45 ind/m^2 and *J. effusus* with 2 ind/m^2. The month with the highest population density was September (10.4 ind/m^2), followed by July (7.3 ind/m^2), November (5.3 ind/m^2), and May (2.8 ind/m^2).

Males were, on average, slightly heavier and larger compared to females, but without a significant difference (Weight M = 8.71 gr, F = 7.92 gr, F = 0.001, d.f. = 1, p = 0.97; TL M = 65.6 mm, F = 61.90 mm, F = 0.08; d.f. = 1, p = 0.77) (SMT 2). May presented significant differences in both weight and length, compared to the other months ($p < 0.000$), while July, September and November did not show significant differences ($p > 0.58$).

By macrophyte species, the highest number of organisms was collected in *P. punctatum* (71.98 %) with a TL range of 8.1-110.6 mm; followed by *L. peruviana* (17.7 %-TL range: 11.6-153.6 mm) and *J. effusus* (10.2 %-TL range: 40.5-106.1 mm). Significant differences in TL, CL, POCL were found comparing *J. effusus* with the other macrophytes ($p < 0.004$). In terms of weight, the only significant differences were found between *J. effusus* and *L. peruviana* ($p < 0.014$).

September was the month when the largest and heaviest organisms were recorded in the three macrophytes, while the smallest organisms were collected in July and May (SMT 2). The largest organisms were found in *L. peruviana*, while the smallest were found in *P. punctatum*. The overall female:male sex ratio was 1 : 0.9. By macrophyte species, in *P. punctatum* it was 1 : 1.1; in *L. peruviana* 1 : 0.8 and in *J. effusus* 1 : 0.9.

Size ranges: Of the nine established size intervals of *P. clarkii*; in *J. effusus*, mainly large crayfish were found (POCL > 27 mm-TL 74.0 mm). In the case of *P. punctatum*, crayfish of all sizes were found (POCL 2.7-43.5 mm), and the highest abundance of organisms was observed in the size interval between 2.6 mm and 12.59 mm POCL. Statistical differences ($p < 0.000$) were found in the length intervals of all catches and also among macrophytes ($p < 0.001$), except between *J. effusus* and *L. peruviana* (p = 0.85) (SMF 2, SMF 3).

In general, the presence of adult crayfish was recorded in all plants during the month of May, and from July onward, a gradual increase of smaller individuals was observed, reaching a maximum abundance in September. In *P. punctatum*, larger organisms were observed in September compared to May ($p < 0.02$). In *L. peruviana* there was a difference in the size intervals evaluated ($p < 0.01$), except between May-November and July-September. In the case of *J. effusus*, similar lengths were found during all months (p = 0.68). (SMF 2).

DISCUSSION

Our results demonstrated a significant influence of macrophytes on the population structure and distribution of *P. clarkii* in high Andean aquatic ecosystems. The selection of various macrophyte species, such as *P. punctatum*, *L. peruviana*, and *J. effusus*, appears to be influenced by the structural complexity of these plants, indicating that plant architecture plays a crucial role in the colonization and survival of different life stages of this invasive species. Specifically, *P. punctatum* served as the primary habitat for the most vulnerable life stages of the red swamp crayfish (juveniles), supporting over 70 % of the studied population. This trend persisted throughout the study period. The complex structure of this macrophyte, reflected in its fractal dimension (FD = 1.44) (Fernández & Florencia, 2019), includes both floating and submerged zones, which create a favorable microenvironment that offers shelter from predation and cannibalism, as well as food resources and spawning grounds (Gherardi & Barbaresi, 2007; Haubrock et al., 2019; Jordan

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et al., 1996; Quirino et al., 2019). Furthermore, among the various macrophytes evaluated, crayfish exhibit a clear preference for *Polygonum*, when this macrophyte is present (Gordon, 2000). Its dense submerged zone, in particular, appears to provide protection for juveniles; this phenomenon has been documented in other studies examining macrophyte-crayfish interactions (Cruz & Rebelo, 2005; Thomaz & Cunha, 2010).

These findings underscore the crucial role that macrophytes play in the ecology of *Procambarus clarkii,* serving not only as a primary food source but also as essential habitats for colonization and survival throughout its various life stages. Previous studies indicate that *P. clarkii* demonstrates a significant preference for consuming macrophytes over animal prey, suggesting that its proximity to these plants is closely associated with the availability of plant-based resources (Gherardi & Barbaresi, 2007; Rivera et al., 2024). This behavior is observed not only in the deeper (profundal) zones of the lake but also extends to active foraging in littoral areas (Dörr et al., 2006; Hamasaki et al., 2020; Haubrock et al., 2019; Rivera et al., 2024). An important aspect of the ecology of *P. clarkii* is its association with *Ludwigia peruviana*. Previous studies have demonstrated a positive interaction between *L. grandiflora* and crayfish, wherein the fragmentation of this macrophyte at high crayfish densities promotes the dispersal of both species (Thouvenot et al., 2017). Additionally, as an emergent or semi-terrestrial species (Lambert et al., 2010; Oziegbe & Faluyi, 2012), *L. peruviana* provides shelter and resources for *P. clarkii* both in and out of the water, enhancing its capacity to colonize new habitats (Gallardo & Aldridge, 2013; Loureiro et al., 2015). Consequently, both *P. punctatum* and *L. peruviana* can be considered “nurseries” for red crayfish, a phenomenon also observed with other macrophytes and microcrustaceans (Choi et al., 2014). In contrast with other macrophytes, *J. effusus* was not utilized by juvenile *P. clarkii*, which may be attributed to its simple structure, making it less suitable for providing shelter during this developmental stage (Yofukuji et al., 2021). In contrast, adult crayfish appear to prefer *J. effusus*, suggesting that this macrophyte offers specific ecological resources or advantages for them. It is possible that it serves as a habitat for organisms that are preyed upon by the adults or that the macrophyte itself is consumed by them. Previous studies have indicated that related species, such as *Juncus bufonius*, have increased in abundance and distribution due to consumption by *P. clarkii* (Lovas-Kiss et al., 2018). Given that *J. effusus* is a cosmopolitan macrophyte that thrives in stagnant water bodies and can withstand both prolonged droughts and floods (Krzciuk & Galuszka, 2020; Syranidou et al., 2017; Visser & Bögemann, 2006; Xu & Chang, 2017), its presence in high Andean ecosystems may provide resources to *P. clarkii* on a continual basis (González-Gamboa et al., 2022), potentially facilitating the expansion of this invasive species. It is important to consider that, in some instances, the presence of *P. clarkii* has led to the local extinction of macrophytes due to excessive consumption (Madzivanzira et al., 2023). This scenario should be taken into account in future studies examining the impact of this invasive species in high Andean ecosystems. The results underscore that macrophytes play a crucial role in the ecology of *P. clarkii*, not only as a primary food source (Gherardi & Barbaresi, 2007; Rivera et al., 2024), which the crayfish frequently forages in littoral zones (Dörr et al., 2006; Hamasaki et al., 2020; Haubrock et al., 2019), but also as essential habitats for its survival throughout various stages of its life cycle.

The population of *P. clarkii* exhibited distinct temporal characteristics. In May, no juveniles were observed; however, in July, a period of juvenile abundance commenced and continued until November, when recruitment peaks seemingly occurred. This pattern appears to be characteristic of populations in all aquatic ecosystems within the high Andean zone of Colombia. In Italy, where the red crayfish is also an invasive species, a similar pattern was identified: the smallest individuals increased in number toward the end of the year, while the highest abundance was recorded in July and September, coinciding with the summer season when recruitment takes place (Barbaresi et al., 2004; Dörr & Scalici, 2013). It is plausible that the bimodal rainfall regime in the Colombian Andes contributes to at least two spawning peaks. Studies of *P. clarkii* in both Mediterranean and tropical regions have documented two annual spawning peaks (Scalici et al., 2010). Environmental factors such as temperature and water availability, including rainfall patterns, are key regulators of reproductive cycles (Anastácio & Marques, 1995; Hamasaki et al., 2023). Future studies should validate this hypothesis through annual analysis of the crayfish population in the region.

Regarding the size and population density of *P. clarkii* in the water body studied, it was found that the organisms are smaller compared to those reported in Europe and Africa. For example, in Morocco they reach a total length of approximately 78.2 mm, in Spain 93.2 mm, and in Italy they have a cephalothorax length of 48.9 mm (Alcorlo et al., 2009; Dörr et al., 2006; El Qoraychy et al., 2011; Peruzza et al., 2015). However, the population density was similar or slightly higher than reported in other countries where the crayfish is invasive (Arteaga, 2009; Piscia et al., 2011). The density of *P. punctatum* found in our study is similar to marshes in Louisiana and macrophytes in South Korea (Choi et al., 2021; Huner & Barr, 1991; Lutz & Wolters, 1986), where established populations of red crayfish exist and continuous data on environmental factors are available.

During our study, we found an optimal temperature in the water body for red crayfish development, similar to other studies (Barbaresi et al., 2004; Liu et al., 2013). However, the temperature values recorded are atypical for the high Andean region of Colombia (Roldán-Pérez & Ramírez-Restrepo, 2008) due to power generation by coal burning, which raises the water temperature to the ideal point for red crayfish development (Chucholl, 2011).

Finally, in our study, we developed a method for the active collection of red crayfish in littoral macrophytes. This method captures individuals of all sizes, from the larval stage to the adult stage (cephalothorax from 4.1 mm), overcoming the limitations of other methods, such as traps (Barbaresi et al., 2004). With this new method, we can evaluate the species in all stages of development in the natural habitat. Although it has some disadvantages, such as its use in deep littoral zones, where the researcher cannot stand close to the shore, it represents a significant advance in the collection of red crayfish and provides valuable information on the species.

Macrophytes play a crucial role in the invasion and establishment of *P. clarkii* in high Andean aquatic ecosystems by providing shelter, food, and essential habitat throughout all life stages. *P. punctatum* hosts more than 70 % of the juvenile population, underscoring its significance as a habitat, while *L. peruviana*, due to its adaptability and dispersal capabilities, is also well-suited for this species. In contrast, *J. effusus* is likely utilized as a food source for adults, offering limited support for other life stages. The structural complexity of macrophytes significantly influences the presence of juveniles and adults, with more complex plants promoting greater juvenile abundance. The ecological plasticity of *P. clarkii* enables it to exploit diverse resources in the ecosystems where it is introduced, facilitating its expansion. Furthermore, the high population density of *P. clarkii* indicates that this species is well established in the ecosystem, and it appears that the reproductive cycle is influenced by the bimodal rainfall regime in the Andean region of Colombia, with peak recruitment occurring from July to November. Future research should focus on analyzing how the implementation of management practices based on macrophyte control, along with an assessment of environmental factors, could help mitigate the adverse

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ecological impacts associated with the invasion of the red crayfish.

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See supplementary material
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