Research Article

*Mediterranean Marine Science*
Indexed in WoS (Web of Science, ISI Thomson) and SCOPUS
www.hcmr.gr
DOI: https://doi.org/10.12681/mms.42458

# Reproductive Characteristics of the Invasive Blue Crab *Callinectes sapidus* (Rathbun, 1896) in the Marchica Lagoon (Alboran Sea, Morocco)

**Nassir KADDOURI[1,2], Douaa SLIMANI[3], Mohamed SELFATI[4], Najib EL OUAMARI[2], and Hocein BAZAIRI[1,5]**

[1] Laboratory of Biodiversity, Ecology and Genome, Faculty of Sciences, Mohammed V University in Rabat, 4 Avenue Ibn Battouta, B.P. 1014 RP, Rabat, Morocco
[2] Fishing Laboratory, Regional Center of the National Institute of Fisheries Research, Nador, Morocco
[3] Laboratory for the Improvement of Agricultural Production, Biotechnology and the Environment, FSO, Mohammed First University, Oujda, Morocco
[4] Laboratory of Health, Environment and Biotechnology, Faculty of Sciences Ain Chock, Hassan II University of Casablanca, Maarif, Casablanca P.O. Box 5366, Morocco
[5] Natural Sciences and Environment Research Hub, University of Gibraltar, Europa Point Campus, Gibraltar

Corresponding author: Nassir KADDOURI; Kaddouri.nassir@gmail.com

Contributing Editor: Thanos DAILIANIS

Received: 22 August 2025; Accepted: 24 March 2026; Published online: 25 May 2026

## Abstract

The blue crab *Callinectes sapidus*, originally native to the western Atlantic coast, is a well-established invasive species along the Atlantic and Mediterranean coasts of Morocco. This study aimed to investigate the reproductive traits of *C. sapidus* along the Moroccan Mediterranean coast, specifically in the Marchica Lagoon, to support post-border biosecurity strategies. The research focused on estimating the gonadosomatic index (GSI), identifying the spawning season, and determining the size at first maturity of female *C. sapidus*. Monthly samples were collected as bycatch of artisanal fishers operating in the lagoon between May 2022 and April 2024. A total of 938 crabs were collected, with an average carapace width (CW) of 119.46 ± 36.65 mm, carapace length (CL) of 54.11 ± 15.68 mm, and body weight of 164.20 ± 129.16 g. The sex ratio was significantly skewed toward males (1.36:1). Ovigerous females were observed from April to October, with two spawning peaks: the first in April and a more pronounced one in July to August, indicated by increased gonadosomatic index and a higher proportion of ovigerous females. The carapace width at 50% maturity ($L_{50}$) was 114.4 mm overall, with females maturing at a larger size (117.8 mm) than males (111.1 mm). These findings provide a foundation for developing targeted strategies to manage the spread of *C. sapidus* in the Marchica Lagoon, reduce its population, and mitigate environmental impacts. They also highlight the potential to valorize the species as a fishery resource, potentially turning its management into an economic and ecological advantage.

**Keywords:** *Callinectes sapidus*; Moroccan Mediterranean; reproductive biology; spawning period; ovigerous females; invasion management.

## Introduction

Biological invasions are among the major threats to global biodiversity and ecosystem integrity, alongside pollution, habitat degradation, and the overexploitation of natural resources (Katsanevakis *et al.*, 2014; IPBES, 2020; Diagne *et al.*, 2020; Verma *et al.*, 2020). These anthropogenic pressures, intensified by climate change, are profoundly altering natural habitats and accelerating biodiversity loss. By modifying key environmental conditions, climate change facilitates the establishment, survival, and spread of invasive alien species (IAS), thereby disrupting ecological balances and threatening native species (Zenetos *et al.*, 2010; Seebens *et al.*, 2017).

In marine ecosystems, biological invasions can lead to long-lasting and, sometimes, irreversible ecological changes across both human and geological timescales (Gravez *et al.*, 2005; Boudouresque, 2005). The expansion of IAS is driven by both direct human-mediated pathways and the indirect effects of global warming (Ramos *et al.*, 2018; Seebens *et al.*, 2021). Rising ocean temperatures influence key physiological and ecological processes, including life cycles, reproductive performance, and population dynamics, ultimately reshaping marine community structure (Atkinson, 1994; Hartnoll, 1982; Sara *et al.*, 2013, 2018). The changes promote range shifts toward higher latitudes and temperate regions, where invasive species may successfully establish and persist. Climate change may also amplify the ecological impacts of IAS and contribute to the spread of marine diseases (IPBES, 2018).

The Mediterranean Sea, including its associated lagoons, is recognized as one of the world's hotspots for marine biological invasions, with 1011 IAS currently identified (Galanidi *et al.*, 2022). Approximately 50% of these species are thought to have been introduced mainly through the Corridor pathway, with the Suez Canal acting as the principal gateway (Galanidi *et al.*, 2022). Since 1870, more than 986 non-indigenous marine species have been recorded in the region, including 91 species of decapod and stomatopod crustaceans, of which at least 18 are considered invasive (Zenetos *et al.*, 2012). Among these, the blue crab *C. sapidus* (Rathbun, 1896), a species native to the western Atlantic coasts of the Americas, has emerged as a particularly impactful invader.

First introduced to European waters in the early 20th century, possibly via ballast water or deliberate releases, *C. sapidus* has demonstrated remarkable ecological plasticity and dispersal capacity (Williams, 1974; Nehring, 2011; Castriota *et al.*, 2012, 2024). Its initial detection in the Mediterranean was reported in the northern Adriatic Sea (Giordani-Soika, 1951), and it has since spread widely, especially throughout the eastern Mediterranean basin (Galil *et al.*, 2002; Nehring, 2011). The species is now established in multiple regions, including the eastern Aegean and the northwestern Mediterranean (Koukouras *et al.*, 1992; Enzenrob *et al.*, 1997; Atar & Secer, 2003; Streftaris & Zenetos, 2006; Onofri *et al.*, 2008; Tuncer & Bilgin, 2008; Dulčić *et al.*, 2010; Eleftheriou *et al.*, 2011; Mancinelli *et al.*, 2017, 2021).

In Morocco, *C. sapidus* was first reported in the Marchica Lagoon in 2017, marking the beginning of its establishment along the country's Mediterranean coast (Oussellam & Bazairi in Chartosia *et al.*, 2018). Since then, the species has become increasingly prevalent and is now considered systematic across various coastal areas (Gourari *et al.*, 2025). The strategic position of Morocco's Mediterranean coast as a major maritime corridor connecting Europe, Africa, and the Middle East likely facilitates the introduction and spread of this and other invasive marine species.

The rapid proliferation of *C. sapidus* has raised significant ecological and socioeconomic concerns. The species poses a serious threat to marine ecosystems through predation, resource competition, and habitat alteration, leading to declines in native biodiversity and changes in ecosystem functioning (Mancinelli *et al.*, 2017; Prado *et al.*, 2020; Zenetos *et al.*, 2022; Clavero *et al.*, 2022; Gavioli *et al.*, 2025). It also competes directly with native crabs and demersal fish, exacerbating ecological imbalances and undermining the sustainability of artisanal fisheries (Nehring, 2011; Labrune *et al.*, 2019; Khamassi *et al.*, 2022). In addition, the damage inflicted on fishing gear, combined with reduced catches of commercially valuable species, underscores the urgency of understanding and managing its impacts.

From a biological perspective, *C. sapidus* exhibits a complex life history, characterized by multiple developmental stages, including planktonic zoeae, post-larval megalopae, benthic juveniles, and rapidly growing adults (Millikin & Williams, 1984). Throughout its ontogeny, the species utilizes a range of marine and estuarine habitats, with marked spatial and behavioral segregation between sexes. Adult males and juveniles typically inhabit low-salinity estuarine zones, whereas ovigerous females migrate seaward toward higher salinity waters to spawn. The resulting planktonic larvae are carried offshore by tidal- and wind-driven currents, where early development occurs on the continental shelf (Aguilar *et al.*, 2005; Epifanio, 2007). Post-larval stages subsequently return to inshore areas, eventually entering estuaries, where they settle and undergo growth and sexual maturation (Tankersley & Forward, 2007; Lipcius *et al.*, 2007; Epifanio, 2007). Brackish environments, such as Marchica Lagoon, provide ideal conditions for the survival and reproductive success of *C. sapidus*, owing to their ecological characteristics and relative trophic richness.

Despite its growing significance on the Mediterranean coast, our understanding of its population structure, reproductive dynamics, and ecological impacts remains limited (Clavero *et al.*, 2022; Gavioli *et al.*, 2025). Further research is, therefore, urgently needed to quantify its effects and identify effective mitigating strategies. One promising approach for controlling invasive populations involves targeted harvesting, particularly during reproductive aggregations at peak spawning periods. Selective fishing during these critical periods could reduce offspring production and, consequently, limit population expansion (Marchessaux *et al.*, 2024). In parallel, developing commercial markets for *C. sapidus* could incentivize local fishers to target the species actively, thereby combining ecological management with economic benefits (Mancinelli *et al.*, 2017).

The success of such integrated management approaches depends on the availability of accurate biological and ecological data. In this context, quantifying key reproductive parameters, such as the Gonadosomatic Index (GSI), Hepatosomatic Index (HSI), and size at first sexual maturity ($L_{50}$), is critical for predicting reproductive cycles and implementing timely control measures. Currently, no such data are available for *C. sapidus* in the Moroccan Mediterranean. Therefore, this study aims to characterize the main reproductive traits of *C. sapidus* in the Marchica Lagoon in order to provide baseline information for science-based management strategies, with the dual objectives of preserving local biodiversity and supporting the sustainability of artisanal fisheries in Moroccan coastal waters.

## Materials and Methods

### *Study area*

The Marchica Lagoon (35.15999° N, 2.83999° W), also known as the Nador lagoon, is the second largest lagoon in North Africa and the only one along the Moroccan Mediterranean coast, covering about 115 km$^2$. It extends approximately 25 km in length and 7.5 km in width, with a maximum depth of 8 m. The lagoon is separated from the Mediterranean Sea by a sandy barrier and connected to it by a 300 m–wide artificial channel that ensures permanent water exchange with the open sea (Fig. 1). This artificial connection has significantly reduced the lagoon's water renewal time from about 80 to 45 days, improving hydrodynamic circulation and water quality (Hilmi, 2005). The hydrological balance of the lagoon is maintained by marine inflows through the artificial inlet, groundwater contributions, and intermittent surface runoff from nearby watercourses (Jeyar *et al.*, 2015). The region has a typical Mediterranean climate with hot, dry summers and cool, wet winters. Annual precipitation is relatively low, averaging around 300 mm, with noticeable interannual variability (El Yaouti *et al.*, 2009; Re, 2010). Wind patterns show clear seasonal variability and play an important role in water circulation, sediment transport, and mixing processes within the lagoon (Tesson, 1977; Hilmi, 2005).

Ecologically, the Marchica Lagoon holds considerable importance. It has been designated a Site of Biological and Ecological Interest (SIBE) since 1996 and a Ramsar Wetland of International Importance since 2005, reflecting its role as a vital habitat for numerous aquatic and migratory species. Socioeconomically, the lagoon supports local artisanal fisheries and provides livelihoods for communities in the surrounding area. However, this unique ecosystem is increasingly threatened by multiple anthropogenic pressures, including rapid urbanization, pollution, overfishing, and intensive tourism development. These threats are compounded by natural stressors, such as climate change and the growing incidence of biological invasions, which together pose serious risks to the lagoon's ecological integrity and resource sustainability.

### *Data Collection and Laboratory*

Between May 2022 and April 2024, blue crab specimens were collected monthly in the Marchica Lagoon as bycatch from artisanal fishers. These fishers primarily employ two traditional fishing gears: the "fyke nets," a type of lift net, and "trammel nets," a three-layered gill net designed to capture various fish species. The majority of fishing activity occurs in the central sector of the lagoon, where water depths are more suitable for gear deployment. Shallow zones and river mouths are typically avoided to minimize the accidental capture of blue crabs, which remain undesirable to local fishers due to their low commercial value. This spatial selectivity underscores an intentional effort to maximize target species catch while limiting bycatch of non-target taxa such as *C. sapidus*.

Collected specimens were transported in plastic coolers to the laboratory of the National Institute of Fisheries Research (INRH) at the regional center in Nador. A total of 938 crabs were analyzed. Morphometric parameters, including carapace width (CW), carapace length (CL), and total wet weight (W), were recorded using precision instruments: digital calipers with a 0.1 mm accuracy for

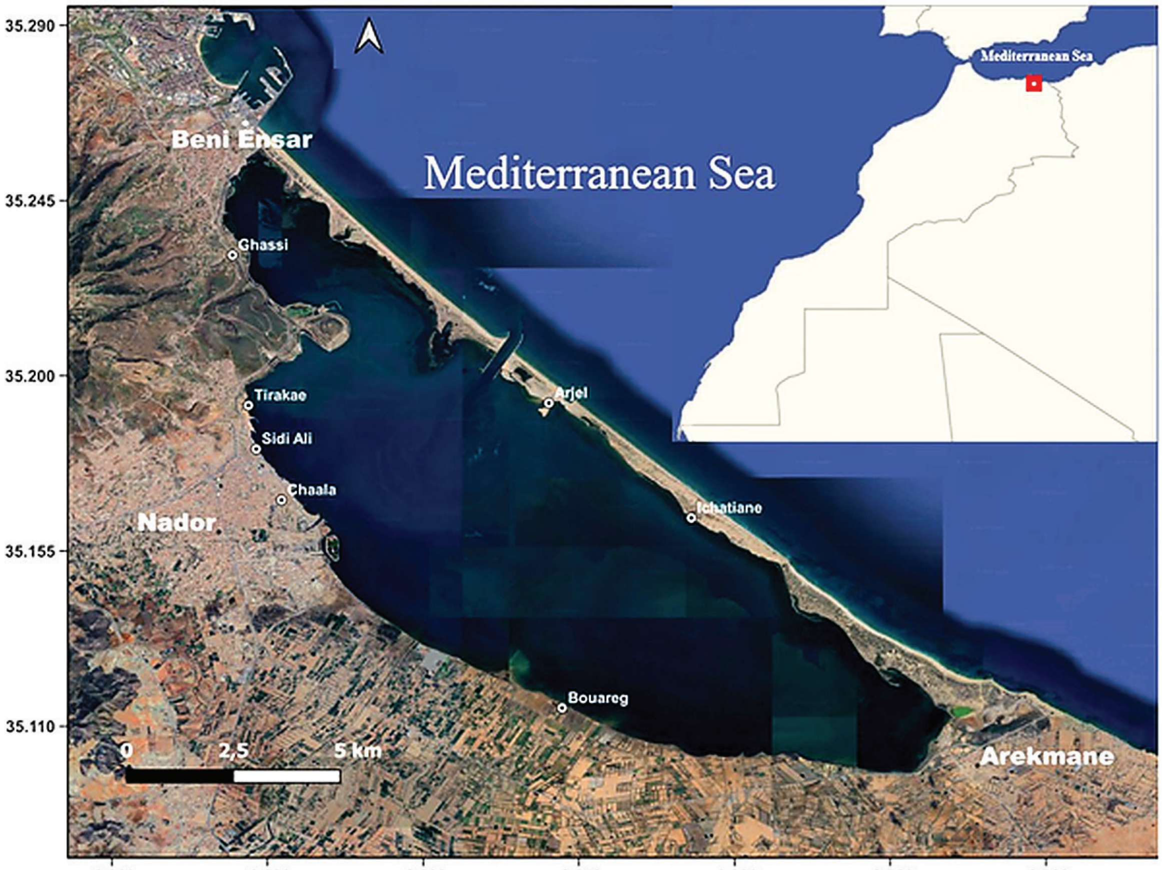

***Fig. 1:*** Location of the Marchica Lagoon showing the main port and fishing sites.

CW and CL measurements and an electronic balance with 0.01 g accuracy for body weight. Carapace length (CL) was measured dorsally along the midline, from the frontal notch to the posterior margin, while carapace width (CW) was defined as the distance between the tips of the posterior lateral spines. Subsequently, crabs were dissected for internal examination. The gonads and hepatopancreas were carefully removed and weighed.

Each month, specimens were carefully dissected to determine their sex through detailed examination of abdominal morphology. Females were classified as immature if they had a narrow, triangular abdominal flap, while mature females were identified by their wider, semicircular abdomen (Millikin & Williams, 1984). For males, immaturity was indicated by a T-shaped abdomen tightly attached to the sternum, whereas in mature males, the abdomen was detached and more flexible (Van Engel, 1990). Female reproductive stages were further determined using Hard's (1942) five-stage classification: Stage I (SM1): Immediately following the last molt, the ovary is small, inconspicuous, and white in color. Stage II (SM2): Ovaries are orange in color and marked by a gradual increase in length and diameter. Stage III (SM3): Mature ovary preceding the first ovulation, the ovary is bright orange in color and of large size, distinguished from Stage IV by the absence of eggshell remnants on swimmerets. Stage IV (SM4): Period between the first and second ovulations; ovaries are orange in color and of large size, and eggshell remnants are present on the swimmerets. Stage V (SM5): Following the second ovulation, the ovary is collapsed, gray or brownish in color, eggshell remnants are present on the swimmerets.

Ovigerous females (OF) were also examined to determine the incubation stage based on the coloration of the egg masses. Egg developmental stages were categorized as follows: stage I, bright orange; stage II, yellow; stage III, brown; stage IV, dark brown; stage V, black.

## Data analysis

### Size structure

To assess the population structure of *C. sapidus* in the Marchica Lagoon, carapace width (CW) measurements were grouped into 5 mm size classes for length frequency distribution analysis (LFDA). This allowed for a detailed evaluation of the size distribution within the sampled population. A comparative analysis of the mean CW between sexes was performed using the non-parametric Wilcoxon rank-sum test.

### Sex Ratio

The sex ratio was calculated as the proportion of males to females within the sampled population. A Pearson's Chi-squared test ($\chi^2$) was applied on a monthly basis to determine whether the observed proportions of males and females each month were statistically different from the theoretical ratio of 1 male to 1 female. The test compares observed (Oi) versus expected (Ei) frequencies under the null hypothesis of equal sex distribution, using the formula:

$$X^2 = \frac{(Oi - Ei)^2}{Ei}$$

### Spawning Period

To characterize the reproductive cycle and determine the spawning period of *C. sapidus*, both qualitative and quantitative approaches were employed. The qualitative approach involved monitoring the monthly frequency of ovigerous females, as their presence is indicative of active spawning. Additionally, a one-way ANOVA was used to test for significant differences in the mean carapace width among ovigerous females across months, providing further insight into reproductive timing. The quantitative approach involved calculating and analyzing the monthly fluctuations in the gonadosomatic index (GSI) and hepatosomatic index (HSI), two key metrics for assessing reproductive status and energy allocation, respectively. These indices were calculated using the following formulas:

$$GSI = 100 \times (GW / BW)$$
$$HSI = 100 \times (HW / BW)$$

Where GW (g) is the gonad weight, HW (g) is the hepatopancreas weight, and BW (g) is the body weight. These indices were analyzed monthly to detect seasonal trends associated with reproductive activity.

### Carapace width at First Sexual Maturity ($L_{50}$)

The carapace width at first sexual maturity ($L_{50}$) was estimated to identify the size at which 50% of the population reaches sexual maturity. This parameter was derived by fitting a logistic regression model to the proportion of mature individuals across size classes. The sigmoid curve used for this analysis follows the logistic function (Dagnelie, 1973):

$$P(CW) = \frac{1}{1+e^{(a+bl)}}$$

Where P represents the proportion of mature individuals, a and b are the regression constants, and CW is the carapace width of the individuals (in mm). The $L_{50}$ value was computed using the sizeMat package in the R software, employing a generalized linear model (GLM) with a binomial error distribution and a logit link function.

## Results

### Size composition of Callinectes sapidus

A total of 938 individuals of *C. sapidus* were collected during the study, comprising 544 males (58%) and 394 females (42%). In males, carapace width (CW) ranged from 26 to 198 mm (mean ± SD: 127.51 ± 1.64 mm), carapace length (CL) from 13 to 96 mm (58.80 ± 0.72 mm), and body weight (W) from 2.19 to 584.6 g (211.22 ± 6.20 g). In females, CW varied between 26 and 173 mm (mean ± SD: 108.35 ± 1.55 mm), CL between 13 and 73 mm (47.65 ± 0.56 mm), and W between 2.32 and 317.8 g (99.37 ± 2.99 g) (Table 1). The most frequent CW classes ranged from 80 to 140 mm in females (52.3%) and from 135 to 175 mm in males (44.2%) (Fig. 2).

The Wilcoxon test revealed a highly significant difference between sexes ($p < 0.001$), with males being significantly larger CW than females. Overall, males exhibited greater body size than females in the Marchica Lagoon.

Crab size showed significant seasonal variation (Kruskal–Wallis test: $p < 0.001$). Post hoc comparisons indicated that the largest individuals were recorded in autumn, with mean size significantly higher than that observed in the other seasons. In contrast, the smallest mean size was observed in spring and differed significantly from those recorded in winter, summer, and autumn (Fig. 3).

### *Sex ratio*

Overall, males were significantly more abundant than females, with a sex ratio of 1.36 and a significant deviation from the expected 1:1 ratio (M:F; $\chi^2 = 22.628$, $p < 0.001$). Monthly sex ratios varied from a minimum of 0.36 in April to a maximum of 5.22 in August (Table 2). Females slightly outnumbered males in March, April, and July, whereas males predominated during the rest of the year.

**Table 1**. Characteristics of carapace width (CW), carapace length (CL), and weight (W) of *Callinectes sapidus* collected from the Marchica Lagoon (F: Female, M: Male, C: Combined sexes).

| Sex | N° | CW (mm) | | | CL (mm) | | | W (g) | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Mean ± SD | Min | Max | Mean± SD | Min | Max | Mean± SD | Min | Max |
| **M** | 544 | 127.51±1.64 | 26 | 198 | 58.80±0.72 | 13 | 96 | 211.22±6.20 | 2.19 | 584.6 |
| **F** | 394 | 108.35 ±1.55 | 26 | 173 | 47.65±0.56 | 13 | 73 | 99.37±2.99 | 2.32 | 317.8 |
| **C** | 938 | 119.46±1.20 | 26 | 198 | 54.11±0.51 | 13 | 96 | 164.21±4.21 | 2.19 | 584.6 |

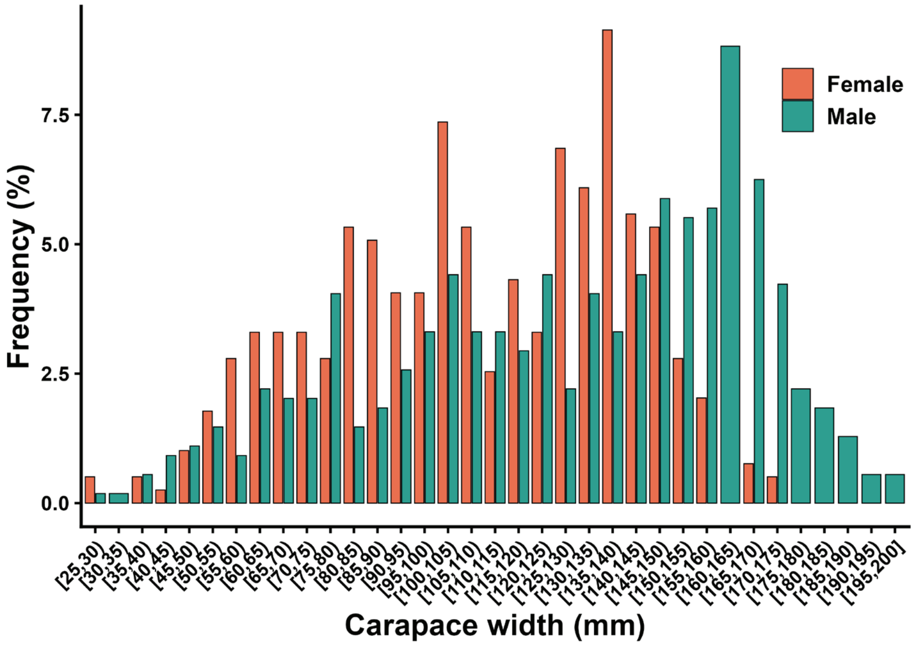

***Fig. 2:*** Frequency distribution of carapace width (CW) of *Callinectes sapidus* in the Marchica Lagoon (F: Female, M: Male).

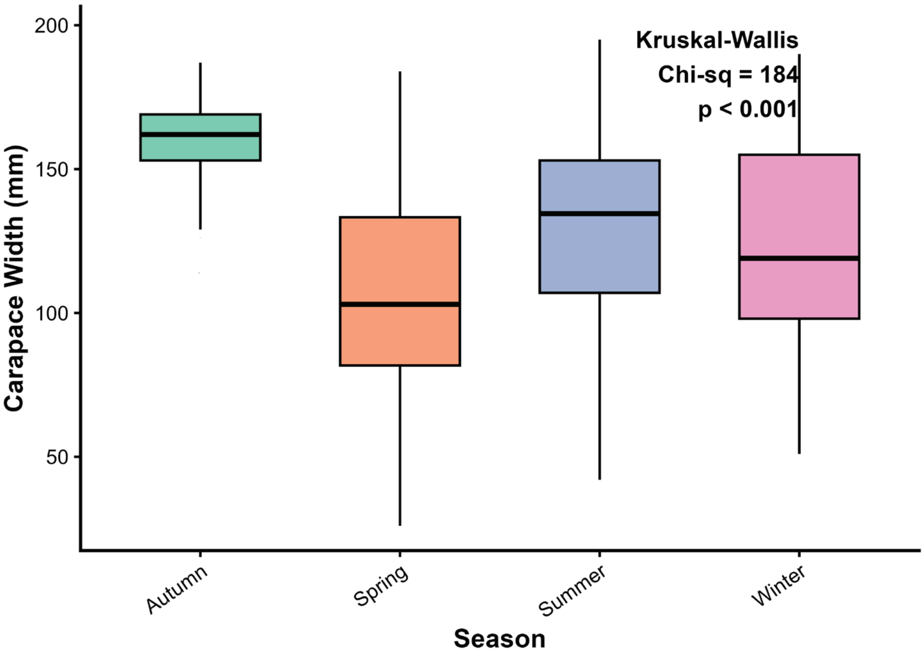

***Fig. 3:*** Seasonal variation in width frequencies of the blue crab *Callinectes sapidus* in the Marchica Lagoon.

**Table 2.** Monthly variation in the sex ratio of the blue crab *Callinectes sapidus* in the Marchica Lagoon.

| Months | Sex Ratio (M/F) | χ2 | P-value |
|---|---|---|---|
| January | 2.28 | 8.97 | 0.0028* |
| February | 1.23 | 0.82 | 0.365 |
| March | 0.86 | 0.6 | 0.4371 |
| April | 0.36 | 16.06 | 0.000061* |
| May | 1.35 | 5.03 | 0.0249 * |
| June | 1.94 | 14.03 | 0.00018 * |
| July | 0.78 | 1.47 | 0.2254 |
| August | 5.22 | 25,79 | 0.00000038 * |
| September | - |  | - |
| October | 2.30 | 5.12 | 0.0236 * |
| November | - |  | - |
| December | 1 | 0 | 1 |

### *Spawning period*

#### *Ovarian Stages*

For blue crab females, mature individuals (N = 170) ranged in size from 105 to 173 mm CW, with a mean (± SD) of (137 ±12.17 mm), whereas immature individuals (N = 224) ranged from 26 to 128 mm CW (mean ± SD: 86 ± 20.93 mm). Individuals in different reproductive phases appeared throughout the year. Immature (SM1) and premature (SM2) ovaries were present mostly in winter (December–March) and from late spring to early summer (June). Females with mature ovaries (SM3 and SM4) were observed from spring (April) to mid-fall (October), with higher percentages found from mid-summer (July) to mid-fall (October). SM4 peaked in mid-summer (July–August), and SM5 peaked in October (Fig. 4).

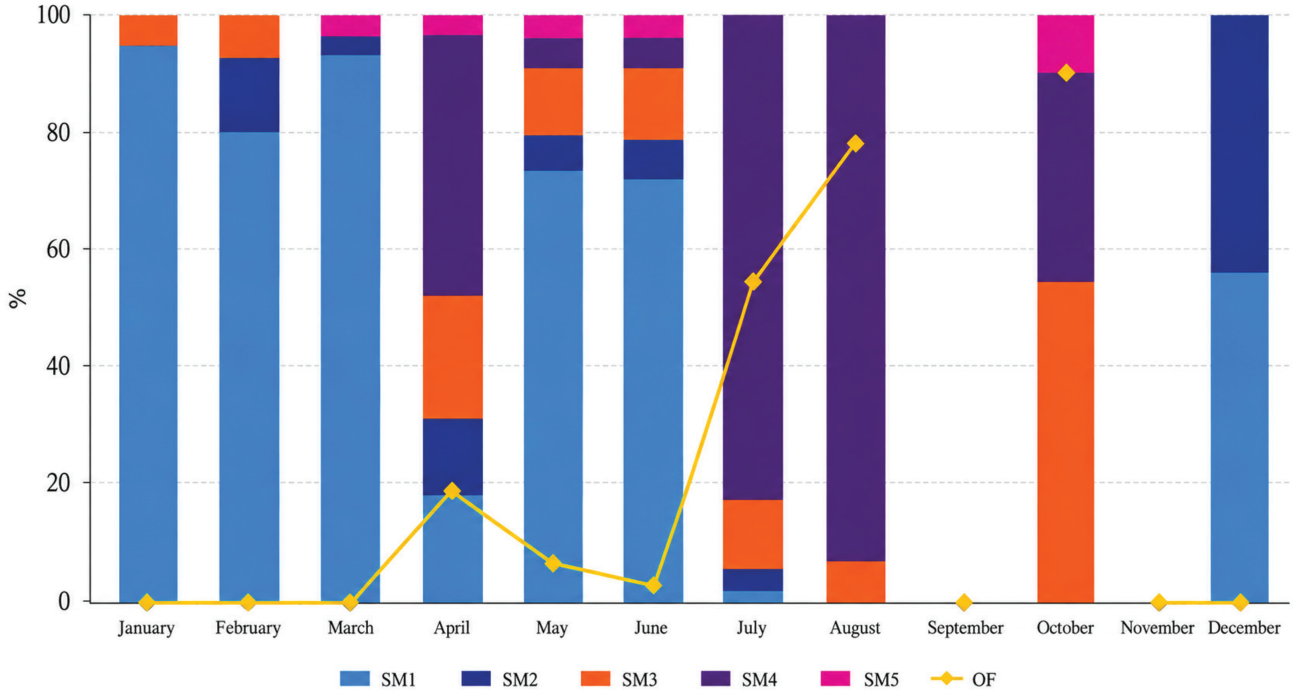

***Fig. 4:*** Evolution of the ovarian stages and ovigerous females of the blue crab in the Marchica Lagoon.

### *Ovigerous Females*

The carapace width (CW) of ovigerous females carrying eggs at developmental stages 4 and 5 extended from 115 to 169 mm (with a mean of 137 ± 9.85 mm) and 119 to 156 mm (with a mean of 134 ± 14.19 mm), respectively. Statistical analysis (one-way ANOVA) revealed no significant differences in mean carapace width among ovigerous females across these different egg development stages ($F = 0.29$, $p = 0.876$). Ovigerous females were recorded exclusively between April and October, with none observed in September. Their presence was limited in May (7%) and June (4%). However, their numbers increased substantially in July, accounting for 55% of the ovigerous females, and peaked in October, when they comprised 90% of the total. Following this peak, a sharp decline was recorded in November, with no ovigerous females captured. Females bearing eggs at advanced developmental stages (SM4 and SM5) comprised about 70% of the total ovigerous females. These advanced stages were predominant in April (100%), suggesting an early spawning peak, followed by high proportions in July (90%) and October (55%), indicating a second spawning peak (Fig. 4).

Another effective method to identify the spawning season of the species is by analyzing the monthly variations in both the gonadosomatic index (GSI) and the hepatosomatic index (HSI) (Fig. 5). Statistical analysis (ANOVA) revealed significant differences in GSI values across the sampling periods ($F = 0.342$, $p < 0.001$), suggesting a clear seasonal variation in gonad development. The highest GSI values were recorded during the months of April, June, July, and August, with respective (means ±SD) of 5.55 ± 3.44, 8.36 ± 3.38, 5.93 ± 2.57, and 7.94 ± 1.45, suggesting two spawning peaks. Conversely, the lowest GSI values were observed in March and January, with means of 0.26 ± 0.23 and 0.7 ± 0.7, respectively. Notably, the GSI values were zero in September, November, and December.

The analysis of variance (ANOVA) conducted on the hepatosomatic index (HSI) values revealed significant temporal differences ($F = 26.73$, $p<0.0001$) throughout the year. In the Marchica Lagoon population, the maximum accumulation of reserves in the hepatopancreas occurred in February to March and May, prior to the spawning periods. The lowest monthly value was recorded in July and August. Notably, the HSI values were found to be zero in September and November, coinciding with months when no female crabs were captured.

### ***Size at first sexual maturity***

The mean carapace width at first sexual maturity for 50 % of *C. sapidus* individuals was calculated as 117.8 mm ($R^2 = 0.89$) for females, 111.1 mm ($R^2 = 0.91$) for males, and 114.4 mm ($R^2 = 0.90$) for both sexes combined (Fig. 6).

## **Discussion**

Amid growing concern over the spread of invasive marine species in the Mediterranean Sea, the Atlantic blue crab *C. sapidus*, listed among the 100 worst invasive species in this region (Streftaris & Zenetos, 2006), has attracted particular attention. The present study provides new insights into the population structure and reproductive biology of the blue crab *C. sapidus* in the Marchica Lagoon (Alboran Sea, Morocco). As an invasive species, *C. sapidus* poses significant ecological and socioeconomic concerns, including competition with native species and

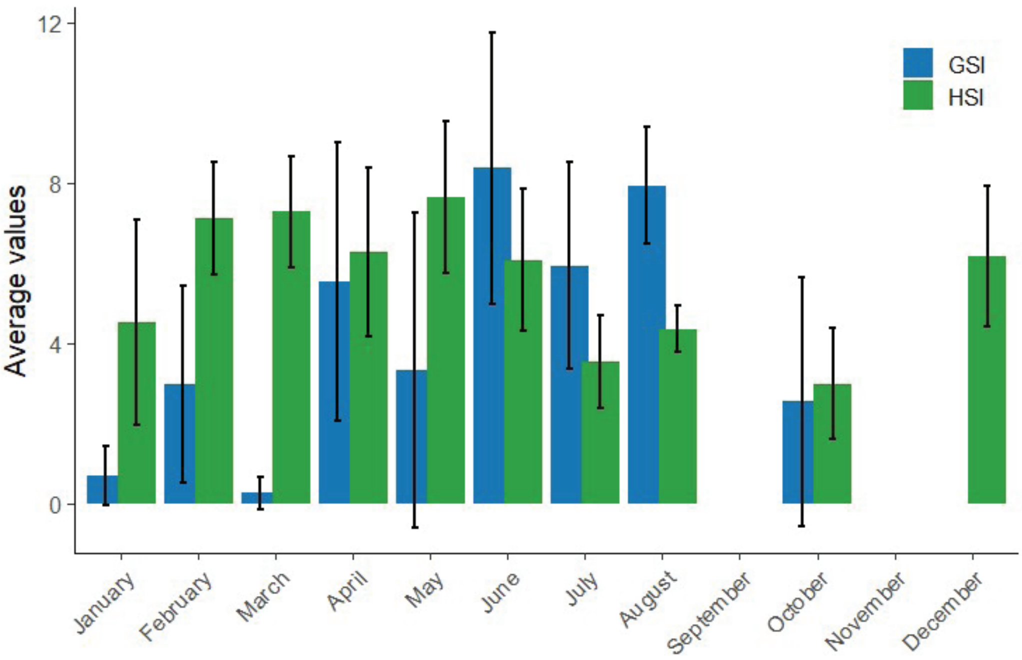

***Fig. 5:*** Monthly variation in GSI and HSI of *Callinectes sapidus* females in the Marchica Lagoon.

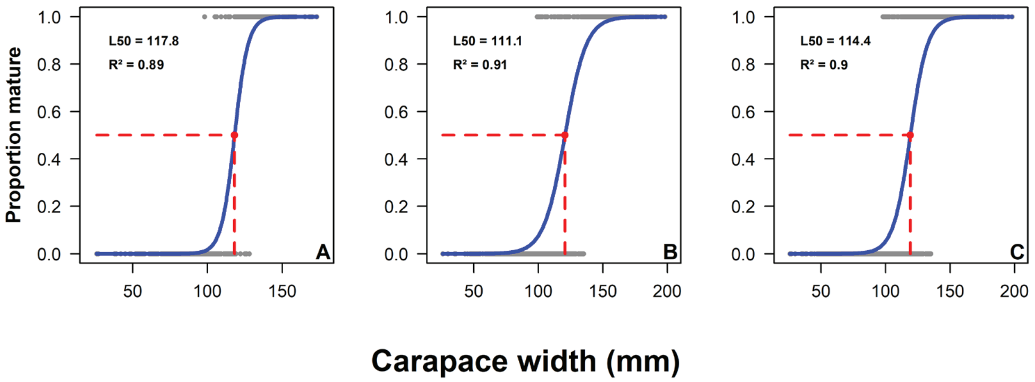

***Fig. 6:*** Carapace width at first sexual maturity (L50) for (A) females, (B) males, and (C) both sexes combined.

potential disruption of ecosystem functioning. A detailed understanding of its reproductive pattern is therefore essential for developing effective, targeted management strategies aimed at limiting its ecological impact while balancing its economic significance through exploitation.

A total of 938 individuals (543 males and 394 females) were analyzed, covering a wide size range (CW: 26–198 mm; CL: 13–96 mm; weight: 2.19–584.6 g). These morphometric values are comparable to those reported for both native and non-native habitats, supporting the strong phenotypic plasticity of *C. sapidus* and its ability to adapt to local environmental conditions. Notably, the maximum CW recorded in the Marchica Lagoon (198 mm) is close to the largest individuals reported from other Mediterranean lagoons (e.g., Greece, Italy), reinforcing the hypothesis that Mediterranean conditions may favor accelerated growth in newly colonized habitats (Kampouris *et al.*, 2020; Marchessaux *et al.*, 2023). In comparison, populations from native regions (e.g., Chesapeake Bay, Tampa Bay) generally reach larger average sizes, likely reflecting more stable environmental conditions and long-established population dynamics (Prager *et al.*, 1990; Steele, 1994). Further south, populations inhabiting the St. Andrews and Suwannee Sound rivers demonstrate average CWs of around 127 mm, reflecting a slight variation within the native range (Hart *et al.*, 2021).

Sexual size dimorphism was also evident in the Marchica population, with males exhibiting significantly larger CWs than females, a pattern commonly reported for Mediterranean populations (e.g., Sumer *et al.*, 2013; Kampouris *et al.*, 2020; Marchessaux *et al.*, 2023) and is attributed to sex-specific growth strategies and reproductive roles. However, this pattern is not universal, as some invaded areas, particularly in Italy, report larger females, suggesting that local environmental factors, such as food availability, temperature, and salinity, may strongly influence growth trajectories and population structure (Kevrekidis *et al.*, 2023).

A first overview of the blue crab population in the Marchica Lagoon was given by the sex-ratio analysis. The male-biased sex ratio (1.36:1) in Marchica reflects trends observed in several other invaded and native regions, including Croatia (Onofri *et al.*, 2008), Egypt (Razek *et al.*, 2016), Greece (Kevrekidis *et al.*, 2018; Kampouris *et al.*,

**Table 3.** Comparison of the carapace width at first sexual maturity ($L_{50}$) of *Callinectes sapidus* between our current study and available data in the literature.

| Country | Study site name | Native (N) / Introduced (I) | Sex | $L_{50}$ (mm) | References |
|---|---|---|---|---|---|
| Morocco | Marchica Lagoon | I | F | 117.8 | Our study |
| Morocco | Marchica Lagoon | I | M | 111.1 | Our study |
| Turkey | Beymelek lagoon | I | F | 118.5 | Sumer *et al.*, 2013 |
| Italy | Trapani Saltmarshes | I | M | 117.5 | Marchessaux *et al.*, 2023 |
| Italy | Trapani Saltmarshes | I | F | 120 | Marchessaux *et al.*, 2023 |
| Greece | Evros River | I | F | 123.9 | Kevrekidis *et al.*, 2023 |
| France | Biguglia Lagoon | I | F | 167.9 | Marchessaux *et al.*, 2024 |
| France | Biguglia Lagoon | I | M | 161.6 | Marchessaux *et al.*, 2024 |
| France | Palo Lagoon | I | F | 138.6 | Marchessaux *et al.*, 2024 |
| France | palo Lagoon | I | M | 143.8 | Marchessaux *et al.*, 2024 |
| Morocco | Moulay Bousselham Lagoon | I | F | 93.7 | Selfati *et al.*, 2025 |
| Morocco | Moulay Bousselham Lagoon | I | M | 86.9 | Selfati *et al.*, 2025 |
| USA | Sarah's Creek and Purtan Bay | N | M | 107 | Van Engel, 1990 |
| USA | Chesapeake Bay | N | F | 147 | Prager *et al.*, 1990 |
| USA | Tampa Bay | N | F | 130 | Steele & Bert, 1994 |
| USA | Louisiana | N | F | 125 | Guillory & Hein, 1997 |
| USA | Chesapeake Bay | N | F | 120 | Rugolo, 1997 |
| USA | Texas Bay | N | F | 120 | Fisher, 1999 |
| USA | Maryland bays | N | F | 116 | Lycett *et al.*, 2020 |
| Brazil | Babitonga Bay | N | F | 102 | Pereira *et al.*, 2009 |
| Brazil | Babitonga Bay | N | M | 89 | Pereira *et al.*, 2009 |
| Brazil | Lagoon-Estuarine of Iguape and Cananeia | N | F | 103.3 | Severino-Rodrigues *et al.*, 2013 |

2020), and Italy (Mancinelli *et al.*, 2013; Carrozzo *et al.*, 2014; Marchessaux *et al.*, 2023). In contrast, female-biased populations have been reported in Turkey (Sumer *et al.*, 2013; Türeli *et al.*, 2016), Brazil (Severino-Rodrigues *et al.*, 2013), the Atlantic coast of Morocco (Selfati *et al.*, 2025), and Chesapeake Bay, USA (Miller *et al.*, 2011; Rains *et al.*, 2016). Such variability likely results from a combination of reproductive migrations, where females move to waters that are more saline during spawning and fishing gear selectivity (Hines *et al.*, 1987; Steele & Bert, 1994). Moreover, several studies have also highlighted a sex ratio to equilibrium, suggesting a relatively homogeneous distribution between males and females, as reported by Sharov *et al.* (2003) in Chesapeake Bay, USA; Lycett *et al.* (2020) in the Maryland Coastal Bays, USA; and Mancinelli *et al.* (2024) in the Lesina Lagoon, Italy.

The analysis of reproductive activity revealed a bimodal spawning pattern, with peaks in spring (April) and summer (July–August). This dual seasonality aligns with findings from other Mediterranean Lagoons (Marchessaux *et al.*, 2023; Kevrekidis *et al.*, 2023; Mancinelli *et al.*, 2024; Selfati *et al.*, 2025). In contrast, a maximum single spawning peak during summer has been reported in the Beymelek Lagoon (Sumer *et al.*, 2013), Algeria's Mellah Lagoon (Bouhali *et al.*, 2022), and Turkey (Türeli *et al.*, 2018). This pattern may reflect a strategy to optimize larval survival under favorable environmental conditions. The observed seasonal peaks appear to be influenced by local temperature and salinity, highlighting the reproductive plasticity of *C. sapidus*. In its native range, spawning phenology also varies widely, further supporting the species' ability to adapt its reproductive timing to environmental cues (Van Engel, 1958; Jivoff *et al.*, 2017; Lycett *et al.*, 2020; Hart *et al.*, 2021; Schneider *et al.*, 2024).

On the other hand, the hepatosomatic index (HSI) exhibited two distinct peaks in February to March and May, occurring prior to GSI increases. This temporal pattern suggests a coordinated mobilization of stored energy in the hepatopancreas to support oocyte development. Such a trend aligns with findings from various studies on different decapod species and highlights the role of the hepatopancreas as a reservoir for reproductive investment (Steele & Bert, 1994). This inverse relationship between HSI and GSI highlights the physiological coordination between energy storage and reproductive effort, supporting successful spawning under seasonal environmental conditions.

Estimating the size at first sexual maturity ($L_{50}$) is critical for both ecological understanding and fisheries management (Hasan *et al.*, 2021). In Marchica Lagoon, $L_{50}$ was estimated at 117.8 mm for females and 111.1 mm for males, values comparable to those reported for other invaded areas such as Turkey (Sumer *et al.*, 2013). These estimates are generally lower than those observed in the native range, where $L_{50}$ reaches up to 147 mm in Chesapeake Bay (Prager *et al.*, 1990; Rugolo, 1997), and about 130 mm in Tampa Bay (Steele & Bert, 1994), suggesting earlier maturation in non-native environments, possibly driven by high growth rates or environmental pressures. Marked regional variability is, nevertheless, evident with much lower $L_{50}$ values reported from Brazil (e.g., 89 mm; Pereira *et al.*, 2009), and substantially higher values from France, e.g., 167.9 mm reported in Biguglia Lagoon (Marchessaux *et al.*, 2024), highlighting the strong influence of local ecological conditions and methodological approaches on maturation size. Size at first sexual maturity varies among populations in relation to temperature, salinity, food availability, and genetic factors (Fisher, 1999), with favorable habitats allowing earlier maturation at a smaller size. However, this variability can be further accentuated by fishing gear selectivity. Passive gear, such as traps and fyke nets, widely used in studies on *C. sapidus*, tend to underestimate the carapace width at which 50% of individuals reach maturity (Atar & Secer, 2003; Smith *et al.*, 2004; Kevrekidis *et al.*, 2023), while active gear, such as beach seines and panel trawls, allows sampling of a wider size range, including juveniles, thus providing more representative estimates of maturity parameters (Able *et al.*, 2002; Bellchambers & De Lestang, 2005).

The invasion of blue crab, *C. sapidus*, in the Marchica Lagoon represents a major challenge for artisanal fisheries, due to direct damage to fishing gear and competition with commercial species. This situation is exacerbated by the absence of a local tradition of crab consumption, which limits immediate commercial valorization.

The concept of transforming invasive species into exploitable resources has already been proposed for *C. sapidus* by Mancinelli *et al.* (2017), who advocated management strategies based on reproductive biology, seasonal dynamics, and ecological context. In this framework, targeted fishing during key reproductive periods could simultaneously reduce population growth and support local economies. However, the effectiveness of such an approach in Marchica Lagoon strongly depends on the development of appropriate fishing practices and market outlets. In the short term, the adoption of more resistant coastal fishing gear adapted to the strong chelae of blue crabs could help reduce local abundance while limiting damage to artisanal fisheries. In the long term, the establishment of regional or international markets remains essential to ensure economic viability and sustained population control (Azzurro *et al.*, 2024; Marchessaux *et al.*, 2024).

Thus, while the "turning a threat into a resource" strategy proposed by Mancinelli *et al.* (2017) provides a valuable conceptual framework, its successful implementation in the Marchica Lagoon requires site-specific adaptation integrating biological knowledge, fishing practices, and socioeconomic constraints.

## Conclusion

This study provides a comprehensive analysis of the reproductive biology of the blue crab *C. sapidus* in the Marchica Lagoon (Moroccan Mediterranean). The findings offer valuable insights that enhance scientific understanding of this invasive species and serve as a foundation for developing targeted management plans. These results are essential for informing effective strategies aimed at the sustainable control and exploitation of *C. sapidus* populations in the region.

## Acknowledgements

This work was carried out as part of a cooperation between Mohammed V University of Rabat and the National Institute of Fisheries Research. We would like to thank the staff of the National Institute of Fisheries Research in Nador. The authors also thank the local artisanal fishers of the Marchica Lagoon for their assistance in sample collection.

## References

Abdel Razek, F.A., Ismaiel, M., Ameran, M.A.A., 2016. Occurrence of the blue crab *Callinectes sapidus* Rathbun, 1896, and its fisheries biology in Bardawil Lagoon, Sinai Peninsula, Egypt. *The Egyptian Journal of Aquatic Research*, 42 (2), 223–229.

Able, K.W., Hagan, S.M., McLellan, J., Witting, D.A., 2002. Characterization and comparison of benthic gears for sampling estuarine fishes and crustaceans. Technical Report. Institute of Marine and Coastal Sciences, Rutgers, The State University of New Jersey, New Brunswick, NJ, USA.

Aguilar, R., Hines, A.H., Wolcott, T.G., Wolcott, D.L., Kramer, M.A. *et al.*, 2005. The timing and route of movement and migration of post-copulatory female blue crabs *Callinectes sapidus* Rathbun from the upper Chesapeake Bay. *Journal of Experimental Marine Biology and Ecology*, 319 (1), 117–128.

Atar, H.H., Secer, S., 2003. Width-length-weight relationships of the blue crab (*Callinectes sapidus* Rathbun, 1896) population living in Beymelek Lagoon lake. *Turkish Journal of Veterinary and Animal Sciences*, 27 (2), 443–447.

Atkinson, D., 1994. Temperature and organism size-a biological law for ectotherms? *Advances in Ecological Research*, 25, 1–58.

Azzurro, E., Bonanomi, S., Chiappi, M., De Marco, R., Luna, G.M. *et al.*, 2024. Uncovering unmet demand and key insights for the invasive blue crab (*Callinectes sapidus*) market before and after the Italian outbreak: Implications for policymakers and industry stakeholders. *Marine Policy*, 167, 106295.

Bellchambers, L.M., De Lestang, S., 2005. Selectivity of different gear types for sampling the blue swimmer crab. *Portunus Pelagicus* l. *Fisheries Research*, 73 (1–2), 21–27.

Boudouresque, C.F., 2005. Les espèces introduites et invasives en milieu marin. Deuxième édition. *GIS Posidonie Publ*., Marseille, 152 p.

Bouhali, K.F., Derbal, M., Kara, M., 2022. First data on the biology and dynamics of the American blue crab *Callinectes sapidus* in Mellah Lagoon, Algeria. p. 9. In: *Proceedings of the 2nd Mediterranean Symposium on the Non–Indigenous Species* (pp. 83–84).

Carrozzo, L., Potenza, L., Carlino, P., Costantini, M.L., Rossi, L. *et al.*, 2014. Seasonal abundance and trophic position of the Atlantic blue crab *Callinectes sapidus* Rathbun 1896 in a Mediterranean coastal habitat. *Rendiconti Lincei*, 25 (2), 201–208.

Castriota, L., Andaloro, F., Costantini, R., De Ascentiis, A., 2012. First record of the Atlantic crab *Callinectes sapidus* Rathbun, 1896 (Crustacea: Brachyura: Portunidae) in Abruzzi waters, central Adriatic Sea. *Acta Adriatica*, 53 (3), 467–471.

Castriota, L., Falautano, M., Perzia, P., 2024. When nature requires a resource to be used - The case of *Callinectes sapidus*: Distribution, aggregation patterns, and spatial structure in northwest Europe, the Mediterranean Sea, and adjacent waters. *Biology*, 13 (4), 279.

Chartosia, N., Anastasiadis, D., Bazairi, H., Crocetta, F., Deidun, A. *et al.*, 2018. New Mediterranean biodiversity records (July 2018). *Mediterranean Marine Science*, 19 (2), 398–415.

Clavero, M., Franc, N., Bernardo-Madrid, R., López, V., Abelló, P. *et al.*, 2022. Severe, rapid and widespread impacts of an Atlantic blue crab invasion. *Marine Pollution Bulletin*, 176, 113479.

Dagnelie, P., 1973. Statistical Theory and Methods: Agronomic Applications (Volume 1). Gembloux Agricultural Press.

Diagne, C., Catford, J.A., Essl, F., Nuñez, M.A., Courchamp, F., 2020. What are the economic costs of biological invasions? A complex topic requiring international and interdisciplinary expertise. *NeoBiota*, 63, 25–37.

Dulčić, J., Dragicevic, B., Lipej, L., 2010. New record of the blue crab, *Callinectes sapidus* Rathbun, 1896, (Decapoda: Brachyura) in the Adriatic Sea. Annales. In: Annales: *Series Historia Naturalis*, 20 (1), 23–28. Scientific and Research Center of the Republic of Slovenia.

Eleftheriou, A., Anagnostopoulou-Visilia, E., Anastasopoulou, E., Ates, A., Bachari, N.I. *et al.*, 2011. New mediterranean biodiversity records (December 2011). *Callinectes sapidus* Rathbun in the Greek Ionian Sea, By K. Kapiris, E. Anastasopoulou and P. Kouraklis]. *Mediterranean Marine Science*, 12 (2), 491–508.

El Yaouti, F., El Mandour, A., Khattach, D., Benavente, J., Kaufmann, O., 2009. Salinization processes in the unconfined aquifer of Bou-Areg (NE Morocco): a geostatistical, geochemical, and tomographic study. *Applied Geochemistry*, 24 (1), 16–31.

Enzenrob, R., Enzenrob, L., Bingel, F., 1997. Occurrence of Blue Crab, *Callinectes sapidus* (Rathbun 1896) (Crustacea, Brachyura) on theTurkish Mediterranean and the adjacent coast and its size distribution in the Bay of Iskenderun. *Turkish Journal of Zoology*, 21 (2), 113–122.

Epifanio, C.E., 2007. Larval biology. p. 513-533. In: The blue crab *Callinectes sapidus*. Kennedy, V.S., Cronin, L.E. (Eds). Maryland Sea Grant College Program, College Park, MD.

Fisher, M.R., 1999. Effect of temperature and salinity on size at maturity of female blue crabs. *Transactions of the American Fisheries Society*, 128 (3), 499–506.

Galil, B.S., Froglia, C., Noël, P., 2002. Crustaceans: decapods and stomatopods. p. 1-192. In: CIESM atlas of exotic species in the Mediterranean. Briand, F. (Ed.). CIESM Publishers, Monaco.

Galanidi, M., Aissi, M., Ali, M., Bakalem, A., Bariche, M. *et al.*, 2022. Refined and updated bon-inigenous species baselines for the Mediterranean sea at the national, sub-regional and national level in the context of the Barcelona convention's integrated monitoringa and assessment programme (IMAP). In: *UNEP/MAP-SPA/RAC, 2022. Proceedings of the 2nd Mediterranean Symposium on the non-indigenous Species (Genova, ITaly, 22-23 September 2022). Bouafif C., Ouerghi, A., edits. SPA/RAC publi. Tunis, 150 p.* (pp. 5-10). Tunis: SPA/RAC.

Gavioli A., Mancinelli, G., Turolla, E., Lanzoni, M., Vadis, P. *et al.*, 2025. Impacts of the invasive blue crab *Callinectes sapidus* on small-scale fisheries in a Mediterranean lagoon using fishery landing data. *Science of the Total Environment*, 974, 179236.

Giordani Soika, A., 1951. Il Neptunus pelagicus(L.) nell'Alto Adriatico (Neptunus pelagicusin the northern Adriatic). *Natura*, 42, 18–20.

Gravez, V., Bernard, G., Boudouresque, C.F., Meinesz, A., Cottalorda, J.M. *et al.*, 2000. *Caulerpa taxifolia* : éléments de synthèse. Programme Life DGXI, DIREN PACA, GIS Posidonie publ., 1–32.

Gourari, K., Mabrouki, Y., Parenteau-Mauffette, É., Legssyer, B., Mancinelli, G. *et al.*, 2025. Assessing the ecological and socio-economic impacts of the invasive bleu crab *Callinectes sapidus* using local knowledge and field surveys in Eastern Morocco. Thalassas: *An International Journal of Marine Sciences*, 41, 118.

Guillory, V., Hein, S., 1997. Sexual maturity in blue crabs, *Callinectes sapidus*. *Proceeding of Coastal Fishing, Louisiana's Blue Crab Resource La. St. University Academy of Science*, 59, 5–7.

Hard, W.L., 1942. Ovarian growth and ovulation in the mature blue crab, *Callinectes sapidus* Rathbun. Chesapeake Biological Laboratory, 46, 3–17.

Hart, H.R., Crowley, C.E., Walters, E.A., 2021. Blue crab spawning and recruitment in two Gulf coast and two Atlantic estuaries in Florida. *Marine and Coastal Fisheries*, 13 (2), 113–130.

Hartnoll, R.G., 1982. Growth. Hartnoll, R.G., 1982. Growth. p. 111-196. In: The biology of Crustacea. Abele, L.G. (Ed.). Academic Press.

Hasan, M.R., Hossain, M.Y., Mawa, Z., Tanjin, S., Rahman, M.A. *et al.*, 2021. Evaluating the size at sexual maturity for 20 fish species (Actinopterygii) in wetland (Gajner Beel) ecosystem, north-western Bangladesh through multi-model approach: A key for sound management. *Acta Ichthyologica et Piscatoria*, 51, 29–36.

Hilmi, K., 2005. Modélisation numérique de la circulation de deux milieux paraliques du littoral marocain : la lagune de Oualidia (Atlantique) et la lagune de Nador (Méditerranée). Ph.D. Thesis. Université Hassan II Mohammedia, Morocco, 186 pp.

Hines, A.H., Lipcius, R.N., Haddon, A.M., 1987. Population dynamics and habitat partitioning by size, sex, and molt stage of blue crabs *Callinectes sapidus* in a subestuary of central Chesapeake Bay. *Marine Ecology Progress Series*, 36 (1), 55–64.

IPBES, 2018. The regional assessment report on biodiversity and ecosystem services for Europe and central Asia. IPBES.

IPBES, 2020. Workshop Report on Biodiversity and Pandemics of the Intergovernmental Platform on Biodiversity and Ecosystem Services. IPBES.

Jeyar, M., Chaabelasri, E., Salhi, N., 2015. Numerical investigation of new alternative Nador Lagoon inlet relocation. *International Journal of Fluid Mechanics Research*, 42 (5).

Jivoff, P.R., Hines, A.H., Quackenbush, S., 2007. Reproduction and embryonic development. p. 255–298. In: Blue Crab: *Callinectes sapidus*, Maryland Sea Grant Program.

Kampouris, T.E., Kouroupakis, E., Batjakas, I.E., 2020. Morphometric relationships of the global invader *Callinectes sapidus* Rathbun, 1896 (Decapoda, Brachyura, Portunidae) from Papapouli Lagoon, NW Aegean Sea, Greece. With notes on its ecological preferences. *Fishes*, 5 (1), 5.

Katsanevakis, S., Wallentinus, I., Zenetos, A., Leppäkoski, E., Çinar, M.E. *et al.*, 2014. Impacts of invasive alien marine species on ecosystem services and biodiversity: a pan-European review. *Aquatic Invasions*, 9, (4), 391–423.

Kevrekidis, K., Antoniadou, C., 2018. Abundance and population structure of the blue crab *Callinectes sapidus* (Decapoda, Portunidae) in Thermaikos Gulf (Methoni Bay), northern Aegean Sea. *Crustaceana*, 91 (6), 641–657.

Kevrekidis, K., Kevrekidis, T., Mogias, A., Boubonari, T., Kantaridou, F. *et al.*, 2023. Fisheries biology and basic life-cycle characteristics of the invasive blue crab *Callinectes sapidus* Rathbun in the estuarine area of the Evros River (Northeast Aegean Sea, Eastern Mediterranean). *Journal of Marine Science and Engineering*, 11 (3), 462.

Khamassi, F., Rjiba Bahri, W., Mnari Bhouri, A., Chaffai, A., Soufi Kechaou, E. *et al.*, 2022. Biochemical composition, nutritional value, and socio-economic impacts of the invasive crab *Callinectes sapidus* Rathbun, 1896 in the central Mediterranean Sea. *Mediterranean Marine Science*, 23 (3), 650–663.

Koukouras, A., Dounas, C., Turkay, M., Voultsoiadou-Koukora, E., 1992. Decapod crustacean fauna of the Aegean Sea: New information, check-list, affinities. *Senckenbergiana Marittima*, 22 (3–6), 217–244.

Labrune, C., Amilhat E., amouroux J.M., Jabouin C., Gigou A. *et al.*, 2019. The arrival of the American blue crab, *Callinectes sapidus* Rathbun, 1896 (Decapoda: Brachyura: Portunidae), in the Gulf of Lions (Mediterranean Sea). *BioInvasions Records*, 8 (4), 876–881.

Lipcius, R.N., Eggleston, D.B., Heck Jr, K.L., Seitz, R.D., van Montfrans, J., 2007. Ecology of juvenile and adult blue crabs. p. 535–564. In: The blue crab *Callinectes sapidus*, Kennedy, V.S., Cronin, L.E. (Eds). Maryland Sea Grant College Program, College Park, MD.

Lycett, K.A., Shields, J.D., Chung, J.S., Pitula, J.S., 2020. Population structure of the blue crab *Callinectes sapidus* in the Maryland Coastal Bays. *Journal of Shellfish Research*, 39 (3), 699–713.

Mancinelli, G., Carrozzo, L., Costantini, M.L., Rossi, L., Marini, G. *et al.*, 2013. Occurrence of the Atlantic blue crab *Callinectes sapidus* in two Mediterranean coastal habitats: temporary visitor or permanent resident. Estuarine, *Coastal and Shelf Science*, 135, 46–56.

Mancinelli, G., Chainho, P., Cilenti, L., Falco, S., Kapiris, K. *et al.*, 2017. The Atlantic blue crab *Callinectes sapidus* in southern European coastal waters: Distribution, impact and prospective invasion management strategies. *Marine Pollution Bulletin*, 119 (1), 5–11.

Mancinelli, G., Bardelli, R., Zenetos, A., 2021. A global occurrence database of the Atlantic blue crab *Callinectes sapidus*. *Scientific Data*, 8 (1), 111.

Mancinelli, G., Lago, N., Scirocco, T., Lillo, O.A., De Giorgi,R. *et al.*, 2024. Abundance, Size Structure, and Growth ofthe Invasive Blue Crab *Callinectes sapidus* in the LesinaLagoon, Southern Adriatic Sea, *Biology*, 13 (12), 1051.

Marchessaux, G., Gjoni, V., Sará, G., 2023. Environmental drivers of size-based population structure, sexual maturity and fecundity: A study of the invasive blue crab *Callinectes sapidus* (Rathbun, 1896) in the Mediterranean Sea. *PLoS One*, 18, e0289611.

Marchessaux, G., Veyssiere, D., Durieux, E.D.H., Sarà, G., Garrido, M., 2024. Using species population structure to assist in management and decision-making in the fight against invasive species: The case of the Atlantic blue crab *Callinect-*

*es sapidus*. *Global Ecology and Conservation*, 54, e03168.

Miller, T.J., Wilberg, M.J., Colton, A.R., Davis, G.R., Sharov, A.F. *et al.*, 2011. Stock assessment of blue crab in Chesapeake Bay. UMCES Technical Report Series TS614.11. University of Maryland Center for Environmental Science, Cambridge, MD.

Millikin, M.R., Williams, A.B., 1984. Synopsis of biological data on the blue crab, *Callinectes sapidus* Rathbun. NOAA Technical report NMFS 51, 1–38.

Nehring, S., 2011. Invasion history and success of the American blue crab *Callinectes sapidus* Rathbun in European coastal waters. In: Galil, B., Clark, P., Carlton, J. (Eds) In: the Wrong Place - Alien Marine Crustaceans: Distribution, Biology and Impacts. p. 607-624. Invading Nature - Springer Series in Invasion Ecology, vol 6. Springer, Dordrecht.

Onofri, V., Dulcic, J., Conides, A., Matic-Skoko, S., Glamuzina, B., 2008. The occurrence of the blue crab, *Callinectes sapidus* Rathbun, 1896 (Decapoda, Brachyura, Portunidae) in the eastern Adriatic (Croatian coast). *Crustaceana*, 81 (4), 403–409.

Pereira, M.J., Branco, J.O., Christoffersen, M.L., Freitas Jr, F., Fracasso, H.A.A. *et al.*, 2009. Population biology of *Callinectes danae* and *Callinectes sapidus* (Crustacea: Brachyura: Portunidae) in the south-western Atlantic Journal of the Marine Biological *Association of the United Kingdom*, 89 (6), 1341–1351.

Prado, P., Peñas, A., Ibáñez, C., Cabanes, P., Jornet, L. *et al.*, 2020. Prey size and species preferences in the invasive blue crab, *Callinectes sapidus*: Potential effects in marine and freshwater ecosystems. *Estuarine, Coastal and Shelf Science*, 245, 106997.

Prager, M.H., McConaugha, J.R., Jones, C.M., Geer, P.J., 1990. Fecundity of blue crab, *Callinectes sapidus*, in Chesapeake Bay: biological, statistical and management considerations. *Bulletin of Marine Science*, 46 (1), 170–179.

Rains, S.A., Wilberg, M.J., Miller, T.J., 2016. Sex ratios and average sperm per female blue crab *Callinectes sapidus* in six tributaries of Chesapeake Bay. *Marine Coastal Fisheries*, 8 (1), 492–501.

Ramos, J., Pecl, G.T., Moltschaniwskyj, N.A., Semmens, J.M., Souza, C.A. *et al.*, 2018. Population genetic signatures of a climate change driven marine range extension. *Scientific Reports*, 8, 27351.

Re, V., 2010. Groundwater in urban coastal areas: Hydrogeochemical based approach for managing the transition areas. The example of the lagoon of Nador (Morocco). PhD Thesis.Universita Ca'Foscari Venezia, Venice, Italy, 153 pp.

Rugolo, L.J., Knotts, K., Lange, A., Crecco, V., Terceiro, M. *et al.*, 1997. Stock assessment of Chesapeake Bay blue crab (*Callinectes sapidus*). NOAA Technical Report, 267 pp.

Sara, G., Palmeri, V., Rinaldi, A., Montalto, V., Helmuth, B., 2013. Predicting biological invasions in marine habitats through eco-physiological mechanistic models: a case study with the bivalve *Brachidontes pharaonis*. *Diversity and Distributions*, 19 (10), 1235–1247.

Sara, G., Mangano, M.C., Johnson, M., Mazzola, A., 2018. Integrating multiple stressors in aquaculture to build the blue growth in a changing sea. *Hydrobiologia*, 809 (1), 5–17.

Schneider, A.K., Fabrizio, M.C., Lipcius, R.N., 2024. Reproductive phenology of the Chesapeake Bay blue crab population in a changing climate. *Frontiers in Ecology and Evolution*, 11, 1304021.

Seebens, H., Blackburn, T., Dyer, E., Genovesi, P., Hulme, P. *et al.*, 2017. No saturation in the accumulation of alien species worldwide. *Nature Communications*, 8, e14435.

Seebens, H., Bacher, S., Blackburn, T.M., Capinha, C., Dawson, W. *et al.*, 2021. Projecting the con-tinental accumulation of alien species through to 2050. *Global change biology*, 27 (5), 970–982.

Selfati, M., Doukilo, I., Erbib, A., El Kemcha, R., Errhif, A., Bazairi, H., 2025. Reproductive biology of the invasive blue crab *Callinectes sapidus* (Rathbun, 1896) on the African Atlantic Coast. *Estuaries and Coasts*, 48 (2), 46.

Severino-Rodrigues, E., Musiello-Fernandes, J., Moura, A.A.S., Branco, G.M.P., Caneo, V.O.C., 2013. Fecundity, reproductive seasonality and maturation size of *Callinectes sapidus* females (Decapoda: Portunidae) in the Southeast coast of Brazil. *Revista de Biologia Tropical*, 61 (2), 595–602.

Sharov, A.F., Volstad, J.H., Davis, G.R., Davis, B.K., Lipcius, R.N. *et al.*, 2003. Abundance and exploitation rate of the blue crab (*Callinectes sapidus*) in Chesapeake Bay. *Bulletin of Marine Science*, 72 (2), 543–565.

Smith, K.D., Hall, N.G., De Lestang, S., Potter, I.C., 2004. Potential bias in estimates of the size of maturity of crabs derived from trap samples. *ICES. Journal of Marine Science*, 61 (6), 906–912.

Steele, P., Bert, T.M., 1994. Population ecology of the blue crab, *Callinectes sapidus* Rathbun, in a subtropical estuary: population structure, aspects of reproduction, and habitat partitioning. *Florida Marine Research Publications*, 51, 24 pp.

Streftaris, N., Zenetos, A., 2006. Alien marine species in the Mediterranean - the 100 "Worst Invasives" and their impact. *Mediterranean Marine Science*, 7 (1) 87–118.

Sumer, C., Teksam, I., Karatas, H., Beyhan, T., Aydin, C.M., 2013. Growth and reproduction biology of the blue crab, *Callinectes sapidus* Rathbun, 1896, in the Beymelek Lagoon (Southwestern Coast of Turkey). *Turkish Journal of Fisheries and Aquatic Sciences*, 13 (4), 675–684.

Tankersley, R.A., Forward Jr, R.B., 2007. Environmental physiology. p. 451-483. In: The blue crab *Callinectes sapidus*. Kennedy, V.S., Cronin, L.E. (Eds). Maryland Sea Grant College Program.

Tesson, M., 1977. Régime hydrologique ct hydrodynamique de la Sebkha Bou Areg (Lagune de Nador, Maroc). Travaux et Documents de Développement des Pêches au Maroc, 27, 67 pp.

Tuncer, S., Bilgin, S., 2008. First record of *Callinectes sapidus* Rathbun, 1896 (Crustacea: Decapoda: Brachyura) in the Dardanelles, Canakkale, Turkey. *Aquatic Invasions*, 3 (4), 469-470.

Türeli, C., Miller, T.J., Gündogdu, S., Yesilyurt, I.N., 2016. Growth and mortality of blue crab (*Callinectes sapidus*) in the northeastern Mediterranean Sea. *Journal of Fisheries Sciences*, 10 (2), 55–62.

Türeli, C., Yeşilyurt, I.N., Nevşat, I.N., 2018. Female reproductive pattern of *Callinectes sapidus* Rathbun, 1896 (Brachyura: Portunidae) in Iskenderun Bay, Eastern Mediterranean. *Zoology in the Middle East*, 64 (1), 55–63.

Van Engel, W.A., 1958. The blue crab and its fishery in Chesapeake Bay. Part 1. Reproduction, early development, growth and migration. *Commercial Fisheries Review*, 20 (6), 6–17.

Van Engel, W.A., 1990. Development of the reproductively functional form in the male blue crab, *Callinectes sapidus*. *Bulletin Of Marine Sciences*, 46 (1), 13–22.

Verma, A.K., Rout, P.R., Lee, E., Bhunia, P., Bae, J. *et al.*, 2020. Biodiversity and Sustainability. p. 255-275. In: Sustainability: Fundamentals and ApplicationsWilliams, A.B., 1974. Swimming crabs of genus Callinectes (Decapoda-Portunidae). *Fishery Bulletin*, 72, 685–798.

Zenetos, A., Gofas, S., Morri, C., Rasso, A., Violanti, D. *et al.*, 2012. Alien species in the Mediterranean Sea by 2012. A contribution to the application of European Union's Marine Strategy Framework Directive (MSFD). Part 2. Introduction trends and pathways. *Mediterranean Marine Science*, 13 (2), 328–352.

Zenetos, A., Gofas, S., Verlaque, M., Çinar, M.E., Raso, J.E.G. *et al.*, 2010. Alien species in the Mediterranean Sea by 2010. A contribution to the application of European Union's Marine Strategy Framework Directive (MSFD). Part I. Spatial distribution. *Mediterranean Marine Science*, 11 (2), 381–493.

Zenetos, A., Tsiamis, K., Galanidi, M., Carvalho, N., Bartilotti, C. *et al.*, 2022. Status and trends in the rate of introduction of marine non-indigenous species in European Seas. *Diversity*, 14 (12), 1077.