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Biological traits and population dynamics for sustainable harvesting of *Carcinus maenas*

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ABSTRACT

Research focusing on the biological patterns and population dynamics of *Carcinus maenas* has not been conducted for the purpose of fishery management along the European coastal systems. This has led to the implementation of fisheries management policies without scientific considerations, adversely affecting fishery profitability. To addrees this gap, we studied the crab species' population dynamics, reproductive biology, and growth patterns across different Portuguese lagoons and estuaries on a monthly basis from 2019 to 2021. Surveys were performed in the Southern (Ria Formosa lagoon and Ria Alvor estuary), Central (Sado river/estuary) and Northern regions (Ria Aveiro estuary) of Portugal. Monthly biological data was used to analyse size-frequency distributions, sex ratios, spawning seasons, recruitment pulses, estimate carapace width at first maturaty and biological growth parameters. It was observed that spawning occurs almost year-round in all systems, with a peak in the colder months, between September and March. In the southern regions of the Portuguese coast, the spawning period starts earlier than in the central and northern systems, with a higher sex ratio recorded for females in all systems. The carapace width at which 50 % (CW_{50}) of individuals reach maturity is similar for both sexes, around 30 mm, a value below to the minimum landing size enforced in Portugal. The analysis of von Bertalanffy growth curves revealed a continuous recruitment with a peak during the colder months, with individuals reaching the size at maturation after six months. The fast growth and continuous recruitment leds to the existence of between four and six growth cohorts for both sexes across all system. The findings of this study can contribute to more effective fisheries management policies for *C. maenas* in Portugal, such as a reduction of the minimum landing size.

1. Introduction

In fisheries management, understanding the biological and life-history parameters of a species is important for enforcing sustainable fishing practices (Laudien et al., 2003; Peharda et al., 2007; Cooke et al., 2023) and crucial for proposing effective conservation measures (Katsanevakis, 2007). This implies a good knowledge of the biological aspects of species, such as growth, reproduction, and mortality rates, which are essential for modelling population dynamics (Nilsson et al., 2019). Species of high economic importance undergo extensive studies on both biological and fishing characteristics (Stagg and Whilden, 1997; Johnston et al., 2011; Liu et al., 2013; Seitz et al., 2014), enabling the determination of minimum landing sizes, maximum daily landings, maximum number of gears, and stock analyses. However, in estuarine fisheries, the lack of information on fishing practices and biological knowledge for some commercially important but data-poor species restricts the enforcement of management strategies (Elliott et al., 2022).

In Portugal, fishing is a traditional activity with strong historical traditions. Fisheries are not just an economic activity but a core part of Portuguese cultural heritage, playing a crucial socio-economic role for many Portuguese families (Leitão and Baptista, 2017; Alves et al., 2021). Among these, estuarine and lagoon fisheries stand out for their local economic importance, deeply embedded in historical contexts (Martins et al., 2004; Braga et al., 2022). Among the estuarine fisheries, the European green crab (*Carcinus maenas*) fishery is assuming increasing importance as seafoodand as fishing bait in recreational and commercial fishery (Gomes, 1991; Leitão and Monteiro, 2022; Leitão et al., 2023).

Carcinus maenas is well-studied globally, with approximately a thousand publications in the past decade (Young and Elliott, 2020). This estuarine crab, native to the Northeast Atlantic, is the most common

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intertidal decapod crustacean in Europe (Klassen and Locke., 2007; Leignel et al., 2014; Waser et al., 2018), and over the past centuries, this species has spread its geographic distribution and settled in five major regions of the globe (Thresher et al., 2000; Young and Elliott, 2020), where it is considered highly invasive (Thresher et al., 2000). An integral component of the success of *C. maenas* as an invasive species lies in its high phenotypic plasticity and broad tolerance to salinity and temperature (Kelley et al., 2013). The high phenotypic plasticity is also observed in morphometric and reproductive parameters (Young and Elliott, 2020; Monteiro et al., 2023), leading to variations in life-history parameters and population dynamics among regions (Kelley et al., 2015; Monteiro et al., 2023). Therefore, studying the biological parameters of *C. maenas* at a population/region level is crucial for enforcing fishery regulations.

Management policies for *C. maenas* fisheries in Portugal have been implemented without considering the biological parameters of this species, leading to incorrect crab biological regulation (Leitão and Monteiro, 2022). For example, the minimum landing size (MLS) of *C. maenas* was set at 50 mm of carapace width (CW) in Portuguese regulation (Portaria nº 27/2001), and it remained in effect until 2022, despite lacking scientific support. This size was potentially enforced due to the Spanish minimum landing size obligation, as most crabs were exported to Spain and needed to comply with fishing regulations at the border. The MLS was revised to 40 mm of CW in 2023 (Portaria nº 255/2022) based on some biological information indicating that *C. maenas* reach sexual maturity at smaller sizes (Leitão and Monteiro, 2022; Portela et al., 2023). Despite advancements in understanding crab fisheries and socio-economic aspects, there is a lack of knowledge on biological characteristics required to enforce output fisheries management strategies (e.g. minimum landing size) in Europe, with the limited biological information available remaining controversial (Leitão and Monteiro, 2022; Portela et al., 2023).

The main goals of this study were to analyze the biological and life-history parameters of *C. maenas* across different regions of Portugal, resolve controversies from previous studies, and enhance scientific biological knowledge applicable to fisheries management. Ultimately, this will lead to proposing better regulations for *C. maenas* fisheries in Portugal. The study includes the analysis of various biological parameters of *C. maenas* populations, such as size-frequency distribution, sex ratio, reproductive periods, size at maturation, morphometric relationships, and life-history parameters of different populations inhabiting estuarine/lagoon systems in Portugal.

2. Materials and methods

2.1. Study area and sampling procedures

In order to assess intra-regional differences, the study was conducted in four coastal systems with different hydrographical characteristics and at different latitudes along the Portuguese coast where *Carcinus maenas* is harvested. In southern Portugal, we sampled in the Ria Formosa lagoon and Ria Alvor estuary; in central Portugal, in the Sado river estuary; and in northern Portugal, in the Ria Aveiro estuary (Fig. 1).

In each system, field samplings were conducted monthly between January 2019 and April 2022 onboard commercial artisanal boats, by professional crab fishers. Crabs were caught using baited fishing traps with small and medium pelagic fish, placed at a mean depth of 2–3 m, and left fishing for periods ranging from 12 to 24 h. At the end of the field sampling, a sub-sample of around three kg of crabs was randomly collected from the total catches. Upon arriving at the laboratory, the crabs were frozen until further analysis.

2.2. Laboratory procedures

Immediately after capture, crabs were placed on ice to reduce their physiological activity. After transport to the laboratory, the crab's activity was further reduced through hypothermic shock by placing specimens in a freezer (-20ºC) for 48 hours. The carapace width at the widest point (5th spine on either side of the carapace)(CW, mm), carapace length (CL, mm) and carapace thickness (CT, mm) of all specimens were measured with a vernier calliper (with an accuracy of 0.01 mm), and the total weight (TW, g) was determined with an analytical digital balance scale (with a precision of 0.0001 g).

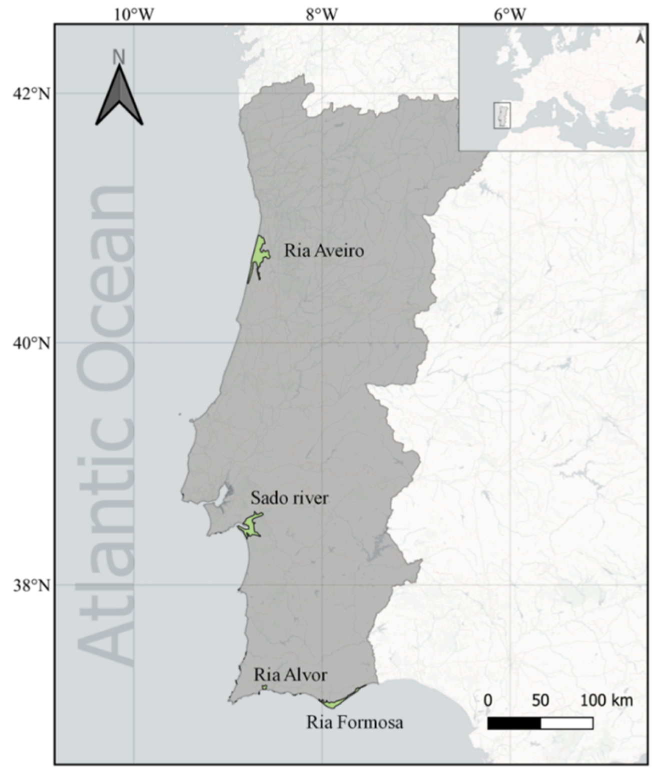

Fig. 1. Geographical location of the different systems in Portugal. Portugal is shaded in grey, and the study areas (Ria Aveiro, Sado river, Ria Alvor and Ria Formosa) are highlighted in green.

The gonadal development of all specimens was assessed macroscopically, using a maturity scale defined by Ovelheiro et al. (2023). In males, the gonad maturity scale was divided into four stages: Immature (0), Developing (I), Spawning (II), and Spent (III), with stages 0 and I classified as immature, and stages II and III as mature. In females, the gonad maturity scale encompassed six stages: Immature (0), Early development (I), Late development (II), Mature (III), Spawning (IV), and Spent (V), with stages 0 and I classified as immature, and stages II, III, IV, and V as mature.

2.3. Data analysis

2.3.1. Morphometric and Sex ratio analysis

Specimens were grouped in CW size intervals (2 mm), and Kruskal-Wallis test was performed to analyse morphometric differences in CW distribution between sexes and systems. Moreover, the overall sex ratio (males:females) and the sex ratio within CW size intervals were examined. Differences in the sex ratio proportion were assessed using the chi-square test (χ^2), with the Bonferroni correction applied to mitigate the potential risk of type I errors. Assuming a sex ratio of 0.5, the null hypothesis was rejected if the χ^2 estimated value exceeded the expected value ($p < 0.05$).

2.3.2. Morphometric relationships

Morphometric relationships of *C. maenas* were estimated separately for females and males in all systems. These relationships were established through regression analysis (least squares method), by fitting the morphometric relationships between linear variables (Carapace width – Carapace length and Carapace width - Carapace thickness) to the linear function (Y= bx + a), and the morphometric relationships between linear and ponderal variables (Carapace width – Body wet weight) to the power function ($Y = ax^b$). The degree of association between variables was assessed for all regressions using the correlation coefficient (r). The relative growth between variables (isometry vs allometry) was analysed through the allometry coefficient (regression slope – b) of the morphometric relationships. In relationships involving the same type of variables (CW-CL and CW-CT), isometry occurs when b = 1, while in relationships with different types of variables (CW-Weight), isometry occurs when b = 3, meaning that growth rates of both variables are identical throughout ontogeny (Huxley and Teissier, 1936). Subsequently, a *t*-test (H0: b = 1 or 3; HA: b ≠ 1 or 3) (Sokal and Rohlf, 1987) was applied to confirm whether the slopes (b) of the morphometric relationships were isometric (b = 1 or 3) or included in the allometric ranges (negative allometry: b < 1 or 3; positive allometry: b > 1 or 3) (Huxley and Teissier, 1936). To verify the similarity of 'b' among systems and sexes, the slopes of the regression lines were compared using Analysis of Covariance (ANCOVA).

The statistical analysis of Sections 2.3.1 and 2.3.2 was carried out using IBM SPSS Statistical 29 software (significance error level α= 0.05).

2.3.3. Reproductive periods and Size at maturation

The annual reproductive period of *C. maenas* was analysed monthly, considering different stages of maturation and classifying the crabs as mature or immature by sex. Pearson correlation test was used to assess the monthly relationship between the peak of the reproductive period and the water temperature. The reproductive period considered for the latter analysis includes only the percentage of pre-spawning and spawning females, specifically those in stages III and IV.

The size at first maturation was determined for each sex by estimating the proportion of mature individuals in every carapace width class (1 mm). The carapace width (CW) at which 50 % (CW_{50}) of individuals were mature was calculated following Roa et al. (1999) by fitting the data to a logistic regression model (Eq. 1). Where P is the proportion of mature crabs, CW the carapace width in mm, α the intercept parameter, and β the slope parameter. The standard errors of CW_{50} were calculated with the delta method by using the package msm (vers. 1.6.9) in R, and a Wald-type confidence interval was also calculated.

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

2.3.4. Growth parameters

The growth parameters were estimated through the von Bertalanffy growth function (VBGF) for males and females of each system separately, using by-monthly CW frequency data derived from the field samplings. To estimate these parameters, the frequency distributions were analysed and fitted with growth curves by the ELEFAN of TropFishR package (v1.2) (Taylor and Mildenberger, 2017). This package include a traditional and updated ELEFAN method (two optimization approaches: generalized simulated annealing ELEFAN_SA, and genetic algorithm ELEFAN_GA) for growth curves fitting and parameters estimates. In this study both methods were utilized, ELEGAN GA and ELEFAN SA, with and without seasonality in growth (i.e., considering or not differences in growth velocity during the year) (Sparre and Venema, 1998). To define the best method, it was considered the best score adjustment (Rn). The value of Rn is used to define an adequate measure of the goodness of fit of the data restructuring. The calculation of Rn is according to the Eq. 2, where ESP is the sum of the explainable points and ASP the sum of the available points. The highest value of Rn (goodness of fit index) was used to determine the best quality of fit of the growth curves in ELEFAN SA with seasonality for all growth curves (see supplementary information table S1aand S2).

$$RN = ESP/ASP \quad (2)$$

The version of the equation with seasonality considers (Eqs. 3, 4 and 5), in addition to the CW_∞, T_{anchor} and K parameters, two other parameters: C (seasonal oscillation amplitude) and T_s.

$$CW_T = CW_\infty \quad \{1 - e^{[-K(T-T_{anchor})+S_T-S_{T0}]}\} \quad (3)$$

$$S_T = \left(C\frac{K}{2\pi}\right)\sin\pi(T - T_{anchor}) \quad (4)$$

$$S_{T0} = \left(C\frac{K}{2\pi}\right)\sin\pi(T_{anchor} - T_s) \quad (5)$$

Where CW_T is the crab carapace width (mm) at age T (year), CW_∞, is the asymptotic width (mm) calculated as $CW_{max}/0.95$, where CW_{max} is the maximum recorded CW. T_{anchor}, describes the fraction of the year where growth curves cross length equal to zero and K is the growth coefficient that expresses how fast ($year^{-1}$) the asymptotic width is approached (Sparre and Venema, 1998). T_s and C are parameters which control seasonal growth oscillation of the period (one year), T_s is the start of a sinusoid growth oscillation with respect to T_{anchor}, and C is a parameter exposing the intensity of the seasonal growth oscillation.

The CW_∞ search range for the ELEFAN_SA analysis was set to CW_∞ ± 20 %, while the growth coefficient (K) ranged from 0.1 to 1.5. Initial seed values for T_{anchor}, C and T_s were set within the range of 0–1. The moving average (MA) was selected based on the rule of thumb and a trial-and-error approach (Taylor and Mildenberger, 2017). Being considered a MA of 7 for all analysis and a bin size of 2.

To determine the growth performance index (Ø) that was used to compare the growth of *C. maenas* over the different systems, the following formula proposed by Pauly and Munro (1984) (Eq. 6) was used:

$$\Phi' = \log(K) + 2\log(CW_\infty) \quad (6)$$

3. Results

3.1. Morphometric and Sex ratio analysis

A total of 55801 specimens were captured, where 20823 were males and 34978 females, specifically: 14407 specimens in Ria Aveiro, 23179 in Sado river, 5618 in Ria Alvor and 12597 in Ria Formosa. *Carcinus maenas* specimens exhibited a range of carapace width (CW) from 4.82 to 81.45 mm (mean ± SD: 41.01 ± 9.23 mm), and their total body weight varied between 0.04 and 118.72 g (mean ± SD: 17.45 ± 11.76 g). A variation in the maximum CW was observed across the systems (Fig. 2 and Table 1). For males, the carapace width ranged from 4.82 to 81.45 mm (mean ± SD: 42.36 ± 11.04 mm), and for females the CW ranged from 4.91 to 74.76 mm (mean ± SD: 40.20 ± 7.85 mm) (Fig. 2 and Table 1), with statistically significant differences in CW recorded between sexes and systems (Kruskal-Wallis test, $p < 0.001$), with the exception of Ria Formosa Ria Formosa and Ria Alvor females ($p = 0.315$), and between sexes in Ria Aveiro ($p = 0.155$). The total weight of males varied between 0.06 to 118.72 g (mean ± SD: 20.40 ± 15.30 g) and for females between 0.04 to 113.55 g (mean ± SD: 15.70 ± 8.57 g) (Table 1).

Overall, regardless of the system, the sex ratio (m/f) of *C. maenas* in this study was 0.60, with sex ratio varying according to the size classes ($\chi^2 = 3558.077$, $p < 0.001$). The proportion of *C. maenas* males in CW size-classes between 4 and 22 mm comprised 60 % of the total sample measured. The proportion of females surpassed that of males in the size class of 24 mm and remained higher in the size classes up to 52 mm CW. The mean proportion of males in above intervals was 34 %. After the size class of 54 mm, the proportion of males in the population increased and remained higher than females until the maximum size class (80 mm) where the proportion of males in the population was 70 %

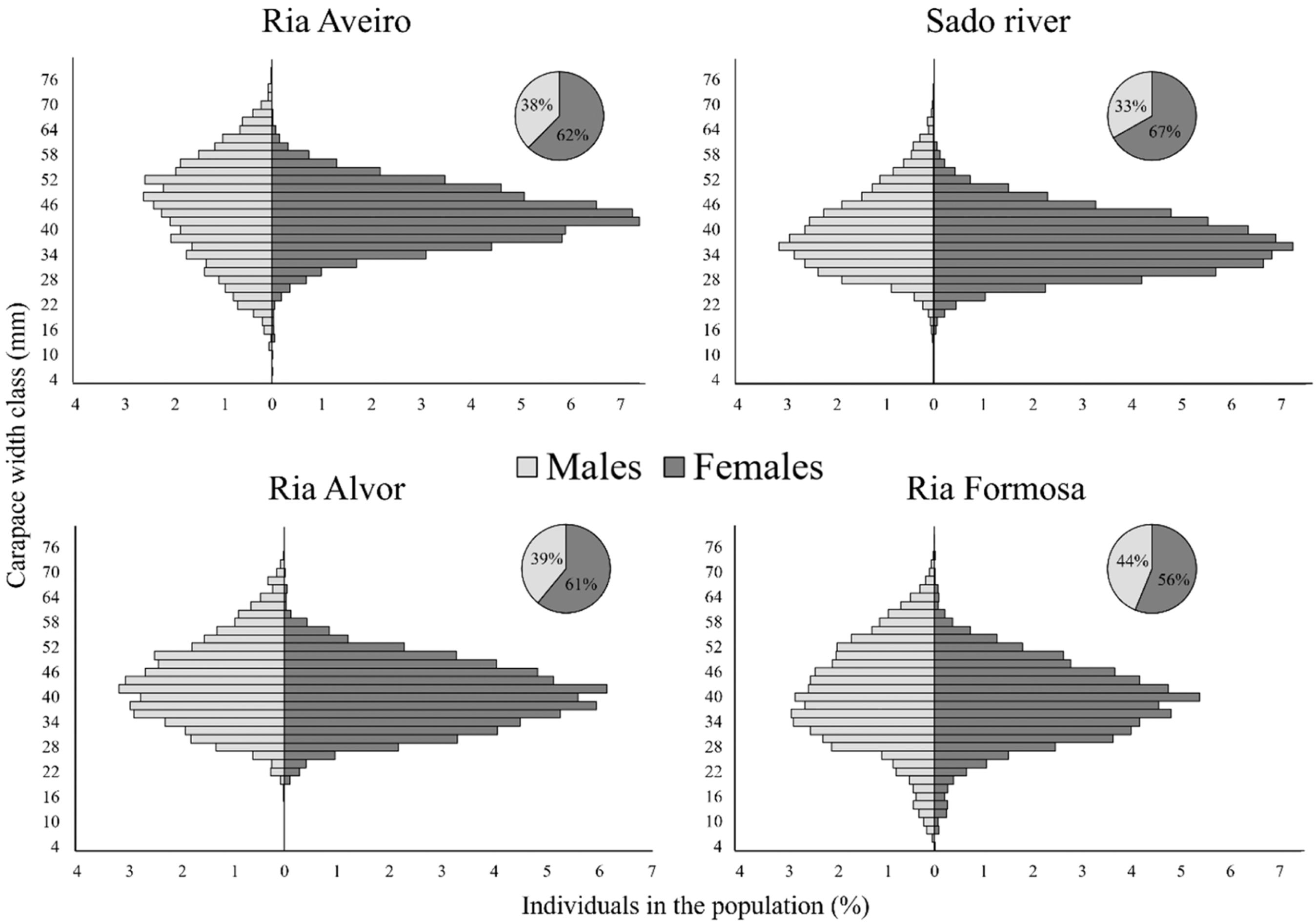

Fig. 2. Carapace width class size frequency of Carcinus maenas populations in each system. Males frequency is represented in the left side (light grey), and females frequency in the right side (dark grey).

Table 1
Summary of range and mean carapace width and body weight of Carcinus maenas for each sex over the different systems. Min, max and SD denote minimum, maximum and standard deviation, respectively.

			Ria Aveiro	Sado river	Ria Alvor	Ria Formosa
Carapace width (mm)	**Males**	Min - Max	8.66 - 81.45	4.82 - 74.79	17.18 - 74.1	5.59 - 78.38
		Mean ± SD	45.39 ± 11.95	40.5 ± 9.13	44.18 ± 9.92	41.27 ± 12.15
	Females	Min - Max	6.83 - 69.99	5.56 - 64.26	20.68 - 70.55	4.91 - 74.58
		Mean ± SD	44.00 ± 6.96	37.97 ± 6.93	41.33 ± 7.58	39.7 ± 8.97
Body Weigh (gr.)	**Males**	Min - Max	0.53 - 113.16	0.06 - 108.91	1.14 - 99.15	0.08 - 118.72
		Mean ± SD	24.95 ± 17.49	16.75 ± 11.89	22.17 ± 15.6	20.11 ± 15.67
	Females	Min - Max	0.52 - 66.97	0.04 - 113.23	2.08 - 66.2	0.14 - 113.55
		Mean ± SD	19.9 ± 8.65	12.87 ± 6.71	16.92 ± 8.93	15.84 ± 9.47

(Supplementary information, Figure S1). The sex ratio exhibits monthly variation ($\chi 2 = 450.408$, $p < 0.001$), with a prevalence of females throughout the year. The variation in sex ratio according to the size classes were also observed for all systems (Ria Aveiro: $\chi^2 = 2148.554$, $p < 0.001$; Sado river: $\chi^2 = 1120.389$, $p < 0.001$; Ria Alvor: $\chi^2 = 320.803$, $p < 0.001$; Ria Formosa: $\chi^2 = 682.013$, $p < 0.001$). In the Ria Aveiro, the sex ratio of the population was m/f= 0.60, with a higher proportion of males between the size classes of 6 and 30, as well as between the CW size classes of 56 to 80 (maximum size class). In the Sado river, the sex ratio of the population was m/f= 0.50, with the higher proportion of males between the size classes of 4 and 16, as well as between the CW size classes of 52 to 74 (maximum size class) (Fig. 2). In the Ria Alvor, the sex ratio of the population was m/f= 0.64, with the higher proportion of males between the size classes of 16 (minimum size class) and 18, as well as between the CW size classes of 54 to 74 (maximum size class). In the Ria Formosa, the sex ratio of the population was m/f= 0.78, with the higher proportion of males between the size classes of 4 and 22, as well as between the CW size classes of 56 to 80 (maximum size class). The sex ratio exhibits monthly variation in all systems (Ria Aveiro: $\chi^2 = 297.949$, $p < 0.001$; Sado river: $\chi^2 = 707.926$, $p < 0.001$; Ria Alvor: $\chi^2 = 294.984$, $p < 0.001$; Ria Formosa: $\chi^2 = 274.618$, $p < 0.001$), with a prevalence of females throughout the year in all systems.

3.2. Morphometric relationships

Relationship between Carapace width (CW) and Body wet weight (Weight) yielded a statistically significant slope ($p < 0.001$) for both sexes across all systems (Fig. 3) with a high coefficient of correlation value ($r^2 > 0.90$). Statistically significant differences were found between

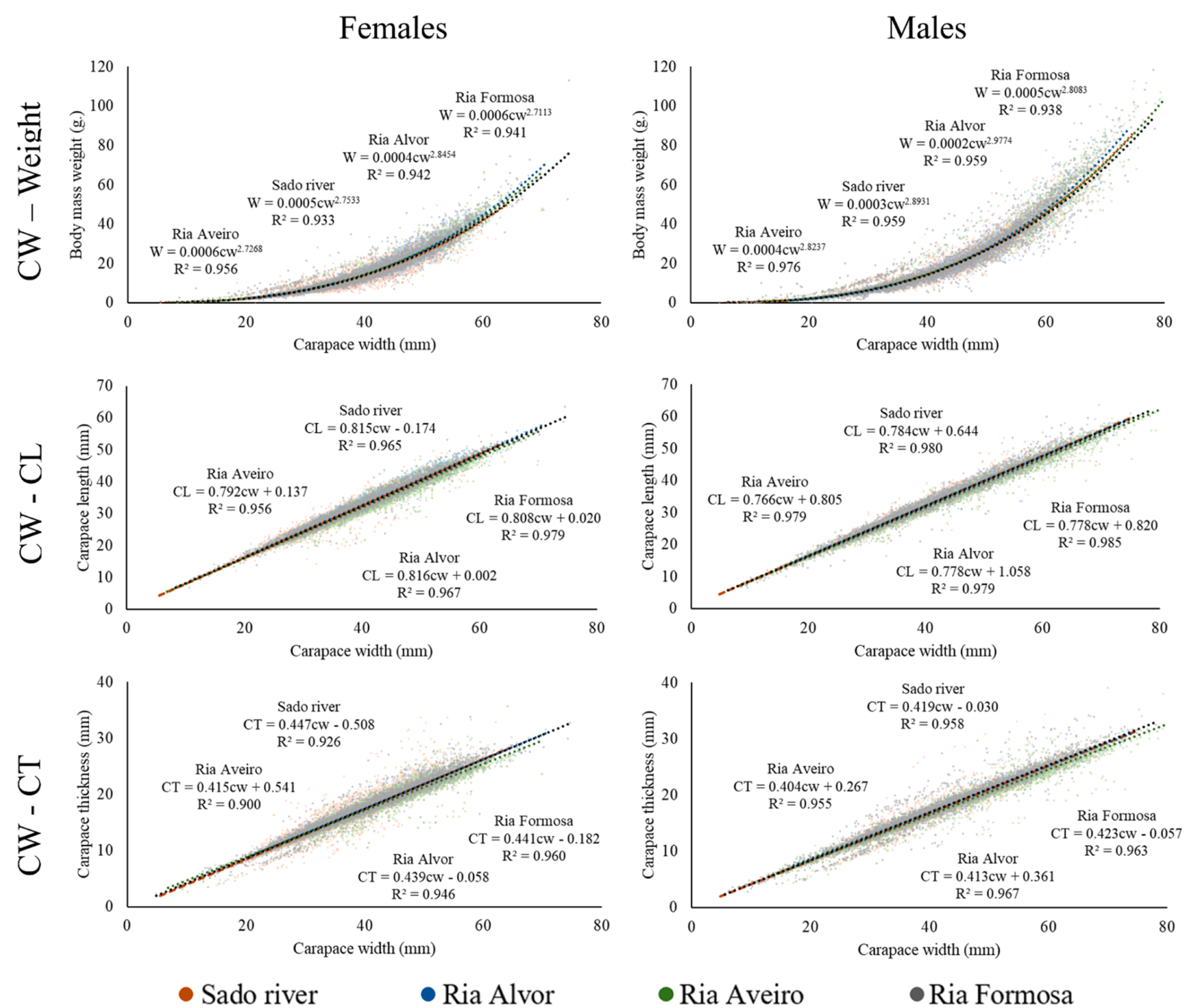

Fig. 3. Morphometric relationships of Carcinus maenas populations for both sexes. The left panels show the relationships for females and the right panels for males. The top panels show the relationship between carapace width and weight (CW-Weight). The middle panels shows the relationship between carapace width and carapace length (CW-CL), and the bottom panels shows the relationship between carapace width and carapace thickness (CW-CT).

CW-W relationships among systems accordingly sex (ANCOVA: Female: F = 33.018; $p < 0.001$; Male: F = 48.295; $p < 0.001$) with a negative allometric growth observed for both sexes in all systems (Table 2). All the CW-CL (carapace width - carapace length) relationships were statistically significant ($p < 0.001$) (Fig. 3) and the fit(s) denoted a high correlation between variables (r^2>0.95), with a negative allometric growth observed for both sexes in all systems (Table 2). Statistically significant differences were found between CW-CL relationships among systems accordingly sex (ANCOVA: Female: F = 48.295; $p < 0.001$; Male: F = 39.312; $p < 0.001$). Lastly, all the CW-CT relationships (carapace width – carapace thickness) were statistically significant ($p < 0.001$), with statistically significant differences observed among the relationships between systems for both sexes (ANCOVA: Female: F = 113.689; $p < 0.001$; Male: F = 54.829; $p < 0.001$). Moreover, it was observed a high coefficient of correlation (r^2>0.90) between carapace thickness and carapace width, with a negative allometric growth observed for both sexes in all systems (Table 2).

3.3. Reproductive periods

The proportion of mature individuals in all populations was always above 50 % (Supplementary Information Figure S2), and all gonadal development stages were observed throughout the year for both sexes (Fig. 4).

It was observed that the gonads of the females developed over the months, with the same seasonal trend in all systems (Fig. 4). A high percentage of females were classified in stages II (Late development) and V (Spent) for all systems throughout the year. These two stages represent transitional phases before the reproductive period that occurs in the colder months, from September to March. This is supported by the high percentage of females in stage III (Mature) and stage IV (Spawning) during this seasonal window, as well by the negative correlation between the monthly percentage of reproducing individuals and water temperature (Pearson correlation: R = −0.665, $p = 0.018$). The peak spawning period for females occurred between December and March in all systems (Fig. 4).

For males, a large percentage of individuals were in stage II throughout the year in all systems (Fig. 4). After the reproductive period

Table 2
Morphometric relationships and type of growth of Carcinus maenas populations for both sexes from Ria Aveiro, Sado river, Ria Alvor and Ria Formosa. CW- Carapace width; CL – Carapace length; CT – Carapace thickness.

	Sex	System	N	Equation	R^2	B ± SE (95 % CI)	Type of growth
CW - Weight	**Female**	**Ria Aveiro**	8980	$W = 0.0006\ CW^{2.7268}$	0.956	2.727 ± 0.006 (2.715 – 2.739)	- Allometry
		Sado river	15045	$W = 0.0005\ CW^{2.7533}$	0.933	2.753 ± 0.006 (2.742 – 2.765)	- Allometry
		Ria Alvor	3425	$W = 0.0004\ CW^{2.8454}$	0.942	2.845 ± 0.013 (2.822 – 2.869)	- Allometry
		Ria Formosa	6903	$W = 0.0006\ CW^{2.7113}$	0.936	2.711 ± 0.009 (2.694 – 2.728)	- Allometry
	Male	**Ria Aveiro**	5419	$W = 0.0004\ CW^{2.8237}$	0.976	2.824 ± 0.006 (2.812 – 2.835)	- Allometry
		Sado river	7383	$W = 0.0003\ CW^{2.8931}$	0.959	2.893 ± 0.007 (2.879 – 2.907)	- Allometry
		Ria Alvor	2182	$W = 0.0002\ CW^{2.9774}$	0.959	2.977 ± 0.013 (2.952 – 2.997)	- Allometry
		Ria Formosa	5256	$W = 0.0005\ CW^{2.8083}$	0.938	2.808 ± 0.010 (2.789 – 2.828)	- Allometry
CW - CL	**Female**	**Ria Aveiro**	8980	CL = 0.792CW + 0.137	0.956	0.792 ± 0.002 (0.788 – 0.796)	- Allometry
		Sado river	15045	CL = 0.815CW - 0.174	0.965	0.815 ± 0.001 (0.812 - 0.817)	- Allometry
		Ria Alvor	3425	CL = 0.816CW + 0.002	0.967	0.816 ± 0.003 (0.811 – 0.821)	- Allometry
		Ria Formosa	6903	CL = 0.808CW + 0.020	0.979	0.808 ± 0.001 (0.805 – 0.811)	- Allometry
	Male	**Ria Aveiro**	5419	CL = 0.766CW + 0.805	0.979	0.766 ± 0.002 (0.762 – 0.769)	- Allometry
		Sado river	7383	CL = 0.784CW + 0.644	0.980	0.784 ± 0.001 (0.781 – 0.786)	- Allometry
		Ria Alvor	2182	CL = 0.778CW + 1.058	0.979	0.778 ± 0.002 (0.773 – 0.782)	- Allometry
		Ria Formosa	5256	CL = 0.778CW + 0.820	0.985	0.778 ± 0.001 (0.775 – 0.781)	- Allometry
CW – CT	**Female**	**Ria Aveiro**	7833	CT = 0.415CW + 0.541	0.900	0.415 ± 0.002 (0.412 – 0.418)	- Allometry
		Sado river	15414	CT = 0.447CW - 0.508	0.960	0.447 ± 0.001 (0.445 – 0.449)	- Allometry
		Ria Alvor	3426	CT = 0.439CW - 0.058	0.946	0.439 ± 0.002 (0.435 – 0.442)	- Allometry
		Ria Formosa	7040	CT = 0.441CW - 0.182	0.926	0.441 ± 0.001 (0.439 – 0.443)	- Allometry
	Male	**Ria Aveiro**	4576	CT = 0.404CW + 0.267	0.955	0.404 ± 0.001 (0.402 – 0.407)	- Allometry
		Sado river	7578	CT = 0.419CW - 0.030	0.958	0.419 ± 0.001 (0.417 – 0.421)	- Allometry
		Ria Alvor	2188	CT = 0.413CW + 0.361	0.967	0.413 ± 0.002 (0.409 – 0.416)	- Allometry
		Ria Formosa	5480	CT = 0.423CW - 0.057	0.963	0.423 ± 0.001 (0.421 – 0.425)	- Allometry

(the colder months), a decrease in the percentage of individuals in stage II, and an increase in the percentage of individuals in stage III (spent) was observed for all populations. From February to April, males in stage III (spent) were most prevalent in all systems.

3.4. *Size at maturity*

The smallest sexually mature specimen captured during this study was a male from Ria Aveiro with a CW of 16.2 mm. In this region, the smallest mature female measured 17.11 mm CW. Furthermore, in Ria Aveiro, the CW_{50} of females was lower than that for males, at 28.44 and 30.44 mm, respectively (Fig. 5; Table 3 and Table S3). In the Sado river, the smallest crab that reached sexual maturity had a CW of 17.64 and 23.02 mm, for females and males, respectively. The CW_{50} of Sado river females was lower than males, 28.66 and 30.84 mm, respectively (Fig. 5 and Table 3). In Ria Alvor, the smallest mature crab had a CW of 22.74 and 23.65 for females and males, respectively. The CW_{50} of Ria Alvor females was lower than males, 29.71 and 30.93 mm, respectively (Fig. 5 and Table 3). In Ria Formosa the smallest sexually mature crab had a CW of 19.37 and 19.17, for females and males, respectively. The CW_{50} of Ria Formosa females was lower than males, 29.85 and 30.88 mm, respectively (Fig. 5 and Table 3). Across all the systems, a CW_{50} latitudinal gradient was observed, with values increasing from north to south (Fig. 5 and Table 3).

3.5. *Life-history traits*

The length-frequency data of *C. maenas* was used to determine the growth parameters of males and females in each system (Fig. 6 and Table 4). Females exhibited a lower CW_{∞} than males in all systems, except in Ria Formosa, with values ranging from 61.08 mm in Ria Aveiro to 79.78 mm in Ria Formosa. On the other side, the CW_{∞} of males ranged from 67.17 mm in Ria Formosa to 84.65 mm in Ria Aveiro (Table 4). The growth coefficient (K) was very similar between sexes in all systems, ranging between 0.51 $year^{-1}$ in females from Ria Aveiro to 0.74 $year^{-1}$ in males from Ria Formosa, indicating a quick growth rate to reach the CW_{∞}. The T_{anchor} values varied between 0.02 $year^{-1}$ and 0.14 $year^{-1}$, suggesting that the massive spawning of *C. maenas* occurred between January and mid-February in all systems. The growth performance index (φ') showed similar results for males and females in all systems with the φ' ranging between 3.28 and 3.58. The seasonal variation of growth (C) varied across systems; it was weak in Ria Aveiro and Ria Alvor ($C < 0.37$ for both sexes), but strong in the Sado river and Ria Formosa ($C > 0.70$). The T_s did not show any temporal trend and varied between sexes and systems. The analysis of von Bertalanffy growth curves revealed the existence of between four and six growth cohorts for both sexes across all systems (Fig. 6).

4. Discussion

Our study provided new insights into the biological traits of *C. maenas*, which can contribute to the European regulation of this crab fishery. These include traits related to maturation, life history, growth, size frequency distribution, reproductive periods and recruitment pulses in various Portuguese coastal systems where crab fisheries occur. In 2023, the minimum landing size for *C. maenas* was reduced from 5 cm carapace width (CW) to 4 cm (Portaria nº 255/2022), based on the preliminary results of this study, however, this work can contribute to a re-evaluation of the regulation of *Carcinus maenas* fishing in Portugal.

Despite extensive research on *C. maenas*, including data on reproductive, developmental, and population characteristics, life cycle, physiological tolerance, control programs, and the potential economic valorization of green crabs (Young and Elliott, 2020), there is a scarcity of information on the biological traits that could be applied for fishery management in different geographical areas. *Carcinus maenas,* the most widely distributed intertidal crab in the world (Rewitz et al., 2004; Young and Elliott, 2020), has been classified by the IUCN as one of the world's 100 worst invaders (Leignel et al., 2014). This high invasive capacity is correlated with variations in biological and reproductive characteristics of the species across different regions (Kelley et al., 2015; Young and Elliott, 2020; Monteiro et al., 2023). Portugal is situated at the southernmost extent of the distribution of *C. maenas* in Europe, a region with relatively high temperatures compared to other areas, which results in the smallest carapace size and early maturation size of Portuguese populations (Young and Elliott, 2020; Monteiro et al., 2023). The population structure of *C. maenas* in each Portuguese system analysed in the present study demonstrated that their size distribution is consistent with those reported for other studies for the species in Portugal (Baeta et al., 2005; Bessa et al., 2010; Souza et al., 2011; Monteiro et al., 2021). A wide range of carapace width was observed in

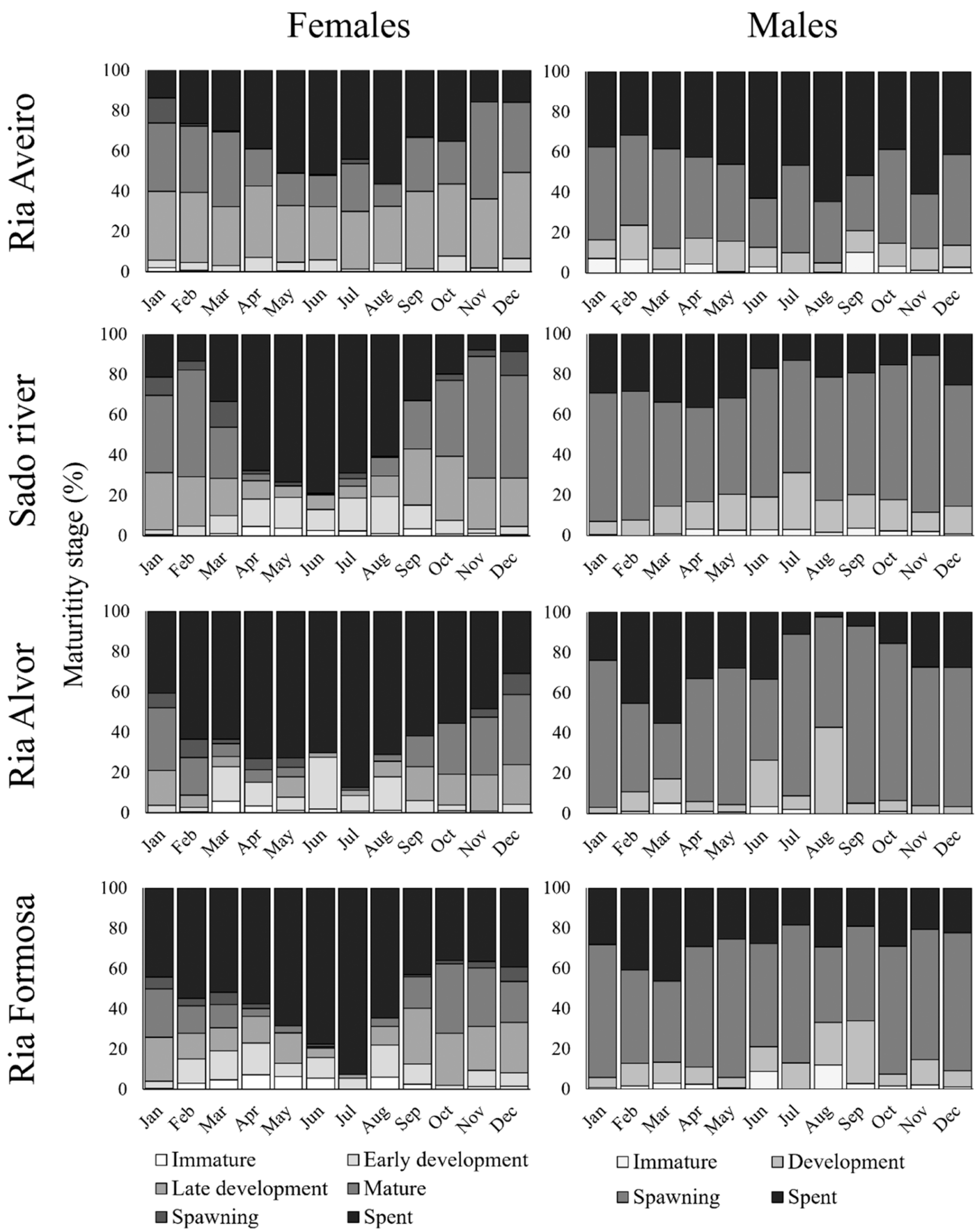

Fig. 4. Monthly variations of gonad stages on mature Carcinus maenas individuals. The left panels show the gonad stages of females and the right panels of males.

the Ria Aveiro system, which is located in the northern region of the country and experiences lower sea surface temperatures. Furthermore, as with the majority of studies on *C. maenas*, it was found that the maximum CW of males was higher than that of females. This is thought to be due to male competition in order to gain access to females and food resources (Klassen and Locke., 2007), as well as a trade-off whereby females invest more energy in reproduction than in growth once females reach sexual maturity (Hartnoll, 2006).

Sex ratio analysis of different CW size classes in this study revealed that the proportion of males was higher in the smaller and larger size classes, while the proportion of females was higher in the intermediate size classes. This trend was observed across all the systems analysed and follows the same pattern observed in previous studies conducted in the Mondego estuary, Portugal (Baeta et al., 2005; Monteiro et al., 2021). It has been postulated that the high proportion of juvenile males could be attributed to behavioural differences among the sexes. The hypothesis of a biased sex ratio over the CW size classes was previously put forth in studies that highlighted the observation that males are more active and competitive than females in smaller size classes (Styrishave et al., 2004; Monteiro et al., 2021). This phenomenon results in a higher mortality rate of males in smaller size classes, consequently leading to a greater number of females than males reaching the intermediate CW size classes. Conversely, the increase in male percentages in the larger size classes can be attributed to the maximum CW attained by each sex. The

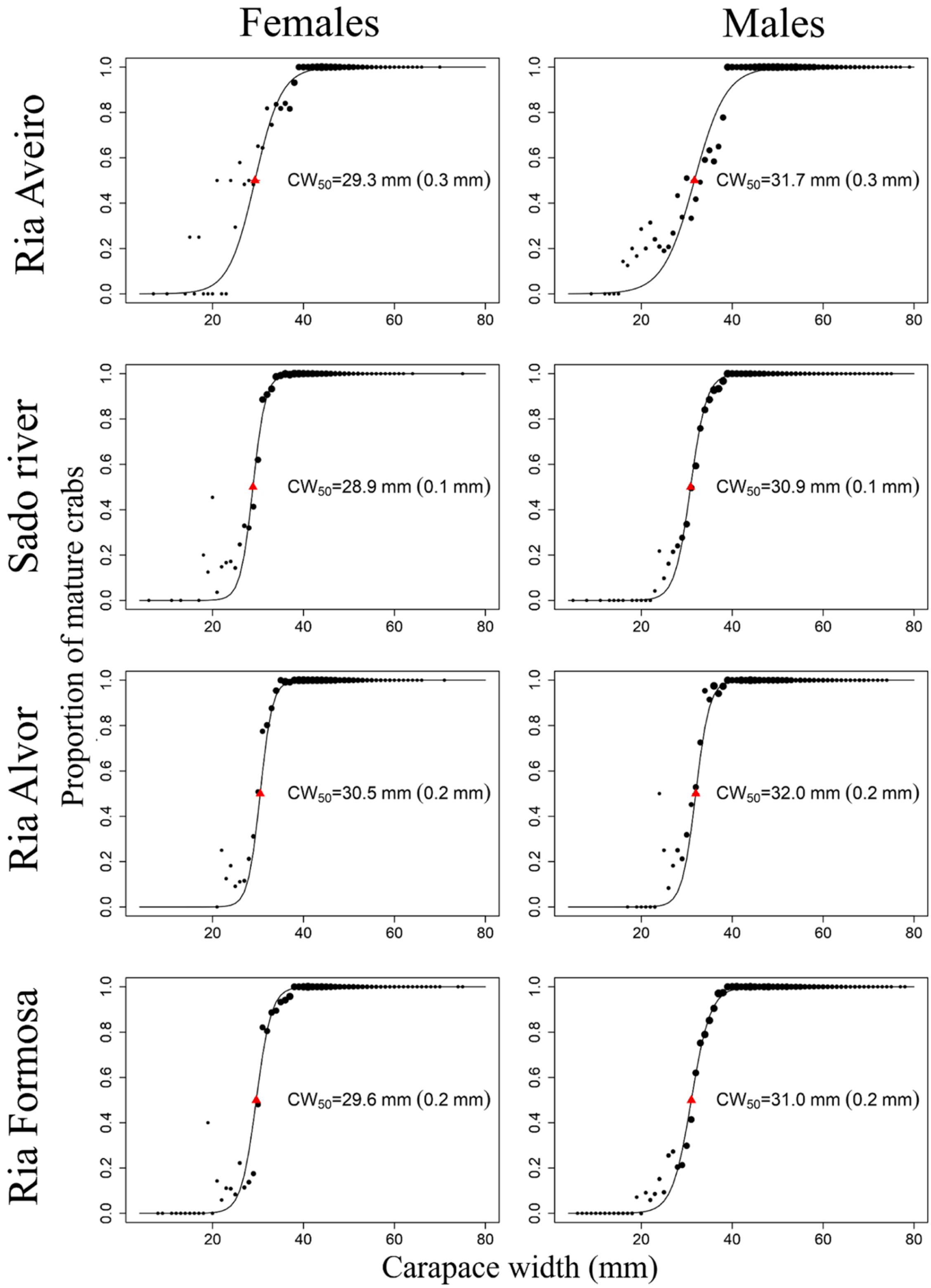

Fig. 5. Progression of sexual maturity with size (dots) and fitted logistic model (line) for females (left) and males (right) specimens of Carcinus maenas on different systems of Portugal (Ria Aveiro, Sado river, Ria Alvor and Ria Formosa). The carapace width at 50 % of maturity and its standard error (in parentheses) are also shown. The red triangle is located at the size at 50 % maturity.

relatively large proportion of crabs in the middle-size classes (20–50 mm) results in a smaller sex ratio in the present study compared to other studies of *C. maenas* populations. This discrepancy could be attributed to the sampling programme employed, as in this study traps were used, which may have resulted in the exclusion of smaller individuals (less than 20 mm). In contrast, in the Mondego studies, trawl nets were used in the samplings, leading to a large number of small crabs being caught (Baeta et al., 2005; Bessa et al., 2010; Monteiro et al., 2021). Consequently, most of the juveniles were males, leading to an overall higher sex ratio in the population. Furthermore, the observed sex

Table 3
Results of the maturity development logistic regression model for females and males specimens of Carcinus maenas on different systems of Portugal (Ria Aveiro, Sado river, Ria Alvor and Ria Formosa). CW_{50}, - Carapace width in mm at which 50 % of individuals were mature; α - Intercept parameter; β - Slope parameter.

System	Females			Males		
	$CW_{50} \pm SD$	α	β	$CW_{50} \pm SD$	α	β
Ria Aveiro	29.34 ± 0.34	−10.15	0.35	31.69 ± 0.25	−9.18	0.29
Sado river	28.90 ± 0.08	−20.94	0.72	30.86 ± 0.11	−17.74	0.57
Ria Alvor	30.49 ± 0.19	−23.02	0.75	31.99 ± 0.23	−21.23	0.66
Ria Formosa	29.62 ± 0.19	−17.90	0.60	31.01 ± 0.15	−14.77	0.48

ratio in our study is relatively low compared to other global populations (for more details see Young and Elliott, 2020). This could be attributed to the warmer waters in Portugal, as the sex ratios are biased towards females in warmer sites (Young and Elliott, 2020). A popular hypothesis is that the sex ratio in crabs is closer to 1:1. However, environmental variables, collection methods, sampling period and crab size seem to influence an inflated sex ratio, biasing the male or female ratio. Therefore, these results here challenge the 1:1 hypothesis, which was also observed in the Mondego estuary (Monteiro et al., 2021).

Establishing morphometric relationships is crucial for developing conversion equations that relate different morphometric variables. These relationships can be utilised in a range of applications, including fisheries analysis, fisheries biology and ecology, population dynamics, stock assessment analysis and the management of fisheries (Laudien et al., 2003; Peharda et al., 2007; Cooke et al., 2023; Mahé et al., 2023). The present study provides relationships in *C. maenas* that have not been previously analysed, including CW-CL and CW-CT. The CW-CL relationship offers crucial information for the determination of optimal mesh sizes. In the case of box traps, the mesh size is dependent on the carapace length of the crabs, with escape or non-escape occurring in accordance with the CL rather than the CW (Herrmann et al., 2021; Yu et al., 2024). The CW-CL relationship would also be of major utility in fishery management, as the thickness of the crab could be employed to determine the optimal space between bars, should it be necessary to sieve the catch after the fishery. In Portugal, specifically in the Ria Aveiro and Sado river, fishers employ an iron grid sieve to sort crabs, enabling the discard of undersized individuals (Leitão and Monteiro, 2022). Both of these relationships demonstrated negative allometric growth (i.e. $b < 1$) across the entire system and sexes, indicating that the growth occurs at the different rate for all carapace measures of *C. maenas*. The estimated b values of the CW–weight relationship for male and female green crabs in all systems indicated that both sexes exhibited a slight negative allometric growth pattern (i.e., $b < 3$). Similarly, Baeta et al. (2005) and Audet et al. (2008) recorded a negative allometric growth for both *C. maenas* sexes collected in the Mondego estuary (Portugal) and in the non-native population of Basin Head (Prince Edward Island, Canada). Furthermore, for the *Carcinus aestuarii* congeneric species of *C. maenas* in the Mediterranean Sea, a negative allometric growth was observed in both sexes (Glamuzina et al., 2017; Aydın, 2018; Tiraşin et al., 2020). In all studies, including the present work, the estimated "b" for males was consistently higher than that for females. This suggests that males are heavier than females at a comparable CW and also grow larger, which is consistent with the previously discussed size-related sexual dimorphism.

Understanding the timing and patterns of reproduction is extremely important for establishing fishing closures, as these closures are set to protect the species during the reproductive period, leading to better reproductive success. (Laudien et al., 2003; Peharda et al., 2007; Cooke et al., 2023). *Carcinus maenas* exhibits a clear peak in reproductive activity during the colder months (September to March), as evidenced by the gonad development stages of females and the negative correlation between sea surface temperature and reproductive periods. Therefore, if required for conservation, a one month closed season between December and February can be enforced due to the higher number of ovigerous females caught. In addition, the discarding of ovigerous females should be mandatory throughout the year. The reproductive period is primarily regulated by the female gonad development, with a high proportion of males maintaining mature gonads throughout the year, exhibiting a slight decline after the colder months, which coincides with the females gonad development. This temporal trend is also observed in the congeneric species *C. aestuarii*, where a clear peak of reproduction occurs in the colder months (Glamuzina et al., 2017; Tiraşin et al., 2020). Additionally, Portuguese studies have reported a high number of ovigerous females in December, January, and February (Baeta et al., 2005; Monteiro et al., 2022; Portela et al., 2023), as well as a high recruitment rate after the colder months (Queiroga et al., 1994; Sprung, 2001;Baeta et al., 2005; Amaral et al., 2009; Bessa et al., 2010). However, the non-native population of North America (Audet et al., 2008; Best et al., 2017) exhibits a different trend, with a peak in reproduction occurring during the warm months. This could be attributed to the high plasticity of *C. maenas* and its capacity for adaptation. Furthermore, Best et al. (2017) postulates that temperature is not the sole factor influencing the observed differences in larval release patterns. Rather, a combination of temperature, salinity, photoperiod, and food abundance is likely to influence the seasonality of the reproductive events of *C. maenas*.

Size at maturation represents a crucial parameter in fisheries management, as it is extensively employed to ascertain the minimum landing size (MLS) (Laudien et al., 2003; Peharda et al., 2007; Pohlmann et al., 2016; Cooke et al., 2023). In Portugal, the MLS of *C. maenas* is defined as 50 mm of carapace width (CW) until 2023 (Portaria nº 27/2001) and 40 mm of CW after 2023 (Portaria nº 255/2022). However, this value is considerably high, as evidenced by fishers (Monteiro et al., in press) and previous studies in Portuguese systems that have documented a considerable number of ovigerous females with carapace widths smaller than 40 mm of CW (Table 5). It is important to note that the size at maturation, and therefore the MLS, should only be determined based on gonad development and not on the presence or absence of ovigerous females in the population. Therefore, some studies should not be considered for advice such as the one conducted by Portela et al. (2023) that determined the size at maturation to be 45.1 mm of CW. However, Portela et al. (2023) determined the size at maturation only according to the presence/absence of ovigerous females. Contrarily, in our study, the estimated size at maturation, 30 mm of CW for both sexes, encompasses inter-annual and inter-systems data collection. As a result, the DGRM, which is responsible for enforcing sustainable precautionary measures based on scientific advice, should consider reducing the current MLS to 35 mm of CW, which would result in fishers catching smaller individuals, ultimately increasing their catches but maintaining the sustainability of the fishery. The size at maturation values determined in our study are supported by the high presence of ovigerous females in all Portuguese systems, with sizes around 30 mm, as well as by the values reported in other *C. maenas* populations (Table 5). The size at maturation of *C. maenas* is influenced by sea surface temperature, with smaller sizes observed in warmer regions (Monteiro et al., 2023). Portugal is located in a warmer region compared with the remaining regions where the size at maturation or ovigerous females' size was studied. This explains the smaller size at maturation determined in our study compared to the findings in the remaining literature (Table 5).

Our study is the first that examines population growth parameters and data that can be used to assess crab stocks in Portugal, as for successful fisheries management, a complete conceptualization of the species' life history parameters is recommended (Hilborn and Walters, 1992). These demographic data are the input for determining the biomass of the stock considering the CW of the age groups/cohorts in the

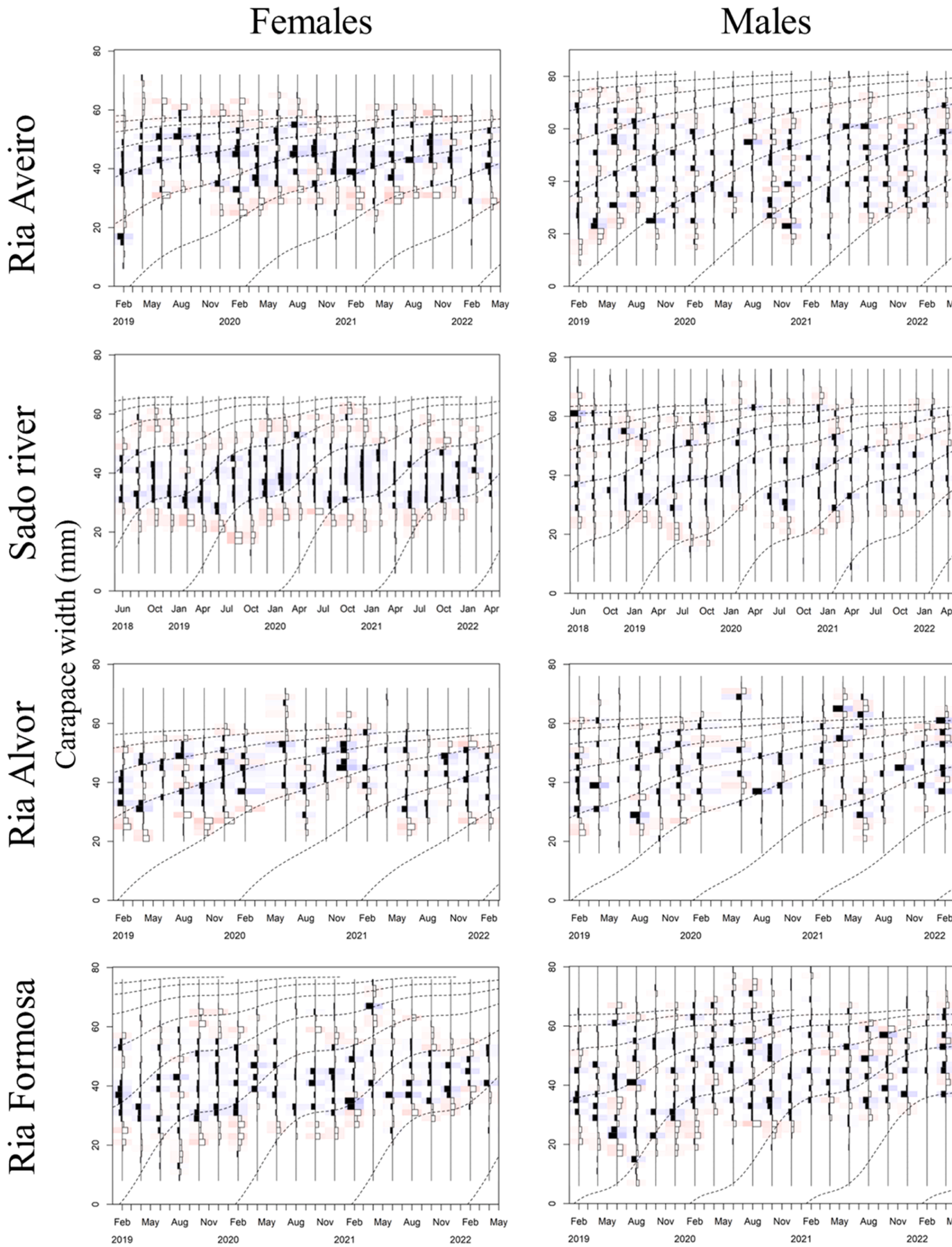

Fig. 6. Von Bertalanffy growth curve for females (left) and males (right) specimens of Carcinus maenas from Portuguese systems (Ria Aveiro, Sado river, Ria Alvor and Ria Formosa), derived from the restructured data with a moving average setting of 7. Black curves represent seasonal growth patterns fitted with ELEFAN_SA. Histograms show negative (white) and positive (black) frequencies, indicating lower or higher counts relative to the moving average. Blue areas indicate alignment of growth curves with LFQ peaks, while red areas indicate misalignment.

stock assessment models (Francis et al., 2016; Punt, 2023). Variations in the growth estimated values were observed across systems and sexes, which could be explained by local hydrographic conditions as discuss previously, such as water temperature and the different behaviors of males and females. CW_{∞} and K showed some variations between systems and sexes, with CW_{∞} determined being lower than CW_{max} observed in all systems except Ria Formosa. Moreover, the CW_{∞} of males was larger than that of females, in accordance with the results of the size-frequency distribution and the CW_{max} of each sex. The K value allowing us to conclude that after six months, *C. maenas* reach sexual maturity (30 mm). This rapid growth is also observed in the cohorts observed in the population, which vary between 4 and 6. These results align with those previously observed in the Mondego Estuary (Baeta et al., 2005). Furthermore, the values of T_{anchor}, i.e. the fraction of the year where CW is equal to zero, were similar in all systems and sexes. The start of growth was determined to occur between January and

Table 4
Von Bertalanffy growth parameters estimated for Carcinus maenas populations for both sexes from Ria Aveiro, Sado river, Ria Alvor and Ria Formosa. CW_∞ -Asymptotic width (mm); T_{anchor} - Fraction of the year where yearly repeating growth curves cross length equal to zero; K - Growth coefficient. T_s – Fraction of the year when start of a sinusoid growth oscillation with respect to T_{anchor}, C - Intensity of the seasonal growth oscillation. φ' is the growth performance index; Rnmax - Goodness of fit indexCWmax – Maximum Carapace width observed in the samplings.

		CW_∞	K	T_{anchor}	C	T_s	φ'	Rn_{max}	CW_{max}
Females	**Ria Aveiro**	61.09	0.51	0.14	0.37	0.18	3.28	0.26	70.00
	Sado river	68.58	0.64	0.04	0.89	0.39	3.48	0.18	75.00
	Ria Alvor	61.24	0.63	0.04	0.21	0.99	3.37	0.19	71.00
	Ria Formosa	79.78	0.55	0.06	0.87	0.32	3.55	0.18	75.00
Males	**Ria Aveiro**	84.65	0.52	0.03	0.08	0.47	3.58	0.14	81.00
	Sado river	67.13	0.53	0.04	0.70	0.12	3.37	0.14	75.00
	Ria Alvor	64.36	0.58	0.02	0.36	0.74	3.38	0.17	74.00
	Ria Formosa	67.17	0.74	0.04	0.78	0.74	3.53	0.20	78.00

Table 5
Summary of published data of range of carapace width (mm) of Carcinus maenas ovigerous females and Size at 50 % of females reach the sexual maturity (CW_{50}). [1] Baeta et al., 2006; [2] Bessa et al., (2010); [3] Monteiro et al., (2022); [4] Portela et al., (2023); [5] Present study; [6] Broekhuysen, (1936); [7] Lyons et al., (2012); [8] Lützen, (1984); [9] Audet et al., (2008); [10] Best et al., 2017; [11] Berrill, (1982); [12] Tremblay et al., (2006).

Local	Ovigerous females Min - Max	Nº of Ovigerous Females	Size at maturity (CW_{50})
Mondego estuary, Portugal[1]	29–64		
Mondego estuary, Portugal[2]	22–56	127	
Ria Formosa, Portugal[3]	32.0–55.4	28	
Ria Alvor, Portugal[3]	30.8–56.3	49	
Sado River, Portugal[3]	32.6–52.0	32	
Ria Aveiro, Portugal[3]	27.0–61.3	51	
Santo André Lagoon[4]	26.7–56.2	173	45.1
Ria Formosa, Portugal[5]	25.9–65.8	193	29.6
Ria Alvor, Portugal[5]	25.7–56.3	147	30.5
Sado River, Portugal[5]	22.5–55.0	626	28.9
Ria Aveiro, Portugal[5]	27.0–61.3	141	29.3
Den Helder, Netherlands[6]	18–29	69	
Bullens Bay, Ireland[7]			49.96
Isefjord, Denmark[8]	30		
Basin Head, PEI[9]	28.6–41.4		
North Harbor, Canada[10]	37–55		
Boothbay Harbor, US[11]	34–67	84	
Bras d'Or Lakes, Canada[12]	40–60	228	

February, which once again coincides with the results observed in the analyses of reproductive periods, as well as with the peak of reproduction observed in other studies in Portugal (Sprung, 2001; Baeta et al., 2005; Monteiro et al., 2022; Portela et al., 2023). The seasonal growth pattern observed in our analysis, which shows a slower growth period in winter for females and in summer for males, is a common phenomenon in decapods such as *Callinectes sapidus, Palaemon adspersus, Crangon rangon* and *Parapenaes longirostris*. This growth pattern is also a consequence of reproduction periods, due to an energy allocation in reproduction rather than growth (Tagatz, 1968; Hartnoll, 2006).

Over the past few decades, *C. maenas* has been fished in the coastal systems of its native region (Gomes, 1991; Sheehan et al., 2008; Leitão and Monteiro, 2022), and more recently in the various non-native populations of North America (Gillespie et al., 2007; Bergshoeff et al., 2019; Favaro et al., 2020; McKenzie et al., 2022). Its socio-economic importance has been on the rise, with the use of crab for both fishing and food purposes (Monteiro et al. in press). Green crab is currently being used as live bait in fisheries (octopus, lobster and seabream fishing), manufactured in shellfish companies, and consumed as soft crab (St-Hilaire et al., 2016; Parks and Thái, 2019; Greiner et al., 2021; McKenzie et al., 2022; Leitão et al., 2023). Despite the increase in green crab catches in Portugal, a recent stock assessment study based on demographic data and these biological data showed that annual landings never exceeded sustainable harvest rates in the Portuguese systems. However, sustainable exploitation and adequate biological data may not prevent the extinction of the crab fishery due to socio-economic hurdles (Monteiro et al. in press). Considering this, the baseline information gathered in this study will allow the proposal of fishery management measures, such as the reduction of the minimum landing size, the discarding of ovigerous females and, if necessary, a closed season between December and February in Portuguese estuaries. These will alleviate the socio-economic problems reported by fishers in the green crab fishery in Portugal.

5. Final considerations

This study gathered biological information that enhances scientific knowledge applicable to fisheries management and resolves the controversies from previous studies, as prior policies have been implemented without consideration of the regional biological parameters of this species, resulting in misguided crab biological regulation in southern Europe. In relation to our climate conditions in Iberia, namely in Portugal, *C. maenas* reach sexual maturity at 30 mm of carapace width, with small variations all over the country. The high percentage of mature individuals observed throughout the year indicates that reproduction occurs throughout the year, although a peak in reproduction occurs during the colder months, between September and March. Furthermore, the analysis of growth parameters revealed that the peak of recruitment occurs during the colder months, with individuals reaching the size at maturation after a few months. This results in a high number of cohorts in the population and a continuous recruitment process. Furthermore, the results indicate that females invest a greater proportion of their energy into reproduction than into growth, resulting in a population comprising large males and a high number of females with carapace widths between 30 and 50 mm. The findings of this study will contribute to more effective fisheries management policies for *C. maenas* in Portugal, such as the reduction of the minimum landing size, the discarding of ovigerous females and, if necessary, a closed season between December and February in Portuguese estuaries.

CRediT authorship contribution statement

Francisco Leitão: Writing – review & editing, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition. **Maria Alexandra Teodósio:** Writing – review

& editing, Supervision, Methodology, Funding acquisition. **Francisco Maia:** Writing – review & editing, Resources, Methodology. **Andreia Ovelheiro:** Writing – review & editing, Investigation. **João Nuno Monteiro:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization.

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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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2024.107243.

Data availability

Data will be made available on request.

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