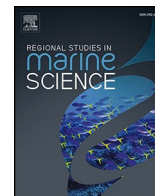


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# Growth patterns of the invasive crab *Cronius ruber* (Brachyura, Portunidae) in the Canary Islands (Central-East Atlantic)

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## ABSTRACT

The growth pattern, including the moult process, relative growth, and estimation of von Bertalanffy growth parameters of the invasive non-indigenous species (NIS) *Cronius ruber* were studied in the Canary Islands. Despite being found in both, native and invaded areas, the life cycle and ecology of this species remain unknown. The study revealed a greater abundance of females than males, with males exhibiting larger carapace sizes and weights than females. Throughout ontogeny, relative growth was observed, with males reaching carapace widths (CW) between 54.5 and 57.8 mm and females reaching 49.9 mm CW. Allometry in the growth of the males' chelae and females' abdomen was consistently positive. *Cronius ruber* was found to be a fast-growing species, reaching the postpubertal growth phase (maturity) between 0.5 and 1 year of age in males and between 0.4 and 0.8 years in females. The intermoult period increased by more than 638% in males and 443% in females with age. Individuals undergo 13 moults during the first phase of life (until 30 mm CW) and then reduced to 6 moults until the end of life, concluding with a final terminal moult. The lifespan until the terminal moult is approximately 2.5 years, followed by a survival time over 1.5 years. von Bertalanffy growth parameters estimated using monthly CW-frequency data for males ( $L_{\infty}=97.4$  mm CW,  $k=1.89$  years<sup>-1</sup>,  $t_0=0.31$  years), and for females ( $L_{\infty}=86.72$  mm CW,  $k=1.91$  years<sup>-1</sup>,  $t_0=0.29$  years). Similar results were obtained using growth increment data.

## 1. Introduction

The spread of non-native marine species into new territories is recognized as a significant environmental issue and a global challenge for ecosystems (Pajuelo et al., 2016). This phenomenon, which involves the introduction, both accidental and intentional, of various species into areas well beyond their indigenous habitats, stands as a critical concern for natural environments worldwide. Such species, which would not have been able to expand into these regions without human involvement, pose threats and challenges to the ecosystems they invade (Bolaños et al., 2012).

*Cronius ruber* (Lamarck, 1818) is a recently reported non-native invader species with a wide distribution in shallow warm waters along the coast of the Atlantic Ocean (González et al., 2017). This species, native to the Brazilian water, has extended its range from the eastern Atlantic coast to Canary Islands (Central East Atlantic) from the

secondary area of distribution (González et al., 2017). It was first reported in the Canary Islands a decade ago, probably transported via oil ring directly from the Gulf of Senegal (González et al., 2017). Once established, these allochthonous species can cause alterations in the ecosystem of the invaded area and economic and social impacts (Carlton and Geller, 1993; Carlton and Ruiz, 2005; Geller et al., 2010; Negri et al., 2018). The impact of *C. ruber* to date is limited and it is related with its widespread carnivorous diet (Triay-Portella et al., 2022). The impact stems from its predatory behavior on native species and competition with native crabs for habitat, especially when some of these local species are endangered, such as *Haliotis coccinea canariensis* (Triay-Portella et al., 2022). In fact, *C. ruber* exhibits a high level of aggressive territorial behavior against other crabs or other species including the octopodid *Callistoctopus macropus* (Triay-Portella et al., 2022).

*Cronius ruber* seeks habitats in its non-native regions, thriving in areas with or without varied structures (Coinva, 2019). Observations

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indicate its presence in soft sediment zones, beneath rocks and debris, along breakwaters, and throughout areas significantly impacted by human activities. The prevalence of *C. ruber* in an ecosystem often leads to decreased populations of other crab species, urchins, polychaetes, gastropods, bivalves, and small fish due to its competitive dominance (Triay-Portella et al., 2022).

Understanding the life cycle traits and population behavior of invasive organisms is crucial for mitigating their negative impacts on the environment (Bolaños et al., 2012). Yet, detailed research on the life cycle and fundamental population parameters of *C. ruber* in both, its original and introduced territories, is lacking. This study aims to elucidate the invasive crab *C. ruber*'s growth patterns in the eastern central Atlantic, encompassing aspects such as age, growth rates, lifespan, molting frequency, and morphometric development.

The findings from this investigation, in conjunction with data on reproductive behaviors, will contribute to a broad comprehension of the species' ecology. This knowledge is essential for implement effective management practices to address the broader ecological consequences instigated by the presence of this invasive species.

## 2. Materials and methods

### 2.1. Sampling and biological data collection

Specimens of *C. ruber* were collected by hand from January 2018 to December 2018 in heavily anthropized areas at depths between 1 and 8 m on rocky/sandy bottoms. Samplings were always conducted after sunset and before midnight, the major peak of activity for *C. ruber* (Triay-Portella et al., 2022).

Measurements for each crab were taken following Triay-Portella et al. (2014) using a digital calliper with 0.01 mm precision: carapace width (CW), carapace length (CL), right/left propodus length (R/L-CHL), right/left propodus height (R/L-CHW), and abdomen width of the fourth abdominal segment (AS4W) in females (Fig. 1). The measurements were specified as follows: CW is the widest transverse distance across the carapace, measured from the antepenultimate to the ultimate lateral spines, excluding the spine itself; CL represents the linear distance along the carapace's center from the diastema to its rear margin; R/L-CHW denotes the propodus's broadest point, measured at its articulation with the dactylus; R/L-CHL is measured from the palm's furthest point to the tip of the dactylus; AS4W describes the broadest part of the fourth segment of the abdomen. Measurements of CW and CL were conducted on the crab's dorsal side, oriented from side to side and front to back, respectively; R/L-CHL was measured along the outer edge of the chelae, from tip to base; AS4W measurements were taken on the ventral side, spanning from side to side. All measurements were recorded with precision to the nearest millimeter. Additionally, the sex of the crabs and their total body weight (TW, accurate to 0.1 g) were documented. Crabs showing signs of damage or with limbs in regeneration were excluded from the study (Mantelatto and Garcia, 2001).

### 2.2. Relationships between size and weight

The CW–TW relationship was determined for males and females by means of a power function. Differences in the CW–TW and CW–CL lineal form of relationships between males and females were evaluated by an F-test, and differences between values of  $b$  and the expected value from isometric growth were evaluated by a t-test (Sachs, 1982). Relationships between CW and CL were calculated to facilitate the comparison of data. The Kolmogorov-Smirnov non-parametric Z-test was used to analyse the differences in CW and TW ranges in males and females (Sokal and Rohlf, 2012).

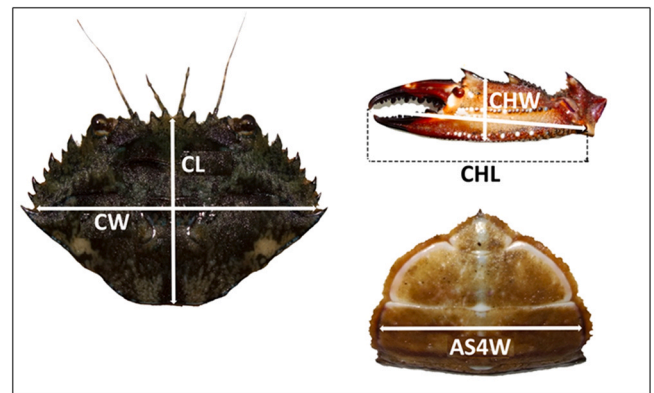


Fig. 1. Measurements taken for each specimen of *Cronius ruber*: carapace width (CW), carapace length (CL), width of chela (CHW), hand-length of chela (CHL), and maximum width of the fifth abdominal somite (AS4W).

### 2.3. Relative growth

The dimensions of the chelae, both in length and width, were compared with the CW for both genders and with the AS4W in females to examine potential shifts linked to the pubertal molt (Somerton, 1980; Attrill et al., 1991). We applied a power function to the dataset using non-linear regression for groups that could be distinctly separated, with transition points determined through iterative searches in increments of 0.1 mm CW (Somerton, 1980). To decide if a dual-model approach provided a better fit than a single unified model, we utilized an F-test that evaluates the differences in the residual sum of squares (Somerton, 1980). Differences in slopes and y-intercepts among the linear relationships, indicative of pre- and post-pubertal growth stages, were assessed using an ANCOVA test (Mantelatto and Garcia, 2001). The differential growth patterns of the chelae (considering both length and width) and the AS4W during the pre- and post-pubertal phases were analyzed using a t-test (Sachs, 1982). The nature of allometry was inferred from the regression slope:  $b=1$  indicates isometry;  $b<1$  signifies negative allometry; and  $b>1$  indicates positive allometry (Mantelatto and Garcia, 2001).

### 2.4. Moulting

A total of 50 individuals (25 males and 25 females) were kept separately in tanks to estimate the number of ecdysis and duration of anecdyosis in this species. Specimens were selected in 10 mm CW size groups. The water temperature in the tanks was the same as that recorded at sea each month ( $\sim 18\text{--}24^\circ\text{C}$ ). The time elapsed between the initial and final process of ecdysis was also recorded. The relationship between percentage of increment in size and carapace width at end of ecdysis was estimated using a linear regression. This equation was used to estimate the number of ecdysis during the first stage of the species.

### 2.5. Growth parameters

The growth increment data obtained from the cultured individuals were used to estimate the parameters of the von Bertalanffy growth function. Two methods were used to estimate the parameters, Appeldoorn (Appeldoorn, 1987; Soriano and Pauly, 1989) and Munro's (Munro, 1982) methods. Both methodologies use growth increment data to estimate the growth parameters  $CW_\infty$  (mm) and  $k$  ( $\text{years}^{-1}$ ).

Appeldoorn's method obtained the von Bertalanffy seasonal growth parameters by minimizing the function using the Marquardt's algorithm

for a nonlinear fit:  $SSE = \sum_i \{ CW_{t+\Delta t} - (CW_\infty - (CW - CW_i) \exp[ - (k\Delta t - S_t + S_{t+\Delta t})]) \}^2$  where  $S_t$  is  $(Ck/2\pi) \cdot \sin(2\pi(t-t_s))$ ;  $S_{t+\Delta t}$  is  $(Ck/2\pi) \cdot \sin(2\pi((t+\Delta t)-t_s))$ ; and  $t_s$  is  $0.5 + WP$ . For  $C=0$  and  $WP=0$ , the simple von Bertalanffy growth function is obtained (Appeldoorn, 1987; Soriano and Pauly, 1989).

Munro's method minimizes the coefficient of variation of the function:  $Ratio = \ln[(CW_\infty - CW_m) - \ln(CW_\infty - CW_r)] / tr$ , where  $CW_m$  is the carapace width before the moulting process (initial carapace width),  $CW_r$  is the carapace width after moulting, and  $tr$  is the time of the intermoult period between two consecutive moulting processes (Munro, 1982).

The monthly CW-frequency data were also used to estimate the parameters of the von Bertalanffy simple and seasonal growth functions by means of the ELEFAN I routine in the FISAT II program (Pauly and David, 1981; Pauly and Morgan, 1987; Gayanilo et al., 1996). The fitted data adhered to a growth curve of the form:  $CW = CW_\infty(1 - \exp(-k(t-t_0) + St_s + St_0))$  where:  $St_s$  is  $(Ck/2\pi) \cdot \sin(2\pi(t-t_s))$ ;  $St_0$  is  $(Ck/2\pi) \cdot \sin(2\pi(t_0-t_s))$ ; and  $L_t$  is the length at time  $t$ , where  $CW_\infty$  is the asymptotic carapace width,  $k$  is the intrinsic growth rate,  $t_0$  is the age at which the carapace width of crabs is 0,  $C$  is the amplitude of seasonal growth oscillation,  $t_s$  is the age at the beginning of growth oscillation, and  $WP = t_s + 0.5$  is the time of year when growth is slowest. For  $C=0$  and  $WP=0$ , the simple von

Bertalanffy growth function is obtained.

### 3. Results

#### 3.1. Relationships between size and weight

In this study, 523 specimens of *C. ruber* were gathered, with 214 males displaying a size range from 27.3 to 90.6 mm in CW and weighing between 7.5 and 233.7 g, and 309 females measuring from 26.4 to 82.3 mm in CW and weighing from 6.2 to 142.5 g (Fig. 2). It was observed that males were generally larger and heavier than females. Analysis revealed disparities in average CW and TW between males ( $66.7 \pm 12.3$  mm and  $86.5 \pm 48.5$  g, respectively) and females ( $62.6 \pm 9.7$  mm and  $62.2 \pm 27.8$  g, respectively), with statistical significance (t-test, CW  $t=4.11$ ,  $p < 0.0001$ ; TW  $t=6.55$ ,  $p < 0.0001$ ). Furthermore, the distribution ranges for both CW and TW significantly varied between the sexes (Kolmogorov-Smirnov non-parametric test, CW  $Z=3.45$ ,  $p < 0.0001$ ; TW  $Z=3.44$ ,  $p < 0.0001$ ).

The analysis of the CW-TW relationship also showed significant sex-based differences (F-test,  $F=4.32$ ,  $p < 0.001$ ), with a consistently positive allometric pattern for males across all measurements (t-test,  $t > 7.746$ ,  $p < 0.001$ ) (Table 1). However, no significant differences were detected

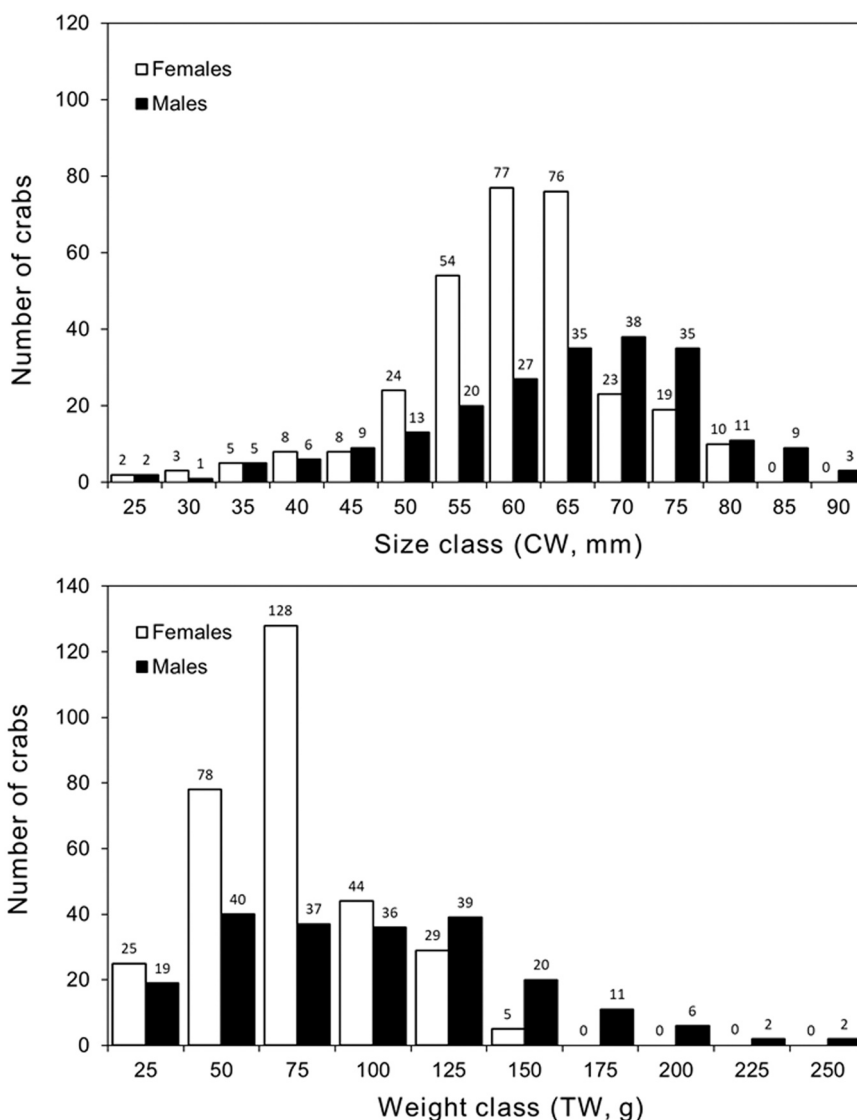


Fig. 2. Number of specimens by carapace width (CW) (top) and total weight (TW) (bottom) of males and females of *Cronius ruber*. Numbers correspond to individuals.

**Table 1**

Parameters of CW-TW ( $TW = a \cdot CW^b$ ) and CW-CL relationships ( $CL = a + b \cdot CW$ ) for males, females and all crabs of *Cronius ruber* a, intercept; b, allometric coefficient; S.E., standard error;  $r^2$ , determination coefficient; n, number of specimens; t, t-test value; \*, significance at 0.05 level.

Relationship	Sex	a	b	S.E.(b)	$r^2$	n	t
CW-TW	Males	0.000033	3.488	0.063	0.954	214	7.746*
CW-TW	Females	0.000248	2.989	0.0704	0.880	309	0.156
CW-TW	All crabs	0.000036	3.458	0.048	0.922	523	9.541*
CL-TW	Males	0.000255	3.311	0.061	0.949	214	5.098*
CL-TW	Females	0.000945	2.937	0.071	0.874	309	0.887
CL-TW	All crabs	0.000205	3.360	0.054	0.911	523	6.501*
CL-CW	Males	0.601	1.459	0.014	0.990	214	32.78*
CL-CW	Females	1.044	1.438	0.0061	0.991	309	73.01*
CL-CW	All crabs	0.551	1.454	0.0090	0.991	523	50.44*

in the CW-CL relationship between males and females (F-test,  $F=1.21$ ,  $p>0.05$ ), with the pattern being positively allometric in all instances (t-test,  $t>32.78$ ,  $p<0.001$ ) (Table 1).

### 3.2. Relative growth

The dimensions of chelae width (R/L-CHW) and length (R/L-CHL) in males were significantly greater and broader than those in females, as determined by ANOVA ( $F>81.15$ ,  $p<0.001$ ). No differences were found in the length or width of the right and left chelae between males and females (ANOVA,  $F<0.17$ ,  $p>0.68$ ). For females, the CW size at which a shift to allometric growth in AS4W occurs was identified at 49.9 mm (Fig. 3). The ANCOVA and F-test highlighted significant disparities between the regression lines for pre- and post-pubertal growth phases (F-test,  $F>7.13$ ,  $p<0.001$ ; ANCOVA  $p<0.001$ ). The allometry of AS4W growth was consistently positive across all subsets analyzed, whether before or after the pubertal phase. The analysis of females exceeding the size at which positive allometric growth begins demonstrated a notable increase in slope magnitude (t-test,  $t=5.25$ ,  $p<0.0001$ ).

The growth of hand length (CHL) and width (CHW) of the right chelae in both males and females was assessed against CW to explore potential shifts linked to the pubertal molt (Fig. 4). The growth patterns of males indicated significant changes throughout their development (F-test,  $F>9.17$ ,  $p<0.001$ ), with transitions observed at 54.5 mm CW (CHL) and 57.8 mm CW (CHW), making different growth patterns before and after these points (ANCOVA  $p<0.001$ ).

The allometry of chelae growth remained positively skewed (t-test,

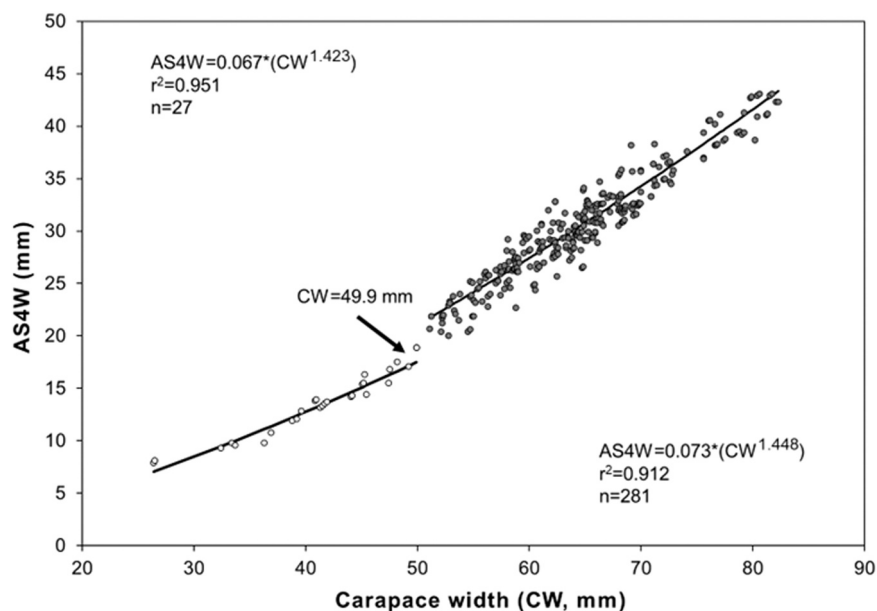
$t>11.42$ ,  $p<0.001$ ), regardless of the chelae's width or length or the developmental phase (pre- or post-pubertal). The model for females exceeding the size at which growth allometry shifts displayed a significant increase in their growth slope. No discontinuities were detected in the relative growth of chelae in females throughout their ontogeny. The allometric growth in chelae length for females was also positively skewed (t-test,  $t>6.78$ ,  $p<0.001$ ).

### 3.3. Moulting

Of the 50 crabs reared in tanks, 21 died before their first moult in the laboratory. The maximum number of moults recorded for the same individual *C. ruber* was 5 times (Fig. 5). The minimum size reared was 37 mm CW (after the first moult in the tank), and the maximum size reached in culture after moulting was 82 mm CW.

The moulting cycle consists of an intermoult period (termed diecdysis if short and anecydysis if longer) which varied from 26 to 32 days for individuals sized between 30 and 39 mm CW, to 142–166 days for individuals in the larger size classes (70–79 mm CW) (Table 2). Ecdysis occurs in an average of  $3.3 \pm 0.8$  hours. During the intermoult period *C. ruber* feeds actively. One male of 87.4 mm CW was reared for 438 days after ecdysis and one female of 80.6 mm CW was reared for 357 days without undergoing a new moult.

Increment in body size after shedding the old exoskeleton varied from 4.9 to 5.3 mm CW for smaller individuals (for males and females) to 10.3–9.1 mm CW for the size classes between 70 and 79 mm CW (Fig. 6). Molting was a short process (less than 2 hours) that was



**Fig. 3.** Maximum width of the fourth abdominal somite (AS4W) plotted against carapace width (CW) in females of *Cronius ruber*. n, number of crabs.  $r^2$ , determination coefficient. Lines fitted correspond to each potential model estimated. Arrows indicate the transition point.

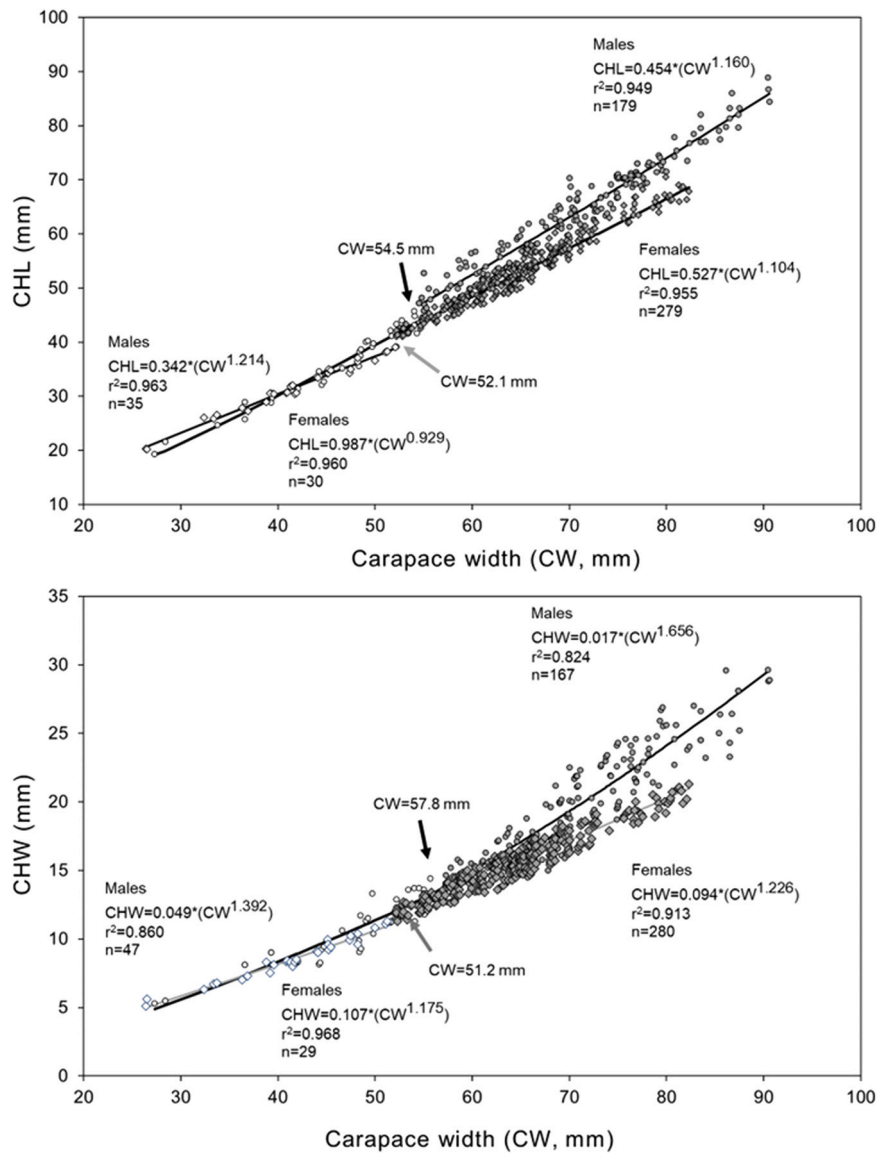


Fig. 4. Chela length (CHL) (top) and chela width (CHW) (bottom) plotted against carapace width (CW). n, number of crabs. r<sup>2</sup>, determination coefficient. Lines fitted correspond to each potential model estimated. Arrows indicate the transition point.

observed in all months of the year (Table 2). The increment in size as a percentage of carapace width at release relationship was estimated for both males and females (Fig. 7). The number of ecdysis events was also calculated for males and females (Fig. 8).

### 3.4. Growth parameters

The von Bertalanffy growth curves determined by Munro and Appeldoorn methods using growth increment data, and the estimated by ELEFAN method using CW-frequency data are presented in Figs. 9 and 10 for males and females, respectively. Males show a higher asymptotic length than females and a similar growth rate when using the Appeldoorn and ELEFAN methods (growth increment data and monthly CW-frequency data). The asymptotic values obtained are consistent with the maximum observed length. However, Munro's method estimates a similar asymptotic length for both sexes and these values are smaller than the highest carapace width recorded.

## 4. Discussion

Individuals were collected from soft bottoms and under rocks;

however, no individuals smaller than 25 mm were found in these habitats. It is important to consider that the failure to detect and collect crabs smaller than 25 mm CW may be due to the sampling protocol, which involved only visual detection of crabs. Smaller crabs are more difficult to detect compared to larger crabs, especially when there is limited air time during dives (Bolaños et al., 2012). Additionally, no small crabs were observed in catches using baited traps were in the same area where adults were found (Coinva, 2019). In other Portunidae species, such as *Charybdis (Charybdis) hellerii*, juvenile individuals are often located in different areas than adults, mainly on patches of algae (Mantelatto and Correa, 1996; Mantelatto and Souza-Carey, 1998; Mantelatto and Garcia, 2001). However, no small crabs were observed in algae patches using three different sampling methods (Triay-Portella et al., 2018). Portunids prefer habitats with high structural complexity (Thiel and Deredde, 1994; Bessa et al., 2010; Young and Elliott, 2020) and avoid open sandy areas without shelter to evade predation and cannibalism (Young and Elliott, 2020). This suggests that there are likely breeding areas that correspond to habitats different from those sampled for this species.

Males reach larger sizes and weight than females. This characteristic is common in many portunid species such as *Charybdis (Charybdis)*



Fig. 5. Ecdysis in a female of *Cronius ruber* reared in tanks in the laboratory.

**Table 2**  
Increment in carapace width in males and females *Cronius ruber* after shedding the old exoskeleton and period of anecdyysis by size class interval.

Size class interval (CW, mm)	Females Size increment (CW, mm)	Anecdysis period (days)	Males Size increment (CW, mm)	Anecdysis period (days)
30–39	5.3±0.53	32.3±4.16	4.9	26.0
40–49	7.0±0.21	51.6±3.79	6.6±0.93	47.5±9.04
50–59	7.4±0.22	62.5±6.36	7.7±0.14	82.5±13.4
60–69	8.1±0.60	94.6±6.66	9.0±0.35	114.1±6.01
70–79	8.8±0.28	142.5±28.9	9.9±0.32	166.0±24.4
80–89	—	357	—	438

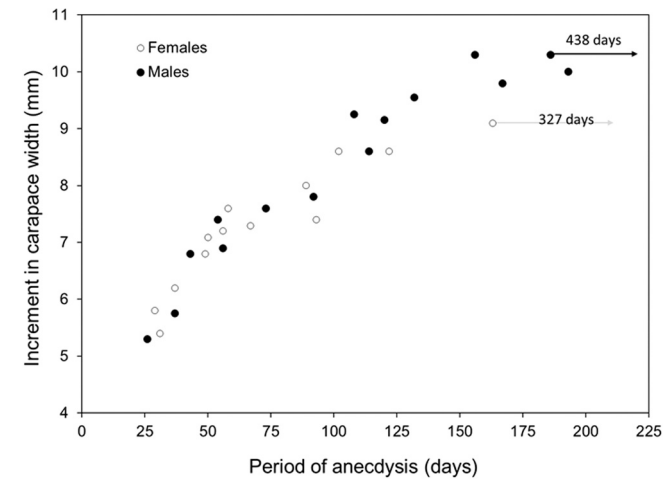


Fig. 6. Increments in carapace width in males and females of *Cronius ruber* in function of the period of time of anecdyysis (in days).

*nator* (Vidhya et al., 2018), *Portunus pelagicus* (Potter et al., 1983), and *Portunus sanguinolentus* (Sukumaran et al., 1986), and it plays an important role during the mating process (Hartnoll, 1982; Abelló et al., 1990). The larger body size of males provides the necessary capacity for manipulating the female during mating (Santos et al., 1995; Sant’Anna

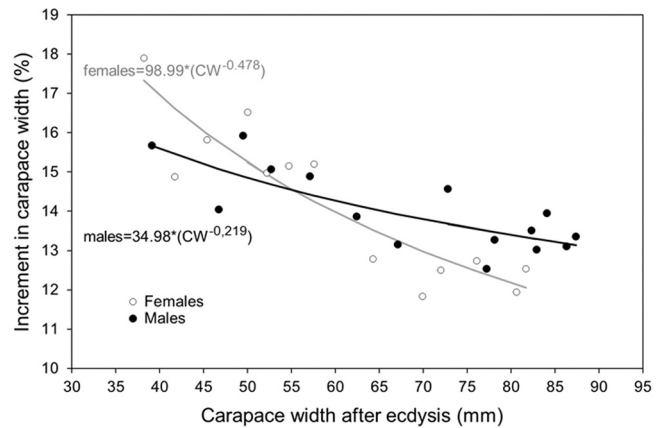


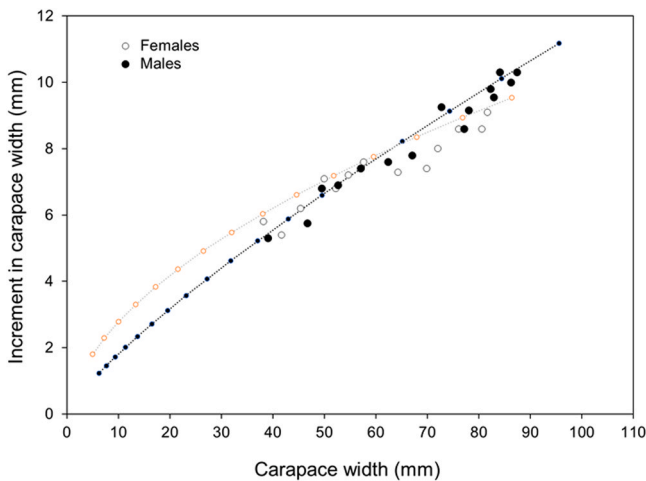
Fig. 7. Relationship between increments in carapace width in percentage and carapace width after ecdysis in males and females of *Cronius ruber*.

et al., 2012). The skewed sex ratio in favor of females in the *Cronius ruber* population is an advantage for the expansion and colonization of new areas. This is because females can generate 5 or 6 clutches of offspring using the sperm stored in the spermathecae to fertilize without mating. On the other hand, a small number of males is sufficient to mate and fertilize all females during their progressive molt, respectively (Triay-Portella et al., 2024).

*Cronius ruber* also exhibited dimorphism in weight, with males reaching higher values. This may be due to the enlargement of male chelipeds, as reported for other portunids such as *C. (C.) natator* (Sallam and Gab-Alla, 2010), *Charybdis (Charybdis) affinis* (Chu, 1999) and *Charybdis (Gonionepturnus) bimaculata* (Doi et al., 2008).

A positive allometry was found in the CL-CW relationship, indicating that the carapace widens relative to its length as size increases. This is likely associated with the development of the gonads which occupy a large volume of the cephalothoracic cavity (Abelló, 1989a, 1989b). This type of allometry has also been observed in other portunid crabs (Davidson and Marsden, 1987; Abelló et al., 1990).

The ontogenic change in the chelae showed a reduction in growth. Portunids exhibit an evolutionary constraint against high positive allometries in the relative growth of appendages, particularly chelae, as it



**Fig. 8.** Relationship between increment in carapace width (estimated from increment size in percentage) and carapace width at release in males and females of *Cronius ruber*.

may negatively affect their swimming ability (Abelló et al., 1990). Portunid crabs are capable of swimming freely in the water column, and it is advantageous for them to remain as light as possible. High positive allometry in the relative growth of the chela, as seen in strictly benthic crabs, tends to reduce this ability. This is likely why allometric growth parameters in most portunid crabs are lower than those shown by strictly benthic crabs (Abelló et al., 1990).

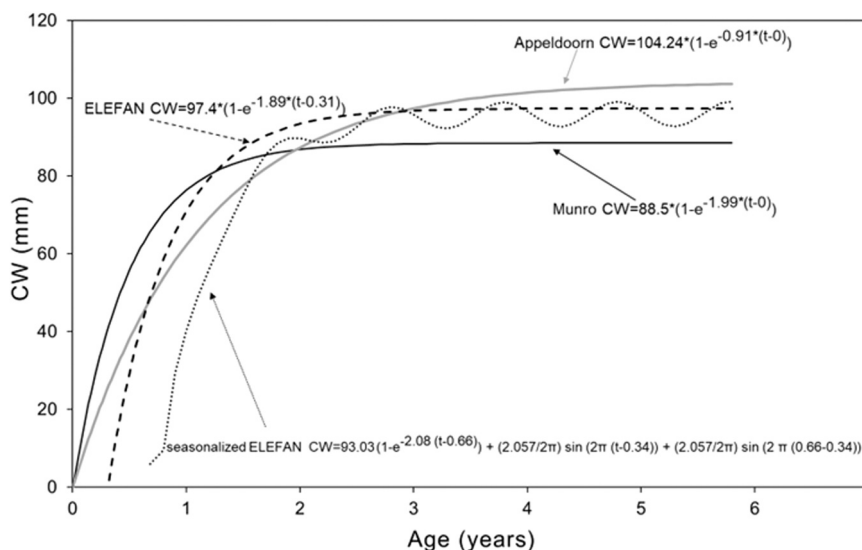
Changes observed in the growth of chelipeds in males and the width of the abdomen in females have been described as playing important roles in the behavior of other portunid species such as *C. (C.) hellerii*, *Charybdis (Charybdis) feriata*, *C. (C.) natator* and *Charybdis (Archias) smithii* (Campbell and Fielder, 1986; Sumpton, 1990; Couwelaar et al., 1997). In the family Portunidae, the abdomen is fixed in immature (prepubertal) females. However, the abdomen become movable in mature (pubertal) females (Van Engel, 1990; Haefner, 1990; Fischer and Wolff, 2006; Bolaños et al., 2012). The ontogenetic change in the growth of the abdomen in females and in the chela in males are secondary sexual character because they are related to reproductive function (Hartnoll, 1978; Yamada et al., 2005). The abdomen of mature females serves as an incubation chamber during the development of eggs, which are attached

to the setose pleopods (Yamada et al., 2005) and the chela is used by males for territorial defence and combat due to their aggressive behaviour. The chela is also used during mating and courtship to transport and support females during copulation (Yamada et al., 2005). While gonopodium development is critical for female insemination and may better reflect male body size at sexual maturity (Doi et al., 2008), relative chela growth can also be used to identify sexual maturity (Yamada et al., 2005). The ontogenetic change in the relative growth of their chela or abdomen at pubertal moult makes these structures fully functional at sexual maturity (Yamada et al., 2005). The values obtained are slightly higher than those on sexual maturity reported by Triay-Portella et al. (2024), who estimate sexual maturity at 52.19 mm CW for males and 49.17 mm CW for females.

During the first phase of life (5–25 mm CW), an estimated 13 moults occur, whereas from then until the end of life, 6–7 moults occur. This is because age is inversely proportional to moult frequency (Klassen and Locke, 2007; Young and Elliott, 2020). Crabs moult much more frequently when young, with short periods of intermediate moult (diecdysis), and intermediate moult intervals becoming much longer (anecdysis) as crabs age, until the crab enters terminal anecdysis (Young and Elliott, 2020).

The longest ecdysis recorded among reared specimens was almost 200 days. Maintenance in rearing conditions for more than 400 days after the last ecdysis suggests the existence of a terminal ecdysis, indicating that they will not moult again. The existence of terminal moult has been observed in other species. Moulting occurs throughout the year in *C. ruber*, as has been observed in other Portunoidea such as the carcinid *Carcinus maenas*. Chronological intermoult times recorded for *Cronius ruber* (26–166 days; crabs 30–79 mm CW) were very similar to those of another invasive Portunidae, *Callinectes sapidus*. This species moults every 18–153 days (crabs 29–85 mm CW) in Chesapeake Bay waters maintained at 16–28 °C (Brylawski and Miller, 2006). However, Bilen and Yesilyurt (2014) observed that *Callinectes sapidus* moults faster in Turkish waters (3–67 days; crabs 14–75 mm CW). This could be due to the higher temperature recorded during culture (30.2 °C) and a shorter experimental period (133 days).

The maximum size attained by *C. ruber* appears to be 80 mm CW for females and over 90 mm CW for males. Females are smaller than males when they reach sexual maturity and begin to incubate eggs (Young and Elliott, 2020). The life-span of *C. ruber* has been estimated at 2.5 years until the terminal moult, with a subsequent survival period more than 1.5 years. These results are consistent with observations for other



**Fig. 9.** The von Bertalanffy growth curves for males *Cronius ruber* determined by the Munro, and Appeldoorn methods (using growth increment data) and by the ELEFAN method (simple and seasonalized using monthly CW-frequency data).

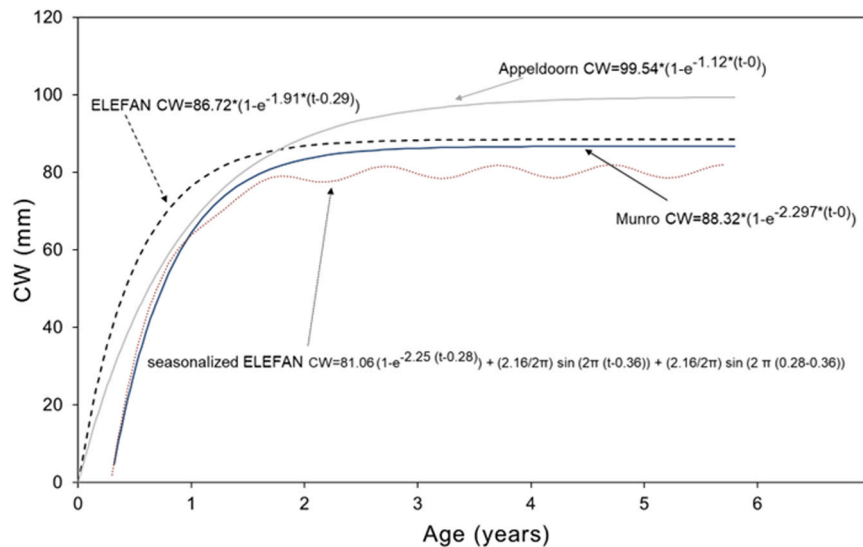


Fig. 10. The von Bertalanffy growth curves for females of *Cronius ruber* determined by Munro, and Appeldoorn methods (using growth increment data) and ELEFAN method (simple and seasonalized using monthly CW-frequency data).

Portunoidea in their Atlantic populations, such as *Carcinus maenas*, which has a life expectancy of 4–7 years (Klassen and Locke, 2007; Yamada et al., 2005; Young and Elliott, 2020). Other portunid crab species have life spans ranging from 2 to 4 years, as seen in *Charybdis (Charybdis) japonica* (Ogawa, 1997) and *Portunus trituberculatus* (Ariyama, 1993), and at least three years, as in the carcinid *Carcinus aestuarii* (Furota et al., 1999).

Differences in growth between sexes are mainly due to the greater energy invested in reproductive production by females. Upon reaching sexual maturity, growth decreases (Hartnoll, 1982) because part of the energy is diverted to reproduction, primarily by females (Lee and Hsu, 2003). As a result of greater investment in reproduction and less growth, females attain smaller size and weight than males (Cobb and Caddy, 1989; Lee and Hsu, 2003). Such differences in the amount of energy expended have been observed in other portunids such as *P. sanguinolentus*, *P. pelagicus*, and *Scylla serrata* (Jacob et al., 1990; Reeby et al., 1990; Sukumaran and Neelakantan, 1997). Size at sexual maturity is reached during their first year of life, as in other portunid species such as *P. sanguinolentus* (Lee and Hsu, 2003).

Gayanilo and Pauly (1997) proposed that asymptotic size must be approximately 5 % larger than the maximum observed size. According to this, the best estimate of asymptotic length and longevity corresponds to the value indicated by the simple von Bertalanffy growth equation estimated from the length frequency distributions.

Among the growth equations estimated for *Cronius ruber*, the equation obtained using the Munro method slightly underestimates growth. The other three equations have similar results, so the simple von Bertalanffy model estimated from CW frequency data is the most appropriate, as it is the simplest model that explains growth with a smaller number of parameters and the most widely used, allowing for comparison the parameters (Bustos et al., 2009). The reduction in growth rate with age is related to diet. Juveniles have a higher ingestion rate than older adults and a greater diversity of preys because they have high energy requirements for growth (Triay-Portella et al., 2022).

It should be noted that the estimated longevity values in the Canary Islands may be slightly lower than those of other Atlantic populations because the Canary Islands and Madeira are the northernmost areas of distribution. Crabs' populations close to the northernmost limit of distribution show slower growth compared to populations from more favourable environments (Young and Elliott, 2020).

Many portunid species that have successfully colonized new habitats

have done so because they possess biological characteristics that confer adaptive advantages for invasion. These characteristics include rapid growth and maturation, high fecundity, short turnover time, the ability of females to store sperm and produce multiple offspring in a single season, a broad carnivorous diet, and the ability to utilize multiple habitats (Sant'Anna et al., 2012). *C. ruber* presents these characteristics in their non-native area (Coinva, 2019; Triay-Portella et al., 2022, 2024).

## 5. Conclusions

The high growth rate of *C. ruber* helps to understand the great expansion and rapid settlement of this species outside its natural area. The short period of time it takes to reach terminal molt is evidence of its great ability to compete with species in the areas it colonizes. The information obtained on the growth pattern increases the baseline on this invasive alien species, expanding the arguments for adding *C. ruber* to the EU list of invasive alien species. Eradication of non-native invasive species as *C. ruber* is practically impossible, so the removal of mature individuals has proven to be an effective strategy to reduce the population and its effects on habitats. This requires intensive fishing with selective traps for this species, especially in anthropized areas (Coinva, 2019). The development of effective management strategies to maintain the *C. ruber* population at the lowest possible levels must be accompanied by measures that lead to the recovery of the populations of their potential predators in the area overexploited by fishing (Coinva, 2019; Triay-Portella et al., 2022).

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## CRedit authorship contribution statement

**José G. Pajuelo:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization, Project administration. **José A. Martín:** Writing – original draft, Investigation, Formal analysis, Data curation, Writing – review & editing. **Raül Triay-Portella:** Writing – original draft, Investigation, Formal analysis, Data curation, Conceptualization.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationship influence the work reported in this paper.

## Data Availability

Data will be made available on request.

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