| SPIXIANA | 48 | 1 | 31–40 | München, November 2025 | ISSN 0341-8391 |
|---|---|---|---|---|---|

# Weight–length relationships and sexual dimorphism in a feral population of *Cherax quadricarinatus* (von Martens, 1868) in temperate Europe

**(Decapoda, Parastacidae)**

**Martina Jaklič & Jaka Jaklič**

Jaklič, M. & Jaklič, J. 2025. Weight–length relationships and sexual dimorphism in a feral population of *Cherax quadricarinatus* (von Martens, 1868) in temperate Europe (Decapoda, Parastacidae). Spixiana 48 (1): 31–40.

The redclaw crayfish (*Cherax quadricarinatus*) is native to northern Australia and Papua New Guinea, and has become increasingly widespread in Europe as a non-indigenous species. The present study investigates morphometric variation, growth patterns, and body condition of a feral population inhabiting a thermally enriched oxbow lake in Slovenia. A total of 1362 individuals collected between 2009 and 2021 were sexed (male, female, intersex) and measured for cephalothorax length (CL), total length, body weight, and chela dimensions.

Sexual dimorphism was evident, with males displaying significantly greater body mass and longer chelae than females. Intersex individuals (10.1 % of the population) exhibited a morphology that was more closely aligned with males, suggesting the potential for endocrine disruption or developmental plasticity. The weight–length relationships exhibited a power function ($W = a * CL_b$), with allometric exponents (b) falling below 3 across all sex groups, indicative of negative allometric growth. General linear models revealed a significant interaction between CL and sex, with males and intersex individuals gaining more weight per unit of CL than females.

The scaled mass index (SMI), utilised as a proxy for condition, exhibited no substantial disparities among the sexes, thereby suggesting optimal physiological well-being across the population. The findings of the present study are in alignment with those of previous aquaculture-based studies, yet they offer rare insights into feral populations in temperate regions. It is important to note that the observed prevalence of intersex individuals, in conjunction with their rapid growth patterns, gives rise to concerns regarding ecological plasticity and invasive potential.

This study contributes to our understanding of the plasticity, growth dynamics and morphological variation in *C. quadricarinatus* under non-native environmental conditions, thereby providing a valuable baseline data set for future comparative research on introduced freshwater crayfish.

Martina Jaklič (corresponding author), University Medical Centre Ljubljana, Zaloška cesta 2, 1000 Ljubljana, Slovenia; e-mail: martina.jaklic@kclj.si

Jaka Jaklič, Goriška 69, 1000 Ljubljana, Slovenia

## Introduction

The study of length–weight relationships (LWR) and condition factors (CF) is of fundamental importance in providing insights into the growth patterns, somatic investment, and ecological adaptability of aquatic organisms, including freshwater crayfish. (Barki & Karplus 2004, Martelloni et al. 2012, Loureiro et al. 2015). These traits are of critical importance for the evaluation of the status of wild populations, particularly those that are non-indigenous and potentially invasive (Loureiro et al. 2015, Bayer et al. 2021, Marn et al. 2022). *C. quadricarinatus* is a tropical species native to northern Australia and Papua New Guinea (Reynolds & Souty-Grosset 2011, Jones & Valverde 2020). Due to its rapid growth, broad environmental tolerance, and economic value, it has been extensively introduced outside its native range for aquaculture and the ornamental trade (Barki & Karplus 2004, Ahyong & Yeo 2007, Marufu et al. 2018, Eprilurahman et al. 2021). Consequently, feral populations of *C. quadricarinatus* have become established in several tropical and subtropical regions (Ahyong & Yeo 2007, Bortolini et al. 2007, Belle & Yeo 2010, Pinder & Harman 2019). As demonstrated in the literature, isolated findings or small, occasionally escaped individuals have been documented in certain temperate regions of Europe, including Italy (D'Agaro et al. 1999, Vecchioni et al. 2022), Spain (Arias & Torralba-Burrial 2021), and Hungary (Weiperth et al. 2020). The first confirmed wild population in Europe was reported from a thermally enriched oxbow lake in southeastern Slovenia in 2009 (Jaklič & Vrezec 2011). Whilst these occurrences confirm the species' capacity to survive in temperate climates, no long-term ecological or morphometric studies have been conducted outside of Slovenia. Consequently, the Slovenian population represents a distinctive European case study in which successful reproduction, population persistence, and sexual dimorphism have been observed under thermally favourable but non-native conditions. Its establishment in a temperate climate is of particular interest, as higher thermal regimes may support reproduction and long-term survival outside the species' typical tropical range. However, there is a paucity of ecological and biometric data on these wild populations. As demonstrated in previous research, r-selected life-history traits – such as early maturation, rapid growth, and high reproductive output – contribute to the invasive potential of freshwater crayfish (Beatty et al. 2003, Haubrock et al. 2021, Miller et al. 2024). The quantification of these traits is facilitated by body condition indices, which reflect the physiological status and fitness of individuals based on body mass and structural length (Froese 2006, Jutagate et al. 2023).The present study investigates the length–weight relationship, growth patterns, and condition factor of wild *C. quadricarinatus* in Slovenia. The objective of this study is to make a comparison between biometric traits and condition among males, females, and intersex individuals. The latter are defined as endocrinologically induced functional males that have been previously documented in aquaculture systems. This is the first detailed ecological and biometric analysis of a feral population of *C. quadricarinatus* in a temperate European habitat.

## Materials and methods

Individuals of *C. quadricarinatus* were collected from a wild population inhabiting the oxbow lake Topla in southeastern Slovenia (45°53'8.25'' N, 15°37'45.7'' E), which is a part of Sava water basin (Fig. 1).The area encompasses 4 hectares, on an altitude of 140 metres.

The population of *C. quadricarinatus* was sampled from 2009 to 2021. Upon capture, the subjects were measured, weighed, and sexed. Sex was determined by external sexual characteristics (male – gonopores at the base of the fifth pair of walking and gonopods (modified first pair of pleopods), red patch on the outer margin of the claws in adults; female – gonopores at the base of the third pair of walking legs (paired openings)). Specimens were categorised as male (M), female (F), or intersex (I). Intersex individuals were identified according to the classification proposed by Sagi et al. (1996), who delineated seven distinct morphological types (type A–G) based on the combination of male and female genital openings and associated internal reproductive structures. In our study only external characteristics were taken in the consideration. Intersexuality in *C. quadricarinatus* is an endocrinologically induced condition occurring in genetic females that function as males. Although these individuals exhibit both male and female gonopores, they are functionally male, possessing testes, sperm ducts, androgenic glands, and viable sperm (Parnes et al. 2003, Shechter et al. 2005).

Three biometric parameters were recorded for each individual: total length (TL: from the tip of the rostrum to the end of the telson), cephalothorax length (CL: length from the tip of the rostrum to the posterior median edge of the carapace), and right chela length (CHL). The measurements were taken to the nearest 1 mm using vernier calipers. The wet weight (W) of the samples was measured using spring balances and recorded to the nearest gram. Individuals exhibiting missing chelae or damaged rostra were excluded from the analysis.

The relationship between CL and W was modeled separately for males, females, and intersex individuals using the power function:

$$W = a * CL_b$$

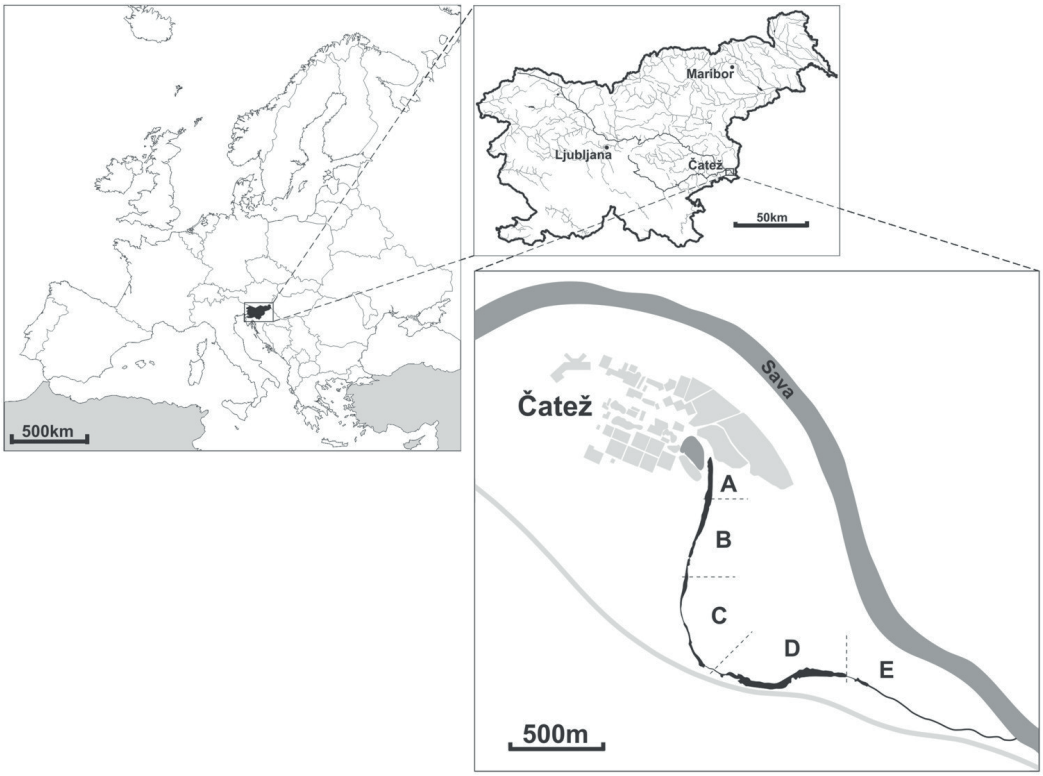


**Fig. 1.** The thermally enriched oxbow lake in Slovenia, where a population of non-indigenous crayfish species *Cherax quadricarinatus* was sampled between 2009 and 2021. The lake, located near Čatež and the Sava River, is marked in black (right lower map) and divided into five habitat zones (A–E) along a natural water temperature gradient. Zone A represents the warmest area, while zone E is the coldest, with water temperatures similar to those in the adjacent Sava River.

To meet the assumptions of normality and homoscedasticity, both variables were log-transformed prior to analysis. The scaling exponent $b$ and intercept $a$ were estimated via linear regression of the form:

$$\mathbf{log(W) = log(a) + b * log(CL)}$$

General Linear Models (GLMs) were applied to assess the effect of sex and the interaction between sex and CL on body weight. One-way ANOVA followed by Tukey's HSD post hoc tests was used to compare morphometric traits (W, TL, CL, CHL, CHW) among the three sex groups.

Body condition was estimated using the Scaled Mass Index (SMI), following the method of Peig & Green (2010). The SMI was calculated for each individual as:

$$\mathbf{SMI_i = W_i\left(\frac{L_0}{L_i}\right)^{bSMA}}$$

where $W_i$ and $L_i$ are the wet mass and cephalothorax length (CL) of individual $i$, $L_0$ is the arithmetic mean of CL for the entire sample, and *bSMA* is the scaling exponent derived from standardized major axis regression of ln(W) on ln(CL). The parameters *bSMA* and $L_0$ were estimated separately for males, females, and intersex individuals using within-group log–log regressions. This approach permits the comparison of predicted body mass at a standardized body length across groups, thus allowing sex-specific inferences about relative condition.

## Statistics

Descriptive statistics (mean, standard deviation, and sample size) of the Scaled Mass Index (SMI) were computed separately for each sex group. Differences in morphometric traits and SMI among sexes were assessed using one-way ANOVA, followed by Tukey's HSD post hoc test. In addition, a General Linear Model (GLM) was employed to evaluate the effects of sex, cephalothorax length (CL), and their interaction on wet weight (model: Weight ~ CL × Sex). Effect sizes, confidence intervals, and p-values were reported. Statistical significance was set at $p < 0.05$. All analyses and visualisations were conducted in R version 4.1.2 (R Core Team 2021).

## Results

A total of 1362 specimens of *C. quadricarinatus* were collected and measured from the Topla oxbow lake between 2009 and 2021. The sample comprised 606 males, 613 females, and 138 intersex individuals. Intersex individuals were categorised into four morphological types (B – female opening on the right, male opening on the left, E – female opening on the left, male openings on both sides, F – female opening on the right, male openings on both sides, and G – female and male openings on both sides) following the classification proposed by Sagi et al. (1996). Furthermore, four specimens could not be reliably sexed and were thus marked as juveniles ("juv"). The body weights of these juveniles ranged from 1.2 to 5.3 g, but carapace length measurements were not recorded.

The smallest female specimen exhibited a cephalothorax length (CL) of 18 mm and a mass of 2 g, while the largest specimen attained a length of 175 mm in total length (TL), 83 mm in CL, and a mass of 113 g. Males ranged from 22 to 95 mm in CL, and from 36 to 193 mm in TL, with weights between 3 and 220 g. Intersex individuals varied between 24 and 95 mm in CL and reached up to 215 mm in TL and 126 g in body mass (Table 1). A total of 138 intersex specimens were recorded, constituting 10.1 % of the entire population. Intersex individuals were categorised into four types: type G was the most prevalent, accounting for 47.8 % (N = 66) of the intersex population, followed by type E (28.3 %, N = 39), type F (22.5 %, N = 31), and type B (0.7 %).

The ANOVA revealed statistically significant differences among the three sex groups (females, males, and intersex individuals) in several morphometric

**Table 1.** The following descriptive statistics were calculated for the morphometric variables of *Cherax quadricarinatus*: mean, standard deviation (SD), minimum (Min), maximum (Max), median, first quartile (Q1), and third quartile (Q3). These statistics were calculated for the following variables: wet weight (W), total length (TL), cephalothorax length (CL), chela length (CHL), and chela width (CHW).

| Parameter | Sex | Mean | SD | Max | Min | Median | Q1 | Q3 |
|---|---|---|---|---|---|---|---|---|
| W (g) | F | 34 | 19 | 113 | 2 | 29.0 | 20 | 46 |
| | M | 43 | 32 | 220 | 3 | 36.0 | 20 | 61 |
| | I | 40 | 27 | 126 | 3 | 35.5 | 20 | 53 |
| CL (mm) | F | 53 | 11 | 83 | 17 | 51.0 | 46 | 61 |
| | M | 56 | 13 | 95 | 21 | 53.0 | 46 | 65 |
| | I | 55 | 12 | 95 | 24 | 55.0 | 46 | 63 |
| TL (mm) | F | 109 | 20 | 175 | 33 | 111.0 | 96 | 127 |
| | M | 113 | 29 | 193 | 36 | 113.0 | 93 | 135 |
| | I | 110 | 31 | 215 | 18 | 112.0 | 90 | 129 |
| CHL (mm) | F | 37 | 10 | 112 | 12 | 36.0 | 31 | 42 |
| | M | 43 | 16 | 81 | 9 | 41.0 | 31 | 50 |
| | I | 41 | 13 | 77 | 16 | 41.0 | 31 | 51 |
| CHW (mm) | F | 22 | 6 | 40 | 5 | 23.0 | 19 | 26 |
| | M | 24 | 6 | 40 | 6 | 23.0 | 19 | 28 |
| | I | 23 | 6 | 40 | 10 | 24.0 | 19 | 27 |

**Table 2.** Results of the analysis of variance (ANOVA) with the Tukey post hoc test for selected morphometric parameters (W, weight; TL, total length; CL, cephalothorax length; CHW, cephalothorax width; CHL, chela length), between sexes (M, males; F, females; I, intersex) are shown below.

| | ANOVA | | | Tukey post hoc test | | |
|---|---|---|---|---|---|---|
| Parameter | F | df | p- value | M vs. F | M vs. I | F vs. I |
| W (g) | 8 | 2 | < 0.001 | < 0.001 | 0.525 | 0.036 |
| CL (mm) | 5.41 | 2 | 0.005 | 0.004 | 0.988 | 0.172 |
| TL (mm) | 3.21 | 2 | 0.041 | 0.036 | 0.423 | 0.974 |
| CHL (mm) | 25.50 | 2 | < 0.001 | < 0.001 | 0.475 | 0.003 |
| CHW (mm) | 2.79 | 2 | 0.087 | 0.056 | 0.072 | 0.477 |

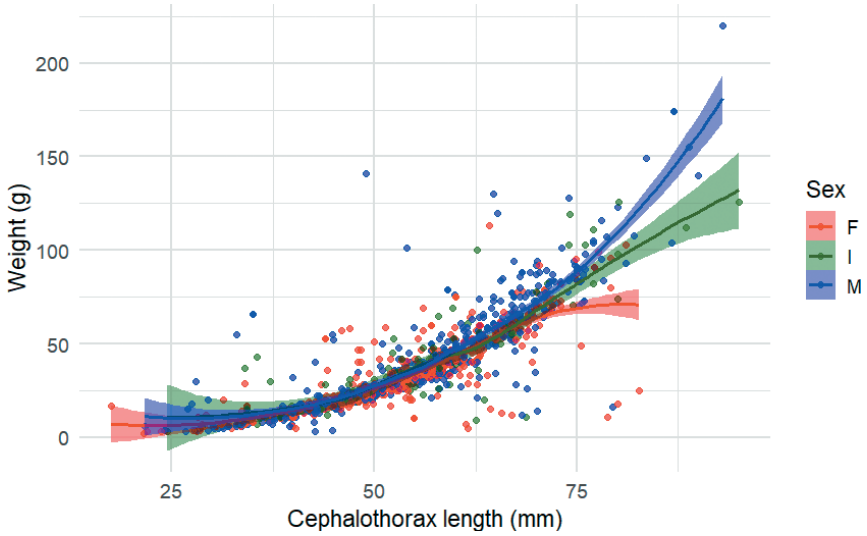


**Fig. 2.** Relationship between cephalothorax length (CL) and wet weight (W) in *Cherax quadricarinatus*, separated by sex (F, female; M, male; I, intersex). Scatter plots show raw values, while smoothed LOESS curves (with 95 % confidence intervals) illustrate the general growth trend for each sex category. Males tend to reach higher weights at larger CL values compared to females and intersex individuals, indicating sex-related variation in growth patterns.

traits (Table 2). A statistically significant difference in body weight was observed between males and females ($p < 0.001$), and between females and intersex individuals ($p = 0.036$). On average, males and intersex individuals exhibited higher body weights compared to females. A statistically significant difference was observed in total length (TL) between males and females ($p = 0.036$). However, no such differences were detected among other sex combinations. Furthermore, a significant variation in cephalothorax length (CL) was observed across sexes, with males exhibiting a substantially greater CL compared to females ($p = 0.004$). No significant differences were observed between males and intersex individuals, nor between females and intersex individuals. With regard to chela length (CHL), males demonstrated significantly elongated chelae in comparison to both females ($p < 0.001$) and intersex individuals ($p = 0.003$), thereby indicating pronounced sexual dimorphism in this trait. No statistically significant differences were observed in chela width (CHW) among the sex groups ($p = 0.332$), although p-values for M vs. F (0.056) and M vs. I (0.072) approached significance.

### Length–weight relationship

The weight–length relationship showed a robust and significant fit across all sex categories (Table 3). In males, the slope (b) was 2.752 ($R^2 = 0.789$), in females 2.5361 ($R^2 = 0.743$), and in intersex individuals 2.516 ($R^2 = 0.721$) (Table 3). All models demonstrated highly significant p-values ($p < 0.001$) (Table 2). The findings suggest a consistent and significant predictive relationship between cephalothorax length and body weight in *C. quadricarinatus* across different sexes. In all groups, the exponent b was significantly lower than 3 ($p < 0.001$), suggesting negative allometric growth, i. e. weight increases at a slower rate than the cube of cephalothorax length. This pattern reflects a common growth trajectory in decapods, where larger individuals gain mass less rapidly relative to their increase in linear dimensions. The regression lines showed that weight increased most rapidly with CL in males, followed by females and intersex individuals, though sex-specific differences were further supported by statistical models (see GLM analysis).

A generalized linear model (GLM) was fitted to assess whether the relationship between cephalothorax length (CL) and wet weight (W) differed across sex categories (Table 4). The analysis revealed a significant main effect of CL (coef. = 1.49, $p < 0.001$), indicating that weight increases significantly with CL across all individuals. Importantly, we included interaction terms between CL and sex to evaluate whether the rate of weight increase per unit of CL differs among males, females, and intersex individuals. The results confirmed this: both interaction terms were statistically significant. The coefficient for the

interaction between CL and intersex individuals was 0.312 ($p = 0.006$), indicating that intersex individuals experience a steeper increase in weight with increasing CL compared to females (the reference group). Similarly, the interaction term for males was 0.448 ($p < 0.001$), suggesting an even stronger positive association between CL and weight for males compared to females.

These significant interaction effects confirm that the slope of the weight–length relationship varies by sex category. This implies that males and intersex individuals gain weight more rapidly than females for each unit increase in CL. The sex-specific growth trajectories are also evident in Figure 2, where LOESS curves show that males, followed by intersex individuals, attain higher weights at larger CLs, consistent with sexual dimorphism in *C. quadricarinatus*.

Figure 3 illustrates the sex-specific variation in body size and mass of *C. quadricarinatus* based on cephalothorax length (CL) and wet weight (W). While the CL distributions appear broadly similar across sex groups, the wet weight histograms indicate a clear right-skewed pattern, with males reaching the highest maximum values, followed by intersex and female individuals. These differences support the observed sexual dimorphism in growth and mass accumulation, as further confirmed by the regression and GLM analyses. The greater weight range in males and intersex individuals, in particular, reflects their higher mass gain per unit CL, in line with their steeper length- weight slopes and positive interaction terms identified in the statistical models.

Based on thresholds for sexual maturity in *C. quadricarinatus* reported in the literature (i.e. 40–50 mm cephalothorax length and approximately 30–50 g wet weight; Rabeni et al. 1997, Sagi et al. 1996, Lawrence & Jones 2002), we classified individuals into juvenile and adult size classes. In our sample (n = 1191), the majority of individuals (61.8 %) exceeded 50 mm CL and 71.7 % weighed less than 50 g. Sex-specific analysis revealed that the majority of females (78.2 %) and intersex individuals (72.2 %) fell within the juvenile size class, while only 21.8 % and 27.8 %, respectively, were classified as adults. Among males, juveniles accounted for 63.7 % of individuals, and adults for 36.3 %. These results suggest that the population is predominantly composed of individuals near or below the conventional thresholds of sexual maturity, although it is likely that a substantial proportion of the juveniles – particularly among males – are already functionally mature. The higher proportion of juvenile-class individuals across all sex categories also reflects the sustained recruitment and potential for continued population expansion under the favourable thermal conditions of the study site. Among females, juvenile individuals dominated the lower weight classes (10–40 g), whereas adults were more frequent above 50 g, with a peak around 60 g. Males exhibited a broader weight range, with juveniles concentrated between 10–50 g and adults spanning up to 120 g, with a gradual decline in frequency at higher weights. The intersex group showed a relatively low number of individuals, mostly juveniles below 50 g, while adult intersex crayfish were rare and more evenly distributed across the 50 100 g range (Fig. 2).

**Table 3.** Summary of regression parameters (log(W) ~ log(CL)) by sex (M, males; F, females; I, intersex).

| Sex | N | Intercept (a) | Slope (b) | $R^2$ |
|---|---|---|---|---|
| M | 533.0 | -3.2431 | 2.7520 | 0.798 |
| F | 536.0 | -2.8999 | 2.5361 | 0.743 |
| I | 122.0 | -2.8426 | 2.5160 | 0.721 |

## Discussion

The study encompassed an extensive dataset of redclaw crayfish collected over a decade from 2009 to 2021 within the Topla oxbow lake, providing a detailed investigation into the species' morphometric characteristics and population structure.

The present study provides compelling evidence of pronounced sexual dimorphism in the feral population of *C. quadricarinatus* inhabiting the thermally enriched oxbow lake in Slovenia. Males were found

**Table 4.** GLM: Interaction between sex (M, males; F, females; I, intersex) and cephalothorax length (CL).

| Term | Coef. | SD | t | p-value | 95 % CI |
|---|---|---|---|---|---|
| Intercept | -45.2881 | 2.9680 | -15.2587 | < 0.001 | -51.1113–-39.465 |
| Sex [F vs. I] | -13.7012 | 6.3228 | -2.1670 | 0.030 | -26.1064–-1.2961 |
| Sex [F vs. M] | -19.3083 | 3.9731 | -4.8597 | < 0.001 | -27.1035–-11.5131 |
| CL | 1.4916 | 0.0547 | 27.2696 | < 0.001 | 1.3843–1.5989 |
| CL x Sex [F vs. I] | 0.3122 | 0.1131 | 2.7612 | 0.006 | 0.0904–0.5340 |
| CL x Sex [F vs. M] | 0.4480 | 0.0718 | 6.2388 | < 0.001 | 0.3071–0.5889 |

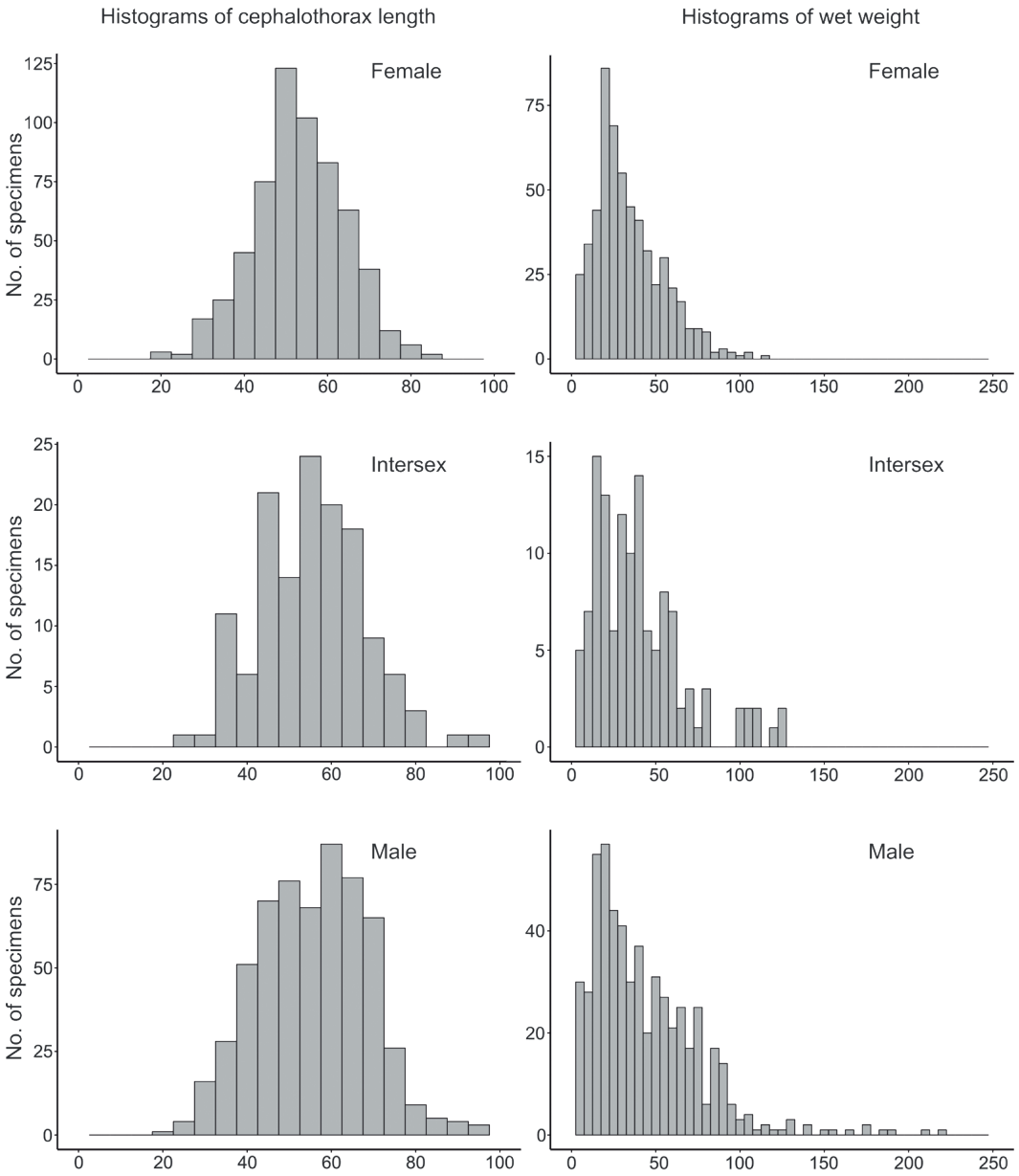


**Fig. 3.** Size-frequency distribution of *Cherax quadricarinatus* by sex (female, male, intersex), based on cephalothorax length (CL) in mm and wet weight (W) in g. The distributions highlight differences in size structure between sex categories, with males and intersex individuals generally attaining larger body sizes.

to have significantly greater body mass and longer chelae than females, a pattern well documented in aquaculture-based research (Austin 1995, Jones 1995, Bortolini et al. 2007, Leland et al. 2012, Eprilurahman et al. 2021). This dimorphism likely reflects reproductive strategies and intraspecific competition; larger chelae in males may serve as secondary sexual traits and as tools in agonistic encounters. However, intersex individuals – genetic females that functionally behave as males – are less commonly reported in field populations. In our population, these individuals accounted for over 10 % of all

specimens and exhibited morphologies that closely resembled those of males, particularly in terms of body size and chela development. These findings corroborate earlier descriptions of hormonally masculinised females in aquaculture systems (Sagi et al. 1996, Parnes et al. 2003, Barki & Karplus 2004, Eprilurahman et al. 2021) and raise significant ecological questions concerning the causes of intersexuality in naturalised populations.

Sex-specific analysis of size classes revealed that the majority of individuals in all sex groups fell within the juvenile size range as defined by published maturity thresholds. Juveniles represented 78.2 % of females, 72.2 % of intersex individuals, and 63.7 % of males. Despite their classification, many of these individuals likely fall within the lower spectrum of functional maturity, particularly among males. The majority of individuals in our sample (n = 1191) exceeded 50 mm in carapace length (CL, 61.8 %) and weighed less than 50 g (71.7 %), indicating a population composed predominantly of subadult to adult specimens. Based on known size at sexual maturity (40–50 mm CL and 30–50 g) (Rabeni et al. 1997, Sagi et al. 1996, Lawrence & Jones 2002), our data strongly suggest that the majority of captured individuals were sexually mature.

It is important to note that our study site – a side-channel (mrtvica) called Topla in northeastern Slovenia – presents environmental conditions highly favorable for the establishment of tropical crayfish species. Throughout the sampling period (2009–2021), surface water temperatures at the site ranged between 20–30° C, regardless of the time of year. This thermal regime is comparable to that of the native habitat of *C. quadricarinatus* in northern Australia and aligns with optimal growth and reproductive temperatures documented for the species in both wild and cultured populations (Jones 1995, Oficialdegui 2023).

Therefore, the body sizes and morphometric differences observed in our population are likely not the result of thermal limitation or poor habitat quality, but instead reflect natural variation within a well-established and environmentally supported feral population. Indeed, the mean CL (54.3 mm) and the size of the largest individual (CL = 93 mm, W = 220 g) fall within the range reported for adult specimens in tropical or subtropical environments (Gu et al. 1994, Marufu et al. 2018, Todd & Hyslop 2023).

Given the suitable abiotic conditions, it is not surprising that *C. quadricarinatus* in Slovenia exhibits size structures, reproductive traits, and sexual dimorphism comparable to those observed in its native range. This supports the interpretation that the observed morphometric traits are ecologically and physiologically representative of natural populations, and not substantially affected by thermal constraints or other stressors commonly found in temperate invader settings. The weight-length relationships observed in all sex categories conformed to a negative allometric growth model ($b < 3$), whereby mass increases at a slower rate than body length. Although aquaculture studies often report positive allometry in males ($b > 3$), our results are consistent with those from wild populations, where environmental constraints may restrict mass gain relative to structural growth (Jones 1990, Purnamasari et al. 2018, Jutagate et al. 2023). Notably, males exhibited steeper slopes in the length–weight regression, reflecting their faster rate of mass accumulation per unit of carapace length compared to females, which is consistent with their larger average size and stronger investment in somatic traits.

Assessment of body condition using the Scaled Mass Index (SMI) revealed no significant differences between the sexes, suggesting that all individuals maintained good physiological status regardless of sex or reproductive morphology. These findings are consistent with observations in related studies of redclaw crayfish and other decapods under different environmental conditions (Peig & Green 2010, Gómez Isaza et al. 2018). The robust condition indices also indicate the high adaptability of *C. quadricarinatus* to non-native environments. Furthermore, the increase in intersex prevalence over time – from 0.6 % in 2009 to over 10 % in recent years – may reflect environmental endocrine disruption, possibly due to pollutants or the effects of population density in the thermally modified habitat.

These findings indicate that *C. quadricarinatus* possesses the capacity to develop natural size structures, sexual dimorphism, and physiological conditions comparable to those observed in tropical native populations, provided that environmental conditions, such as thermal regime, are favourable. This capacity is evident even within temperate European habitats, albeit in a habitat that is likely to include thermal springs. The present study combines morphometric, condition and demographic analyses in order to provide valuable ecological insight into the biology of redclaw crayfish in feral European environments.

**Acknowledgements**

We would like to thank the numerous volunteers who assisted in monitoring the *C. quadricarinatus* population over more than a decade. Special thanks go to the National Institute of Biology, Slovenia, for their valuable scientific and financial support. We also thank the Fisheries Research Institute of Slovenia for enabling the long-term monitoring of the population in the field. This

study was funded by the Slovenian Research and Innovation Agency (ARIS) within the framework of the "Young Researcher" programme and the research project "Invasive potential of alien crayfish species and their effects on native species in Slovenia" (project no. L1-2169-0105), supported by the same agency.

## References

Ahyong, S. T. & Yeo, D. C. J. 2007. Feral populations of the Australian red-claw crayfish (*Cherax quadricarinatus* von Martens) in water supply catchments of Singapore. Biological Invasions 9 (8): 943–946.

Arias, A. & Torralba-Burrial, A. 2021. First record of the redclaw crayfish *Cherax quadricarinatus* (von Martens, 1868) on the Iberian. Limnetica 40 (1): 33–42.

Austin, C. M. 1995. Length–weight relationships of cultured species of Australian freshwater crayfish of the genus *Cherax*. Freshwater Crayfish 10 (4): 410–418.

Barki, A. & Karplus, I. 2004. Size rank and growth potential in redclaw crayfish (*Cherax quadricarinatus*): are stunted juveniles suitable for grow-out? Aquaculture Research 35 (6): 559–567.

Bayer, L. M., Fournier, R. J. & Magoulick, D. D. 2021. Modelling effects of disturbance on population dynamics of generalized crayfish life history strategies. Aquatic Conservation Marine and Freshwater Ecosystems 31 (3): 457–468.

Beatty, S. J., Morgan, D. L. & Gill, H. S. 2003. Reproductive biology of the large freshwater crayfish *Cherax cainii* in south-western Australia. Marine and Freshwater Research 54 (5): 597–608.

Belle, C. C. & Yeo, D. C. J. 2010. New observations of the exotic Australian re-claw crayfish *Cherax quadricarinatus* (von Martens, 1868) (Crustacea: Decapoda: Parastacidae) in Singapore. Nature in Singapore 3: 99–102.

Bortolini, J. L., Alvarez, F. & Rodríguez-Almaraz, G. 2007. On the presence of the Australian redclaw crayfish, *Cherax quadricarinatus*, in Mexico. Biological Invasions 5: 615–620.

D'Agaro, E., De Luise, G. & Lanari, D. 1999. The current stats of crayfish farming in Italy. Freshwater Crayfish 12 (1): 506–517.

Eprilurahman, R., Simarmata, A. K., Hakim, L. & Trijoko, T. 2021. Morphological and molecular characters of *Cherax quadricarinatus* (von Martens, 1868) from Sermo Reservoir and Tambakboyo Retention Basin, Daerah Istimewa Yogyakarta, Indonesia. Biogenesis Jurnal Ilmiah Biologi 9 (1): 18–25.

Froese, R. 2006. Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. Journal of Applied Ichthyology 22 (4): 241–253.

Gómez Isaza, D. F., Cramp, R. L. & Franklin, C. E. 2018. Negative impacts of elevated nitrate on physiological performance are not exacerbated by low pH. Aquatic Toxicology 200: 217–225.

Gu, H., Mather, P. B. & Capra, M. F. 1994. The relative growth of chelipeds and abdomen and muscle production in male and female redclaw crayfish, *Cherax quadricarinatus*. Aquaculture 123 (3–4): 249–262.

Haubrock, P. J., Oficialdegui, F. J., Zeng, Y., Patoka, J., Yeo, D. C. J. & Kouba, A. 2021. The redclaw crayfish: a prominent aquaculture species with invasive potential in tropical and subtropical biodiversity hotspots. Reviews in Aquaculture 13 (3): 1488–1530.

Jaklič, M. & Vrezec, A. 2011. The first tropical alien crayfish species in European waters: the Redclaw *Cherax quadricarinatus* (von Martens, 1868) (Decapoda, Parastacidae). Crustaceana 84 (5–6): 651–665.

Jones, C. M. 1990. The biology and aquaculture potential of the tropical freshwater crayfish *Cherax quadricarinatus*. 109 pp., Brisbane, Australia (Queensland Department of Primary Industries).

Jones, C. M. 1995. Production of juvenile redclaw crayfish, *Cherax quadricarinatus* (von Martens): I. Effects of density and shelter on survival and growth. Aquaculture 138 (1–4): 221–238.

Jones, C. M. & Valverde, C. 2020. Development of mass production hatchery technology for the redclaw crayfish, *Cherax quadricarinatus*. Freshwater Crayfish 25 (1): 1–6.

Jutagate, T., Kwangkhwang, W. & Saowakoon, S. 2023. Growth and competitions of the Australian redclaw crayfish, *Cherax quadricarinatus* (von Martens, 1868) in Thailand: the experimental approaches. Aquatic Invasions 18 (1): 103–117.

Lawrence, C. & Jones, C. M. 2002. *Cherax quadricarinatus* (von Martens) – biology, culture and production. Pp. 702–716 in: Holdich, D. M. (ed.). Biology of freshwater crayfish. Oxford (Blackwell Science Ltd. Osney Mead Press).

Leland, J. C., Coughran, J. & Furse, J. M. 2012. Further translocation of the Redclaw, *Cherax quadricarinatus* (Decapoda: Ptarastacidae), to Lake Ainsworth in northeastern New South Wales, Australia. Crustacean Research 7: 1–4.

Loureiro, T. G., Anastácio, P., Araujo, P. B., Souty-Grosset, C. & Almerão, M. P. 2015. Red swamp crayfish: biology, ecology and invasion – an overview. Nauplius 23 (1): 1–19.

Marn, N., Hudina, S., Haberle, I., Dobrović, A. & Klanjšček, T. 2022. Physiological performance of native and invasive crayfish species in a changing environment: insights from Dynamic Energy Budget models. Conservation Physiology 10 (1): 373–380.

Martelloni, G., Bagnoli, F. & Libelli, S. M. 2012. A dynamical population modeling of invasive species with reference to the crayfish *Procambarus clarkii*. Rivista di Biologia 105 (2): 47–69.

Marufu, L., Nyikahadzoi, K. & Nyamupingidza, B. T. 2018. Population dynamics of a recently introduced crayfish, *Cherax quadricarinatus*, in the Sanyati Basin of Lake Kariba, Zimbabwe. African Zoology 53 (1): 17–22.

Miller, S. B. O., Davis, A. R. & Wong, M. Y. L. 2024. The impacts of invasive crayfish and other non-native species on native freshwater crayfish: a review. Biology 13 (8): 1–24.

Oficialdegui, F. J. 2023. *Cherax quadricarinatus* (redclaw crayfish) datasheet. In: Invasive Species Compendium. CABI International, Wallingford, UK. World Wide Web electronic publication. https://www.cabidigitallibrary.org/doi/10.1079/cabicompendium.89135 [accessed 12-Jul-2025].

Parnes, S., Khalaila, I., Hulata, G. & Sagi, A. 2003. Sex determination in crayfish: are intersex *Cherax quadricarinatus* (Decapoda, Parastacidae) genetically females? Genetical Research 82 (2): 107–116.

Peig, J. & Green, A. J. 2010. The paradigm of body condition: a critical reappraisal of current methods based on mass and length. Functional Ecology 24 (6): 1323–1332.

Pinder, A. C. & Harman, A. 2019. Spread of the non-native redclaw crayfish *Cherax quadricarinatus* (von Martens, 1868) into natural waters of the Pilbara region of Western Australia, with observations on potential adverse ecological effects. BioInvasions Records 8 (4): 882–897.

Purnamasari, R., Hariati, A. M. & Priyono, A. D. 2018. Growth patterns and condition factor of redclaw crayfish (*Cherax quadricarinatus*) in freshwater aquaculture ponds. International Journal of Fisheries and Aquatic Studies 6: 154–170.

R Core Team 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at https://www.r-project.org/

Rabeni, C. F., Collier, K. J., Parkyn, S. M. & Hicks, B. J. 1997. Evaluating techniques for sampling stream crayfish. New Zealand Journal of Marine and Freshwater Research 31 (5): 693–700.

Reynolds, J. & Souty-Grosset, C. 2011. Management of freshwater biodiversity: crayfish as bioindicators. 384 pp., Cambridge (Cambridge University Press).

Sagi, A., Khalaila, I., Barki, A., Hulata, G. & Karplus, I. 1996. Intersex red claw crayfish, *Cherax quadricarinatus* (von Martens): Functional males with pre-vitellogenic ovaries. Biological Bulletin 190 (1): 16–23.

Shechter, A., Aflalo, E. D., Davis, C. & Sagi, A. 2005. Expression of the reproductive female-specific vitellogenin gene in endocrinologically induced male and intersex *Cherax quadricarinatus*. Biology of Reproduction 73 (1): 72–79.

Todd, S.-R. L. & Hyslop, E. J. 2023. Morphometrics, diet, reproductive biology and ecological interactions of the introduced redclaw crayfish (*Cherax quadricarinatus*) in Jamaica. Caribbean Journal of Science 53 (2): 397–410.

Vecchioni, L., Marrone, F., Chirco, P., Arizza, V., Tricarico, E. & Arculeo, M. 2022. An update of the known distribution and status of *Cherax* spp. in Italy (Crustacea, Parastacidae). BioInvasions Records 11 (4): 1045–1055.

Weiperth, A., Kouba, A. & Csányi, B. 2020. The present status of non-native decapod (Crustacea: Decapoda) species in Hungary. Tudomany 113 (2): 61–69.