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Research Article

Ecology and biology of *Callinectes sapidus* in the Northern Adriatic Sea: could the small spatial scale explain its outbreak?

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Abstract

The Atlantic blue crab (*Callinectes sapidus*) is among the 100 worst invasive species in the Mediterranean Sea, causing significant ecological and economic impacts. The aim of this study is to investigate key aspects of the species' biology and ecology during its demographic outbreak in a Northern Adriatic area significantly affected by the species' invasion. Year-round sampling was carried out across a short spatial gradient encompassing lagoon, estuarine, and marine habitats. This comprehensive approach aimed to elucidate the invasive success of the blue crab. Our findings shows that the species resulted widely distributed across all habitat types, with significant differences among stations, seasons, and sexes, with females being prevalent in higher salinity marine and outer lagoon waters during spawning season. These findings, along with the spatiotemporal analyses of the condition factor and the presence in the lagoon of various cohorts of juveniles over the year, highlight the completion of the complex life cycle of the blue crab on an extremely small spatial scale. Moreover, with an average of over 2 million eggs laid per female and a prolonged spawning season, the species reveals a robust reproductive potential, likely favoured by the short distance between mating and spawning habitats. In conclusion, the results of this study underscore the critical role of the short spatial environmental mosaic in facilitating the invasive success of *C. sapidus*, providing relevant data for managing this unprecedented demographic explosion.

Key words: Atlantic blue crab, fecundity, invasion, reproductive cycle, salinity gradient

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Introduction

The Atlantic blue crab *Callinectes sapidus* Rathbun, 1896 is a decapod crustacean of the Portunidae family (Hill et al. 1989), native to the western Atlantic coast, from Nova Scotia to Argentina (Mancinelli et al. 2017). Due to its characteristics that make it a very adaptable species when colonizing new areas (Epifanio 2019), *C. sapidus* is listed among the 100 worst invasive species in the Mediterranean (Streftaris and Zenetos 2006). It is a large-sized aggressive species, with high fecundity, rapid mobility, osmoregulation capacity, and strong tolerance to temperature variations: all characteristics that allow it to compete effectively for food and space (Hill et al. 1989; Gennaio et al. 2006; Nehring 2011; Epifanio 2019).

In Europe, the blue crab was first recorded in 1900 along the French coasts (Kampouris et al. 2020), while in the Mediterranean it was first officially documented in 1949 in Italy, along the coasts of the northern Adriatic (Mizzan 1993). Probably introduced several times through ship ballast water, the blue crab has been spreading to various European basins, including the Baltic (Czerniejewski et al. 2020) and the Black Sea (Kvach et al. 2025), and is now present in almost all Mediterranean countries (Nehring 2011; Mancinelli et al. 2017). It first successfully established in the Eastern Mediterranean Sea (e.g., Greece and Turkey; Perdikaris et al. 2016; Türeli et al. 2016; Kevrekidis and Antoniadou 2018; Öztürk et al. 2020; Kevrekidis et al. 2023), and only later in the western part of the basin (e.g., Southern Italy, Spain and France; Gennaio et al. 2006; López and Rodon 2018; Fuentes et al. 2019; Labrune et al. 2019). The expansion of the blue crab has then been rapidly proceeding along the Adriatic Sea (e.g., Italy, Albania, Croatia; Cilenti et al. 2015; Manfrin et al. 2015; Mancinelli et al. 2017; Milori et al. 2017; Glamuzina et al. 2023) and resulted in an unprecedented outbreak in the Northern Adriatic occurring since spring and summer 2023 (Azzurro et al. 2024; Chiesa et al. 2025). The exponential increase in abundance of the species is raising concerns about the impacts that it may have on local ecosystems and the fishing industry. *C. sapidus* is a keystone species in coastal ecosystems and is a very versatile predator, although it prefers bivalve molluscs and crustaceans (Hines 2007; Rady et al. 2018). The blue crab competes and preys on native fauna, compromising the survival of native species such as the Mediterranean green crab *Carcinus aestuarii* Nardo, 1847, threatened and probably already extirpated locally in some areas of Greece and Spain (López and Rodon 2018; Kampouris et al. 2019; Clavero et al. 2022). Moreover, the impact of the blue crab has also been recorded on relevant commercial molluscs such as the Common cockle *Cerastoderma edule* Linnaeus, 1758 at Ebro Delta (Spain, López and Rodon 2018) and Manila clam *Ruditapes philippinarum* A. Adams & Reeve, 1850 at Po Delta (Italy; Chiesa et al. 2025), with considerable economic impacts on the local economies. Small-scale fisheries targeting several local species have also been affected by the blue crab in invaded areas as the Ebro Delta (Clavero et al. 2022) and the Po Delta (Gavioli et al. 2025), with drastic abundance decreases observed for some species following the recent outbreak of the species. Moreover, the blue crab directly impacts some fishing gear, such as traditional fyke nets, which require constant maintenance with significant economic and time costs for retrieval and repair of the nets (Glamuzina et al. 2021).

Although the complete eradication of the species is unlikely due to its high adaptability and mobility (Garrido and De Basquiat 2023), investigating biological and ecological characteristics of *C. sapidus* in the new invaded areas is essential to better understand the reasons for the success of the species in the area and manage the invasion emergency. The blue crab has deeply been studied in its native distribution range, where its biology and ecology are extremely well known (see Newcombe 1945; Van Engel 1958; Millikin and Williams 1984; Perry and McIlwain 1986; Hill et al. 1989; Jivoff 1997; Turner et al. 2003; Hines 2003, 2007; Aguilar et al. 2005; Jivoff et al. 2007; Tilburg et al. 2008; Ramach et al. 2009; Epifanio 2019). However, the way invasive species react and adapt to newly invaded areas and proliferate can vary greatly from their spread areas.

Several factors can be hypothesized to have contributed to the outbreak of *C. sapidus* that occurred in the Northern Adriatic in 2023. Firstly, increased temperatures associated with climate change appear to favour the progressive expansion of the species to higher latitudes. Indeed, under various RCP scenarios, it has been predicted that in the near future *C. sapidus* will experience an increase in habitat suitability in the Northern Adriatic (Cavraro et al. 2022). Furthermore, high connectivity in the dispersal of blue crab larvae was observed along both the eastern and western Adriatic coasts (Marchessaux et al. 2023a). This is probably linked to the large-scale cyclonic meander circulation of this sea, characterized by a northerly flow along the eastern coast and a southerly return flow along the western coast (Orlic et al. 1992). Additionally, the Northern Adriatic is an area with exceptionally high trophic availability (Barausse et al. 2009), with the presence of numerous lagoon environments that maximize resource availability (Franzoi et al. 2010). These environments promote the proliferation of bivalve molluscs, supporting extensive clam farming and simultaneously providing abundant resources for the blue crab (Chiesa et al. 2025). Lastly, this type of environment, where river mouths, lagoons, and the sea interface over short distances, can provide the ideal conditions for the blue crab, as the salinity is a crucial parameter regulating the biological and reproductive cycles of the species (Van Engel 1958; Epifanio et al. 2019). Therefore, a short spatial salinity gradient could exceptionally increase the dispersal potential and invasiveness of *C. sapidus*, as it can find the perfect conditions for speeding up its life cycle. The occurrence of this phenomenon has also been suggested for another invaded area of the Mediterranean, the Thermaikos Gulf in Greece (Kevrekidis and Antoniadou 2018).

This study aims to investigate key aspects of the species' biology and ecology during its demographic outbreak in a Northern Adriatic area. We present an annual insight about *C. sapidus* across various habitat types (riverine estuary, lagoon and marine coast). The investigation was carried on simultaneously with the species demographic explosion in the area and we focused on: I) Spatial and temporal distribution to determine habitat preferences and year-round migration patterns. II) Main morphological relationships to study growth, weight gain and condition factor across stations and seasons. III) Size structure within lagoon sites using two fishing gears to identify crabs at various maturation stages. IV) Species fecundity by analysing the distribution and fertility of ovigerous females across stations and seasons. This comprehensive approach aimed to elucidate the invasive success of this allochthonous species in an area characterized by different habitats along a short spatial gradient.

Materials and methods

Study area

The present study was conducted in four locations near Chioggia (northeastern Italy), along a salinity gradient which extends from the outlet of the Brenta River to the Adriatic Sea, including the southern part of Venice lagoon (Figure 1). The northern Adriatic coast of Italy is characterized by the presence of many waterways that flow into the sea, creating a mosaic made of different environments such as riverine estuaries, lagoons and marine coastal habitats, close and connected to each other. The Venice lagoon is a shallow transitional water body, covering an area of about 550 km^2. It is the largest Italian lagoon, and it is connected to the sea through three large navigable inlets (Lido, Malamocco and Chioggia; Solidoro et al. 2010). The environmental complexity of this transitional water system, a

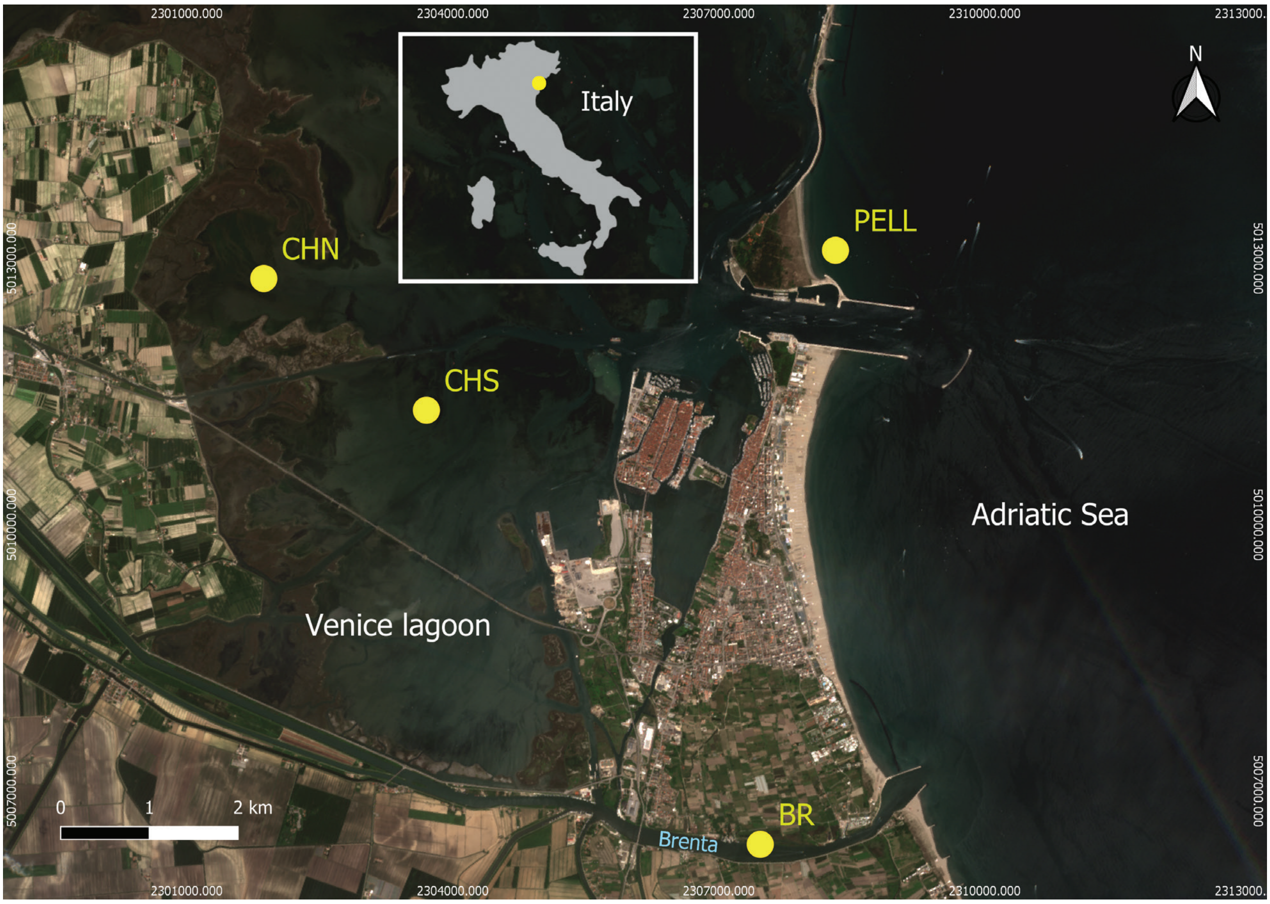

Figure 1. Map of sampling stations near Chioggia: CHN and CHS (Venice Lagoon), PELL (Adriatic coast), and BR (Brenta River mouth).

network of interconnected habitats such as saltmarshes, channels and shallow bottom areas, generates a great variety of ecological niches and plenty of resources to be used by a wide number of species (Molinaroli et al. 2009; Solidoro et al. 2010). The diversity in morphological and environmental features ensures the importance of the Venice lagoon for its multi-functional role, being exploited by resident and marine migrant nekton species as feeding, shelter, reproductive, and nursery grounds (Franco et al. 2006; Franzoi et al. 2010; Scapin et al. 2022). Just a few kilometres south of the Chioggia inlet, the Brenta River outflows into the Adriatic Sea (Figure 1) with an average annual discharge of 65 m^3/s (ARPAV 2023).

In the northwestern Adriatic, salinity gradients occur on an extremely small spatial scale, around two orders of magnitude smaller than in Atlantic environments such as the Chesapeake Bay, where the blue crab is most prevalent and females undergo post-mating migrations for 150–200 km (Turner et al. 2003; Aguilar et al. 2005). To study the effect of the steep salinity gradients typical of the area, four sampling stations were selected near Chioggia to represent distinct environmental characteristics, all located between 2 and 9 km of each other and include: two lagoon stations, CHN (northern Chioggia, at 7 km from the sea, 45°13'58.06"N, 12°13'11.35"E) and CHS (southern Chioggia, at 5 km from the sea, 45°13'21.15"N, 12°14'21.25"E); a coastal marine station, PELL (Pellestrina, 45°14'13.00"N, 12°18'32.21"E) and a station at the Brenta River mouth, BR (Brenta, at 2 km from the sea, 45°10'33.90"N, 12°17'27.15"E).

The two lagoon stations exhibit salinity levels that generally range from polyhaline to euhaline, and partial macrophyte cover. Despite their geographical proximity, CHN is more confined by saltmarshes and undergoes a minor influence from both freshwater and saltwater inputs into the lagoon. Conversely, CHS is more exposed to freshwater inputs from a large canal (Canale Novissimo) and to seawater inputs from tidal flow through Chioggia inlet. PELL, a marine site, is characterized by higher and more stable salinities and presents a bare sandy substrate. BR, located at the Brenta river mouth, typically presents oligohaline waters and a bare muddy substrate. However, at this station, salinity undergoes significant fluctuations, primarily driven by meteorological conditions. The distribution of the sampling stations was arranged following the salinity gradient on a spatial transect of only a few kilometres.

Sampling methods

Sampling activities using wire crab pots were carried out from June 2023 to June 2024. A total of 14 sampling events were performed at each of the four sampling stations during this period (9 in 2023 and 5 in 2024). During each sampling event, six wire pots of two different types (3 pots per type) were deployed at each site and retrieved 24 hours later. The first type measured 52.5×42.5×22.5 cm (L×W×H; 4×4 cm square mesh) and featured four entry funnels, no internal chambers, and three circular escape vents (6 cm diameter) for non-target species. The second type measured 40×61×40 cm (L×W×H; 5×5 cm square mesh) and was equipped with four entry funnels, an internal chamber, and no escape vents. All wire pots were baited with low-value fish species, primarily grey mullets and sardines. One sampling event in 2023 was not conducted at the PELL due to adverse sea conditions. Sampling using the fyke nets (locally named “tresse con cogolli”, a traditional fishing gear with a mesh size of 0.6 cm (Zucchetta et al. 2016; Scapin et al. 2022) was also conducted for a total of 6 sampling events from October 2023 to June 2024. The nets were positioned within the lagoon, in the area between sites CHN and CHS. During each sampling event, 20 “bertovelli” were inspected from the numerous ones actively used by local fishermen in their routine fishing operations. Environmental parameters were recorded at each sampling event using a multiparameter probe (Hanna Instrument 9829). These included: temperature (± 0.01°C), pH (± 0.01), salinity (± 0.01 PSU), turbidity (± 0.1 FNU), and dissolved oxygen (± 0.1% saturation).

Laboratory analyses

All the crabs sampled with pots and a sub-sample of crabs (representative of the sex-ratio and size distribution) collected during each fyke nets check were culled using a two-step ethical protocol as described in de Souza Valente (2022) and analysed in the laboratory. Each specimen was identified to species level and sexed based on Rathbun 1930, weighed (W) with a technical balance (± 0.01 g) and measured using a standard Vernier calliper (± 0.1 mm) according to the method in Fazhan et al. (2021) adapted for blue crab as in Figure 2. Measurements of blue crab’s carapace taken include Total Carapace Width (TCW), Carapace Width at the basis of spines (CW) and Carapace Length (CL). A total of 1171 crabs were analysed.

The methodology for fertility estimates used was adapted from Chenery (2002) and Rodrigues et al. (2011). The egg masses or “sponges” were removed from ovigerous females, taking care to remove the crab’s pleopods, and weighed. The total number of eggs was estimated from a subsample of approximately 50–100 mg, the exact weight of which was measured using an analytical balance (± 0.001 g). This subsample was then spread as homogeneously as possible in a gridded Petri dish (10 mm × 10 mm). Using a stereomicroscope (Nikon SMZ1270, with

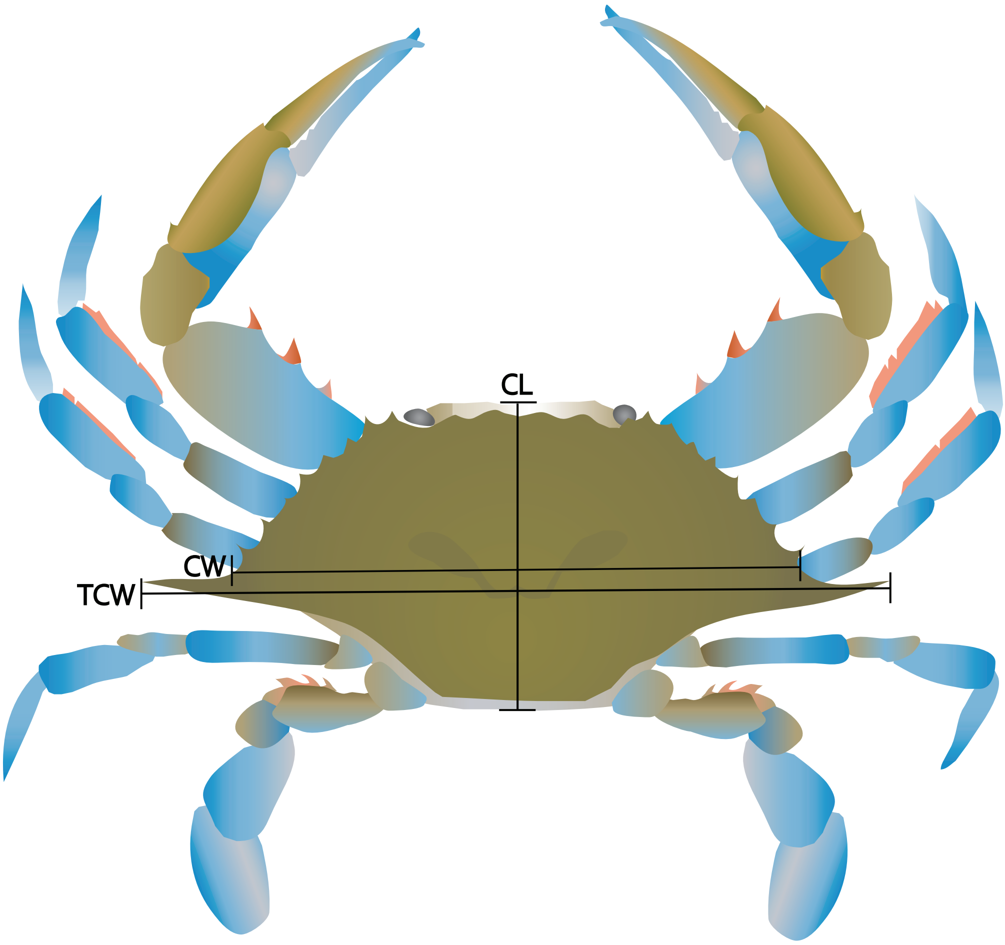

Figure 2. Measurement of blue crab's carapace: Total Carapace Width (TCW), Carapace Width at the basis of spines (CW) and Carapace Length (CL). Source: ian.umces.edu/media-library.

magnification ranging from ×6.3 to ×80), the number of eggs was counted in 30 cells of the gridded Petri dish. From this count, the total number of eggs in the subsample was estimated, from which the total number of eggs in the sample was then extrapolated. Additionally, the diameters of 30 randomly selected eggs from each egg mass were measured (± 0.01 mm) using a digital controller (Nikon DS-L3 with the attached camera Nikon DS-Fi2). The egg masses were subsequently classified into maturation stages based on colour observation and stereomicroscopic analysis. Three stages were identified: 1) Early maturation stage (yellow-light orange colour); 2) Intermediate maturation stage (dark orange-brown colour); 3) Pre-hatching (dark brown-black colour) (Severino-Rodrigues et al. 2013; Kelly and Taylor 2018). A total of 86 egg masses were analysed.

Data analyses

The distribution of crabs captured with wire pots over stations and seasons by sex was analysed by performing a GLM (negative binomial family; significant $p < 0.05$; n = 660). Post hoc exploring relevant interactions between the three factors was conducted through Estimated Marginal Means (EMMs) with False Discovery Rate (FDR) adjustment method (significance at $p < 0.05$). To perform graphical representation and statistical analysis, data were organized into seasonal periods, broadly defined as: Summer (Jun-Aug 2023), Autumn (Sep-Dec 2023), Winter (Feb-Mar 2024), and Spring (Apr-Jun 2024).

The relationships between the main morphological parameters and the total weight of all sampled crabs (wire pots and fyke nets) were compared using regression models, with log-transformed variables. The following comparisons were performed (W-CL; W-CW; W-TCW; TCW-CW; TCW-CL) separately for males and females. Specimens lacking one or both chelae were excluded from the regressions involving weight and eggs weight was removed in ovigerous females. The slope of the linear relationship (parameter ‘b’) was used to determine isometry ($b = 1$ or $b = 3$) and allometry ($b \neq 1$ or $b \neq 3$) by means of linear F-test (significant allometry at $p < 0.05$) (Hartnoll 1978). Moreover, ‘b’ values were compared between sexes through ANCOVA analysis in order to evaluate sexual dimorphism in growth. The condition of adult crabs over stations and seasons by sex was investigated using the relative condition factor (Kn) (Blackwell et al. 2000). The relative condition factor K_n was determined using the formula $K_n = W/W'$, where W' represents the expected weigh derived from the TCW-W relationship for a specimen of its size (TCW). Natural logarithm-transformed data were fitted to the linear equation $\ln(W) = m \ln(TCW) + \ln(q)$. Two separate linear equations were fitted for females and males and then used to estimate the expected weight, as the slopes of the two regression lines were found to be statistically different (ANCOVA, $p < 0.001$). For the calculation of K_n, specimens lacking one or both chelae were excluded. Missing TCW data due to broken spines were estimated using regression based on CW. The factor was calculated solely for adult crabs collected with wire pots and data organized into seasonal periods as previously reported. Statistical differences of K_n over stations and seasons by sex were tested by performing a GLM (gamma family; significant $p < 0.05$; $n = 701$). Post hoc exploring all interactions between the three factors was conducted through Estimated Marginal Means (EMMs) with False Discovery Rate (FDR) adjustment method (significance at $p < 0.05$).

Population size distribution was seasonally calculated for females and males using TCW with 1 cm frequency and distinguishing fyke nets data from wire pots data, as the latter only capture adult crabs. Moreover, only data from the lagoon stations were included, as sampling data with both gear types were available. No statistical analysis was performed as the fyke net data presents a polymodal distribution that could not be fitted by a suitable model.

Spatial and temporal distribution of ovigerous females was tested using a binomial presence/absence GLM (significance at $p < 0.05$; $n = 330$). The odds ratio was calculated, and Tukey HSD post hoc for pairwise comparisons was performed (significance at $p < 0.05$). The tests included solely data of crabs collected by wire pots and data organized into seasonal periods as previously reported. As ovigerous females were only sampled from April to September, for further investigations three periods were identified within the egg-laying season: 1 – spring (April and May; $n = 33$); 2 – early summer (June and July; $n = 27$); 3 – late summer (August and September; $n = 25$). A total of 86 ovigerous females were analysed, but one was excluded from statistical analyses as an outlier using the Interquartile Range (IQR) Method. The estimated egg numbers were analysed as a function of sampling station, period, and maturation stage by means of One-Way ANOVA and Tukey post hoc test in case of significant differences ($p < 0.05$; $n = 85$). The linear equations, the adjusted coefficient of determination (Adjusted R^2) and the p-value (significance at $p < 0.05$) were obtained. Slopes comparisons were tested by means of ANCOVA analysis (significance at $p < 0.05$).

Statistical analyses were performed and graphics plotted using R (v 4.5.0; R Core Team 2025) within RStudio (v 2024.12.1+563; Posit team 2025). The most appropriate model was selected for each analysis and assumptions were tested using DHARMa library (v 0.4.7; Hartig 2024), including residual distributions, uniformity, dispersion and outlier tests (Suppl. material 3: figure S1).

Results

Environmental characterization of stations

The seasonal and yearly average values of water environmental parameters, detected at each sampling station, are shown in Table 1. BR showed overall lower temperatures, pH and salinity alongside higher turbidity with notable variability in salinity and turbidity, compared to other stations. The two lagoon stations, while displaying similar parameter values with yearly average salinity above 30 PSU, saw CHN exhibit greater variability in dissolved oxygen and turbidity. PELL recorded the highest salinity and dissolved oxygen, and the lowest turbidity, generally showing low variability across most of the parameters. Seasonal variations show a clear pattern only for temperature, with summer peak and winter minimum. Salinity was lower in spring in all the stations. Dissolved oxygen was lower in summer in all the stations except PELL. Turbidity and pH did not show any clear seasonal variation.

Table 1. Seasonal and yearly average (± SD) values of water environmental parameters detected per sampling station (BR, CHN, CHS, PELL): Temperature (°C); ph; Salinity (PSU); Dissolved Oxygen (%); Turbidity (FNU).

Station	Season	Temp. (°C)	pH	Sal. (PSU)	DO (%)	Turb. (FNU)
BR	Summer	23.15 ± 2.86	7.83 ± 0.10	3.11 ± 3.61	85.01 ± 0.46	20.08 ± 6.86
	Autumn	13.56 ± 8.17	8.04 ± 0.20	15.42 ± 15.46	104.19 ± 13.18	68.87 ± 97.92
	Winter	11.74 ± 1.76	8.02 ± 0.11	2.15 ± 0.91	106.38 ± 6.32	20.11 ± 0.30
	Spring	17.76 ± 2.76	7.83 ± 0.45	0.70 ± 0.80	116.39 ± 1.29	52.80 ± 59.95
	Full year	**16.37 ± 6.00**	**7.92 ± 0.25**	**5.64 ± 9.54**	**102.32 ± 14.42**	**42.32 ± 56.01**
CHN	Summer	23.54 ± 1.60	8.38 ± 0.35	32.85 ± 2.20	74.35 ± 15.66	3.39 ± 2.36
	Autumn	17.57 ± 8.13	8.25 ± 0.20	31.60 ± 2.47	105.37 ± 18.50	1.78 ± 1.09
	Winter	12.22 ± 1.35	8.47 ± 0.07	29.98 ± 3.87	109.74 ± 7.11	3.40 ± 2.40
	Spring	21.98 ± 4.34	8.50 ± 0.30	26.21 ± 0.59	108.12 ± 51.56	25.90 ± 41.98
	Full year	**19.88 ± 5.99**	**8.38 ± 0.26**	**30.66 ± 3.29**	**95.50 ± 28.94**	**7.76 ± 19.26**
CHS	Summer	23.96 ± 1.47	8.39 ± 0.38	30.77 ± 5.46	81.92 ± 9.25	11.52 ± 6.96
	Autumn	17.95 ± 7.95	8.30 ± 0.16	32.94 ± 2.08	104.88 ± 12.98	2.52 ± 0.86
	Winter	12.14 ± 1.34	8.43 ± 0.08	31.25 ± 3.22	110.17 ± 5.64	3.91 ± 1.17
	Spring	21.72 ± 4.45	8.43 ± 0.08	24.87 ± 3.98	102.20 ± 11.97	6.92 ± 3.81
	Full year	**20.07 ± 6.00**	**8.38 ± 0.24**	**30.19 ± 4.75**	**96.86 ± 15.14**	**6.87 ± 5.74**
PELL	Summer	27.11 ± 2.21	8.14 ± 0.22	33.45 ± 2.16	122.01 ± 7.02	0.37 ± 0.36
	Autumn	19.56 ± 6.07	8.35 ± 0.05	35.10 ± 1.56	112.65 ± 5.56	1.65 ± 1.75
	Winter	11.92 ± 1.70	8.37 ± 0.13	34.21 ± 0.54	133.17 ± 7.88	1.52 ± 0.49
	Spring	21.37 ± 2.48	8.52 ± 0.02	29.31 ± 0.83	146.12 ± 6.33	2.39 ± 2.08
	Full year	**20.54 ± 6.17**	**8.34 ± 0.15**	**33.25 ± 2.68**	**123.99 ± 13.90**	**1.50 ± 1.52**

Spatial and seasonal distribution

Spatial and seasonal distribution of the blue crab, assessed through catch per unit effort (CPUE), demonstrated extreme variability and complexity as shown in Figure 3. Both sexes were present at every station and in every season. A Generalized Linear Model (GLM), using a negative binomial family revealed significant differences when considering three-way interactions between stations, seasons and sexes ($p < 0.001$). These findings indicate that variations in crab distribution between

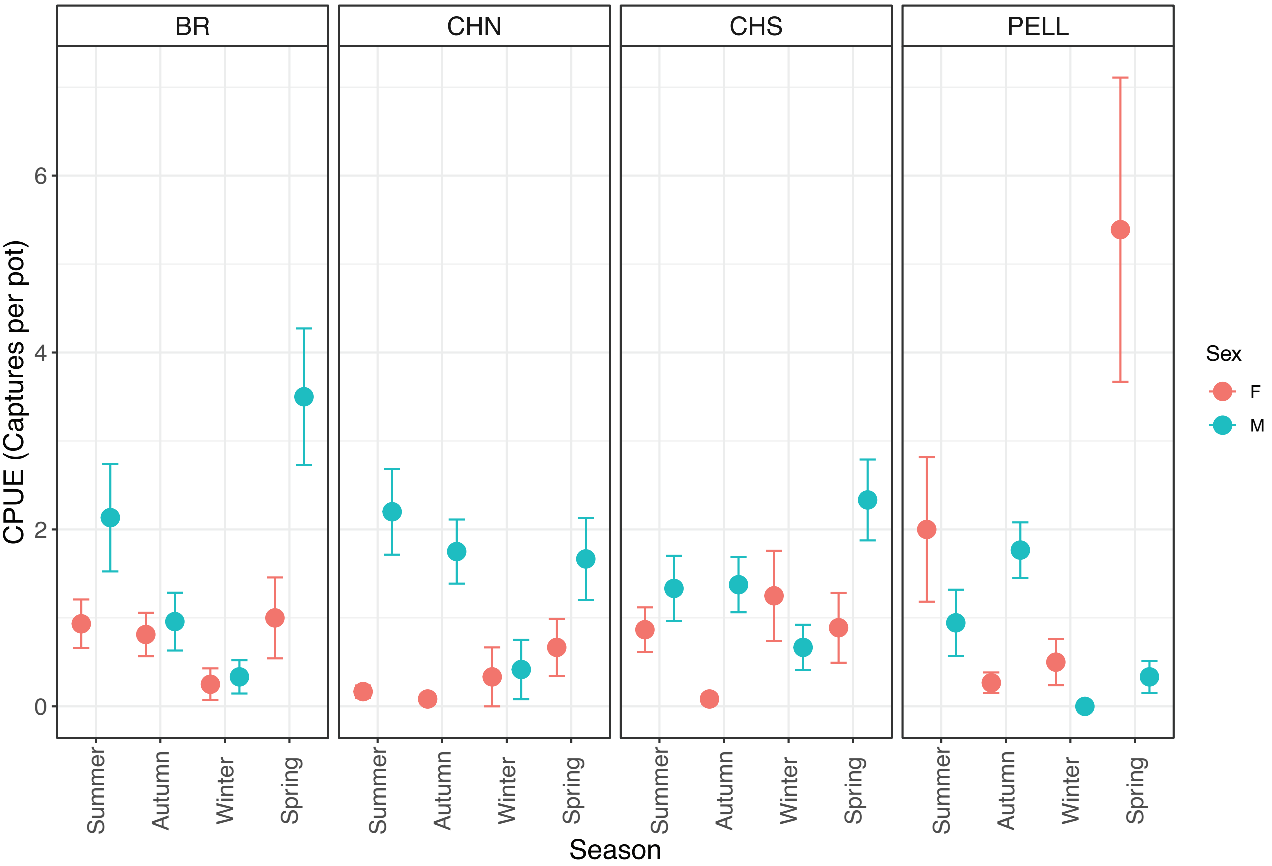

Figure 3. CPUE (mean ± SE) of male and female crabs per station (BR, CHN, CHS, PELL) and per season: summer (n pots = 30), autumn (n = 24), winter (n = 12), spring (n = 18).

males and females are dependent on the season, and this seasonal-sex pattern itself varies among stations. Significant seasonal variations, detected through post hoc analysis showed that females at PELL were more abundant in spring compared to autumn ($p < 0.001$) and winter ($p = 0.006$) and in summer compared to autumn ($p = 0.008$), while males at BR were more abundant in spring compared to winter ($p = 0.024$). Station-level significant differences showed that females in spring were more abundant at PELL compared to all the other stations ($p < 0.05$) and in summer at PELL compared to CHN ($p = 0.003$), while males in spring were less abundant at PELL compared to both BR ($p = 0.004$) and CHS ($p = 0.039$). Moreover, many significant differences between sexes were detected, most of the time with males more abundant than females. Specifically, males were more abundant in autumn at all stations ($p < 0.05$) and in summer at CHN ($p < 0.001$). Females were only significantly more abundant than males in spring at PELL ($p < 0.001$).

Morphological relationships and condition factor

The outputs of the relationships between the main morphological parameters and the total weight of crabs (W-CL; W-CW; W-TCW; TCW-CW; TCW-CL) are summarized and reported in Suppl. material 1: table S1 separately for female and male crabs. Adjusted R^2 and p-values exhibit a strong significance between all the relationships investigated. For each pair of variables, the comparison of the slope of the regression lines for females and males showed significant differences (ANCOVA, $p < 0.001$; Suppl. material 1: table S1). The relations between crab weight W and carapace measures always exhibit negative allometry in females (b < 3; F test, $p < 0.05$), while in males they either exhibit positive allometry for W-CW and W-CL relations (b > 3; $p < 0.05$) or isometry for W-TCW relation (b = 3; $p > 0.05$). Instead, TCW-CW and TCW-CL exhibit positive allometry in females (b > 1; $p < 0.05$) and isometry in males (b = 1; $p > 0.05$).

The relative condition factor (K_n) was calculated based on the regression lines for females, $y = 2.249x - 1.0093$ (adjusted $R^2 = 0.7944$, $p < 0.001$), and for males, $y = 2.797x - 2.130$ (adjusted $R^2 = 0.8334$, $p < 0.001$) (Figure 4). The two regression lines exhibited significantly different slopes (ANCOVA; $p < 0.001$), with adult males showing a greater increase in weight compared to females for a given increase in carapace width.

The results of the relative condition factor (K_n) for female and male crabs are shown in Figure 5, and their complexity was explored with a gamma family GLM. The three-way interaction between station, season, and sex implies that the combined influence of station and season on K_n is distinct for each sex ($p = 0.002$). Post hoc analysis of three-way interaction revealed many significant differences, mostly among stations. Specifically, males exhibited a higher K_n at both lagoon stations compared to BR in all seasons ($p < 0.05$), while at PELL K_n was only significantly lower than CHN in autumn ($p = 0.03$) and never higher compared to BR ($p > 0.05$), revealing a clear pattern with K_n being higher at CHN and CHS, intermediate at PELL and lower at BR. Consistently, females did also often exhibit significantly higher K_n at lagoon stations compared to BR ($p < 0.05$), while in spring K_n was higher at PELL compared to both CHS ($p = 0.026$) and BR ($p < 0.001$), showing a more complex pattern compared to males. Differences at seasonal and sex level were only seldomly significant. Specifically, K_n was only higher in summer compared to spring for females at CHS ($p = 0.043$) and for males at BR ($p = 0.042$). Sex differences only detected higher K_n for males compared to females in spring at CHN ($p = 0.029$) and CHS ($p = 0.013$).

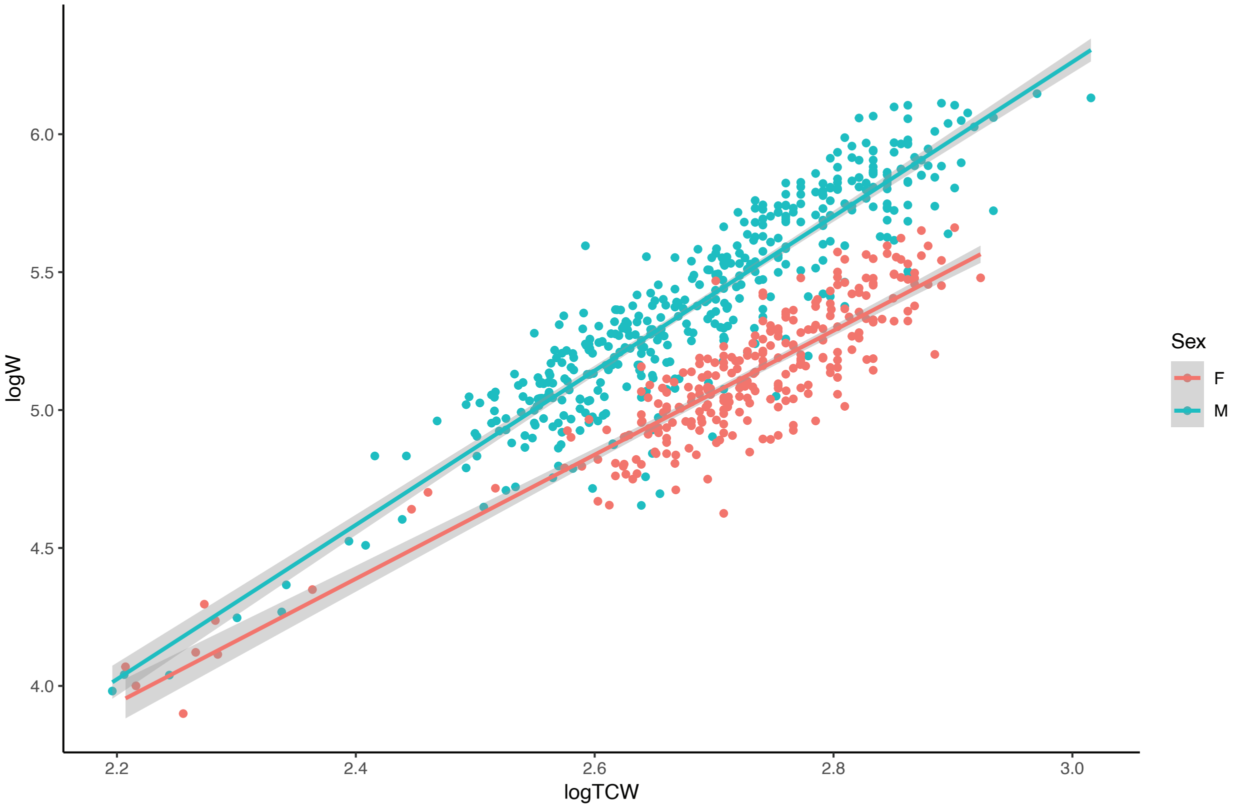

Figure 4. Regression lines between the logarithms of total carapace width (TCW) and weight (W) for male (blue) and female (red) crabs.

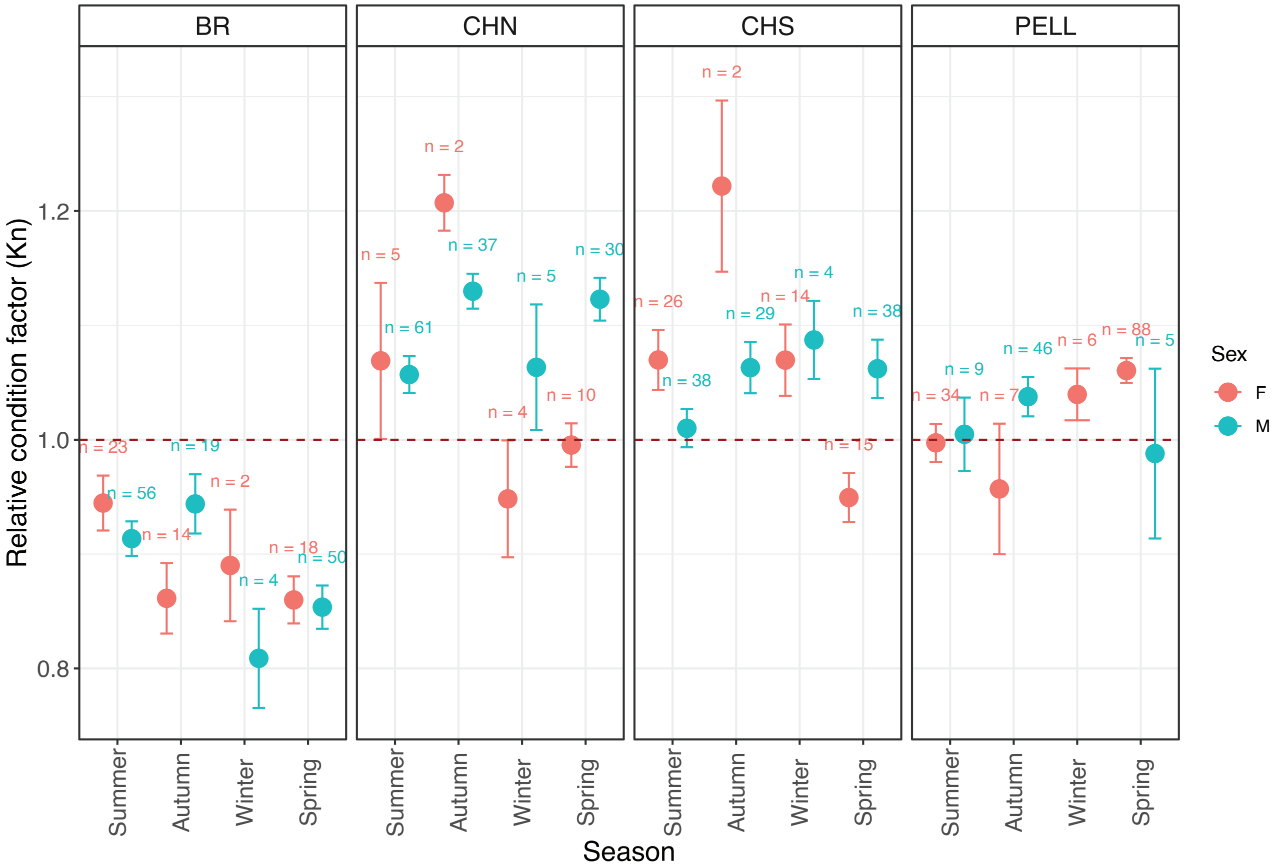

Figure 5. Relative condition factor Kn (mean ± SE) of male and female crabs per station (BR, CHN, CHS, PELL) and per season (summer, autumn, winter, spring). The number of analysed crabs are reported as "*n*".

Size distribution

Population size structure analysis (Figure 6; Suppl. material 2: table S2) shows that wire pots (large mesh size) only capture adult crabs (min TCW = 9.71 cm), with females always exhibiting high abundance around 15 cm TCW, and males progressively increasing their abundance peaks from 13–14 cm in summer 2023 to 17 cm in spring 2024. Indeed, the overall mean TCW of crabs captured with wire pots increased during the year-round sampling period, from 14.22 ± 1.44 cm of summer 2023 to 16.28 ± 1.53 cm of spring 2024. Conversely, fyke nets (fine mesh size) deployed in the same area and period (excluding summer) also caught juveniles of various sizes, with minimum TCW of 2.47 cm. The polymodal size structure of fyke nets highlights multiple crab recruitment events in lagoon waters throughout the year, probably occurring from spring to autumn.

Spawning and fecundity

The distribution of ovigerous females per station and season is shown in Figure 7, as the percentage of presence or absence in the crab wire pots. The earliest ovigerous female was sampled at PELL in mid-April, while the latest were sampled at CHS and PELL in mid-September. Significant differences were observed in the presence or absence of ovigerous females between seasons (GLM, binomial family, $p < 0.001$). Ovigerous females were primarily sampled during spring and summer with no significant differences ($p = 0.949$). Both spring and summer exhibit significant differences ($p = 0.004$; $p = 0.010$) and markedly greater odd presence

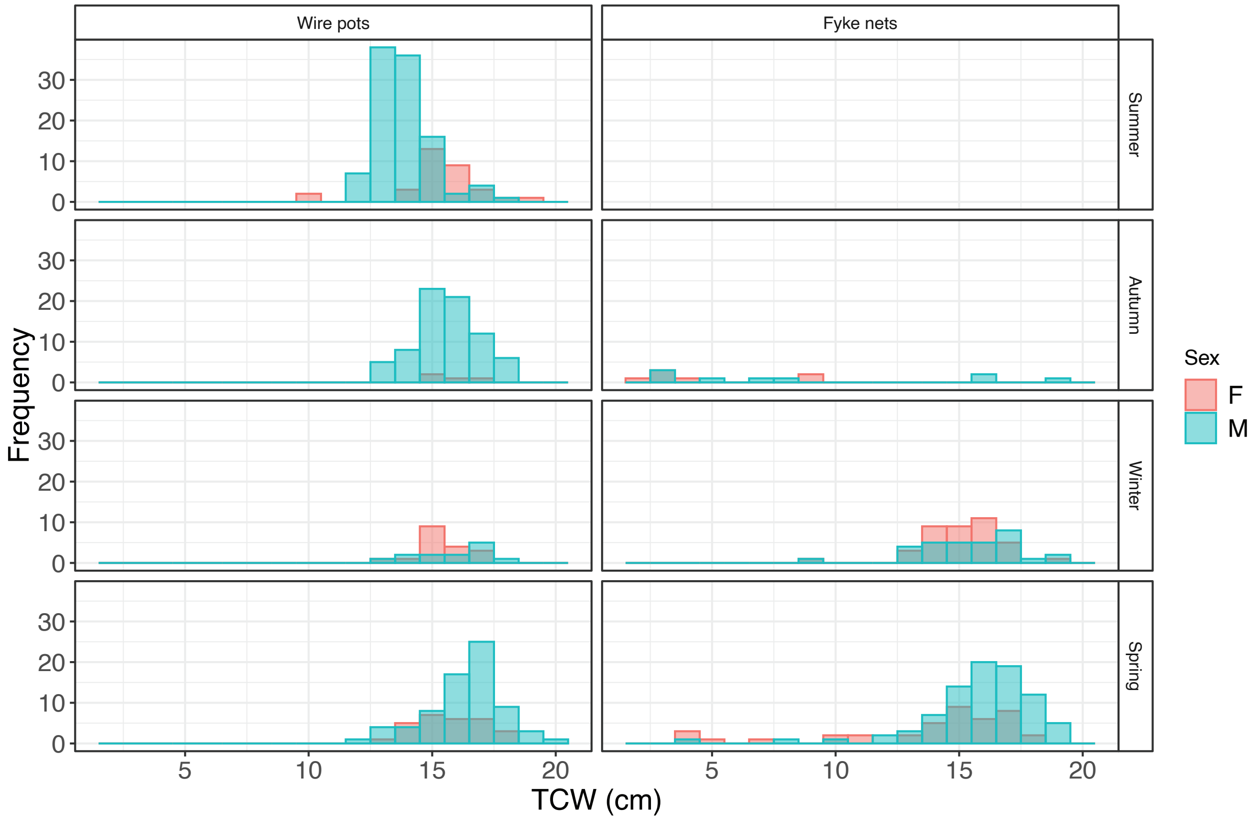

Figure 6. Size structure of crabs (separated by males and females) per season (summer, autumn, winter, spring) and gear type (crab wire pots and fyke nets).

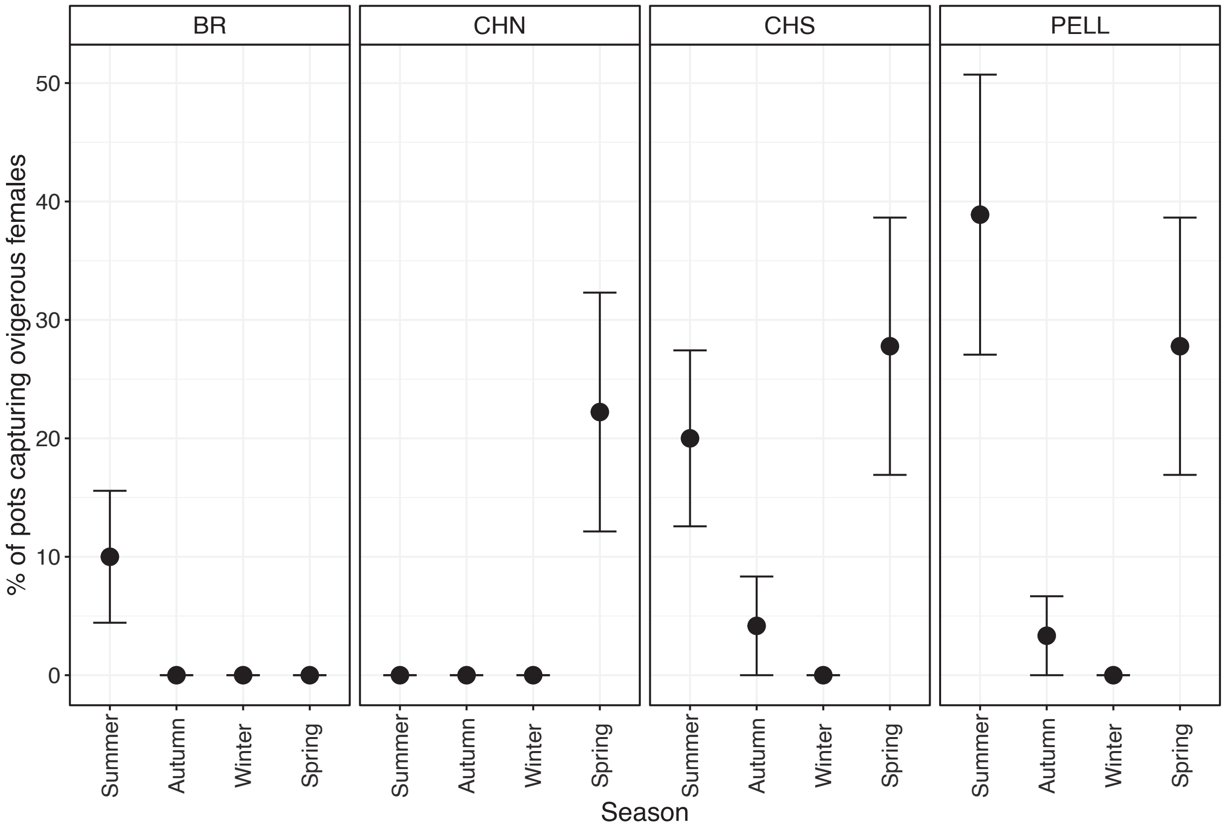

Figure 7. Percentage of pots where ovigerous females were sampled (mean ± SE) per station (BR, CHN, CHS, PELL) and per season: summer (n pots = 30), autumn (n = 24), winter (n = 12), spring (n = 18).

compared to autumn. No ovigerous female was sampled during winter. Significant differences were also observed in the presence or absence of ovigerous females across stations (p = 0.005), with PELL showing significant differences with BR (Tukey HSD p = 0.017) and CHN (p = 0.030). CHS showed only slight but not significant differences with BR (p = 0.090) and CHN (p = 0.160). No significant differences were detected between PELL and CHS (p = 0.800) and between BR and CHN (p = 0.980). No evidence of a significant interaction between station and season was detected by the model, suggesting that the effects of station and season on the presence of ovigerous females are largely independent of each other.

The ovigerous females weight ranged from 112.99 g (12.51 TCW cm) to 308.50 g (17.80 TCW cm). The egg mass weight wet ranged from 10.16 to 55.50 g (average 30.27 ± 9.12 g), representing an average of 15.16 ± 2.69% of the total female body wet weight. The number of estimated eggs ranged from 518,717 to 4,106,743 (average 2,072,450 ± 745,464), but a high of 5,982,200 was recorded and excluded from the analyses as outlier. The average egg diameter of each egg mass ranged from 217.3 to 310.3 μm (average 251.4 ± 17.6 μm). No significant relationship was found between estimated egg numbers and the three periods within the reproduction season (spring, early summer and late summer) (One-Way ANOVA, p = 0.800) (Figure 8A, Table 2) or between estimated egg numbers and sampling stations (One-Way ANOVA, p = 0.416). Conversely, a significant correlation was detected between estimated egg number and the maturation stage (p = 0.006) (Figure 8B, Table 2), with Tukey post hoc test showing significant difference between early maturation and pre-hatching stages (p = 0.005). The average number of estimated eggs in the pre-hatching stage was 30.19% lower than in the early maturation stage. The average egg mass weight (g), the estimated egg number and the egg diameter (μm) per maturation stage are shown in Table 1. Egg diameter did also show a significant dependence on the maturation stage (One-Way ANOVA, $p < 0.001$), with significant differences detected by Tukey post hoc test for all pairwise ($p < 0.05$).

Relations between the egg mass weight (g), female crab weight (g) and estimated egg number were also explored. Results showed a positive correlation between female weight (W) and the egg mass weight (EggW), following the equation: EggW = 0.1633 × W – 2.1937, with adjusted R^2 = 0.6768 and $p < 0.001$ (Figure 9A).

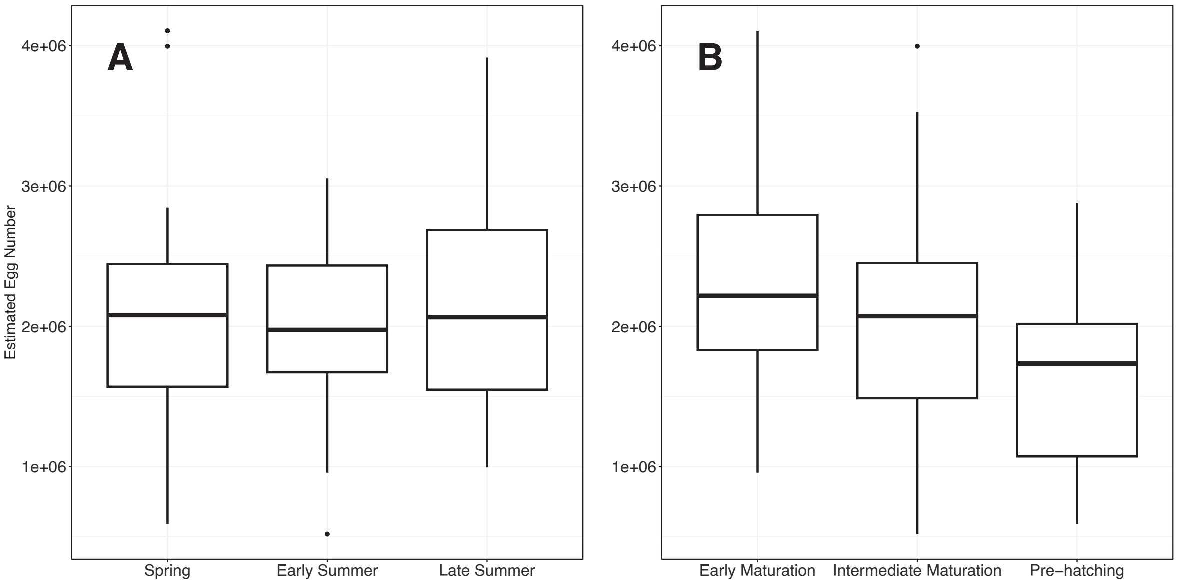

Figure 8. Boxplot of estimated number of eggs per period (**A**) and develop stage (**B**). Maximum, minimum and median values are shown for each sampling site; boxes represent first and third quartiles.

Table 2. Average (± SD) egg mass weight (g) estimated egg number and egg diameter (µm) per maturation stage (early, intermediate and pre-hatching) and in total. The number of analysed crabs is also reported (n).

Eggs Maturation Stage	n	Egg Mass Weight (g)	Estimated Egg Number	Egg Diameter (µm)
Early	33	31.08 ± 7.61	2,330,196 ± 735,218	240.0 ± 11.7
Intermediate	36	30.83 ± 8.96	2,034,355 ± 707,586	254.2 ± 14.9
Pre-hatching	16	27.31 ± 11.99	1,626,563 ± 654,900	268.6 ± 17.8
Total	**85**	**30.27 ± 9.12**	**2,072,450 ± 745,464**	**251.4 ± 17.6**

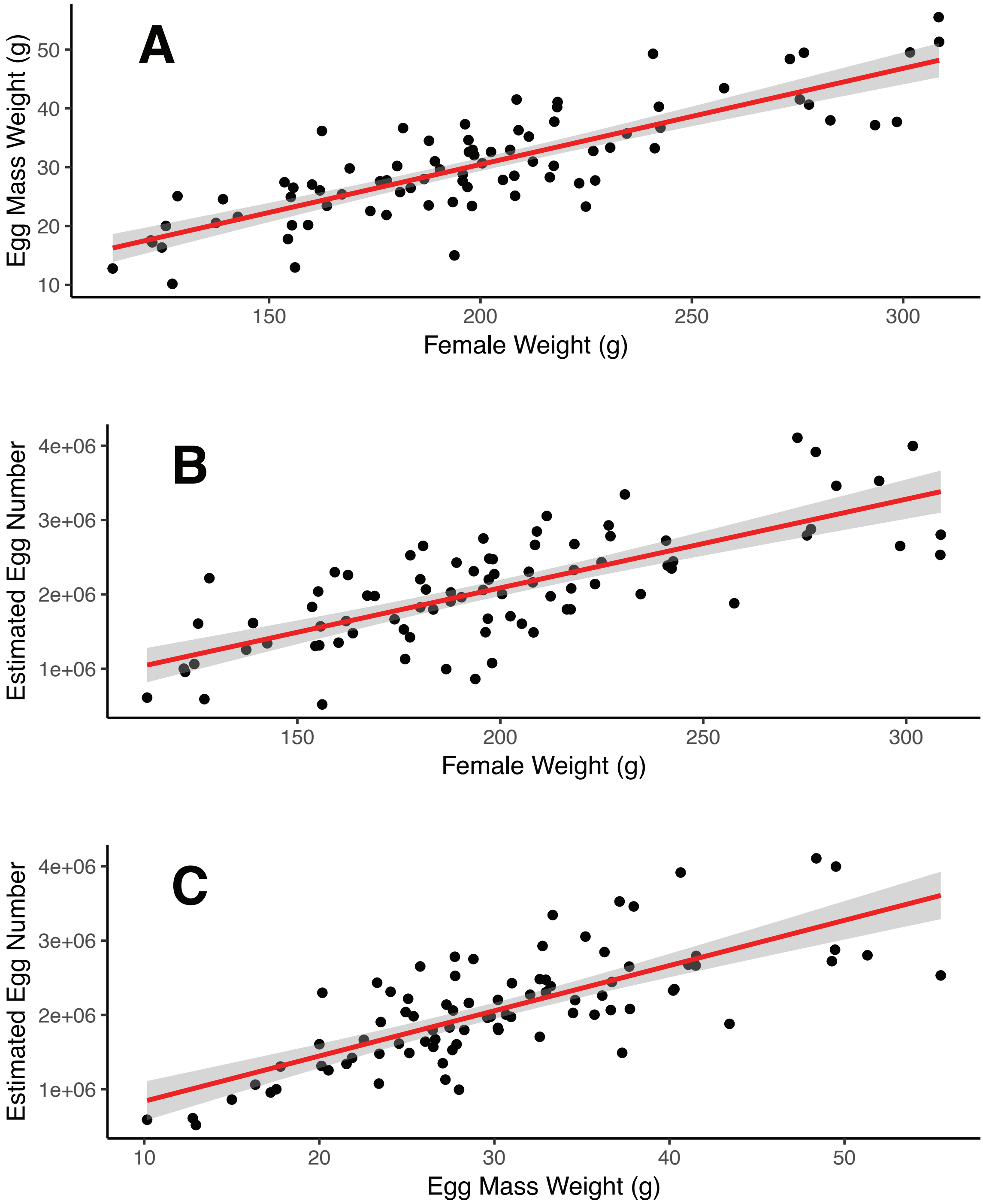

Figure 9. Regression lines between **A)** crab weight (g) and egg mass weight (g); **B)** crab weight (g) and estimated egg number; **C)** egg mass weight (g) and estimated egg number.

Results also showed a positive correlation between female weight (W) and the estimated egg number (EggN) following the equation: EggN = 11939 × W – 300846 with adjusted $R^2 = 0.5393$ and $p < 0.001$ (Figure 9B). Lastly, a positive correlation was also detected between egg mass weight (EggW) and the estimated egg number (EggN), following the equation: EggN = 60859 × EggW + 230450, with adjusted $R^2 = 0.549$ and $p < 0.001$ (Figure 9C).

Discussion

Spreading and distribution

Data of abundance and distribution of *C. sapidus* in four distinct aquatic habitats (two brackish, one freshwater and one coastal marine) in the area of Chioggia highlighted the magnitude of the outbreak of the species that occurred during spring and summer 2023, and its rapid and successful establishment. The blue crab was indeed found to be abundantly present in all the aquatic environments where samplings were carried out. The high significance of the three-way interaction (station:season:sex) highlights the complex distribution pattern of the species in an area where different aquatic habitats are present nearby and deeply connected between each other, showing that males and females have different space-time dynamic in the habitat use. The overall greater abundance of male specimens in the riverine station confirms their preference for lower salinity waters (Hines et al. 1987; Steele and Bert 1994). On the contrary, the greater abundance of females in marine environments, particularly during spring and summer, reflects the necessity of spawning eggs at higher salinities to ensure larval development (Van Engel 1958; Perry and McIlwain 1986; Hines 2003). The remarkably higher probability of encountering ovigerous females in the marine and in the outer lagoon stations compared to the riverine and the more confined lagoon stations detected in our study is a further confirmation of the occurrence of female's migration to water with higher salinity for egg laying, as also supported by the finding of many seasonal significant variations of CPUE between stations for females. Understanding this aspect of the blue crab's life cycle, including the periods and sites of mating and females' migration, may prove fundamental for species management via targeted, intense, and localized fishing, such as at river estuaries (Cilenti et al. 2016). Our findings about the distribution pattern of male and female crabs are consistent with the findings of other studies in newly invaded areas in the Mediterranean Sea (Glamuzina et al. 2021, 2023; Kevrekidis et al. 2023; Marchessaux et al. 2024). Nevertheless, the presence of specimens of both sexes in all stations highlights the species' high mobility and remarkable adaptability to diverse abiotic conditions (Gennaio et al. 2006; Nehring 2011). Moreover, it confirms that within our study area, the blue crab can find the habitats suitable to all stages of its life cycle. Furthermore, the close proximity of all these environments suggests this is a highly favourable area where to speed up the life cycle and increase fitness, enhancing a rapid and extensive expansion of the species (Mancinelli et al. 2017). This was also suggested for the Thermaikos Gulf in Greece (Kevrekidis and Antoniadou 2018). The short "river to sea" gradient represents a clear advantage compared to its native range where environments with all these different characteristics could only be found at long distances. For instance, in the Chesapeake Bay, females must undertake long migrations up to 200 km to brood eggs in the sea, which might only happen the year after mating (Turner et al. 2003; Aguilar et al. 2005; Epifanio 2019). On the contrary, in our study area, it is likely that most females can brood eggs the same year of mating, without the need of overwintering during migration from estuaries to the sea due to the very short distances. Moreover, the capture of juvenile individuals with fyke nets set within the lagoon, suggest that in this area the blue crab could also find suitable nursery habitats for the young crabs, as also stated by Lipcius et al. (2005) and Epifanio et al. (2019) about transitional waters. Indeed, these environments comprise numerous distinct habitats and ecological niches rich in resources and shelters (Franco et al. 2006; Franzoi et al. 2010; Scapin et al. 2022).

Condition factor

Although the blue crab was found to be abundantly present all over the study area, analysis of the relative condition factor (K_n) reveals significant differences among specimens captured in different stations and seasons. The station has a strong overall effect, as both males and females captured at the riverine site exhibit a poorer condition compared to all other stations. Despite the blue crab is slightly more abundant at the riverine site, the lower K_n might be caused by the high energy consumption for osmoregulation in a oligohaline environment (Tan and Van Engel 1966) or due to the lack of their favourite food source, bivalve molluscs (Hines 2007; Rady et al. 2018), abundant in lagoon and marine coastal habitats (Chiesa et al. 2025). The influence of seasons on K_n turned out to be lower but still significant when related to the other factors. Specifically, in spring, females were in better conditions at sea compared to most of the other stations, possibly indicating that females who had accumulated more energy had already migrated to sea for reproduction (Aguilar et al. 2005; Epifanio 2019). Consistently, at riverine site males were in poorer condition in spring compared to summer, likely due to energy expenditure associated with mating. This process indeed generally occurs in oligo- and mesohaline regions of estuaries during the warm season (Van Engel 1958; Hines 2003; Ramach et al. 2009; Epifanio 2019) and requires long starvation in order to protect the females during their pubertal molt (Van Engel 1958; Millikin and Williams 1984; Jivoff 1997). The climatic conditions of the northern Adriatic Sea, particularly influenced by increasing global warming (da Costa et al. 2024), do probably also permit prolonged activity of the species, which, according to our findings, although reduced in winter, did not result entirely absent. Moreover, K_n in winter was never detected to be lower compared to the other seasons. Year-round activity of the species is in contrast to its general inactivity status during colder periods in its native area (Hill et al. 1989; Hines 2007; Epifanio 2019), but consistent with findings from other Mediterranean countries, as reported for Greece (Kevrekidis and Antoniadou 2018; Kevrekidis et al. 2023), Croatia (Glamuzina et al. 2021) and France (Marchessaux et al. 2024), where the blue crab was also sampled all over the year. The longer activity period of the species is likely responsible for more rapid growth of individuals, which have more time to feed and develop, accelerating the life cycle compared to its native area.

Spawning and fecundity

Fecundity of the blue crab might also benefit from the longer activity period, being reproductive for almost six months. Coupling our samples with the reports of local fishermen (F. Riccato, personal communication) ovigerous females were collected from late March to mid-September. The length of egg brooding period is consistent with other recent studies conducted in the Mediterranean Sea (Kevrekidis et al. 2023; Vivas et al. 2025), and together with the advantage of females not undertaking long migrations, suggests the possibility that a female, once mated, may spawn eggs two or three times within a single reproductive season. This hypothesis is supported by the population structures, as different cohorts of juvenile crabs were caught in both spring and autumn. The lack of samplings with fyke nets during summer represents a limitation of our study, as our results suggest that they result more suitable for juvenile crab collection than traps; nevertheless, it is likely that juveniles are present in the lagoon during the whole warm period, from spring to autumn. At the end of the reproductive season, females might face high mortality, as during autumn they were significantly less abundant than males at the coastal marine station and at both lagoon stations and did often present lower abundances in autumn compared with the other seasons. This hypothesis finds support in Hines et al. (2007), stating that usually mature females do not move back to lower salinity zones of estuaries. On the contrary, male specimens might survive longer, as total carapace width of the most abundant size class showed a progressive increase from an average of 14.22 ± 1.44 cm in summer 2023 to 16.28 ± 1.53 cm in spring 2024. This could represent a consequence of the 2023 outbreak, as in that year older age class crabs were rare and only became abundant the following year, after the demographic explosion and the high availability of food in the newly invaded area (Chiesa et al. 2025). The average number of eggs per mass estimated in our study, slightly over 2 million, is consistent with what is usually reported by studies in its native area (Perry and McIlwain 1986; Jivoff et al. 2007; Epifanio 2019). The number of eggs per mass varied greatly, from half a million to over 4 million, with a peak of almost 6 million, reflecting the wide range of sizes of ovigerous females, from 12.51 cm (112.99 g) to 17.80 cm (308.50 g) and highlights the high reproductive potential of the species in the area. In other areas of the Mediterranean Sea, ovigerous females, ranged from 10.10 cm (79 g) to 15.60 cm (180 g), with a consequently lower number of laid eggs (1.65 million) (Marchessaux et al. 2023b). The reasons why in our study area females reach maturity at larger sizes could be related to the high productiveness and wide food availability of the Northern Adriatic Sea (Barausse et al. 2009; Franzoi et al. 2010). The number of eggs laid by ovigerous females in the Chioggia area throughout the reproductive season was constant from April-May to August-September. Generally, the first egg laying is the most abundant, then the number of eggs tends to decrease progressively in subsequent brooding (Epifanio 2019). The high number of eggs per mass in our study area lets hypothesize that new females start to brood at different times during the reproductive period, extending it. On the other hand, the number of eggs decreases with the advancement of egg development, as eggs ready to hatch were on average 30% less than eggs in an earlier developmental stage. The same finding was also reported by Jivoff et al. (2007) referring to numerous factors for the loss of embryos during development, which usually takes around two weeks to be accomplished (Newcombe 1945; Van Engel 1958; Tilburg et al. 2008). Lack of embryo adhesion to the pleopods, mechanical losses, embryo predation, disease, and parasites are most of the most frequent factors. Significant linear relationships also demonstrated that egg mass and brooded eggs number are directly proportional to female weight, confirming that larger females are also more fecund, as previously reported by Vivas et al. (2025) in Spain. Similarly, larger males could also improve the species' fecundity by better protecting the females during copulation and by producing and ejaculates more sperm, that females store to fertilize their lifetime production of eggs (Jivoff et al. 2003), enhancing the need of understanding growing mechanism of the species in the area.

Conclusions

In conclusion, the findings of our study highlight the massive spread of the blue crab *C. sapidus* in the Northern Adriatic Sea, in an area comprising diverse aquatic environments at short distances: lagoon, river estuary and marine coast, all located between 2 and 9 km from each other. Spatial and seasonal distribution of males and females appeared to be strongly connected with the reproductive cycle of the blue crab. Therefore, the proximity of all these environments represents an extremely crucial factor in favouring the rapid successful establishment of the species, which can take advantage of all the different habitats to foster a faster and more efficient life cycle compared to its native range. Based on our results, the effect of the small spatial scale " from river to sea" gradient may be equivalent or even stronger than other factors favouring the invasive success of *C. sapidus*. This study represents a relevant starting point for further investigations in the area; more information are, in fact, necessary to provide a better understanding of the species biological and ecological characteristics in Northern Adriatic, such as its trophic role and importance of other drivers, such as temperature rise, larval connectivity and food availability. While the complete eradication of the species is unlikely due to its high adaptability and mobility, our findings provide one of the first insights that could be helpful for the development of targeted management strategies, such as intensive and localized fishing, and for understanding the invasive success of this allochthonous species on the Northern Adriatic ecosystems.

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- "Monitoraggio della distribuzione e abbondanza della specie alloctona *Callinectes sapidus* in Laguna di Chioggia [Monitoring the distribution and abundance of the invasive species *Callinectes sapidus* in the Chioggia Lagoon.]" between Fondazione della Pesca di Chioggia and Ca' Foscari University of Venice (Department of Environmental Sciences, Informatics and Statistics- DAIS) n. 57/2023 Prot.54475 - 15/02/2023.
- "Monitoraggio della distribuzione e abbondanza della specie alloctona *Callinectes sapidus* in Laguna di Chioggia: impatti sulla pesca tradizionale ed indicazioni gestionali [Monitoring the distribution and abundance of the invasive species *Callinectes sapidus* in the Chioggia Lagoon: impacts on traditional fishing and management measures]" between Veneto Region and Ca' Foscari University of Venice (Department of Environmental Sciences, Informatics and Statistics- DAIS) n 425/2022 Prot n. 128484 - 30/11/2022.

- "Continuazione del monitoraggio della distribuzione e abbondanza della specie alloctona *Callinectes sapidus* in Laguna di Chioggia. Valutazione degli effetti del granchio blu sugli attrezzi e sulle rese alieutiche della pesca tradizionale e della piccola pesca costiera [Continuing the monitoring of the distribution and abundance of the invasive species *Callinectes sapidus* in the Chioggia Lagoon. Evaluation of the blue crab's effects on the gear and fishing yields of traditional and small-scale coastal fisheries.]" between Fondazione della Pesca di Chioggia and Ca' Foscari University of Venice (Department of Environmental Sciences, Informatics and Statistics- DAIS) n. 68/2024 Prot. n. 73241 - 18/03/2024.

Author contribution

Marco Boschiero: sample design and methodology, investigation and data collection, data analysis and interpretation, writing – original draft; Chiara Facca: sample design and methodology, writing – review & editing; Francesco Cavraro: sample design and methodology, writing – review & editing; Simone Redolfi Bristol: investigation and data collection, writing – review & editing; Anna Gavaioli: writing – review & editing; Federico Riccato: investigation and data collection, writing – review & editing; Matteo Zucchetta: data analysis and interpretation, writing – review & editing; Piero Franzoi: Research conceptualization, sample design and methodology, writing – review & editing, funding provision.

Ethics and permits

All research pertaining to this article did not require ethics approval. All research pertaining to this article was allowed by the research permit Decreto n. 50 - 24/01/2023 issued by Veneto Region (Italy).

Data availability

Species georeferenced records are available at the European Alien Species Information Network: https://easin.jrc.ec.europa.eu/easin/RJD/Download/37b1faca-07d0-46d9-a05c-cd4aaf654bbf.

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Supplementary material 1

Suppl. table S1

Authors: Marco Boschiero, Chiara Facca, Francesco Cavraro, Simone Redolfi Bristol, Anna Gavioli, Federico Riccato, Matteo Zucchetta, Piero Franzoi

Data type: xlsx

Explanation note: Regression equations with corresponding R_2 values and p-values for all pairs of morphometric parameters tested for females and males; (b) coefficients are reported in red for negative allometry, in green for positive allometry and in blue for isometry. The results of the ANCOVA test, which compared the slopes of the regression lines between sexes, are also provided.

Link: https://doi.org/10.3391/ai.2026.21.1.180751.suppl1

Supplementary material 2

Suppl. table S2

Authors: Marco Boschiero, Chiara Facca, Francesco Cavraro, Simone Redolfi Bristol, Anna Gavioli, Federico Riccato, Matteo Zucchetta, Piero Franzoi

Data type: xlsx

Explanation note: Min, max and mean ± SD values of blue crab's total carapace width (TCW) caught with wire pots and fyke nets across the four sampling seasons

Link: https://doi.org/10.3391/ai.2026.21.1.180751.suppl2

Supplementary material 3

Residuals and normality diagnostics of the most complex GLM

Authors: Marco Boschiero, Chiara Facca, Francesco Cavraro, Simone Redolfi Bristol, Anna Gavioli, Federico Riccato, Matteo Zucchetta, Piero Franzoi

Data type: png

Explanation note: **figure S1:** Residuals and normality diagnostics of the most complex GLM **A)** negative binomial family GLM for crabs' distribution; **B)** gamma family GLM for the relative condition factor; **C)** binomial presence/absence GLM for ovigerous females' distribution.

Link: https://doi.org/10.3391/ai.2026.21.1.180751.suppl3