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Original research article

Using species population structure to assist in management and decision-making in the fight against invasive species: The case of the Atlantic blue crab *Callinectes sapidus*

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ABSTRACT

The blue crab *Callinectes sapidus* Rathbun, 1896 is an invasive species in the Mediterranean, with a remarkable ability to adapt to various habitats, and thereby having significant impacts on biodiversity and artisanal fishing activities. Currently, fishing is a measure being considered to control blue crab populations in invaded sites. However, it is necessary to understand the temporal structure of blue crab populations (e.g., growth, reproduction, sexual maturity) to determine specific periods when control measures need to be implemented. Considering the species' ability to adapt to various habitats, it is crucial to evaluate how temperature and salinity influence population structure. In this study, we present fishers-dependent monitoring on the temporal population structure of blue crabs in two lagoons in Corsica (France) over 12 months. Through this approach, we provide new information that can assist in decision-making for the implementation of control measures. Even though these two lagoons are geographically close, blue crab populations showed differences, particularly in terms of sexual maturity. Specimens from Biguglia mature later (males: 16.16 cm; females: 16.79 cm) than those in the Palo Lagoon (males: 14.38 cm; females: 13.86 cm). Seasonal size distribution also showed differences between the lagoons and within the same lagoon between males and females. Temperature and salinity had a significant effect on the monthly relationship between carapace width and wet weight (referred to here as growth rate) for males and females and between the lagoons. In the Biguglia Lagoon, the higher the temperature, the greater the growth rate over a wide salinity window (16–30 psu); for females, the environmental window was restricted (temperature: 20–30°C; salinities $>$ 16 psu). The dynamics differed in the Palo Lagoon, with a more restricted high growth rate window for males, and females showed a much wider window, with high growth rates over the entire temperature and salinity range. By employing blue crab's populations monitoring along with environmental parameters, we were able to determine how the environment influenced the blue crab's population structure, thus identifying periods conducive to species control. The most effective strategy would undoubtedly be to eliminate females before their period of sexual maturity and copulation ensue. In our case, this would involve intensive control in summer for

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Biguglia and in spring for Palo. These recommendations have been translated into operations to be implemented as part of the "Territorial Plan for Combating the Blue Crab (*Callinectes sapidus*) in Corsica (2024–2027)".

1. Introduction

An essential aspect of ecology is understanding the impact of environmental factors on species distribution and population structure (MacIsaac, 1996), including the effects of species disturbances (Sousa, 1984). This paradigm necessitates examining population size structure, dynamics, reproductive strategies, and species' capacity to adapt to environmental shifts (Hare et al., 2011). Among the crucial factors to consider, species body size stands out as a primary performance trait with significant potential to influence the adverse effects of environmental factors on local population composition (De Bie et al., 2012; Gjoni et al., 2023). The analysis of population size distribution and how environmental factors influence size-based population structures is a strong indicator of the health of marine ecosystems. (Petchey and Belgrano, 2010). In the case of Non-Indigenous Species (NIS), this approach introduces new monitoring descriptors, including quantifying the NIS's adaptability to new habitats and understanding how environmental factors influence population size structure, dynamics, and biology at local scales.

The blue crab *Callinectes sapidus* Rathbun, 1896, native from the Atlantic coasts of America, was first reported in the Mediterranean Sea in 1949 and in the Black Sea and the Sea of Azov in 1967 (Nehring, 2011). Known for its high fecundity (Darnell et al., 2009; Hines et al., 1987) and wide temperature tolerance (Marchessaux et al., 2022), this species has successfully invaded, expanded, and thrived in the Mediterranean over recent decades (Streftaris and Zenetos, 2006). Widely distributed along the Mediterranean coasts, *C. sapidus* in northern (from Spain to Turkey) and southern (Egypt, Tunisia, Algeria and Morocco; Mancinelli et al., 2021) regions, are opportunistic predators (Hoeinghaus and Zeug, 2008; Laughlin, 1982) with aggressive behavior (Millikin, 1984) that leads to significant impacts on local biodiversity (e.g. mollusks, invertebrates, seagrasses, etc.; Prado et al., 2020; Clavero et al., 2022) and artisanal fisheries (Marchessaux et al., 2023a). Removal efforts through fishing remains the accepted method for controlling this species, as blue crab fisheries are valued for their commercial importance and catch volume in its native range (NOAA, 2023). Despite being a major fishing interest in the USA and Mexico (Churchill, 1919; Perry, 1975), the blue crab fishery also serves as a population control measure in certain Mediterranean regions (e.g. in Tunisia, Rifi et al., 2023 or Turkey, Öndes and Gökçe, 2021), compensating for economic losses in artisanal fisheries (Cannarozzi et al., 2023; Glamuzina et al., 2021).

With its complex life cycle, *C. sapidus* thrives in diverse habitats and across a wide salinity gradient (Millikin, 1984): reproduction typically occurs in low salinity waters, with females migrating to polyhaline zones for egg production and larval release (Aguilar et al., 2005). The eggs mature in seawater, leading to the release of planktonic zoeae larvae, which eventually return to low salinity areas acting as nurseries (Epifanio, 2019; Lipcius et al., 2005). Juvenile crabs use a diverse nurseries throughout ontogeny, mainly in structurally complex habitats (dense aquatic vegetation) for individuals smaller than 25 mm carapace width (Hines et al., 1995; Perkins-Visser et al., 1996; Lipcius et al., 2007; Shervette et al., 2011), then non-vegetated secondary nurseries with a sandy-muddy substrate and low salinity for individuals $>$ 25 mm (Lipcius et al., 2005; Posey et al., 2005). Juvenile blue crabs remain in sandy-muddy substrate until they reach sexual maturity at about 100–200 g body weight (age at maturity and longevity $\sim$ 1–2 years and 3 years, respectively, depending on phenology and geographic location) (Jivoff et al., 2007; van Montfrans et al., 2003). The complex blue crab life cycle currently presents a barrier to the possible control measures and some answers are urgent about when and how to implement an effective control measure. Thus, studying the blue crab life cycle, especially the population structure and growth is the key to define the sensitive periods where control measures could be implemented.

In the Mediterranean Sea, *C. sapidus* is found in various productive coastal habitats (e.g., river mouths, brackish lagoons, coastal marine) offering to blue crabs protection and ample food resources to sustain growth and reproduction (Johnston and Caretti, 2017; Perkins-Visser et al., 1996; Posey et al., 2005; Ruas et al., 2014). On the Mediterranean French coasts, *C. sapidus* was historically recorded in the Berre Lagoon in 1962 (French continent, Zibrowius, 2002), was recorded in the 1990s in the Palo and Diana lagoons, and in 2014 in the Biguglia Lagoon in Corsica island (pers. comm.). Between 2014 and 2018, the species spread along Corsica's eastern coastline and between 2020 and 2022, the number of individuals exploded, particularly in the Biguglia and Palo lagoons, with the first observations of ovigerous females attesting to its reproduction in 2020.

Even if *C. sapidus* is widespread in the Mediterranean Sea, it appears that even if the blue crab invasion is a global concern in the Mediterranean Sea, it is increasingly necessary to focus efforts on local systems invaded by the species because the species response appears to be dependent of the location where the species is (Marchessaux et al., 2023b). These aspects are fundamental to implement species' management control plans. One of the main management measures for this species would be to implement selective "control" fisheries concentrating on specific periods and locations to reduce the number of spawning individuals and thus reduce the production of new generations. However, to implement such measures, it is necessary to know the temporal population size distribution, growth periods and sexual maturity, taking into account local environmental conditions.

Population size distribution analysis offers an invaluable approach to determine how the species is adapted to local environmental conditions. Size distribution is a very important tool addressing how the species respond to environmental factors (such as temperature and salinity) in each location and how they will respond to climate change (Gjoni et al., 2023). The invasive blue crab *C. sapidus*, is known to be a generalist species is the perfect example showing a high adaptability to different habitats (Marchessaux et al., 2023a). Using such descriptors allows quantification of environmental factors influencing population size structure, enabling the implementation of adaptive and effective management plans, including population control (Marchessaux et al., 2022).

The objective of this study was to evaluate the size structure of blue crab populations within the same geographic region on Corsica Island and to compare size structure, sexual maturity, and fecundity across different lagoons. We hypothesize that there are significant differences in the size structure, sexual maturity, and fecundity of blue crab populations between different lagoons on Corsica Island. Additionally, we describe the participation of fishers-monitors to help quantify the blue crab population structure in relation to environmental factors that can help practitioners design effective NIS management measures in the Mediterranean Sea.

2. Materials and methods

2.1. Study sites

This study was carried out in two lagoons (Biguglia and Palo) in Corsica (France), which are strongly affected by *Callinectes sapidus*. The Biguglia Lagoon is the largest wetland in Corsica Island, covering a surface of 14.5 km^2 with a watershed of 182 km^2 (latitude: 42.597, longitude: 9.481; Fig. 1). This semi-enclosed lagoon (*sensu* Kjerfve, 1994) is characterized as a shallow brackish coastal lagoon, separated from the Tyrrhenian Sea by a sandy beach barrier, and connected to the sea via a long, narrow, and shallow natural inlet at its north end (1.5 km). Artificial interventions occasionally re-establish the connection with the sea but without a regular management pattern (Ligorini et al., 2022). Freshwater inputs, primarily from rivers, streams, agricultural pumping stations, sewage plants, and

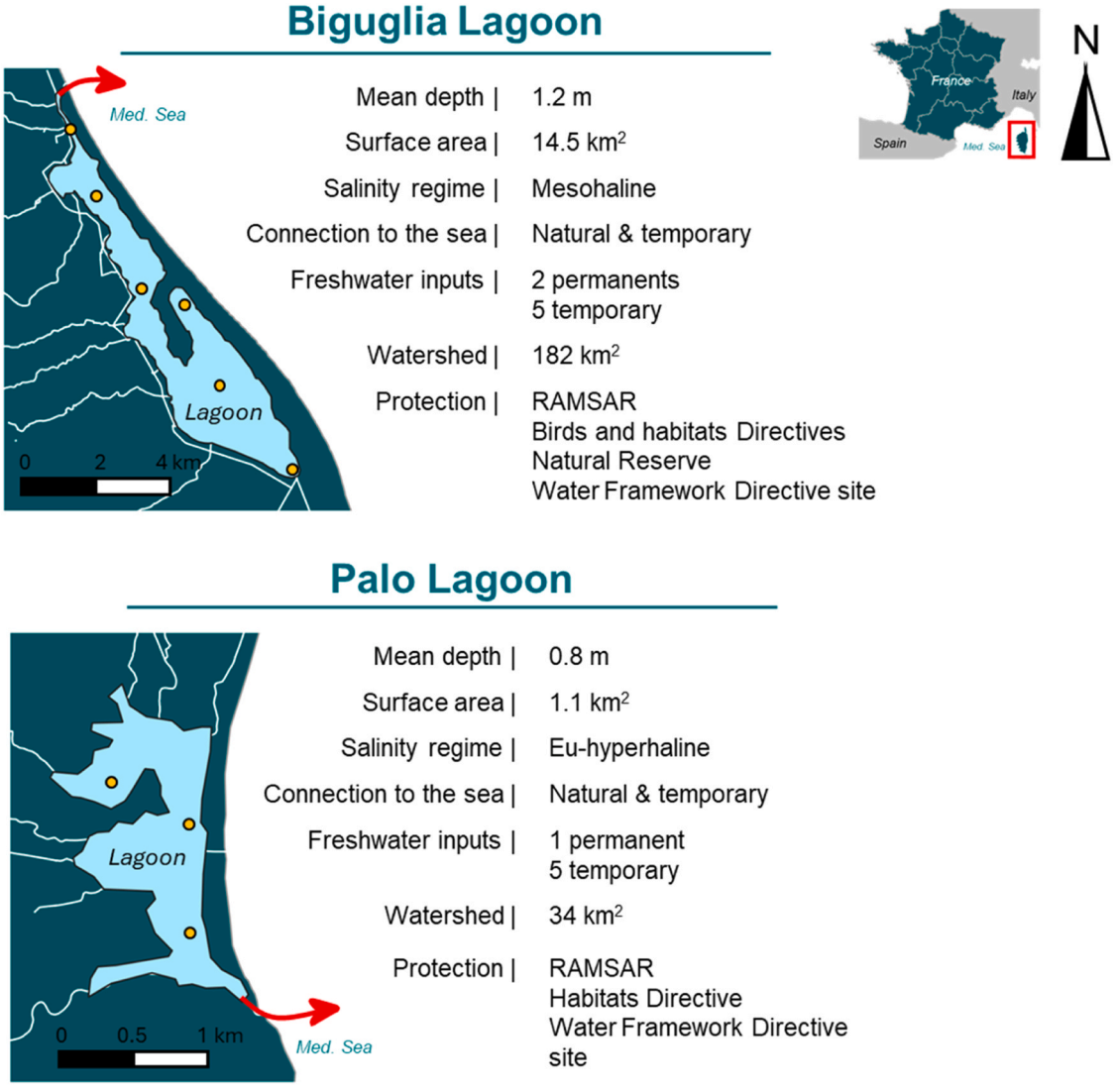


Fig. 1. Maps and descriptions of study sites in Corsica Island (France): the Biguglia and Palo lagoons. The red arrows on the lagoon maps represent the connections between the lagoons and the Mediterranean Sea (Med. Sea). The orange dots represent the monitoring stations for environmental parameters (temperature and salinity).

runoff, dominate the water budget, with significant contributions from the Fossone canal connecting the Golo river to the lagoon at its southern end, and from the Bevinco river in the North (Fig. 1) (Dufresne et al., 2017). These inputs are directly influenced by inter-annual and inter-seasonal climatic variability, shaping lagoon salinity, which decreases sharply from north to south due to freshwater inputs from the Golo River via the Fossone canal. This hydrological variability drives aquatic biodiversity (Garrido et al., 2016; Ligorini et al., 2022). Recognized as a wetland conservation area since 1991 by the RAMSAR Convention and designated as a Natural Reserve since 1994 (Gardner and Davidson, 2011), the Biguglia Lagoon provides essential ecosystem services, including fish exploitation and provision of drinking water for the urban area of Bastia. Despite its ecological significance, the lagoon faces challenges such as eutrophication, disturbances to its natural functioning, and postponements in achieving ecological status objectives under the Water Framework Directive, exacerbated by factors such as increasing urbanization, agricultural exploitation of its watershed, and high environmental variability impacting salinity gradients and connectivity to adjacent marine environments (Erostate et al., 2022; Pasqualini et al., 2020).

The Palo Lagoon (latitude: 41.948, longitude: 9.407; Fig. 1) is the fourth largest lagoon on the Corsica Island, covering an area of 1.1 km^2 and is characterized as a relatively undeveloped watershed with a small surface area (34 km^2). This lagoon is also a semi-enclosed lagoon (*sensu* Kjerfve, 1994) characterized as a shallow brackish coastal lagoon with an average depth of 0.8 m, separated from the Tyrrhenian Sea by a sandy beach barrier, and connected to the sea via a narrow and shallow natural inlet at its southern end (Fig. 1). The lagoon inlet is occasionally opened to facilitate professional fishing activities. This system is fed by six small freshwater streams collecting runoff from the watershed. Spring rains result in a significant influx of nutrients into the pond through runoff, leading to eutrophication, which sometimes causes anoxia phenomena in summer. Owned by the Coastal Conservancy since 1994, the Palo Lagoon has been a Natura 2000 site since 1998, managed by the Corsican authorities, and designated as a RAMSAR convention protected site since 2008. Due to its shallow depth and small surface area, Palo is a particularly responsive and sensitive lagoon to temperature increases. Hydrological parameters show pronounced variations from year to year, impacting the biological components.

2.2. Sampling strategies

In 2023, a collaboration between fishers and scientists was set up with the financial and logistical support of the Environmental Agency of Corsica. This cooperative agreement involved mobilizing and training participating fishers who provided blue crabs, and captured opportunistically each month as a way to monitor and assess this population.

Blue crabs, an invasive species in the Mediterranean, are considered by-catch for fishers, as blue crabs are not currently marketed in France. As a result, there is no specific blue crab fishing gear in these lagoons; instead, blue crabs caught in these areas are destroyed by local fishers, as is the common practice. A CPUE (Catch Per Unit Effort) measurement was not possible as blue crabs were only incidentally fished, but in order to estimate the total weight of blue crabs caught each month (from January to December), a local ecological knowledge (LEK) approach (Begossi, 2015; Lima et al., 2017) was carried out with the fishers, who indicated the total weight (in kg) of blue crabs they had caught to Marie Garrido each month by SMS or telephone. Based on the total quantity of blue crabs monthly caught by fishers, prior to the destruction of blue crabs by fishermen, 30 specimens were randomly sub-sampled for the measurements presented in this study (see below).

Fishers used fyke nets (60–80 m long) in the Biguglia Lagoon; and bordigues (2 m in diameter), a type of trap used for catching fish, in the Palo Lagoon. Fishers were paid to supply blue crabs once a month at a cost of €8 per crab, a high price compared with prices per kilogram elsewhere in Europe. Alongside blue crab catches, environmental data (temperature and salinity) were recorded on the same day each month by the managers (Collectivité de Corse) in the subsurface using a multiparameter probe (In-Situ AquaTROLL 500) at several stations in each lagoon (7 stations in Biguglia lagoon, 3 stations in Palo lagoon). Temperature and salinity data were measured at each station and then averaged for each month over the course of the study.

2.3. Size structure, sexual maturity and females fecundity

In the laboratory, for each blue crab individual, the carapace width (CW, the horizontal distance between the dorsal spines) was measured using a graduated ruler (± 1 mm accuracy), wet weights (WW) were measured using a digital balance (± 0.1 g accuracy), and an assessment of sexual maturity, based on morphological analysis of the abdomen (Jivoff, 1997; Marchessaux et al., 2023a; Millikin, 1984). Female blue crabs were evaluated for maturity based on the shape of their abdomen: a triangular abdomen (locked to the abdomen) was considered immature; whereas a mature adult female exhibited a characteristic enlarged, heavily pigmented, and fully expandable abdomen along with developed pleopods (Van Engel, 1958). Male blue crabs were deemed immature if their abdomen was closed and/or partially locked to the abdomen with the penis inserted into the gonopods (Pyle and Cronin, 1950; Perry, 1975; Van Engel, 1990; Olmi III and Bishop, 1983; Marchessaux et al., 2023a). Conversely, a mature adult male displayed a free and fully expandable abdomen. In the case of ovigerous females, egg masses were delicately extracted from the pleopods, and their wet weight was measured with a digital microbalance, with an accuracy of ± 0.1 g.

2.4. Data analysis

Total blue crabs' catches were presented monthly with temperature and salinity recorded in the same period. The width-weight (CW-WW) allometric relationship was established using an exponential equation for both males and females. Monthly size ranges for males and females for both lagoons were plotted as boxplots. To test the temperature and salinity differences between lagoons, and seasonal differences in size range between sexes and lagoons, an ANOVA and a Bonferroni post-hoc test (significant difference = $p <$

0.05) were performed using the software SigmaPlot 12.5.

The length at first maturity (L_{50}) for males and females, defined as the size at which 50 % of individuals reach maturity, was determined by examining the relationship between the percentage of mature crabs (males and females separately), and CW. To calculate the L_{50}, the proportion (P) of sexually mature (males and females) was fitted to the logistic equation (3): $P = \frac{1}{(1+\exp^{[-r(L-\ Lm)]})}$ which in straight line form is: $\ln\left[\frac{1-P}{P}\right] = rL_m - rL$ where r (-b) is the slope of the curve and L_m is the mean length at sexual maturity on the CW which corresponds to a proportion of 50 %. All plots and regressions were performed using the software SigmaPlot 12.5.

To determine the monthly allometric regressions carapace width (CW) and wet weight (WW) variations, CW-WW regressions were log-transformed for males and females separately, and the slopes post-linearization were extracted (Marchessaux et al., 2023a). To link the effect of temperature and salinity on the monthly CW-WW allometric regressions, a principal component analysis (PCA) was performed using R software (version 4.2.2.). After the transformation of the data into log(n+1), the latter were normalized (Shapiro-Wilk test). The PCA was traced as well as the circle of correlations allowing to identify the factors influencing the males and females CW-WW regressions in both lagoons studied.

3. Results

For both lagoons, temperature showed a seasonal variation with a minimum in January (7.9 ± 0.5 °C for Biguglia and 7.7 ± 0.21 °C for Palo) and a maximum in July (30.8 ± 0.8 °C for Biguglia and 31.1 ± 0.52 °C for Palo) (Fig. 2). No significant difference in temperature values was observed between the lagoons. Salinity was variable from 9.9 ± 4.5 psu (February) to 23.4 ± 3.8 psu (October) for the Biguglia Lagoon and from 27.9 ± 1.7 psu (January) to 51.3 ± 1.8 psu (August) for the Palo Lagoon (Fig. 2). Palo Lagoon salinity was significantly higher in summer (ANOVA, Bonferroni post-hoc test, $p = 0.002$) and autumn (ANOVA, Bonferroni post-hoc test, $p = 0.033$) than Biguglia.

The total weight (kg) exhibited for both lagoons a strong temporal variability with maximum values recorded in summer (2 110 kg for Biguglia; 2 549 kg for Palo) and decreased values in the winter season reaching a minimum in January (0.70 kg for Biguglia; 12.6 kg for Palo); following the seawater temperature seasonal variations (Fig. 2). No significant difference in seasonal catches values was observed between the lagoons.

A total of 378 blue crabs (257 males and 121 females) for Biguglia Lagoon and 311 blue crabs (214 males and 94 females) for the Palo Lagoon were used for size-length characteristics and sexual maturity. In the Biguglia Lagoon, the size distribution of immatures and matures males and females ranged for males from 5 to 12.7 cm (immatures) and from 9.6 to 23 cm (matures); for females from 4.7 to 13.7 cm (immatures) and from 13.0 to 20.0 cm (matures; Table 1A). In the Palo Lagoon, the size distribution followed the same trends with for males from 8 to 8.8 cm (immatures) and from 9.5 to 19.6 cm (matures); for females from 6.2 to 7.5 cm (immatures) and from 10.1 to 17.3 cm (matures; Table 1B).

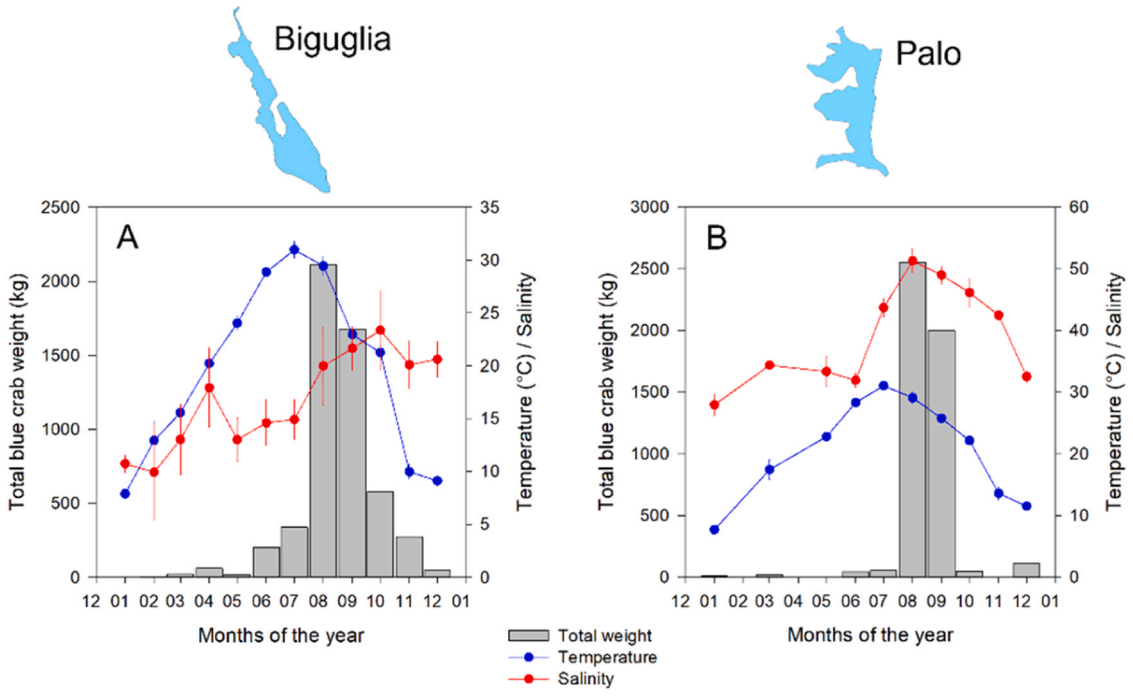


Fig. 2. Monthly evolution of temperature, salinity and total monthly catch (kg) of blue crab *Callinectes sapidus* (A) in Biguglia and (B) Palo lagoons for the year 2023.

Table 1
Carapace Width (CW) and wet weight (WW) characteristics (mean, minimum (Min.), maximum (Max.)) for the blue crab for (A) the Biguglia Lagoon, (B) the Palo Lagoon. SE = standard error.

A | Biguglia Lagoon			**CW characteristics (cm)**				**WW characteristics (g)**			
Sex	Maturity	n	Mean	SE	Min.	Max.	Mean	SE	Min.	Max.
Males	Immatures	37	8.0	± 1.8	5.0	12.7	35.4	± 20.2	8	106
	Matures	220	16.1	± 3.2	9.6	23.0	275.5	± 146.2	48	611
Females	Immatures	41	10.7	± 2.1	4.7	13.7	84.6	± 45.9	8.0	223
	Matures	79	16.8	± 1.8	13.0	20.0	192.4	± 53.9	102	333
B | Palo Lagoon			**CW characteristics (cm)**				**WW characteristics (g)**			
Sex	Maturity	n	Mean	SE	Min.	Max.	Mean	SE	Min.	Max.
Males	Immatures	2	8.4	± 0.6	8.0	8.8	47.5	± 19.1	34	61
	Matures	212	14.5	± 1.8	9.5	19.6	220.7	± 69.4	69	413
Females	Immatures	3	6.8	± 0.7	6.2	7.5	23.0	± 8.9	16	33
	Matures	94	13.9	± 1.3	10.1	17.3	134.0	± 31.5	65	242

The width-weight relationships (CW-WW) followed an exponential curve for both sex in both lagoons (Fig. 3; Table 2). For the Biguglia Lagoon the slope coefficient b values were similar for both immature sex: $b = 0.13$ for immatures males, and $b = 0.19$ for immatures females (Table 2A). Whereas b values showed differences between mature males and females ($b = 0.05$ and $b = 0.13$ respectively). For Palo Lagoon, the low number of immatures specimens did not allow us to determine de CW-WW relationships separately (Table 2B), however we were able to determine the CW-WW relationship for mature specimens. b values were similar between both sex (males: 0.07 and females: 0.04) but were lower than values obtained in Biguglia Lagoon (Table 2A).

The size distribution of males and females showed a seasonal pattern in the two lagoons studied (Fig. 4). The carapace width (CW) of males and females at Biguglia Lagoon showed similar dynamics, with an increase in CW between winter (males: 10.5 ± 3.7 cm; females: 12.8 ± 6.7 cm) and summer (males: 17.3 ± 2.8 cm; females: 16.4 ± 2.3 cm). No significant differences were observed between males and females except in spring, when the CW of males was significantly (ANOVA, Bonferroni post-hoc text, $p < 0.05$) higher than that of females (Fig. 4). In the Palo lagoon, the CW of males and females showed a different trend to that of Biguglia, with CW distributions that were relatively constant (males: 14.4 ± 1.9 cm; females: 13.7 ± 1.8 cm) independently of the seasons (Fig. 4). As in Biguglia, no significant differences were observed between males and females except in spring, when the CW of males was significantly (ANOVA, Bonferroni post-hoc text, $p < 0.05$) higher than that of females (Fig. 4). Comparison of male and female CW distributions between lagoons showed significant differences for all seasons, except winter and spring for females (Fig. 4).

The size at first maturity (L_{50}) showed different values between male and females but also between both lagoons (Fig. 5). In the Biguglia Lagoon similar values were observed for both sexes (males: 16.16 cm; females: 16.79 cm) (Fig. 5A). On the contrary in the Palo Lagoon males and females were matures on smallest sizes (males: 14.38 cm; females: 13.86 cm).

The seasonal evolution of sex ratio Males:Females (M:F) showed highest values in winter for both lagoons (Biguglia: M:F = 3, Palo: M:F = 4) and in summer/spring (M:F between 2 and 3) in Biguglia, and spring (M:F = 6.6) in Palo (Fig. 5 C,D) indicating a dominance of males during these periods and a decrease in the number of females. For the rest of the time, the M:F sex ratio was close to 1 suggesting a relative equilibrium between both sex in the both lagoons. The ovigerous females CW ranged from 11.5 to 17.3 cm and the egg mass weight wet from 10 to 53 g representing an average of 18 ± 7 % of the total female body wet weight (all lagoons combined). Ovigerous females were observed between August and November in Biguglia, and between June and December in Palo, all presenting orange sponges eggs corresponding the early-stage embryonic development.

The relationship between temperature, salinity, and the CW-WW regressions showed opposite results between males and females and between lagoons (Figure S1). In the Biguglia lagoon, for males the CW-WW regression slope coefficient increased exponentially with increasing temperature (reaching a plateau at 25°C) and with salinity (Figure S1A). For females, CW-WW regression slope coefficients were highest at the highest temperatures and salinities (Figure S1C). In the Palo lagoon, the trends were similar for males for temperature (Figure S1B) but no trends were observed in response to salinity. For the Palo Lagoon's females, the CW-WW regression slope coefficient increased exponentially with temperature and decreased with salinity (Figure S1D). These results were corroborated by principal component analysis (PCA), which showed that CW-WW regression slope coefficients were correlated with temperature but opposed to salinity; whereas for females salinity had the greater influence (Fig. 6).

4. Discussion

4.1. Environment and population structure

The results obtained in this study showed that the morphometric relationships and allometric growth of the American blue crab *Callinectes sapidus* were lagoon specific and differed from the data available in the literature (Table 3). For females, the maximum carapace width (CW) values obtained in our study were in the same ranged for Palo (CW = 17.3 cm) with females measured in Turkey ((Atar and Seçer, 2003; Gokce et al., 2006), and in Morocco (Chaouti et al., 2022). On the other hand, maximum CW values (CW = 20.0 cm) for females in the Biguglia Lagoon were higher than in Palo, and similar to values recorded in Albania (Beqiraj and Kashta, 2010) and Italy (Cilenti et al., 2015). For males in the Palo Lagoon the maximum CW (= 19.6 cm) was similar than in Morocco (Marchica Lagoon, Oussellam et al., 2021) and in Italy (Saltmarshes of Trapani, Marchessaux et al., 2023a). In the Biguglia Lagoon, our data showed that the maximum males CW = 23.0 cm was the highest value recorded to date in the Mediterranean Sea: the highest

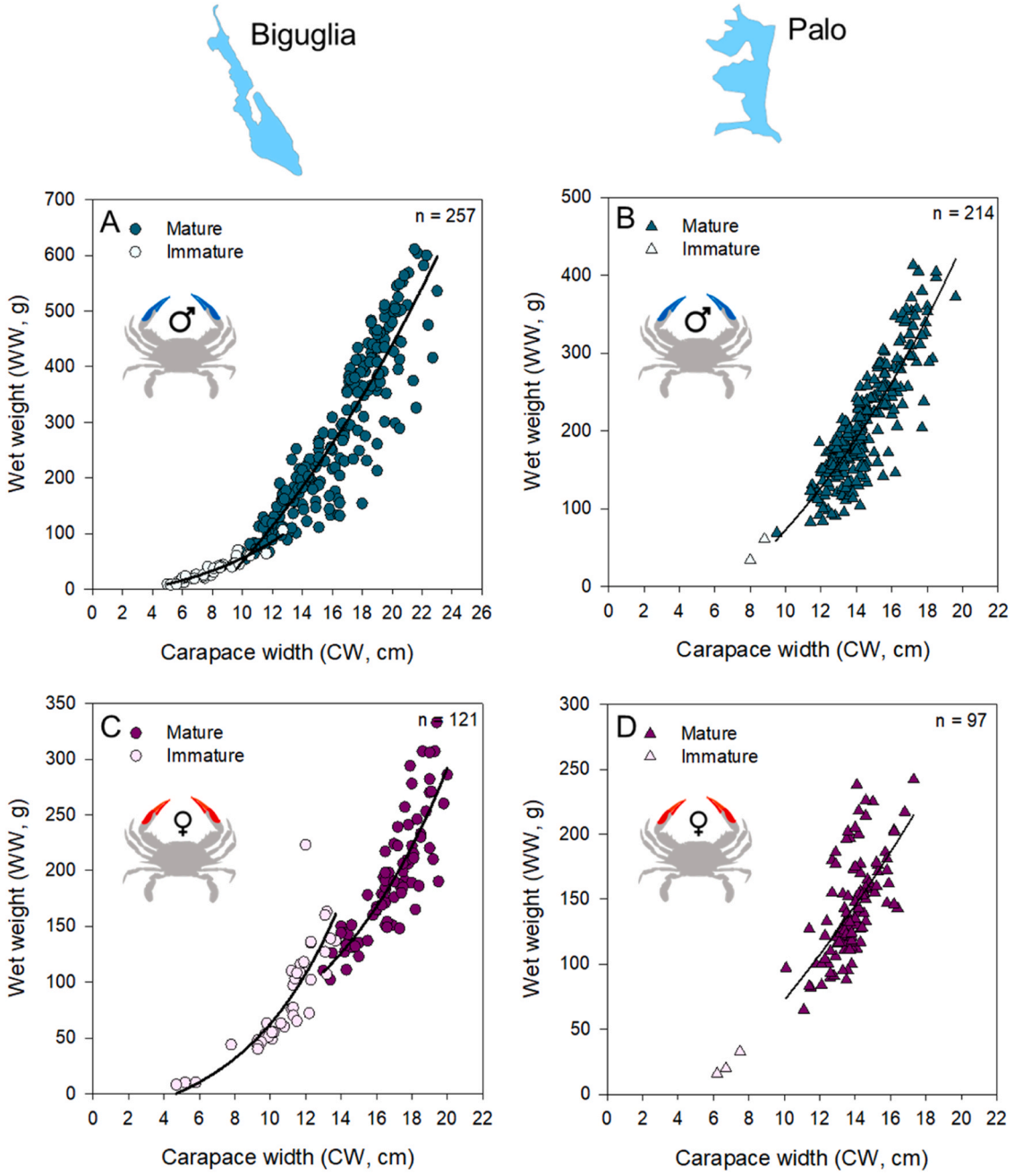


Fig. 3. Relationship between carapace width (CW) and wet weight (WW) for the Biguglia Lagoon: (A) males and (C) females; and for the Palo Lagoon: (B) males and (D) females.

value available in the literature was CW = 21.0 cm for the Ugento Lagoon, Italy (Gennaio et al., 2006).

Comparing our size distribution, males and females of blue crabs showed positive allometric relationships for the two lagoons studied in Corsica which agreed with that presented for Greek (Kevrekidis, 2019) and Italian (Marchessaux et al., 2023a) blue crab populations. The variability of blue crab size ranges and allometric slopes equations aligned with the observation that decapods and crustaceans demonstrate considerable flexibility in their physical morphology, which could be influenced by various environmental and genetic elements (Maguire et al., 2017) including seasonal variations, temperature, availability of food, level of satiation, age stage of maturity, and gender (Bagenal, 1978; Pauly, 1984).

Our study in the two Corsican lagoons has shown that *C. sapidus* has a locally complex life cycle specific to each area studied, certainly involving seasonal and spatially specific migrations for copulation and reproduction linked to temperature and salinity (Aguilar et al., 2005; Carr et al., 2004; Forward et al., 2005; Hines et al., 1995; Jivoff et al., 2007; Perry, 1975), thus generating

Table 2
Allometric parameters of the relationship (WW = a*exp(b*CW) + y0) between the carapace width (CW) and the weight (WW) for (A) Biguglia; (B) the Palo lagoons. *: significant difference. For the Palo Lagoon, due to the low number of immatures specimens, it was not possible to analyze the allometric parameters.

A | Biguglia Lagoon				Parameters of CW-WW relationship WW = a*exp(b*CW) + y0				
Sex	Maturity	n	a	b	SE(b)	R^2	p value	y0
Males	Immatures	37	24.58	0.13	0.04	0.91	< 0.0001*	−39.45
	Matures	220	407.66	0.05	0.02	0.83	< 0.0001*	−602.91
	Both	257	122.26	0.08	0.02	0.88	< 0.0001*	−214.48
Females	Immatures	41	15.43	0.19	0.08	0.72	< 0.0001*	−36.80
	Matures	79	21.45	0.13	0.08	0.72	< 0.0001*	−10.90
	Both	151	79.53	0.08	0.02	0.87	< 0.0001*	−113.00

B | Palo Lagoon				Parameters of CW-WW relationship WW = a*exp(b*CW) + y0				
Sex	Maturity	n	a	b	SE(b)	R^2	p value	y0
Males	Matures	214	186.94	0.07	0.03	0.74	< 0.0001*	−298.77
Females	Matures	97	275.53	0.04	0.05	0.53	< 0.0001*	−340.90

spatio-temporal variability in population abundance at local scale.

In the two Corsican lagoons, the decrease in catch over winter at temperatures < 12 °C with an almost total absence of blue crabs in January (only a few individuals caught), which is consistent both with what was observed in the literature (Marchessaux et al., 2022) supporting the idea that this temperature represents a critical lower thermal threshold making local conditions unfavorable for *C. sapidus* metabolism, as it has been reported that blue crabs become inactive during cold periods in other Mediterranean and Atlantic regions (Millikin, 1984; Hines et al., 1987; Lipcius and Van Engel, 1990; Mancinelli et al., 2013; Marchessaux et al., 2023a; Pereira et al., 2009). However, this phenomenon was observed in our study only in January, as blue crabs were caught even into the winter season (February and March) although in this case temperatures remained > 12 °C with a mild winter. Total blue crab catch showed the same trends in the two lagoons with an increase in spring to reach a maximum in summer.

The distribution of carapace width (CW) presented in our study showed different seasonal trends between the sexes and from one lagoon to another. At Biguglia, CW of males and females increased between winter and summer with a significant difference in CW of males in spring, which were larger than females, highlighting that males grew faster than females and similar results were observed in a saltmarsh system in Italy (Marchessaux et al., 2023a); however, at Palo Lagoon, there were no seasonal variations. Two hypotheses may be put forward to help explain this result. First, there may be an effect of fishing technique used by the fishers (e.g. "bordigue", a type of trap used for catching fish) which would select specimens of a certain size; but given the wide CW range of the specimens caught in our study (from 6.2 to 19.6 cm) this seems unlikely. Second, and probably a more likely hypothesis, is that environmental conditions have an affect on the size of the crabs (male and female). As demonstrated in the PCA performed in our study, we showed that temperature had a significant effect on the CW of males, while for females it was salinity. In Palo Lagoon, salinity values > 30 psu had a negative effect on the CW-WW regression for males, and salinity > 36 psu for females. On the contrary, lower salinity values were measured in the Biguglia Lagoon showing a positive effect on CW-WW regressions for both sexes, illustrating here that Palo's salinities would not be optimal for blue crab growth and would therefore limit their size. These new results obtained in Corsica clearly demonstrate the plasticity of *C. sapidus* and its response to local environmental conditions enabling it to take advantage of each area where it is present.

4.2. Sexual maturity and reproduction

Size at sexual maturity (L_{50}) is a good indicator in terms of species management, particularly for invasive species, since it gives an estimate of when male and female populations are sexually mature (Hasan et al., 2021). In our study, the estimated L_{50} showed an important difference between males and females in the same lagoon, but also between the two lagoons studied (Table 4). In the Biguglia Lagoon the L_{50} for males was estimated at 16.16 cm, higher than in the Palo Lagoon (L_{50} = 14.38 cm). A similar situation exists for female blue crabs that mature for a bigger size in the Biguglia Lagoon (L_{50} = 16.79 cm) compared with the Palo Lagoon (L_{50} = 13.86 cm). In other words, males and females reached sexual maturity quickly in the Palo Lagoon than in the Biguglia Lagoon. The L_{50} values of males obtained in our study were higher than those available in the literature (Table 4), where males are generally mature at

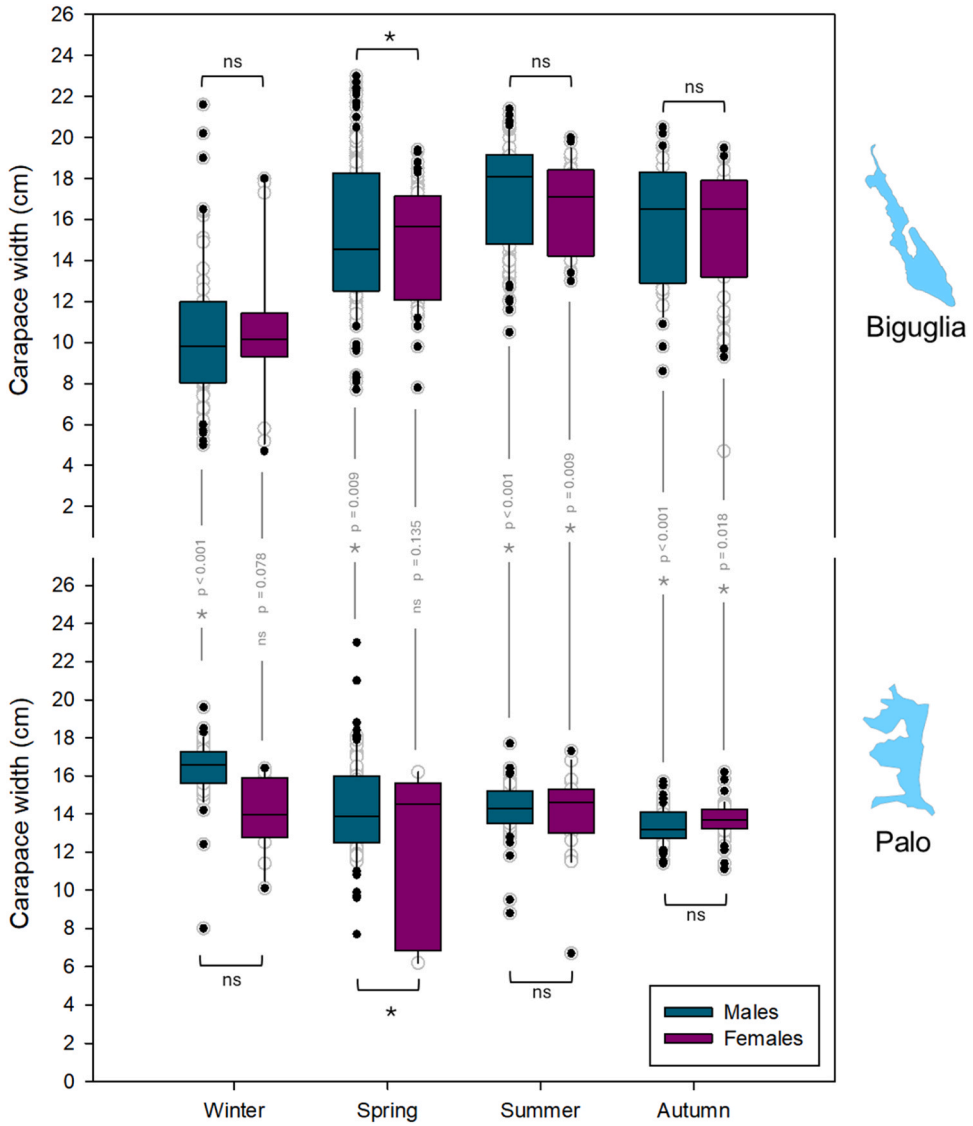


Fig. 4. Seasonal blue crab size ranges of males (dark cyan) and female (dark pink) in the Biguglia Lagoon (on the top) and the Palo Lagoon (on the bottom). *: significative differences; ns: non-significative differences, based on the ANOVA, Bonferroni post-hoc test ($p < 0.05$). Black horizontal brackets represent statistical differences between males and females for each season. Vertical lines in light grey and values represent significant differences between lagoons for males and females for each season.

smaller sizes (Italy: $L_{50} = 11.75$, Marchessaux et al., 2023a; USA: L_{50} between 10.7 and 11.2 cm). For females, however, the L_{50} obtained in the Palo Lagoon was within the same range of values as American populations (Tampa Bay, $L_{50} = 13$ cm, Guillory and Hein, 1997; Chesapeake Bay, $L_{50} = 14.7$ cm, Prager et al., 1990), whereas for Biguglia, the values were close to those measured in the St John River (USA) ($L_{50} = 15$–16 cm, Tagatz, 1968). In other areas documented in the literature, females are generally sexually mature at smaller sizes (10.2 cm (Brazil) to 12.5 cm (USA)).

The variation of the monthly sex ratio Males:Females (M:F) estimated in our study showed similar trends with the highest values at the end of winter for both lagoons as well as in summer (Biguglia Lagoon) and autumn (Palo Lagoon); over the remainder of the time, sex ratios were close to 1:1 in the Biguglia Lagoon while variable in the Palo Lagoon. The variation in sex ratio among species of the genus *Callinectes* is known to be often associated with reproductive behavior, female migrations, seasonal temperature variations, and salinity gradients (Perry, 1975; Tagatz, 1965). A seasonal transition in the sex ratio based on water temperature has been reported for *C. sapidus*, with a positive response in the number of male crabs, and a negative response in the case of females (Harding and Mann, 2010). These observations align with the findings of our study, as the monthly variation of the sex ratio showed an almost total absence of females (dominance of males) in early autumn (October-November) for both studied lagoons, likely due to the migration of adult females towards waters with higher salinity, where they release their larvae (Branco and Masunari, 2000). Overall, the populations of Biguglia and Palo lagoons were in favor to males as observed elsewhere in the Mediterranean (Croatia: Dulčić et al. 2008; Egypt: Razek

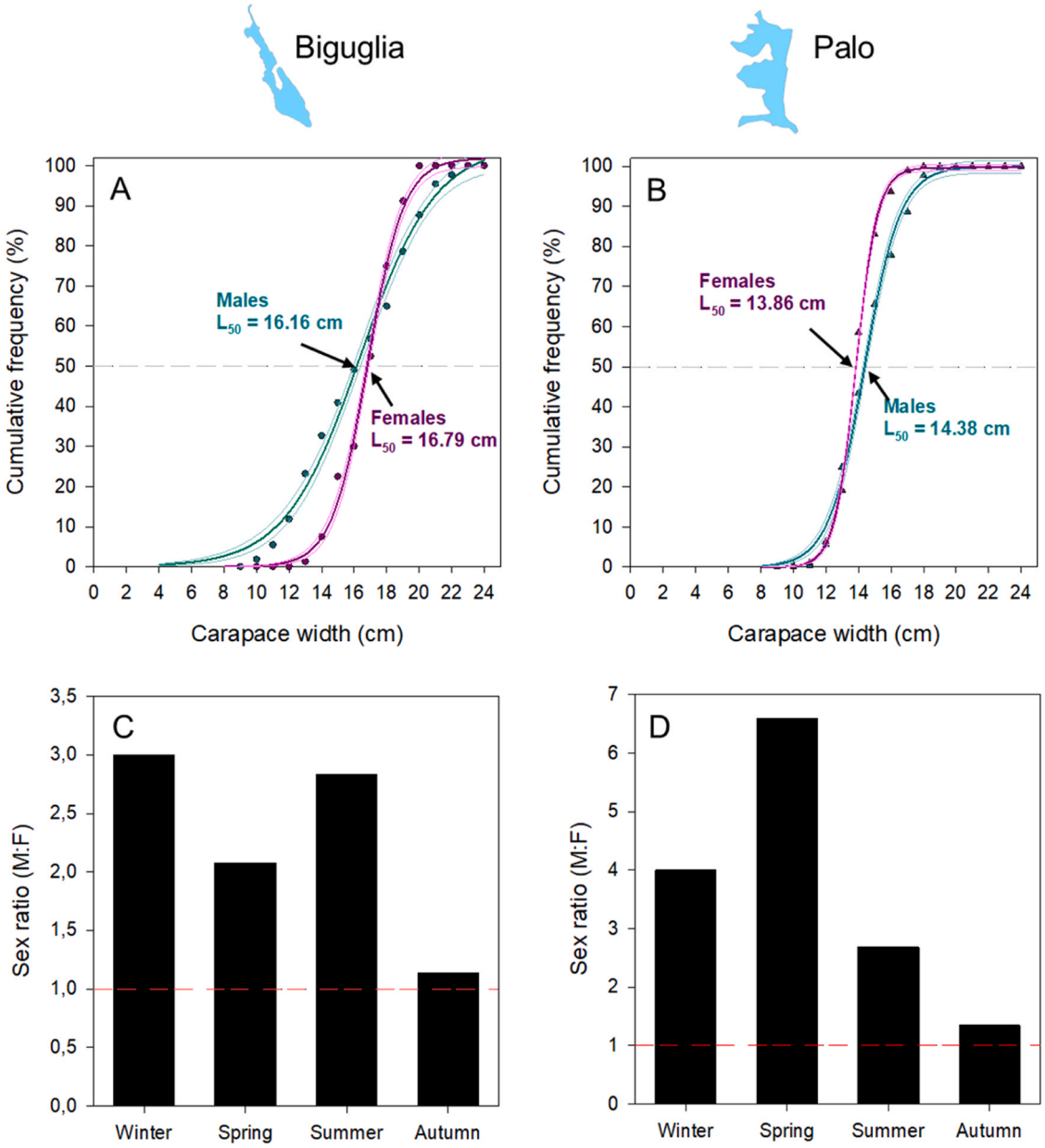


Fig. 5. Logistic regressions fitted to the percentage of mature males and females based on the carapace width (CW), L_{50} values represent the CW when 50 % of the population was mature, (A) Biguglia Lagoon, (B) Palo Lagoon; and temporal sex ratio (M:F) for (C) Biguglia and (D) Palo. The red dotted line indicates a sex ratio = 1.

et al., 2016; Italy: Carrozzo et al., 2014; Mancinelli et al., 2013; Marchessaux et al., 2023a), but diverged from lagoon in southern Turkey, where the population was in favor to females (Sumer et al., 2013).

4.3. Fishers-monitors survey to manage invasive species

This study supports the notion that the management of NIS species, such as the blue crabs in the Mediterranean Sea requires fishers-monitors strategies that are both lagoon specific and context-dependent to local ecological conditions. Context-dependent monitoring is specifically designed to identify changes that are critical within the unique ecological framework of a given area. The sensitivity of these approaches is essential for the early detection of ecological changes that may escape more generic monitoring systems, thus enabling the implementation of management measures precisely adapted to local conditions (*sensu* Lindenmayer and Likens, 2010).

Indeed, by employing long-term and frequent blue crab populations monitoring along with environmental variables such as

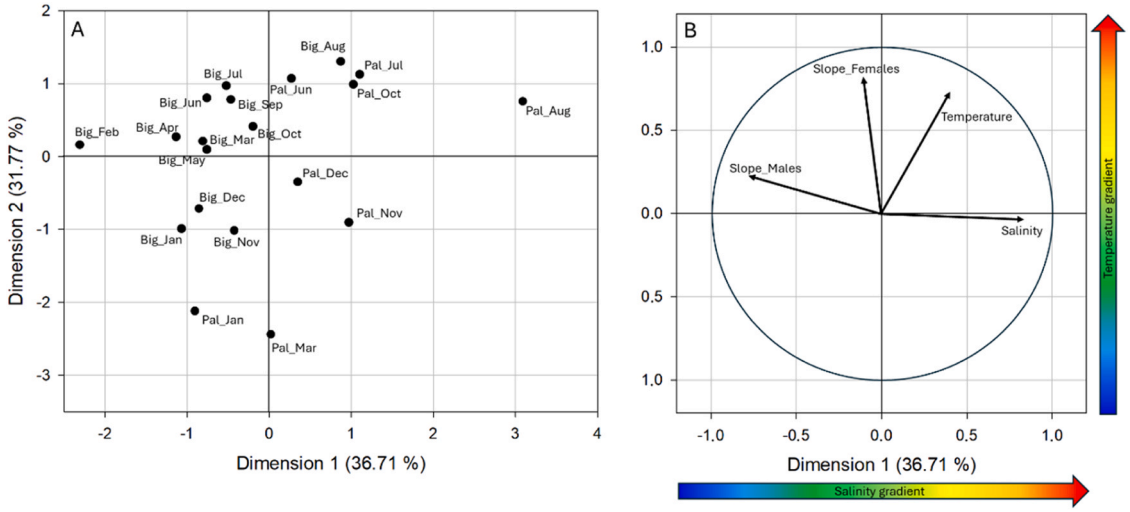


Fig. 6. Principal components analysis (PCA): (A) Projection of monthly groups (BIG: Biguglia; PAL: Palo), and (B) correlation circle.

temperature and salinity (measured monthly), we were able to accurately determine how the environment influenced blue crab population structure, thus identifying the most appropriate periods to design species control measures. In the case of the two Corsican lagoons considered in our study, and based on our findings, the most sensitive periods for the species (and therefore the period requiring population control) was when the highest percentage of mature females was recorded (over 50 %), coinciding with seasons where the growth rate was highest within a narrow environmental window. Additionally, considering that the populations in both lagoons were in favor to males, it is thus the females that would likely be key to effective population control. Two strategies can be highlighted for implementing control measures through intensive fishing of blue crabs:

- A first strategy would involve intensive fishing of males to reduce the sex ratio and prevent copulation by selecting a specific size, for example, the L_{50} (in our case CW ~ 16 cm for Biguglia; CW ~ 14 cm for Palo) of males can alter the size structure of males and the sex ratio of local populations (*sensu* Jivoff, 2003), especially for crustacean species (Ogburn, 2019).
- A second strategy would be to also remove the females directly after copulation, bearing in mind that females need 1–2 months to produce eggs (Wolcott et al., 2005). This strategy could be applied in particular in the connecting zones between lagoons and the sea, where the females have to pass through to release the larvae into the open sea. This second strategy could be carried out in parallel with the control of males to remove as many individuals as possible.
- A third strategy is that intensive fishing of mature females has the greatest impact on populations, and intensive fishing of males is only effective if their number is such that females cannot find a mate, as observed in North America (Rains et al., 2018). This second hypothesis certainly could not apply in the two lagoons studied here because the populations favored males, which were twice as abundant as females.

These two strategies should be explored in the near future in Corsica. The most effective strategy would undoubtedly be to eliminate females before the period of sexual maturity and potential copulation. In our case, this would involve intensive control in summer for Biguglia and in spring for Palo. These recommendations have been translated into operations to be implemented as part of the 'Territorial Plan for Combating the Blue Crab (*Callinectes sapidus*) in Corsica (2024–2027)' drafted by the Environmental Agency of Corsica and currently submitted to the relevant authorities at regional and national levels.

5. Conclusion

The blue crab *C. sapidus* is a case study in the Mediterranean Sea and it is known to have negative ecological and socioeconomics impacts on invaded habitats in the Mediterranean Sea. Due to its adaptability and high plasticity, this species exhibits populations that operate differently from one area to another, adapting to local environmental conditions. Despite its wide distribution in the Mediterranean, we still have limited knowledge of how populations of this invasive blue crab are structured in response to local environmental conditions.

Brackish coastal lagoons are known to be favorable to the species in its native range, where the blue crab can perform its entire life cycle (growth and reproduction). In the two studied lagoons in our study, we observed all size classes ranging from small juveniles (4 cm) to large adults (more than 18 cm) and the presence of ovigerous females indicating that these sites are favorable for *C. sapidus'* life cycle.

Analyzing size distribution is a powerful approach to describe the relationship between species size and the environment. This is especially the case for invasive species like the blue crab *C. sapidus*, and this approach is highly useful for defining sensitive periods for

Table 3
Comparison of *Callinectes sapidus* carapace width (CM) and wet weight (WW) distribution between our present study and the information available in the literature in native and introduced areas. "–" = no data; temperature (T°C, minimum and maximum), Salinity (minimum and maximum), n: number of specimens, CW: carapace width (cm); WW: wet weight (g).

							Females					Males					
Country	Location name	Native (N) / Introduced (I)	Min T°C	Max T°C	Min Salinity	Max Salinity	n	Min CW (cm)	Max CW (cm)	Min WW (g)	Max WW (g)	N	Min CW (cm)	Max CW (cm)	Min WW (g)	Max WW (g)	References
Albania Albania	Patok Lagoon	I	6.8	28.6	15.7	39.1	9	15.83	20.20	115	285	3	12.55	17.73	115	380	(Beqiraj and Kashta, 2010)
	Vaini Lagoon	I	–	–	–	–	9	11.9	15.1	76	162	36	11.3	16.7	102	294	(Kamberi et al., 2020)
Croatia	Neretva	I	9.2	26.7	7.2	33.4	10	11.2	16.6	158	520	42	11.2	14.2	158	367	(Jakov and Glamuzina, 2011)
France	Biguglia Lagoon	I	7.9	30.8	9.9	30.9	120	4.7	20.0	8.0	333	257	5.0	23.0	8	611	Our study
France	Palo Lagoon	I	7.7	31.1	27.9	51.3	97	6.2	17.3	16	242	214	8.0	19.6	34	413	Our study
Greece	Papapouli Lagoon.	I	24.7	30.3	23.5	32.1	226	5.26	18.33	8	292	290	5.09	20.90	12	540	(Kampouris et al., 2020)
Italy	Saltmarshes of Trapani	I	11.9	30.6	15	42	305	0.74	16.2	0.02	196	445	0.75	19.8	0.02	524.00	(Marchessaux et al., 2023a)
Italy	Lesina	I	10	27	11	29	5	19.0	23.0	246.9	352	3	11.5	21.0	104.9	480.5	(Cilenti et al., 2015)
Italy	Varano	I	10	29	24	29	10	18.0	21.4	219.2	369	1	–	–	–	–	(Cilenti et al., 2015)
Italy	Ugento	I	–	–	0.8	23	1	–	–	–	–	4	17.0	21.0	350	568	(Gennaio et al., 2006)
Morocco	Marchica Lagoon	I	–	–	–	–	27	9.0	18.5	58.52	274.73	77	9.4	18.7	61.49	470.35	(Oussellam et al., 2021)
Morocco	Coastal	I	–	–	–	–	59	9.71	17.97	68.2	273.5	94	10.91	18.54	108.0	412.6	(Chaouti et al., 2022)
New England	Seekonk River	N	17.9	29.0	1.2	24.0	–	1.1	16.4	–	–	–	0.8	17.1	–	–	(Taylor and Fehon, 2021)
New England	Taunton River	N	18.4	29.5	0.3	27.8	–	1.2	16.0	–	–	–	1.2	18.5	–	–	(Taylor and Fehon, 2021)
Poland	Lake Dąbie	I	–	–	–	–	1	12.6	–	100.19	–	–	–	–	–	–	(Czerniejewski et al., 2020)
Tunisia	Ghar El Melh Lagoon	I	–	–	–	–	32	11.14	11.86	90.21	101.83	30	10.02	10.85	81.28	98.66	(Fassatoui et al., 2021)
Turkey	Beymelek	I	–	–	–	–	317	5.5	17.5	12	290	710	5.1	18.1	8.92	448	(Atar and Seçer, 2003)
Turkey	Camlik	I	11.9	30.3	13.9	17.8	355	3.90	17.30	4.20	253.00	356	4.00	17.80	0.70	301.00	(Gokce et al., 2006)
Turkey	Yumurtalik	I	–	–	–	–	184	4.9	19.0	–	–	234	3.7	18.6	–	–	(Türeli et al., 2016)

Table 4
Comparison of the size at first maturity for *Callinectes sapidus* between our present study and the information available in the literature in native and introduced areas.

Country	Study site name	Native (N) / Introduced (I)	Sex	Size at maturity (cm)	References
France	Biguglia Lagoon	I	Males	16.16	Our study
France	Palo Lagoon	I	Males	14.38	Our study
Italy	Trapani saltmarshes	I	Males	11.75	(Marchessaux et al., 2023a)
Brazil	Babitonga Bay	N	Males	8.9	(Pereira et al., 2009)
USA	Sarah's Creek and Purtan Bay	N	Males	10.7	(Van Engel, 1990)
USA	Chesapeake Bay	N	Males	11.2	(Perry, 1975)
France	Biguglia Lagoon	I	Females	16.79	Our study
France	Palo Lagoon	I	Females	13.86	Our study
Italy	Trapani saltmarshes	I	Females	12.00	(Marchessaux et al., 2023a)
Greece	Evros River	I	Females	12.39	(Kevrekidis et al., 2023)
Turkey	Beymelek Lagoon	I	Females	11.85	(Sumer et al., 2013)
Brazil	Lagoon-Estuarine of Iguape and Cananéia	N	Females	10.33	(Severino-Rodrigues et al., 2013)
Brazil	Babitonga Bay	N	Females	10.2	(Pereira et al., 2009)
USA	St. Johns River	N	Females	15–16	(Tagatz, 1968)
USA	Tampa Bay	N	Females	13.0	(Steele and Bert, 1994)
USA	-	N	Females	12.5	(Guillory and Hein, 1997)
USA	Maryland bays	N	Females	11.6	(Lycett et al., 2020)
USA	Texas bay	N	Females	12.0	(Fisher, 1999)
USA	Chesapeake Bay	N	Females	14.7	(Prager et al., 1990)
USA	Chesapeake Bay	N	Females	12.0	(Rugolo, 1997)
USA	Chesapeake Bay	N	Females	11.2	(Perry, 1975)

implementing management measures. Using this strategy, our study once again demonstrates that populations of *C. sapidus* in both the Biguglia and Palo lagoons are well-established, comprising juveniles, subadults, and adults. The results presented in this study provide evidence of the species' local adaptation to invade different types of habitats. The analysis of size distribution has revealed comprehensive results on how the environment (temperature and salinity) influences blue crab populations in terms of growth and sexual maturity, highlighting significant differences in the functioning of blue crab populations between the two geographically close lagoons in Corsica.

Our study has highlighted an innovative approach to studying an invasive species, particularly the blue crab *C. sapidus*. Corsica is an island with around 200 coastal wetlands, predominantly brackish coastal lagoons with high diversity (95 coastal lagoons), that are favorable to *C. sapidus* and where the species is primarily observed (> 20 highly impacted lagoons. in Corsica; see https://orzhc.oec.fr/Action_Callinectes_sapidus_mpage_258.htm).

The results presented in this study show the importance of long-term monitoring of blue crab populations at a local level scale and helps to refine our knowledge of how populations respond to local environmental conditions, as well as to implement control measures adapted to each environment invaded by blue crabs.

Ethics Statement

Not applicable: This manuscript does not include human or animal research. If this manuscript involves research on animals or humans, it is imperative to disclose all approval details.

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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.

Data availability

Data will be made available on request.

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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.gecco.2024.e03168.

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