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Effect of warming on European green crab (*Carcinus maenas)* populations from larvae to sexual maturity

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ABSTRACT

Understanding the effects of climate change on the physiology of marine species, particularly during their early life stages (larvae and juveniles), is essential for predicting population dynamics. *Carcinus maenas* is a widely distributed species of significant ecological and economic importance. This experimental study investigates the effects of warming on the early life stages of the European green crab, *C. maenas,* through two complementary experiments: (1) larval development and survival were assessed under three temperature regimes—approximately 18.5 °C (representing the annual average Portuguese seawater temperature between 1980 and 2020, used as the control), and two projected climate change scenarios: RCP 4.5 (+1.5 °C) and RCP 8.5 (+3.5 °C), and (2) juvenile survival and growth were monitored in mesocosms from early settlement to sexual maturity. Results indicated that larval mortality exceeded 90 % across all treatments, with 75 % occurring within the first 8 days (95 % CI: 7–8), and that warming enhanced larval survival, with the RCP 4.5 scenario yielding the highest survival rates compared with the control. Additionally, warming also reduced the pelagic larval duration, which declined from 27 (±2) days at 18.5 °C to 16 (±1) days at 22 °C. Similarly, the duration of the megalopa (settlement) stage decreased from 10 to 6 days. Therefore, despite high mortality, accelerated development under warming may enhance population resilience. Juvenile mortality was also high, with 50 % of settled individuals dying within the first 50 (95 % CI: 31–46) days, and differences in growth and survival between sexes were observed: females reached sexual maturity faster than males 83 ± 12 and 109 ± 20 days, respectively. Moreover, only 24 % (95 % CI: 16–34) of the settled females reached sexual maturity, compared to just 9 % of males (95 % CI: 5–18). These results indicate that *C. maenas* reach reproductive maturity within six months. The biological data reveal a fast growth increment, high larval and juvenile mortality, and suggest that projected climate change scenarios through the end of the century will have a limited impact on the species' population dynamics and recruitment.

1. Introduction

Climate change, particularly global warming, can impact biodiversity and the ecosystem services provided by marine environments, affecting marine species and ecosystems in multiple ways across various spatial and temporal scales (Bueno-Pardo et al., 2021; Albo-Puigserver et al., 2022; Pinto et al., 2023; Leitão and Cánovas, 2025). Coastal and estuarine areas are among the regions most vulnerable to global warming (Biguino et al., 2023). These habitats play a critical role in the early life stages of many fish and invertebrate species, serving as nurseries that support successful recruitment (Beck et al., 2001). Their high food availability and structural complexity offer both nourishment and protection, enhancing juvenile growth and survival (Cardoso et al., 2004; Pinto et al., 2021). Warming could lead to a reduction in the success of connectivity between ocean and coastal systems, and affect invertebrate species' physiology and consequently growth and reproduction, thus ultimately threatening the development of early life stages of fish and invertebrates (Pinto et al., 2021; Monteiro et al., 2023).

Like all the brachyuran crustaceans, the European green crab, *Carcinus maenas*, has a complex life cycle, including a pelagic larval phase

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and a benthic juvenile-adult phase, which also undergoes a process of connectivity between oceanic and coastal systems (Mohamedeen and Hartnoll, 1989; Sprung, 2001). Larval development takes place across a range of habitats, including oceanic waters as well as coastal waters such as estuaries and coastal lagoons, and can last from several days to months. This development is influenced by environmental factors such as salinity and temperature (Dawirs, 1985; Nagaraj, 1993; Sprung, 2001; Torres and Giménez, 2020), and involves a series of moults from one zoea stage to the next, culminating in four zoea stages while drifting to nearshore areas where semi-benthic larva, the megalopa stage, will be formed (Spitzner et al., 2018). The transformation of the megalopa into a benthic juvenile marks its settlement, which occurs in estuaries, lagoons, or rivers, where it undergoes further development (Baeta et al., 2005; Bessa et al., 2010).

The geographical expansion of *C. maenas* into non-native regions is influenced by global warming (Kelley et al., 2015; Monteiro et al., 2023). Despite its high phenotypic plasticity and environmental resilience, the distribution and development of *C. maenas* are influenced by environmental conditions (Monteiro et al., 2023). Adult green crabs are physiologically resilient, tolerating short-term exposure to sea temperatures ranging from as low as −1 °C up to 30 °C (Young and Elliott, 2020). However, larvae and juveniles are more thermally sensitive, with a thermal preference range of 10–25 °C (Spitzner et al., 2019). Global warming presents a challenge to the survival of *C. maenas* in warmer regions, such as southern Europe, where sea surface temperatures (SST) during summer months approach the species' upper thermal limits, potentially reducing the survival of early life stages. Conversely, rising temperatures may facilitate the establishment of new populations in colder regions (Kelley et al., 2015; Monteiro et al., 2023).

As a consequence of global warming, SSTs are projected to rise between 1.7 °C (Representative Concentration Pathway 4.5 (RCP 4.5) and 3.5 °C (RCP 8.5) by the end of the 21st century) (IPCC, 2018). Although reaching 1.5 °C of global warming above pre-industrial levels — a limit agreed under the Paris Agreement — may seem like a distant prospect, it could happen sooner than expected, with experts suggesting it will occur by 2030 (C3S global temperature trend monitor, May 2025). The ecological implications for *C. maenas* under these scenarios are complex due to various trade-offs and constraints governing life history traits in different regions (Young and Elliott, 2020). However, increases in SST are expected to cause reductions in body size, longer reproductive seasons, and smaller crab sizes at maturity (Kelley et al., 2015; Monteiro et al., 2023), and also affect early life stages, shortening the duration of larval development and increasing larval mortality (Anger, 2006; Young et al., 2006).

Settlement and early juvenile stages represent critical periods in the life cycle of crab species, marked by high mortality due to predation, cannibalism, and the scarcity of suitable refuge habitats (Hunt and Scheibling, 1997). Successful recruitment depends on the ability of the megalopa to settle in appropriate habitats and survive during the vulnerable early benthic stages (Eggleston and Armstrong, 1995; Shanks, 1995; Wahle, 2003). *Carcinus maenas* is an estuarine species with great ecological importance as it is a key epibenthic species (Baeta et al., 2005; Monteiro et al., 2021), and it is also listed among the world's top 100 most invasive species by the IUCN (Leignel et al., 2014). In addition, *C. maenas* also has high economic importance. Economically, *C. maenas* is relevant, as in its native range, it is harvested for use as bait in both recreational and commercial fisheries (Leitão et al., 2023), while in regions where it has become invasive, its predation on bivalves results in economic losses amounting to millions of dollars (Kouba et al., 2022). Therefore, given the ecological and economic significance of *C. maenas* globally, understanding how environmental factors, such as SST and climate change affect its early life stages is essential (Klassen and Locke, 2007; Monteiro et al., 2024).

This study aimed to examine: (1) the duration of larval development under projected SST scenarios related to climate change in the Algarve coast (southern Portugal), and (2) the survival and growth development of *C. maenas* juveniles through to maturity.

2. Materials and methods

Two laboratory experiments were conducted to assess the effects of climate change on *C. maenas*. *Experiment 1* evaluated how climate warming scenarios, in particular, increasing SST influence larval development and survival. *Experiment 2* focused on determining juvenile survival and growth from early settlement through to sexual maturity. Both experiments were carried out during the summer months, when the highest annual temperatures occur in the Ria Formosa lagoon, spanning from July 2019 to July 2020. The trials took place at the Ramalhete Marine Research Station/CCMAR (Faro), located within the Ria Formosa Natural Park (37°0′22" N; 7°58′3" W). In this region, annual surface temperatures typically range from 12 °C to 27 °C, and salinity fluctuates between 20 and 30 (Newton and Mudge, 2003; Barbosa et al., 2010).

Experiment 1: Larval development under climate scenarios.

Larval development experiments were conducted from June to July 2020. During these experiments, we examined the larval development of *C. maenas* under two temperature warming scenarios, and compared it to development at the average annual SST in Ria Formosa between 1980 and 2020 (~18.5 °C). In Portugal, most ovigerous females are observed between October and May (Monteiro et al., 2025). This study was conducted at the end of the reproductive season, when SSTs are warmer, to assess the potential impact of elevated temperatures on larval survival under a worst-case climate scenario.

The two scenarios, RCP 4.5 and RCP 8.5, considered SST increases of 1.5 °C and 3.5 °C by the end of the century. These scenarios describe different climate change end points, all of which are considered possible depending on the level of greenhouse gas (GHG) emissions in future years. The RCP 4.5 is described by the IPCC as an intermediate scenario, and the RCP 8.5 is considered to be the worst-case scenario for climate change (IPCC, 2018).

Large egg-bearing females of *C. maenas*, expected to have high fecundity, were collected using fishing traps near the Ramalhete Marine Station on 27th May 2020. Four females of similar size (40 mm carapace width, CW) and at the same ovigerous stage (with brown-coloured egg masses) were individually placed in 8-l tanks with a constant flow of seawater. The tanks maintained an average natural temperature of 18.4 ± 0.4 °C (mean ± SD), representing the typical spring SST conditions in the Ria Formosa system. The females were kept under these natural environmental conditions until larval hatching (20th July 2020), after which they were released back into the lagoon.

Following hatching, 40 larvae from each ovigerous female ($n = 4$) were allocated to each temperature treatment, resulting in four replicate Erlenmeyer flasks per treatment (one replicate per female). Thus, each treatment comprised a total of 160 larvae (40 larvae × 4 females), with each 150 mL Erlenmeyer flask containing exclusively larvae from a single female (Fig. 1). Each Erlenmeyer presented its own aeration and was filled with filtered seawater to the top. The water was changed every day. To maintain a homogeneous temperature, the flasks were partially submerged (70%) in a 30 L water bath. To minimize temperature fluctuations, the experiments were conducted in a temperature-controlled room set to 16 °C. Since this ambient temperature was lower than the predefined experimental treatment temperatures, the water temperature in each 30 L water bath was adjusted using PID (Proportional Integral Derivative) controllers connected to thermostats. These systems ensured that the replicates maintained their respective treatment temperatures throughout the experiment. The three temperature levels tested were 18.5 °C, representing average spring temperatures (control level), 20 °C for the intermediate level (RCP 4.5), and 22 °C, temperature projected for the worst-case scenario (RCP 8.5).

Larvae of *C. maenas* were fed daily with *Artemia salina* (5 ind./ml) enriched with *Isochrysis galbana*. *Artemia* cysts (Sanders®, Ogden, UT, USA) were hatched in seawater according to the methodology described

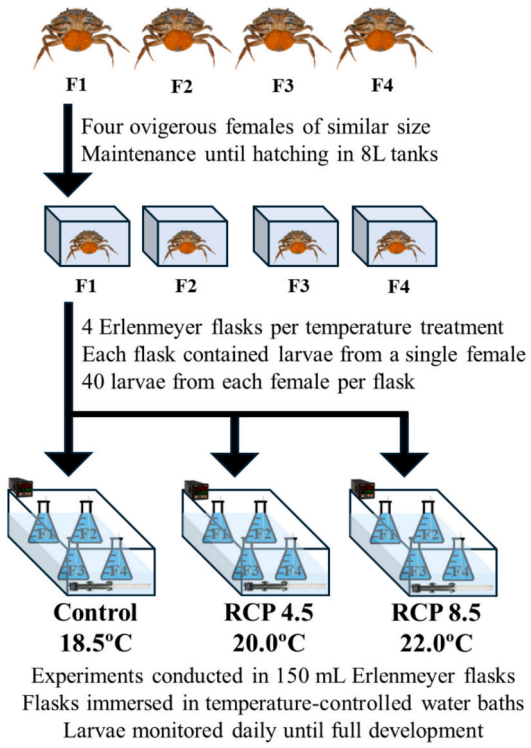

Fig. 1. Schematic representation of the experimental design used to assess larval development of *Carcinus maenas* under different temperature scenarios. Larval development and survival were assessed under three temperature regimes—approximately 18.5 °C (representing the current average Portuguese sea surface temperature, used as the control), and two projected climate change scenarios: RCP 4.5 (+1.5 °C) and RCP 8.5 (+3.5 °C). Larvae from four ovigerous females were used for the experiment, with 40 larvae per replicate flask per female per treatment. The experiments were conducted in temperature-controlled water baths using 150 mL Erlenmeyer flasks, and larval development was monitored daily.

by Sorgeloos et al. (1986). Within 24 h post-hatching, newly hatched nauplii (Instar I) were transferred to a 20-L acrylic cylindrical-conical tank containing a suspension of *Isochrysis galbana*. The nauplii remained in this enriched seawater for 24 h at a maximum concentration of 50,000 *Artemia* L^{-1}, under constant moderate aeration and at a room temperature of 20–22 °C. This 24-h period encompasses the nauplii's developmental transition from the non-feeding Instar I stage to the feeding Instar II stage, allowing for subsequent active ingestion and enrichment with the microalgae. Daily water changes were performed in each Erlenmeyer flask to maintain water quality by removing uneaten food and dead larvae. To analyse survival and larval development, the number of live larvae was recorded daily, and each larva's developmental stage was determined based on external morphology and size. The staging followed the classification of four zoeal stages and one megalopa stage, as described by Spitzner et al. (2018).

The probability of larval survival over time (in days) under different temperature scenarios was estimated using Kaplan-Meier survival curves: Control (18.5 °C), RCP 4.5 (18.5 °C + 1.5 °C), and RCP 8.5 (18.5 °C + 3.5 °C). Kaplan-Meier curves were generated with 95 % confidence intervals. Survival probability was plotted against time (days). Pairwise comparisons of survival times across treatments were conducted using the log-rank test. Additionally, a Cox regression model was applied to determine the hazard ratio, quantifying the effect of temperature on larval survival for each scenario relative to the control. A hazard ratio greater than 1 indicates an increased risk of mortality due to elevated temperatures in the tested scenarios.

The average duration of the larval stage and the total larval development time were determined for each temperature treatment and then statistically compared between the control and experimental scenarios to assess the effect of temperature on larval development. Since the data did not meet normality assumptions (as tested by the Shapiro-Wilk test), the Kruskal-Wallis test was applied. For pairwise comparisons between the control and scenarios, Dunn's post-hoc test with Bonferroni correction was used.

All statistical analyses were conducted in R (version 4.3.1), using the survival and survminer packages for survival analysis, and the tidyverse package for data processing and visualization.

Experiment 2: Survival and growth development of juveniles.

Juvenile growth experiments were conducted in mesocosms between July 2019 and April 2020. These experiments analysed the growth of *C. maenas* from the onset of the benthic stage until all the crabs reach the size at sexual maturity. The maturity size of crabs was defined as 30 mm CW for both sexes according to previous studies in Ria Formosa populations (Monteiro et al., 2025).

In July 2019, the smallest available juveniles of *C. maenas* ($N = 150$; Fig. 2) were collected from the intertidal zone near the Ramalhete station (Faro, Portugal). The crabs were randomly distributed among three outdoor tanks (1 m × 1 m × 1 m), which maintained a constant flow of seawater at an average temperature of 19.4 ± 4.4 °C (mean ± SD) throughout the experiment. The tanks were filled with water to a depth of 70 cm. To replicate the crabs' natural habitat, the bottom was covered with a 4–5 cm layer of sediment collected from *C. maenas* natural environments, consisting of shells and small stones. A continuous flow-through water system was used to maintain optimal conditions, with the water level regulated by an overflow pipe to ensure a steady depth of 70 cm. The crabs were fed daily *ad libitum* with frozen mussels (*Mytilus galloprovincialis*), and any uneaten food from the previous day was promptly removed to maintain water quality.

Twice a month, the crabs in each tank were counted and sexed. CW was measured at its widest point—between the fifth spines on each side of the carapace—using a vernier calliper with an accuracy of 0.01 mm. Following each survey, the tanks were cleaned, the sediment was replaced, and the water level was adjusted to the desired depth. The experiment concluded in April 2020, when only nine crabs remained alive, with CWs ranging from 32 to 48 mm. These measurements indicated that all surviving individuals, regardless of sex, had reached maturity, as egg-bearing females were observed.

Juvenile data analysis was conducted using the same statistical approach as for the larvae. Kaplan-Meier survival curves (with 95 % confidence intervals) were applied to assess the probability of juvenile survival over time, categorized by sex until maturity. Additionally, survival rates were examined in relation to crab size (carapace width in mm) using Kaplan-Meier estimation and the log-rank test.

The Von Bertalanffy growth model was applied to analyse the growth pattern of *C. maenas* juveniles. This model estimates the asymptotic carapace width (CW_∞), the growth coefficient (k), and the theoretical

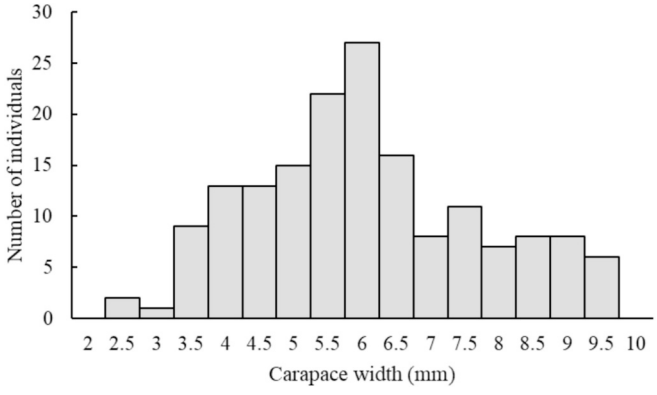

Fig. 2. Initial size-frequency distribution ($n = 150$) of juvenile *Carcinus maenas* at the start of the growth experiment (July 2019).

time at which the crabs would have zero size (T_0). Growth data were fitted separately for males and females using non-linear least squares regression (Eq. 1) using the previously estimated values for the Ria Formosa population (Males: $CW_\infty = 84.65$ mm $K = 0.52$ year^{-1}; Females: $CW_\infty = 79.785$ mm $K = 0.55$ year^{-1}; Monteiro et al., 2025).

$$CW(t) = CW_\infty \left(1 - e^{-K(t-t_0)}\right) \quad (1)$$

The progression of maturity over time (days) for both sexes was analysed using the logistic regression model. The model fit was plotted along with 95 % confidence intervals for the predicted maturity probabilities. The duration (days) until individuals reached size at maturity was calculated by fitting the data with a logistic binary (mature = 1 size >30 mm; immature = 0) regression model (Eq. 2 from Roa et al., 1999). Where P is the proportion of mature crabs, D is the number of days since the start of the experiment, α is the intercept parameter, and β is the slope parameter. The time at which 50 % of crabs reached sexual maturity (D_{50}), standard errors, and the selection of 95 % confidence limits (Wald-type confidence interval) were calculated using the delta method (R-package msm).

$$P(D) = 1/\left(1 + e^{-(\alpha+\beta CW)}\right) \quad (2)$$

Growth increment was determined by calculating the relative difference between successive carapace width values (Eq. 3). The log regression model ($y = a + b \cdot \log(x)$) was fitted to determine the species' daily growth. Where y is the mean growth increment and x is the time in days. To visualize growth increments, a plot of the observed data was generated along with the fitted logarithmic regression curve.

$$\textit{Relative growth increment} = \frac{CW_t - CW_{t-1}}{CW_{t-1}} \quad (3)$$

3. Results

3.1. Larval development under climate scenarios

The survival probability results indicated that, regardless of temperature, more than 75 % of *C. maenas* larvae died by day 8 (Fig. 3). The duration until 75 % of larvae perish was 7.52 days (95 % CI: 7–8) under control conditions, 7.96 days (95 % CI: 7–8) under RCP 4.5, and 7.20 days (95 % CI: 7–8) under RCP 8.5. Significant differences between the control and the future warming scenarios were observed in the survival probability ($\chi^2 = 12.6$; df = 2; $p = 0.002$). The Cox proportional hazards model presented evidence that individuals under the RCP 4.5 scenario presented a lower mean hazard rate compared with the control treatment (HR = 0.725; 95 % CI: 0.576–0.912; $p = 0.006$), indicating a greater probability of survival at 20 °C. In contrast, RCP 8.5 did not differ significantly from the control (HR = 1.062; 95 % CI: 0.850–1.328; $p = 0.596$). Overall, these findings indicated a greater chance of *C. maenas* larvae survival for RCP 4.5 (20 °C) in comparison to RCP 8.5 (22 °C). Moreover, it was observed that RCP4.5 treatment led to a greater survival probability between days 4 to 10. However, the survival rates between treatment groups were very similar after day 12.

Significant differences among control and scenarios were observed in the duration of larval development stages, with a reduction of larval development duration under the future scenarios (KW test: $\chi^2 = 9.881$, df = 2, $p = 0.007$). The duration of larvae development stage varied significantly between the Control and RCP 8.5 scenario (Dunn test: $p = 0.005$), whereas between Control and RCP 4.5 (Dunn test: $p = 0.348$), no significant differences were found (Fig. 4A and B). Overall, larvae in the RCP 8.5 scenario exhibited significant differences compared with the Control, with the reduction of the duration of development time in all larval stages, except in stages Zoea II and IV (Fig. 4A). A significant overall reduction of cumulative larval development time was detected for RCP 8.5 scenario in comparison to the Control (Fig. 4B). Therefore, the pelagic larval duration (PLD) of *C. maenas* is around 27 ± 2.29 (mean ± SD) days at 18.5 °C, 20 ± 3.44 days at 20.0 °C, and 16 ± 1.13 days at 22.0 °C, and the duration of the megalopa (settlement) stage is 10 days at 18.5 °C, 6.83 ± 0.62 days at 20.0 °C, and 6 days at 22.0 °C, respectively. These results suggested that increasing ocean warming will accelerate larval development.

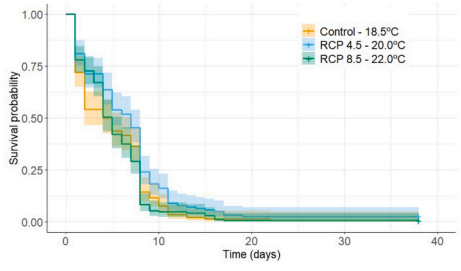

Fig. 3. Kaplan-Meier survival curves for green crab, *Carcinus maenas,* larvae under different treatments with an initial number of 160 larvae per treatment. Survival probability was monitored over time in three temperature treatments: Control (18.5 °C, yellow), RCP 4.5 (20 °C, blue), and RCP 8.5 (22 °C, green). Shaded bands represent the 95 % confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

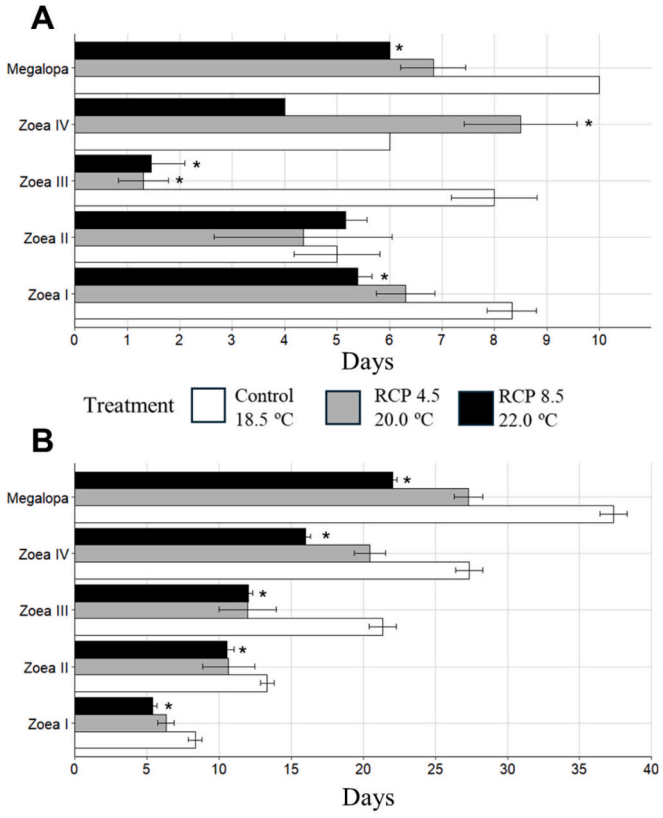

Fig. 4. Green crab (*Carcinus maenas)* larval development stages duration (days) under different treatments (Control, RCP 4.5 and RCP 8.5) with an initial number of 160 larvae per treatment. (A) Mean duration and standard deviation (error bars) of each larval stage (Zoea I–Megalopa) across three temperature treatments: Control (18.5 °C, white), RCP 4.5 (20 °C, grey), and RCP 8.5 (22 °C, black). (B) Mean cumulative larval development duration with standard deviation (error bars) from Zoea I to Megalopa across treatments. * Indicate statistically significant differences compared with control ($p < 0.05$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

3.2. Survival and growth development of juveniles

Juvenile *C. maenas* exhibited similar survival patterns between sexes, with 50 % mortality occurring around 50 days post-initiation. The estimated time to 50 % mortality was 33.76 days for males (95 % CI: 31–46) and 35.50 days for females (95 % CI: 31–46) (Fig. 5A). Moreover, females tended to have a higher survival probability compared with males during the period 50–120 days but the overall difference in survival rate was not significant ($\chi^2 = 1.5$, $p = 0.2$). Conversely, the probability of survival with growth increase (CW) revealed a significant difference in survival between sexes ($\chi^2 = 4.7$, $p = 0.03$), indicating that males exhibited lower survival probabilities than females as carapace width increased (Fig. 5B). Survival analysis revealed that 50 % mortality occurred at approximately 10 mm carapace width (CW) for both sexes, with males reaching this threshold at 9 mm (95 % CI: 8–12) and females at 11 mm (95 % CI: 9–14). Only 15 % of individuals overall reached sexual maturity. However, females exhibited higher survival until the size at sexual maturity (~30 mm CW), with 24 % (95 % CI: 16–34) of females compared to 9 % of males (95 % CI: 5–18) reaching sexual maturity. The Cox proportional hazards model estimated a HR of 1.424 (95 % CI: 1.036–1.957, $p = 0.029$), suggesting that males had a 42.4 % higher risk of mortality compared with females.

The estimated asymptotic carapace width of experimental crabs (CW_∞) was similar between sexes (Fig. 6A). However, females exhibited a significantly higher growth rate (K) than males. Females had an estimated CW_∞ of 44.59 mm (95 % CI: 41.94–48.18), with a K of 0.0114 day^{-1} (95 % CI: 0.0090–0.0141) and an initial time parameter (t_0) of −6.52 days (95 % CI: −14.76 to −0.34), indicating that the females settled approximately 6.5 days before the start of the experiment. In contrast, males had an estimated CW_∞ of 44.59 mm (95 % CI: 41.81–48.49), a K of 0.0085 day^{-1} (95 % CI: 0.0068–0.0103), and a t_0 of −13.96 days (95 % CI: −21.78 to −7.80), indicating an earlier settlement of approximately 14 days before the experiment. These results indicate that while both sexes reach similar asymptotic sizes, females grow at a faster rate than males, highlighting a sex-based difference in growth dynamics in early juvenile stages.

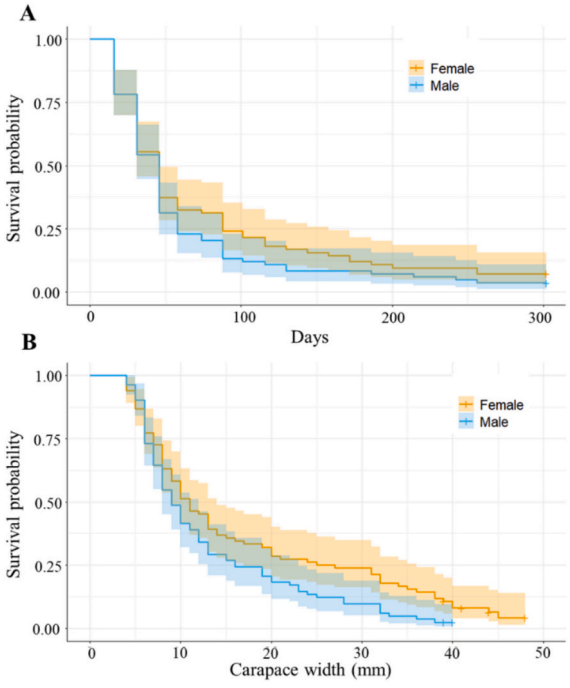

Fig. 5. Kaplan-Meier survival probability estimates for juvenile green crabs, *Carcinus maenas*, for both female (orange) and male (blue) individuals over time (days) (A) and size (carapace width in mm) (B), with an initial number of 150 juvenile crabs. Shaded bands represent the 95 % confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

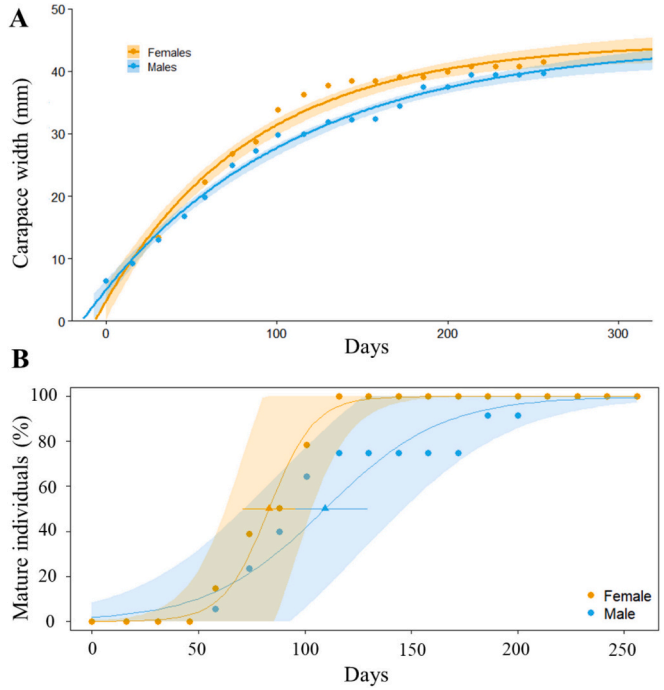

Fig. 6. Growth and maturation of juvenile green crabs (*Carcinus maenas*) for female (orange) and male (blue) individuals. (A) Carapace width (mm) growth modelled using the von Bertalanffy growth function. (B) Probability of crabs reaching sexual maturity as a function of time (days), with an initial number of 150 crabs. Triangular markers indicate the time required for 50 % of the population to reach maturity, with horizontal bars representing standard errors. Shaded bands represent 95 % confidence intervals. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

The probability of 50 % of individuals to reach maturity (D_{50}) differed significantly between sexes (Fig. 6B). Females reached D_{50} at 83.07 ± 12.25 days, whereas males reached D_{50} at 109.47 ± 19.83 days, indicating that females matured significantly earlier than males. These results evidence sex-based differences in maturation timing, with females achieving maturity earlier than males.

The growth increment analysis denoted a negative trend of the species growth increment over time (Fig. 7). Initial measurements revealed a growth increment of 0.4 (±0.18) per sampling measurement, while over time, the growth increment between measurements

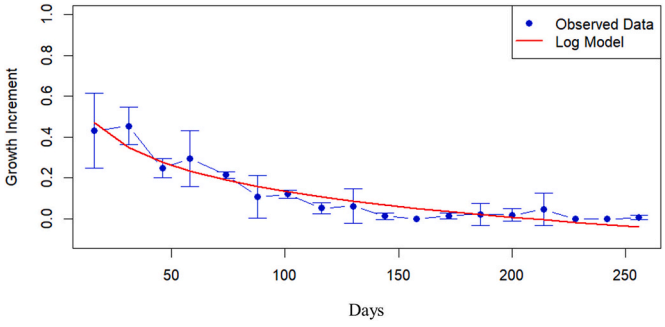

Fig. 7. Growth increment of the green crab, *Carcinus maenas*, over time. Blue dots represent the observed data; the blue bars represent the standard deviation and the red line represents the estimated model. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

decreased. After ~150 days (D) of experiment, reduced growth increments (GI) were detected between measurements. This observation is further corroborated by the logarithmic regression model (Eq. 4). The model exhibited a high degree of fit to the observed data ($R^2 = 0.905$, $F_{(1,16)} = 152.4$, $p < 0.001$), indicating a negative relationship between growth increment and time.

$$GI = 0.98254–0.18396 \times \log(D) \quad (4)$$

4. Discussion

The present study indicates that global warming is likely to significantly affect the life cycle of *C. maenas*. Our results show that larval survival was highest at 20 °C (corresponding to the RCP 4.5 scenario) compared with both the current average temperature of 18.5 °C (control) and the elevated temperature of 22 °C (RCP 8.5). The reduced survival observed at 22 °C suggests the existence of a thermal threshold beyond which larval viability declines. Conversely, these findings imply that moderate warming may enhance larval survival, potentially promoting larval development and settlement, which could in turn lead to increased population sizes and broader larval dispersal. These results are consistent with previous studies, which observed that the optimal temperature for *C. maenas* larval development and survival is around 20 °C (Mohamedeen and Hartnoll, 1989; Spitzner et al., 2019; Geißel et al., 2025a). Nevertheless, one study reported high larval survival at lower temperatures (Nagaraj, 1993), suggesting that survival outcomes may be influenced by a range of environmental and biotic factors, such as food availability and salinity (Dawirs, 1985; Torres and Giménez, 2020). Additionally, intraspecific variation may play a role in shaping larval responses to climate-related environmental changes (Spitzer et al. 2019; Geißel et al., 2025b). The highest survival rate was observed at 20 °C in our study. That, along with findings from previous research, suggests *C. maenas* can adapt to a broad temperature range (Spitzer et al. 2019; Geißel et al., 2025b). However, the lower survival rates recorded in our experiments compared with some earlier studies may be attributed to differences in egg batch quality. It has been shown that egg batches produced earlier in the reproductive season tend to exhibit higher quality, which can significantly influence larval survival (Lyons et al., 2012; Glamuzina et al., 2017). In our study, this variable was controlled by using eggs from the same batch period and females of similar size.

Temperature also affects the duration of larval development. Our results are consistent with previous studies that reported an acceleration in the duration of all larval developmental stages at higher temperatures (Mohamedeen and Hartnoll, 1989; Nagaraj, 1993; Spitzner et al., 2019). We observed a reduction of 14 days for a difference of 3.5 °C in comparison to control (control and RCP 8.5 treatments), to complete larval development (34 days at 18.5 °C and 20 days at 22 °C). These results have also been observed in metadata studies where a reduction of pelagic larval duration (PLD) (~30 %) occurs in Portugal under the worse-case warming scenario RCP8.5 (Monteiro et al., 2023). Reducing larval development time could lead to earlier settlement and a decrease in mortality from pelagic predators. However, it could also increase the vulnerability of the early benthic stages due to their smaller size, which could reduce settlement success (Raventos et al., 2021). The accelerated development was especially observed in the Zoea III stage, suggesting that key physiological and biochemical processes during this stage may be very sensitive to temperature. This pattern could have important implications for understanding the duration of *C. maenas* larvae development under climate change and deserves direct study in future research.

Warming of 1.5 °C above pre-industrial levels by the end of the century (RCP 4.5), the critical threshold established under the Paris Agreement, seemed a distant reality. However, warming is occurring at such a rapid pace that climate experts suggest that this scenario can be a reality by the end of this decade. Despite *C. maenas* being a widely distributed species with significant ecological and economic importance and having received extensive research attention (Young and Elliot, 2020), the effects of global warming on the survival and growth of its early larval stages remain poorly understood namely within the scope of future temperature changes. This study addresses this gap by experimentally analysing the responses of the early larval and juvenile stages of *C. maenas* to warming conditions.

Information on early benthic stages is essential for the management of fisheries in native regions and for controlling the spread of this crab in invasive regions (Hart, 2003; Young et al., 2006; Almeida et al., 2008). Juvenile mortality was high, with approximately 50 % of settled individuals perishing within the first 50 days. However, in this study, we did not test the effects of predation or foraging behaviour, which implies that the results should be interpreted with caution, given that survival is expected to be even lower under natural conditions. No differences in survival probability were observed over time between sexes; whereas, survival probability as a function of size (CW) differed between sexes, with males having a lower probability of survival as CW increased. The male mortality decreases with increasing body size (the slope of the relationship between CW and survival is weaker at large CW, meaning that their survival rate is rather high); mortality is greater at CW between 5 and 10 mm. Females had the highest probability of reaching larger sizes, with 25 % reaching sexual maturity, while only 15 % of males reached sexual maturity. These findings suggest that male mortality increases with body size, aligning with observations from studies conducted in natural environments. This pattern is likely driven by physiological stress or behavioural factors, such as increased competition among males for access to females during reproduction (Styrishave et al., 2004; Monteiro et al., 2021).

Carcinus maenas populations in Portugal have a life span of 4–6 years and a maximum CW of 81 mm (Baeta et al., 2005; Bessa et al., 2010; Monteiro et al., 2025). Growth results showed that both sexes reached similar asymptotic sizes, which was expected given that individuals of both sexes were projected to grow beyond the maximum sizes observed during the experiment. This is consistent with previous studies (Young and Elliot, 2020; Monteiro et al., 2025), as the experimental period ended before individuals attained their maximum size. Nevertheless, this experiment demonstrated that the juvenile growth increment was higher in females than in males, suggesting that females reach maturity sizes faster than males. This is further supported by the analysis of the time required for each sex to reach sexual maturity. Approximately 50 % of females reached this size after 83 days, whereas males required around 109 days. These values are comparable to those reported by Mohamedeen and Hartnoll (1989), who observed that crabs reached 30 mm CW after approximately 150 days at 15 °C and 120 days at 20 °C. The earlier maturation in females may confer a reproductive advantage in comparison to males, allowing females to reproduce earlier (Hartnoll, 2006; Young and Elliot 2020; Monteiro et al., 2025). Moreover, the duration of the early life stages recorded in our study was shorter than recorded in previous studies, *e.g.,* the time to reach sexual maturity was approximately 7 to 8 months in England (Orton, 1936; McVean and Findlay, 1979) and two years in western Sweden (Eriksson and Edlund, 1977). However, it is important to note, that our study was conducted under controlled laboratory conditions (juveniles with less than 10 mm CW were reared in 1 m^3 tanks with running seawater for 300 days), and the chosen initial size distribution likely influenced survival and growth outcomes. Therefore, the observed patterns of growth and the duration necessary for the crabs to reach maturation need to be considered with caution when applied to natural populations, as these patterns were analysed in experimental conditions that did not consider natural stresses such as predation or food availability. Moreover, the differences in duration from settlement to sexual maturity across regions are likely related to the temperature of each region (Monteiro et al., 2023).

We observed that growth increments showed a decreasing trend over time, with large growth increments in the early life stages and a smaller growth increment after the crabs reached sexual maturity. This growth pattern is consistent among crustacean species (Crothers, 1967;

Hartnoll, 2001), where during the early developmental stages juveniles prioritise moulting and a fast increase in individual size, then gradually divert most of their energy towards reproduction and maintenance, resulting in smaller growth increments (Styrishave et al., 2004; Monteiro et al., 2025).

Our results can be used to infer specific stages in the life cycle of *C. maenas*. Green crabs can reproduce during the first year of life, with the hatching of embryos spanning about 1 month (Young and Elliot, 2020). Larval development is completed in another month, and juvenile crabs reach sexual maturity 3–4 months later. Therefore, at approximately six months, crabs are sexually mature.

5. Conclusion

The effect of global warming is expected to be species/specific and influenced by regional factors. This study provides insights into the early life stages of *C. maenas*, highlighting the effect of global warming on larval survival and developmental duration, as well as the duration and incremental growth of early settlement crabs until sexual maturity. These results contribute to improving our understanding of how this species may impact non-native regions. Global warming is expected to enhance larval survival and accelerate development. Predicted temperature increases for the RCP 4.5 suggest an increase in survival rate compared with the current average sea surface temperature. These changes can favour crab populations inhabiting the Portuguese coastal systems, where the species is economically relevant. Experiments with juveniles demonstrated growth and survival differences between sexes, with females reaching maturity fastest and green crab reproductive maturity occurring within six months. This increases our understanding of green crab population dynamics in the context of a commercial fishery.

CRediT authorship contribution statement

João N. Monteiro: Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization. **Andreia Ovelheiro:** Writing – review & editing, Investigation. **Laura Sordo:** Writing – review & editing, Methodology, Investigation. **Jorge Palma:** Writing – review & editing, Investigation. **Miguel Pinto:** Writing – review & editing, Investigation. **Maria Alexandra Teodósio:** Writing – review & editing, Funding acquisition. **Francisco Leitão:** Writing – review & editing, Methodology, Funding acquisition, Formal analysis.

Declaration of competing interest

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

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Data availability

Data will be made available on request.

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