STATUS OF THE BLUE CRABS IN THE MEDITERRANEAN

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Introduction

The latest report from the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) raises alarms about the global proliferation of Non-Indigenous Species (NIS) (Roy *et al.*, 2023). Among the **37,000 recorded NIS**, **3,500 are Invasive Alien Species (IAS)**, contributing to **60 % of global species extinctions**, **impacting biodiversity** through ecosystem modifications, resource competition, and predation (Roy *et al.*, 2023). **Climate change exacerbates species distribution changes**, indirectly facilitating IAS spread, often at the expense of indigenous species. Monitoring both indigenous and invasive species is crucial for understanding the impacts of climate change and implementing effective conservation measures (DeLong *et al.*, 2018).

The introduction of Non-Indigenous Species (NIS) has profound and **dramatic ecological and socioeconomic impacts** and is considered a major threat to biodiversity conservation (Bright, 1998; Carlton, 1996; Occhipinti-Ambrogi, 2007). With the continued increase in the number of species, specimens, and/or individuals being transported, as well as the speed of these transports (Sheppard *et al.*, 2018), the threat to biodiversity posed by NIS (i.e., populations introduced by humans and expanding in regions beyond their past or current ranges) has become particularly concerning. This phenomenon is all the more worrisome as it is irreversible on both human and even geological timescales, especially in marine environments (Boudouresque *et al.*, 2005).

The Mediterranean Sea is one of the world's regions most severely affected by biological invasions, with **1 011 NIS identified** (Galanidi *et al.*, 2022). Approximately **half of the NIS in the Mediterranean are introduced primarily via the Corridor pathway**, likely entering through the **Suez Canal** (Galanidi *et al.*, 2022). **Shipping vectors**, including **Ballast Water and Fouling**, collectively account for the introduction of nearly one-third of NIS in the Mediterranean (Galanidi *et al.*, 2022).

Among the 91 exotic species of decapod and stomatopod crustaceans recorded in the Mediterranean since 1870, **85 are believed to have an anthropogenic origin** (6 species are thought to have migrated), **and 18 are considered invasive**, including two species of blue crabs from the Portunidae family: the American blue crab *Callinectes sapidus* and the blue swimming crab *Portunus segnis*.

Currently present throughout the Mediterranean, **the American blue crab**, *Callinectes sapidus* (Rathbun, 1896) — **native to the temperate and subtropical Atlantic coasts of the Americas** — has recently become **emblematic of significant socio-economic and environmental impacts**. This invasive species raises concerns among oyster farmers, lagoon fishermen, and scientists. It is considered **one of the most invasive species in the Mediterranean** (Streftaris and Zenetos, 2006). Indeed, this crustacean proliferates rapidly and possesses the biological and physiological capabilities to expand across the entire Mediterranean basin. With its distinctive morphology, it can travel up to 15 km in a single day.

In 2023, a historic shift occurred in the invasion dynamics of the **Red Sea swimming blue** crab, *Portunus segnis* (Forskål, 1775), in the Mediterranean Sea. **The unprecedented warming of Mediterranean waters facilitated its exponential expansion**, with new sightings in the Gulf of Cadiz (Spain) and the Italian Adriatic coasts, surpassing its previous confinement to the southeastern Mediterranean (de Carvalho-Souza *et al.*, 2023; Grati *et al.*, 2023). **Originating from the Indo-Pacific**, *P. segnis*, **an early Lessepsian invader**, was first recorded in Egypt in 1898 after the Suez Canal's construction. Since the 2000s, it has established across the south Mediterranean, posing threats to local biodiversity and artisanal fisheries (Marchessaux *et al.*, 2023d; Tureli and Yesilyurt, 2017). While the crab's aggressive behavior negatively impacts native species and habitats, the challenge lies in devising effective conservation measures for such invasive organisms reaching new habitats (Blackburn *et al.*, 2011). The potential expansion of *P. segnis* underscore the urgency of implementing robust conservation strategies to mitigate local biodiversity losses and safeguard ecosystem integrity.

These two blue crab species from the Portunidae family share numerous similarities: rapid colonization capabilities, aggressive behavior, voracious omnivorous predation, and significant ecological and socio-economic impacts.

The current situation regarding the invasion of these two species is alarming, and significant management measures must be implemented to counter the spread of these blue crabs, thereby protecting Mediterranean biodiversity and human activities.
In this report, we present the current state of knowledge, and the challenges related to the invasion of blue crabs in the Mediterranean. This report is divided into different parts:

- The state of knowledge on the American blue crab *Callinectes sapidus*,
- The state of knowledge on the Red Sea swimming blue crab *Portunus segnis*,
- The challenges associated with the presence of these two species in the Mediterranean,

1 Methodological note

The aim of this document is to review the current state of knowledge on the invasive Portunidae blue crabs Callinectes sapidus and *Portunus segnis* in the Mediterranean. A search of relevant literature was carried out to explore several aspects for each species: (i) morphological characteristics, (ii) distribution and invasion history, (iii) population dynamics and life cycle, (iv) ecology, and (v) socio-economic and ecological impacts. Information was extracted from existing scientific literature available from SCOPUS, Google Scholar and Web of Science platforms. Keywords were used for each category of information:

Categories	Keywords used
General characteristics	Morphological, Anatomy, Morphological characteristics
Distribution and invasion history	Distribution, Invasion history, Occurrences
Population dynamics and life cycle	Population dynamics, Life cycle, Larvae, Larval connectivity, Allometry, Sexual maturity, Reproduction, Larval growth rate, Population structure
Ecology	Diet, Stable isotopes, Ecology, Food consumption, Food items, Thermal tolerance, Salinity tolerance, Habitat, Feeding ecology
Socio-economic and ecological impacts	Impacts, Fisheries, Socio-economic impacts, Ecological impacts, Net damages, Aquaculture

* for each category, the specific name of each species was used: for *Callinectes sapidus:* "American Blue crab" OR/AND "Callinectes sapidus"; for *Portunus segnis*: "Swimming blue crab" OR/AND "Portunus segnis".

2 Current knowledge of the American blue crab *Callinectes sapidus*

2.1 General characteristics of the species

The American blue crab *Callinectes sapidus* (Rathbun, 1896), whose etymology means "savory graceful swimmer", is a decapod crab in the Portunidae family, subfamily Portunidae. This species is easily recognized by its **"electric" blue color** (Figure 1). The carapace is brownish in color and more than twice as wide as it is long; 9 spines on the arched anterolateral margin on the front of the carapace and 2 large spins on the extremities. Most of the convex dorsal surfaces are smooth and granular. The claws are robust and longitudinally ridged; the fifth legs are flattened in the shape of paddles. The claws are blue in males and rather red at the tip in adult females. Legs are blue (Chace and Hobbs, 1969; Churchill, 1919).

The maximum dimensions recorded are **carapace length: 9 cm and width** (measured from one end of the large lateral spines to the other): **23 cm** (Holthuis, 1987). In terms of weight, a 17 cm wide individual can weigh 331 g, and a 20.5 cm wide one can weigh 585 g.

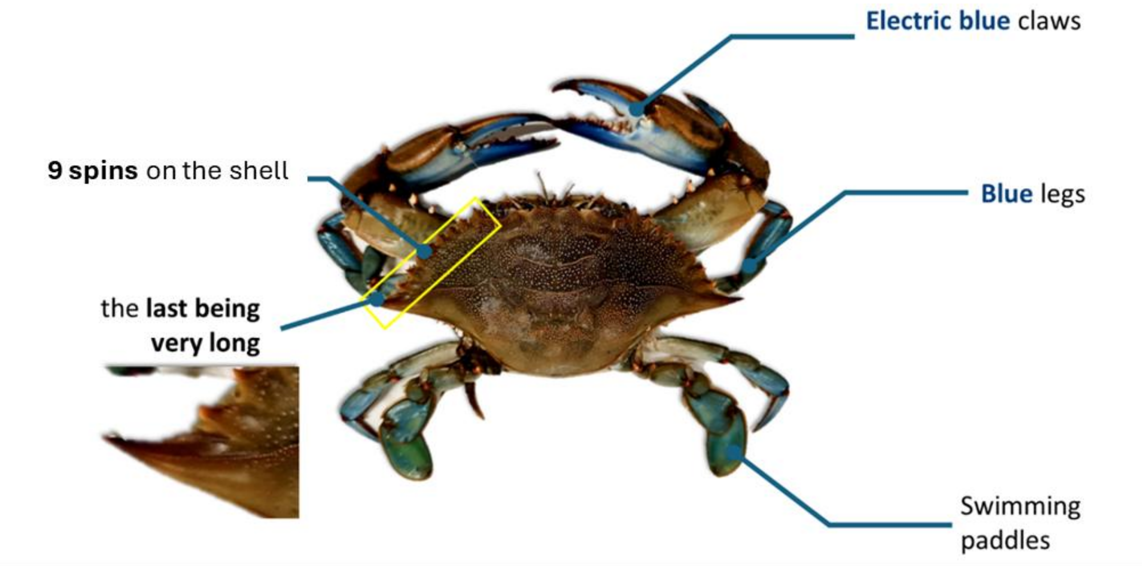


Figure 1. Morphological characteristics of the American blue crab *Callinectes sapidus*. Photography: Guillaume Marchessaux.

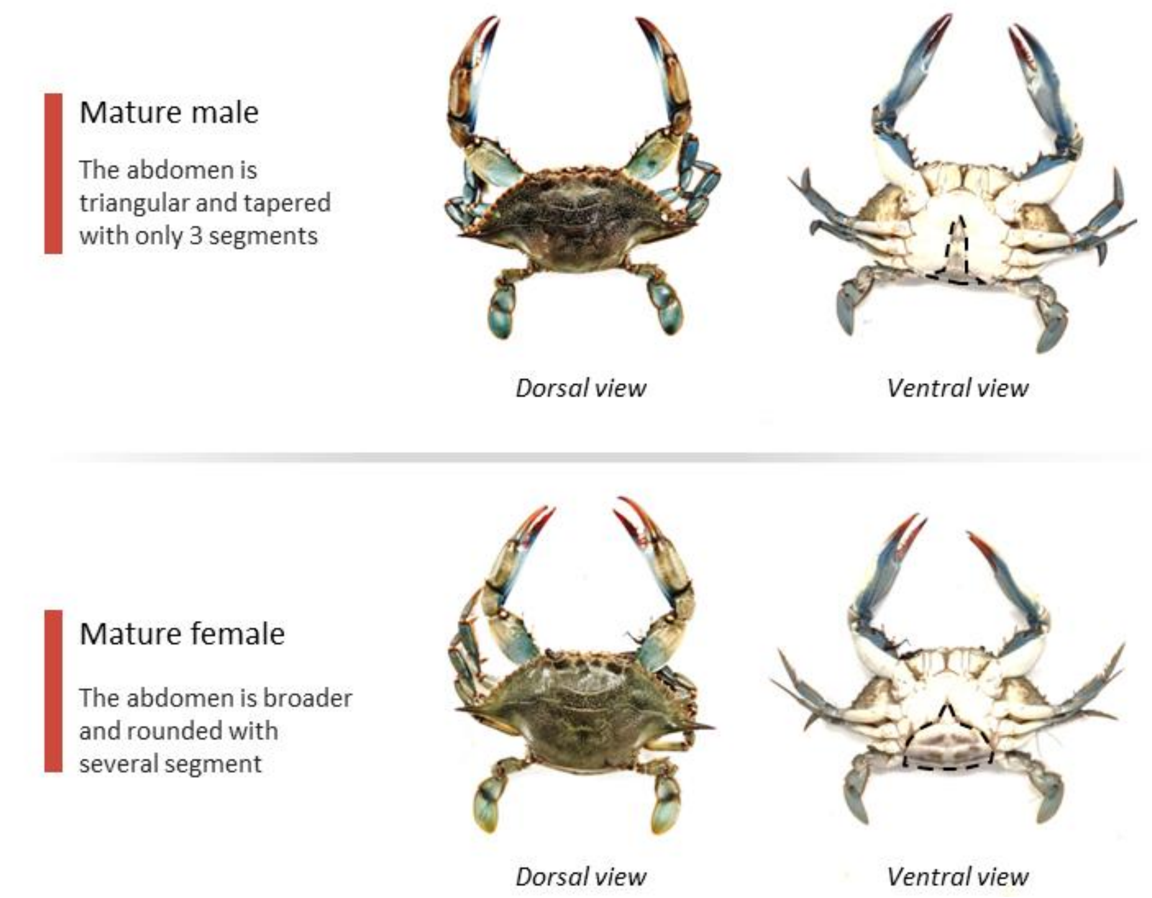


Figure 2. Morphological characteristics of males and females of the blue crab *Callinectes sapidus*. Photography: Guillaume Marchessaux.

Although females tend to have red claw tips, the difference between males and females is identifiable on the ventral side of the abdomen (Figure 2). In **males**, the **abdomen is triangular**, **T-shaped** and tapered with only 3 segments. In females, the abdomen is wider and rounded, with several segments. In **females**, the shape of the abdomen is a **key indicator for differentiating mature from immature females**. In

immature females, the **abdomen is triangular**, **narrow** and **pointed**, and **fused with the plastron** (underside of the carapace). In **mature females**, the abdomen is **rounded or broadly dome-shaped**, often **compared to a horseshoe**. The abdomen is wider and more pronounced to accommodate eggs during reproduction (egg sac or sponge). These differences are linked to the morphological evolution of females as they reach sexual maturity, a change essential to their reproductive role.

2.2 Distribution and invasion history

Callinectes sapidus is native to the **temperate and tropical Atlantic coasts of America** (Rathbun, 1930). It is found from Nova Scotia (southern Canada), where the species does not reproduce, to northern Argentina, the southern limit of distribution in its native range (Williams, 1984). Mancinelli *et al.*, (2021) have carried out a large world-wide inventory based on bibliographical data (Figure 3). Introduced to the Mediterranean region during the 20th century, probably via ballast water from ships, *Callinectes sapidus* has successfully established itself in numerous coastal habitats. In recent years, the species appears to be expanding its range northwards in the Northern Hemisphere (Johnson, 2015; Mancinelli *et al.*, 2021).

The first record of the American blue crab *Callinectes sapidus* in Europe was in 1900 on the French Atlantic coast (Figure 4). Individuals were subsequently detected in the North Sea (1932), Mediterranean Sea (1949, probably as early as 1935), Baltic Sea (1951), Black Sea (1967) and Sea of Azov (1967). It would appear that several independent introduction vectors have taken place, such as ballast water and the introduction of the species for aquaculture purposes, which remains the most likely introduction vector (Nehring, 2011).

Since 2011, the species has greatly expanded in Europe, particularly in the Mediterranean (Labrune *et al.*, 2019; Mancinelli *et al.*, 2017). *Callinectes sapidus* has spread to the German and Danish coasts (Nehring and van der Meer, 2010), the northernmost area where it has been recorded. The American blue crab is therefore located at higher latitudes than its range due to warmer waters linked to the Gulf Stream (Mancinelli *et al.*, 2021). *Callinectes sapidus* is now reported throughout the Mediterranean basin, with the exception of a few regions such as the Libyan coast (Figure 4) (Castriota *et al.*, 2024; Mancinelli *et al.*, 2021).

Since the last review of the species' distribution by Mancinelli *et al.* (2021), **the distribution of the American blue crab has continued to increase**, particularly on European coasts, where it is now present from the southern coasts of Portugal (Atlantic coast), to Spain, France, the whole of Italy, the Adriatic Sea and the Aegean Sea (Figure 4).

In the southern Mediterranean, the species is present from Morocco to Egypt. Numerous hot spots have recently been identified, notably in the Balearic Islands (western Mediterranean), the islands of the Western Basin (Corsica, Sardinia), the Strait of Sicily and the Adriatic Sea (Figure 4) (Castriota *et al.*, 2024). Castriota *et al.* (2024) showed that the invasion of *Callinectes sapidus* in Europe and the Mediterranean was long, with a latency period of almost 60 years before populations exploded in the 2000s.

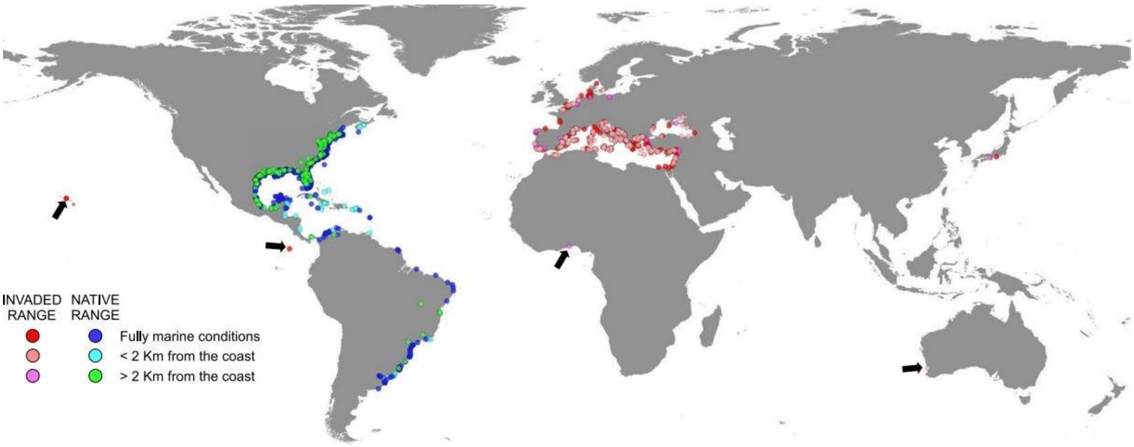


Figure 3. Global distribution of *C. sapidus* according to coastal distance of census, geographical area of origin and geographical area of introduction (figure taken from Mancinelli *et al.*, 2021).

In the Mediterranean, however, **the species' expansion phase became particularly strong from 2014** onwards, whereas it was much slower in Northwest Europe. In the Mediterranean, the American blue crab *Callinectes sapidus* **is considered established**, and the species **is currently expanding rapidly.**

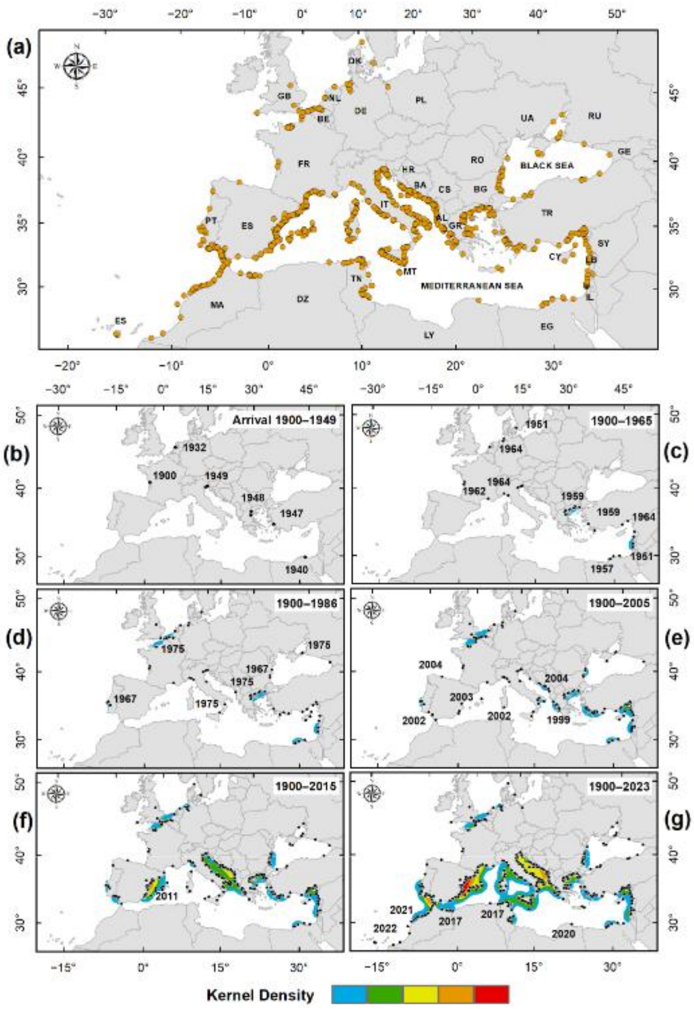


Figure 4. Distribution of *Callinectes sapidus* in Europe and the Mediterranean, Figure extracted from Castriota *et al.* (2024).

2.3 Population dynamics and life cycle of *Callinectes sapidus*

2.3.1 Population dynamics and size spectra

Size spectra analysis is a powerful approach to **describe the relationship between species size and abundance with environment** (Petchey and Belgrano, 2010). Especially, in the case of invasive species, this approach in very useful **to define the sensitives periods** to implement management measures (Buba *et al.*, 2017; Petchey and Belgrano, 2010). The analysis of the size spectra distribution showed integrative results on how environment was driving the blue crab's population in term of growth, sexual maturity and copulation.

The population dynamics of *Callinectes sapidus* show significant differences across its native range and in the Mediterranean (Mancinelli *et al.*, 2024; Marchessaux *et al.*, 2023c, 2024c). It has been observed that **each *Callinectes sapidus* population is unique**, and **size-weight relationships vary** from one area to another **due to environmental conditions** (e.g., temperature, salinity) influencing these relationships. Table 1 highlights the differences in size-weight relationship coefficients reported in the literature, revealing significant variations between males and females as well as between sites.

Table 1. Allometric parameters of *Callinectes sapidus.* Source: https://www.sealifebase.se

a	b	Doubtful?	Sex	Length (cm)	Length type	No.	Country	Locality
0.3913	2.199	No	female	5.5 - 17.5	CW	317	Türkiye	Beymelek Lagoon Lake, Antalya/2000
0.2489	2.396	No	female	6.8 - 14.7	CW	55	Egypt	Bardawil Lagoon, Sinai Peninsula/2015
0.2331	2.413	No	female	7.6 - 18.6	CW	1342	Türkiye	Beymelek lagoon/2009-2010
0.2016	2.554	No	male		CW		Türkiye	Mediterranean Sea/2006
0.2186	2.561	No	mixed	6.5 - 15.5	CW	140	Egypt	Bardawil Lagoon, Sinai Peninsula/2015
0.1752	2.568	No	female		CW		Brazil	Babitonga Bay, Santa Catarina/2003-2004
0.1263	2.570	No	female		CW		USA	Chesapeake Bay
0.1646	2.589	No	female		CW		Türkiye	Mediterranean Sea/2006
0.1834	2.613	No	male	5.1 - 18.1	CW	710	Türkiye	Beymelek Lagoon Lake, Antalya/2000
1.3898	2.626	No	male		CL		Türkiye	Mediterranean Sea/2006
0.1256	2.639	No	female		CW		USA	Galveston Bay, Texas
0.1216	2.670	No	male		CW		USA	Chesapeake Bay
0.1284	2.700	No	mixed		CW		Türkiye	Mediterranean Sea/2006
0.1764	2.769	No	male	6.5 - 15.5	CW	85	Egypt	Bardawil Lagoon, Sinai Peninsula/2015
0.1182	2.772	No	male	6.0 - 21.3	CW	869	Türkiye	Beymelek lagoon/2009-2010
0.1084	2.775	No	male		CW		USA	Galveston Bay, Texas
0.1193	2.775	No	female	6.7 - 16.3	CW		Egypt	Bardawil Lagoon/2016-2018
0.0887	2.899	No	mixed	6.3 - 16.3	CW		Egypt	Bardawil Lagoon/2016-2018
0.6825	2.931	No	female	3.6 - 7.7	CL	55	Egypt	Bardawil Lagoon, Sinai Peninsula/2015
0.7490	2.943	No	mixed		CL		Türkiye	Mediterranean Sea/2006
0.0805	2.954	No	male		CW		Brazil	Babitonga Bay, Santa Catarina/2003-2004
0.7005	2.971	No	female		CL		Türkiye	Mediterranean Sea/2006
0.5310	3.123	No	mixed	3.6 - 7.7	CL	140	Egypt	Bardawil Lagoon, Sinai Peninsula/2015
0.5433	3.133	No	male	4.4 - 7.5	CL	85	Egypt	Bardawil Lagoon, Sinai Peninsula/2015
0.3220	3.307	No	male	6.3 - 15.2	CW		Egypt	Bardawil Lagoon/2016-2018

The largest blue crab specimen are generally **caught in spring-summer** and **the smallest** specimens in **autumn-winter** as observed in populations in the Mediterranean Sea (e.g. Lesina Lagoon, Italy (Cilenti *et al.*, 2015) and Monolimni Lagoon, Agean Sea (Kevrekidis *et al.*, 2023), Trapani Saltmarshes (Marchessaux *et al.*, 2023c), Corsican lagoons (Marchessaux *et al.*, 2024c)). Local conditions are indeed crucial factors in addressing local presence of species as showed by the analysis of size spectra. **The recruitment period of juveniles** was identified between **September and November** and at the **end of winter** (Marchessaux *et al.*, 2023c). The population's growth period was identified from the end of winter to early summer. For many populations in native areas and Mediterranean Sea, it is known that *Callinectes sapidus* hibernates during the winter at temperatures **below 14°C putative critical lower thermal threshold** making local conditions unfavorable to the metabolism of *C. sapidus* (Hines *et al.*, 1987; Lipcius and Van Engel, 1990; Mancinelli *et al.*, 2013; Pereira *et al.*, 2009).

2.3.2 Sexual maturity and reproduction

American blue crabs reach sexual maturity after numerous post-larval molts (between 18 and 19 molts for males and 18 to 20 molts for females) (Van Engel, 1958). **The time required to reach sexual maturity varies according to geographic area, mainly latitude**; the warmer the water, the faster the development of the species (Churchill, 1919). As an example, sexual maturity is reached between 10 and 12 months for individuals studied in the Gulf of Mexico and up to 20 months for individuals in Chesapeake Bay (Millikin, 1984; Van Engel, 1958).

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). Recent studies in the Mediterranean have shown that **sexual maturity is reached differently from one area to another** (Table 2), depending in particular on environmental conditions (e.g. temperature, salinity) (Marchessaux *et al.*, 2023c, 2024c). For example, in Sicily (Italy), males were mature at 11.75 cm, while in Corsica they were mature at 16.16 cm (Biguglia Lagoon), and 14.38 cm (Palo Lagoon) (Marchessaux *et al.*, 2023c, 2024c). For females, the results are the same: in Sicily, sexual maturity was reached at 12.0 cm, while it was expected at 16.79 cm and 14.38 cm in Biguglia and Palo lagoons respectively. Differences were also noted in other areas of the Mediterranean and in its native range (Table 1).

Table 2. **Comparison of the size at first maturity for *Callinectes sapidus* in the information available in the literature in native and introduced areas. Extracted from** Marchessaux ***et al.***, (2024c).

Country	Study site name	Native (N) / Introduced (I)	Sex	Size at maturity (cm)	References
France	Biguglia Lagoon	I	Males	16.16	(Marchessaux *et al.*, 2024c)
France	Palo Lagoon	I	Males	14.38	(Marchessaux *et al.*, 2024c)
Italy	Trapani saltmarshes	I	Males	11.75	(Marchessaux *et al.*, 2023c)
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	(Marchessaux *et al.*, 2024c)
France	Palo Lagoon	I	Females	13.86	(Marchessaux *et al.*, 2024c)
Italy	Trapani saltmarshes	I	Females	12.00	(Marchessaux *et al.*, 2023c)
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)

The life cycle of *Callinectes sapidus* takes place in different types of habitats: bays, lagoons and estuaries. It includes (i) population stratification, (ii) migratory activities mainly linked to genus, ontogeny and reproduction, and (iii) trophic aspects (Marchessaux *et al.*, 2023a; McClintock *et al.*, 1993; Ramach *et al.*, 2009). **Despite its preference for medium-salinity** waters, **the American blue crab has also been described in very low-salinity or even freshwaters** (Churchill, 1919). **In lagoon environments, estuaries and low-salinity regions, juveniles of both sexes predominate**. While **adult males remain in the estuary or lagoon**, **adult and ovigerous females migrate to saltier waters** (Aguilar *et al.*, 2005; Archambault *et al.*, 1990; Ortiz-Leon *et al.*, 2007; Ramach *et al.*, 2009). In summer, blue crabs are found in shallow waters, and in winter they migrate to deeper waters (Churchill, 1919).

The life cycle of *Callinectes sapidus* is divided into **two phases**: the juvenile/adult **benthic phase**, and the **planktonic** (larval) **phase** (Figure 5). American blue crab reproduction is influenced by several factors, including the salinity and temperature of the waters frequented. **Reproduction takes place in brackish water**. Males can mate several times a year, unlike females, who lay eggs only after their terminal molt. Females migrate upstream from the estuaries/lagunes where the males are located (Williams, 2004). The male carries and seems to protect the female before her terminal molt (this behavior is called "prenuptial strolling") so as to be able to mate and fertilize her as soon as she has molted. As the female's carapace is still soft, fertilization can only take place during this period (Churchill, 1919). Mating can take place day or night, and lasts between 5 and 12 hours (Van Engel, 1958).

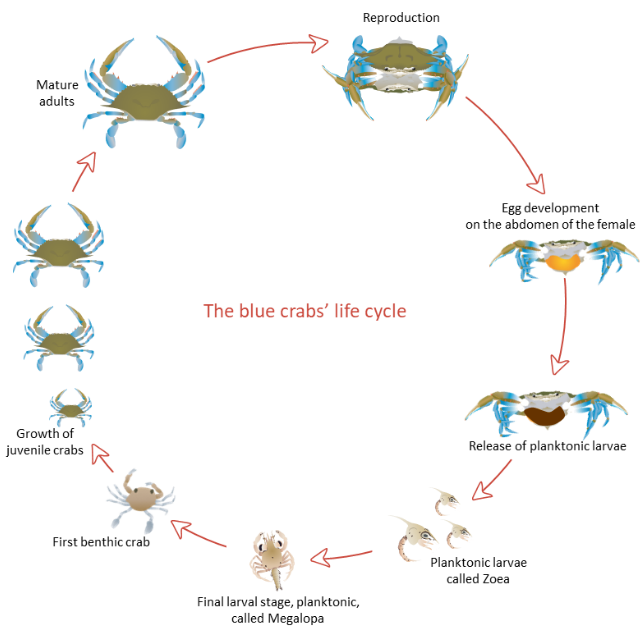


Figure 5. Schematic representation of the life cycle of *Callinectes sapidus,* figure by Guillaume Marchessaux.

In its native area, **oviposition begins in May, with a peak** (100 % of females caught oviposit) **from June to August** (Havens and McConaugha, 1990). However, ovigerous females have been observed throughout the year in Brazil, with a peak between December and March (corresponding to the summer period in this part of the world; Severino-Rodrigues *et al.*, 2013). *Callinectes sapidus* reproduction periods vary from one area to another in the Mediterranean Sea. **Ovigerous females are generally observed between April and October,** but in certain areas ovigerous females are also observed in November and December, as is the case in the Biguglia lagoon in Corsica (France).

Female eggs are yellow/orange when laid, but turn brown and then black before hatching as incubation progresses (Figure 6) (Hench *et al.*, 2004). The **number of eggs per clutch ranges from 700,000 to 2,100,000 depending on female size** (Churchill, 1919; Graham and Beaven, 1942; Pyle and Cronin, 1950; Van Engel, 1958), in the Mediterranean the number of eggs appears to be equivalent (Cilenti *et al.*, 2015). At the end of eggs incubation, in their native range and in the Mediterranean Sea, fe**males migrate to the open sea or to waters with high salinity**, so that the eggs can hatch and the larvae can complete their development cycle off the coast. **Eggs hatch between 14 and 17 days after laying in water at 26°C** and

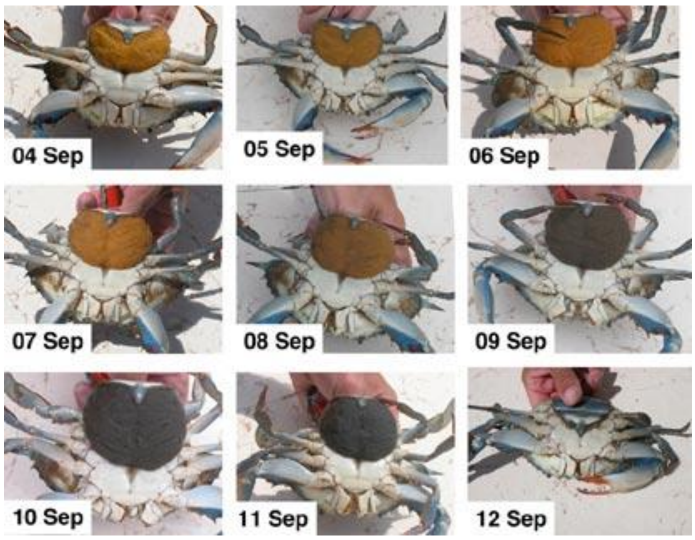


Figure 6. Photographs of ovigerous females of *Callinectes sapidus* at different stages of egg maturation. Figure taken from Hench *et al.*, (2004).

between 12 and 15 days in water at 29°C (Churchill, 1919), all at a salinity of at least 20 psu (Millikin, 1984). **Larval development** can last **between 1 and 2 months**, depending on water temperature. Zoe larvae, averaging 1 mm in length, go through 7 to 8 stages before becoming megalopas. The size of the megalops is between 1 and 3 mm long (Churchill, 1919; Costlow and Bookhout, 1959). Zoe larvae need between 31 and 49 days to complete all the Zoe stages before becoming a megalops (Costlow and Bookhout, 1959).

The megalopa stage lasts several days and completes its cycle in the benthos, generally in coastal areas. Costlow and Bookhout (1959) proved, through an experimental study, that the time from metamorphosis of the megalopa stage to a juvenile crab (Figure 7) was dependent on salinity at a temperature of 25°C (between 6 and 9 days for a salinity varying between 20.1 and 26.7 psu and between 10 and 20 days for a salinity higher than 31.1 psu). A recent study characterized the larval phase of *C. sapidus* populations on the Balearic Islands in Spain (Png-Gonzalez *et al.*, 2021). Costlow and Bookhout (1959) remains the benchmark study of larval development; however, this work is based on observations in the geographical area of origin of *C. sapidus*.

Figure 7. Photography of a juvenile American blue crab, caught in Sicily (Italy). Guillaume Marchessaux.

The megalopa will then differentiate into juvenile crabs, which are considered benthic. These juveniles will tend **to camouflage themselves in seagrass beds** (e.g. Sea Grasses, *Cymodocea, Ruppia*, etc.) and/or silted up **in muddy substrates to avoid predators** (Marchessaux *et al.*, 2023a, 2023c).

Cheng *et al.* (2022) have shown that coastal vegetation and bathymetry are the main features influencing the relative abundance and distribution of adult *C. sapidus* over wide spatial scales (a few meters to several kilometers). Indeed, adult crabs seem to be found in deeper water than young individuals or juveniles; **juveniles can be found in just a few centimeters of water** (Marchessaux *et al.*, 2023c). In general, the closer to the shore, the smaller the individuals (Churchill, 1919). The various factors that can influence the distribution of the American blue crab in its native range have been studied/observed and have enabled us to highlight local distribution preferences through: the presence of sparse grass beds, depth, salinity and temperature (Cheng *et al.*, 2022; Churchill, 1919). For example, on the Virginia coast, the maximum number of observed males and females (both grained and un-grained) was found in sparse seagrass beds, corresponding to a density of 200 to 300 clusters per m² (Cheng *et al.*, 2022). A study carried out during the summer in Croatia showed that females were concentrated mainly in waters with high salinity (above 30 psu), while males seemed to prefer brackish waters between 20 and 25 psu (Jakov and Glamuzina, 2011).

As in almost all crustaceans, growth is linked to molting (Gray and Newcombe, 1938; Newcombe *et al.*, 1949). Autotomy and regeneration occur, especially in growing juveniles (Churchill, 1919). After molting, the cuticle hardens in 2 or 3 days (Churchill, 1919). Contrary to the general rule, this crab does not molt throughout its life; it has a pubertal molt which is also the terminal molt; the latter is linked to the regression of the Y organ or molting gland (Carlisle, 1957; Haefner and Shuster, 1964). Growth is rapid. During its lifetime, the crab molts around 18 (females) to 20 times (males); males grow slightly faster than females. **An average growth of 120 % per molt has been observed**, with an average intermolt duration of 16 days (Bilen and Yesilyurt, 2014). The usual lifespan does not exceed 3 or 4 years (Churchill, 1919; Van Engel, 1990, 1958); however, a lifespan of up to 5 to 8 years has also been suggested (Fischler, 1965). **The frequency of molting depends on the age of the crab and the temperature**; the higher the temperature, the more often the crab molts (Churchill, 1919). Conversely, individuals with parasites such *Loxothylacus texanus* Boschma, 1933 molt less frequently.

2.3.3 Larval connectivity

The larvae of *Callinectes sapidus* are planktonic, meaning **they are transported by ocean currents** throughout their development. Therefore, it is essential to understand the role of ocean currents in the Mediterranean to determine the larval connectivity of *C. sapidus* populations. A study showed that the larval dispersion dynamics for *C. sapidus* different **clusters of connectivity in the Mediterranean Sea** (Marchessaux *et al.*, 2023b) (Figure 8). There are several connectivity clusters in the Mediterranean:

- Balearic Islands, Spanish coasts and mainland France
- Northern Italy, Corsica, Sardinia, Sicily and Tunisia
- Morocco, Algeria, Tunisia
- Sicily, Southern Italy
- All Adriatic Sea countries
- All Aegean Sea countries
- Turkey, Cyprus to Egypt.

These clusters clearly identify the importance of collaboration between countries. The distance traveled by *C. sapidus* larvae ranged from 0 km to 600 km, with the highest frequencies observed for **distances < 100 km** (64.2%), highlighting recruitment near the release zones and emphasizing **medium-scale connectivity challenges** (Marchessaux *et al.*, 2023b).

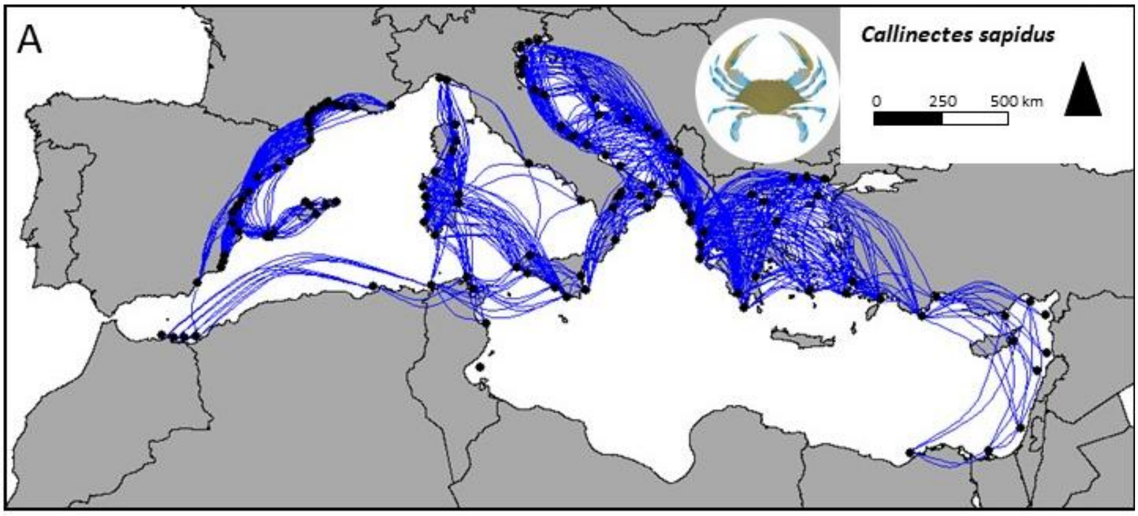


Figure 8. Clusters of larval connectivity identified in the Mediterranean Sea for *Callinectes sapidus.* Figure extracted from Marchessaux *et al.*, (2023a).

2.4 Ecology of *Callinectes sapidus*

2.4.1 Habitat

The American blue crab *Callinectes sapidus* primarily inhabits environments with **significant salinity gradients**. It is predominantly found in **estuaries and brackish lagoons** in both its native range and the Mediterranean. However, it is also often encountered at the interface of these habitats, in coastal marine zones, where it can survive at **depths of up to 35 meters**. *Callinectes sapidus* is an **active**, **aggressive** and **epibenthic omnivore** abundant in shallow habitats. Juveniles are frequently observed in shallow macroalgal fields, while larger crabs are found in deeper waters (Churchill, 1919; Epifanio *et al.*, 2003).

The American blue crab occupies diverse habitats due to its life cycle, living in different environments on **sandy or muddy substrates**, in coastal waters, lagoons, and estuaries with salicornia vegetation (Holthuis, 1987; Mancinelli *et al.*, 2013; Powers and LW, 1977). It is also **present in seagrass meadows**, which serve as critical nursery grounds for juveniles and adults (Heck and Thoman, 1984; Orth and van Montfrans, 1990). Additionally, *C. sapidus* can be found **in mangrove** ecosystems in its tropical native areas. The species is **euryhaline**, capable of surviving in waters with **salinity ranging from 0 to 65 g/L** (Marchessaux *et al.*, 2024a), and even up to 117‰ in the Laguna Madre de Tamaulipas in Mexico (Diez-García *et al.*, 2013). It is also **eurythermal**, tolerating temperatures between **3°C and 40°C** (Marchessaux *et al.*, 2022a).

2.4.2 Environmental tolerance

The invasion of *Callinectes sapidus* in Europe and the Mediterranean has demonstrated the American blue crab's ability to adapt to a wide variety of environments and habitats. This is due in part to its **tolerance to temperature and salinity**, as well as the unique characteristics of its life cycle, including reproduction in brackish waters and larval release and growth in marine environments.

One of the challenges associated with the invasion of *Callinectes sapidus* in the Mediterranean was determining its metabolic tolerance to temperature. Identifying the thermal window of the American blue crab was essential to anticipate the species' expansion and/or persistence in the Mediterranean under climate change scenarios (Marchessaux *et al.*, 2022a). Analyzing the shape of its tolerance curve, along with lethal and optimal temperatures, provided crucial insights into the environmental limits of the species.

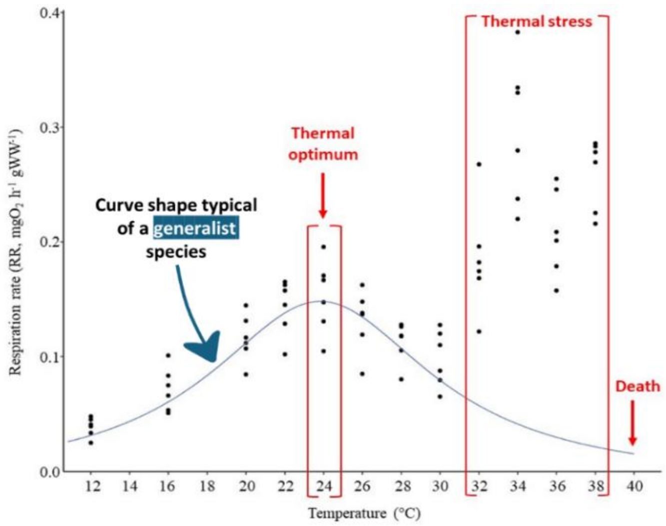


Figure 9. Thermal tolerance curve of *Callinectes sapidus.* Figure extracted and modified from scenarios Marchessaux *et al.*, (2022).

Adult *Callinectes sapidus* exhibited a broad thermal tolerance curve, characteristic of a **generalist species in terms of temperature** (Figure 9). Models estimated a minimum lethal temperature of 0°C and a maximum lethal temperature of 40°C. The species' **optimal temperature was determined at 24°C**, but *C. sapidus* tolerates a very wide temperature range, allowing it to survive under almost all seasonal conditions (Marchessaux *et al.*, 2022a).

Determining the temperature tolerance curve not only helped define the species' thermal window but also allowed researchers to map favorable thermal habitats for *C. sapidus* across the Mediterranean under current and future conditions (Figure 9).

Predictive metabolic maps revealed that the Thermal Habitat Suitability (THS) of *Callinectes sapidus* in the Mediterranean Sea varies seasonally across different sections of the basin (Figure 9).

Under future climate scenarios (IPCC RCP 4.5 optimistic and RCP 8.5 pessimistic), the monthly **THS increased by an average of +0.2**. This indicates that under both current and future conditions, *C. sapidus* will likely find favorable conditions year-round for its persistence. Consequently, the species may expand its range and maintain long-term stability in the Mediterranean. **This ability to adapt to a wide range of thermal conditions underscores the importance of monitoring *Callinectes sapidus* populations and**

developing management strategies to mitigate its ecological and economic impacts in invaded regions (Marchessaux *et al.*, 2022a).

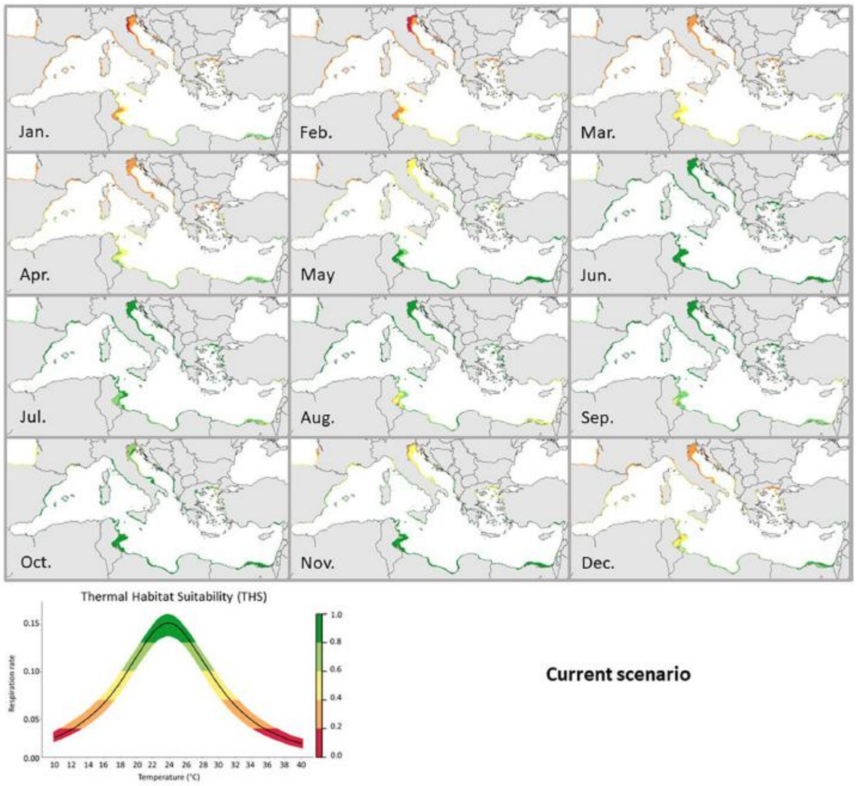


Figure 10. Distribution of thermal habitats based on the thermal tolerance curve of *Callinectes sapidus* in the Mediterranean Sea. Figure extracted from scenarios Marchessaux *et al.*, (2022).

Another **critical aspect** to consider in the study of the environmental tolerance of *C. sapidus* is its **salinity tolerance**. As previously mentioned, (Section III.3.1.), **salinity gradients play a crucial role in the species' reproduction**. To recall, males and females' mate in brackish environments near rivers, eggs mature at higher salinity levels, and planktonic larvae develop in marine environments.

A recent study explored the salinity tolerance of adult *C. sapidus* (both males and females) across a broad range of salinities (from 0 to 65 psu) (Marchessaux *et al.*, 2024a). The results indicated no significant differences between males and females, both displaying a wide range of salinity tolerance (Figure 11). **In freshwater** (salinity = 0 psu), **specimens did not survive**, with an estimated survival time of 18 hours in freshwater conditions. However, starting at a salinity of 5 psu, all specimens survived. **The optimal conditions for the American blue crab were estimated at 18.5 psu**, corresponding to brackish water. Beyond this optimum, the metabolism of *C. sapidus* decreased (Figure 11). **Mortality began to occur at salinities of 55 psu, and all specimens were dead at 65 psu.**

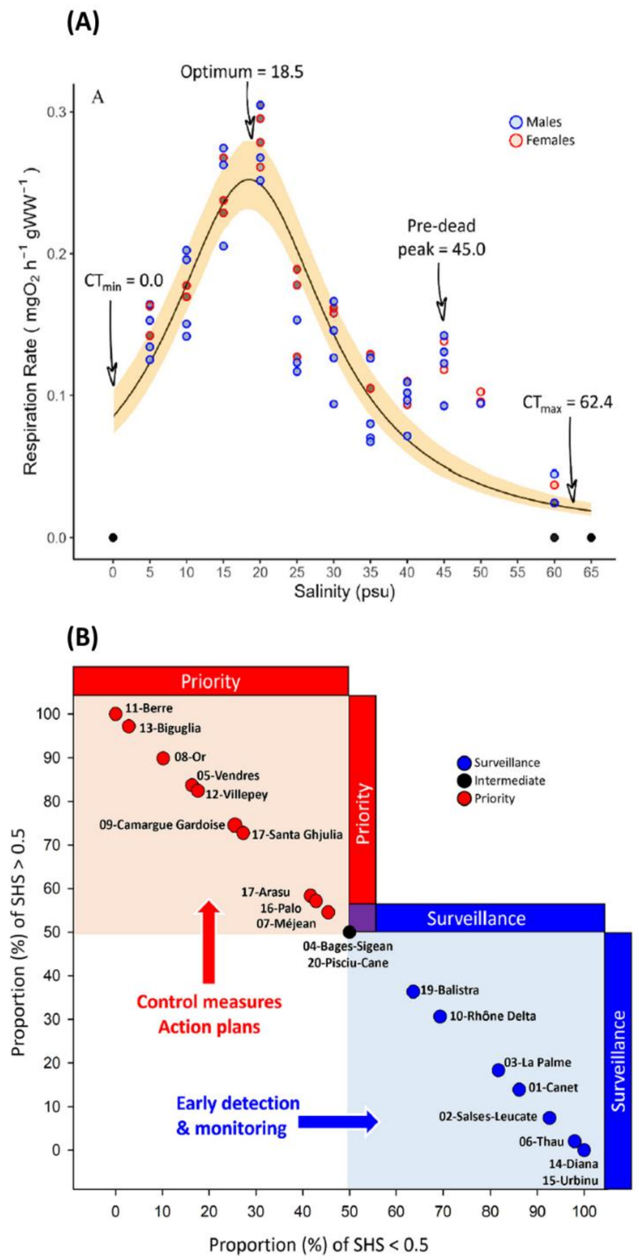


Figure 11. (A) Tolerance of *Callinectes sapidus* to various salinities, and (B) priorization plot based on habitat suitability in 20 french Mediterreanean Lagoons. Figures extracted and modified from Marchessaux *et al.*, (2024a)

This study highlighted a previously underexplored aspect of the American blue crab, the effect of salinity on its metabolism.

Similarly to temperature, the authors also mapped the distribution of salinity-related favorable habitats on a small-scale lagoon level, which are crucial environments for the species' reproduction. Mapping efforts were conducted across 20 French Mediterranean lagoons exhibiting varying levels of invasion (refer to the article for detailed maps).

Based on the mapping and available data on favorable habitats for the American blue crab, the authors proposed a **prioritization index for management measures based on the species' tolerance** across the 20 studied lagoons. Using this tool, the lagoons were classified into three categories: **priority**, **intermediate**, and **monitoring**, with specific recommendations provided for each category.

In conclusion, these two studies on the temperature and salinity tolerance of *Callinectes sapidus* have provided significant new insights into the species' biology and the anticipation of its expansion. Additionally, leveraging this data enables the development of support tools for the management and control of the species in the Mediterranean.

2.4.3 Diet and Feeding Ecology of *Callinectes sapidus*

Callinectes sapidus is an **omnivorous** and **opportunistic predator**. It is a highly **aggressive crab**. Its diet consists of **various trophic groups**, varying according to prey availability and the individual's developmental stage. Studies show that this crab primarily consumes **mollusks**, **crustaceans**, **fish**, **decomposed organic matter**, and **algae**.

The American blue crab is also necrophagous and cannibalistic (Peery, 1989) competiting with other crabs, including *Callinectes similis*, *C. ornatus*, *Panopeus herbstii*, *Menippe mercenaria*, and *Carcinus maenas* (Gennaio *et al.*, 2006).

The diet of the American blue crab, adapted to a wide variety of trophic resources, is a key factor in its success as an invasive species:

- **Mollusks |** Mollusks, especially bivalves and gastropods, constitute a significant portion of *C. sapidus*' diet. In the Mediterranean, mussels (*Mytilus galloprovincialis*), clams (*Ruditapes decussatus*), and wedge shells (*Donax trunculus*) are frequently predated (Mancinelli *et al.*, 2016). Predation on another invasive mollusk *Rapana venosa* was also reported (Harding, 2003). These prey items are often abundant in the lagoonal and estuarine habitats where the blue crab lives.
- **Crustaceans |** Crustaceans, including small decapods and amphipods, also represent a significant component of the diet of *C. sapidus* (Seitz *et al.*, 2011). The crab is known for its cannibalistic behaviors, a phenomenon documented both in its native range and in the Mediterranean (Dittel *et al.*, 2006).
- **Fish |** *Callinectes sapidus* preys on fish in particular in the fishers' nets.
- **Plant Matter and Detritus |** In addition to living organisms, the blue crab consumes decomposed organic matter and algae (Annabi *et al.*, 2018; Aslan and Polito, 2021; Seitz *et al.*, 2011). This behavior allows it to survive in environments where animal prey is scarce (Davie, 2021; Lee *et al.*, 2021). Algae from the genus *Ulva sp.* and grasses from the genus *Spartina sp.* (Gennaio *et al.*, 2006).
- **Cannibalism |** The American blue crab is also known for its cannibalistic behavior. Cannibalism can account for up to 13% of the species' diet (*bluecrab.info*; (Peery, 1989). Individuals most likely to be consumed by their peers are those that are: (i) in poor health, (ii) missing significant appendages, (iii) molting or immediately post-molt, and (iv) heavily fouled by other organisms (*bluecrab.info*).
- **Jellyfish |** Predation on the hydromedusa *Gonionemus vertens* (Carman *et al.*, 2017) living in seagrasses was recorded.

In their native range, the diet composition of blue crabs generally consists of **mollusks** (from 30 % to 40 %; mussels, clams, oysters), from 15 % to 20 % of **crustaceans** (decapods, amphipods), 15–20 % of **fishes**, <5 % of **polychaetes**, and a highly variable percentage of **algae**, **sediment**, and **detritus** (Belgrad and Griffen, 2016).

Adaptability and Feeding Ecology in the Mediterranean

There is still limited information available on the trophic characteristics of the crab in the Mediterranean. However, *C. sapidus* appears to compete with native crab and fish species, potentially causing significant ecological impacts (Labrune *et al.*, 2019; Nehring, 2011). The establishment of *C. sapidus* in the Mediterranean is **largely tied to its opportunistic feeding habits**. Its ability to exploit a wide variety of trophic resources, combined with its tolerance for salinity and temperature variations, supports its invasion of coastal ecosystems (Nehring, 2011). In the Mediterranean Sea, *C. sapidus* was identified as a fully carnivorous predator and share the same set of trophic resources with these benthivores fish species in Croatia (Mancinelli *et al.*, 2016). Due to the aggressiveness and omnivorous diet, the impact of blue crabs species (like *C. sapidus*) is important especially on the commercial species witch are decreasing (Öndes and Gökçe, 2021) as perceived by the artisanal small-scale fishermen in this present study.

In Mediterranean lagoons such as the Berre Lagoon and the Po Delta, studies have shown that *C. sapidus* exerts significant **predatory pressure on local species**. This **includes economically important species** such as **oysters** (*Crassostrea gigas*) and **clams** (Aslan and Polito, 2021; Kara and Chaoui, 2021; Longmire *et al.*, 2021). These trophic interactions have **major ecological consequences**, including increased competition with native predators and disruptions to local food webs.

The study by Clavero *et al.* (2022) demonstrated that ecosystems dominated by *C. sapidus* **cause decrease and consistent declines in several species**, including those that are threatened or commercially exploited (Figure 12). The impacts of the blue crab seem to manifest even at low abundances, likely hindering the recovery of declining species. The blue crab is becoming a keystone species in invaded systems.

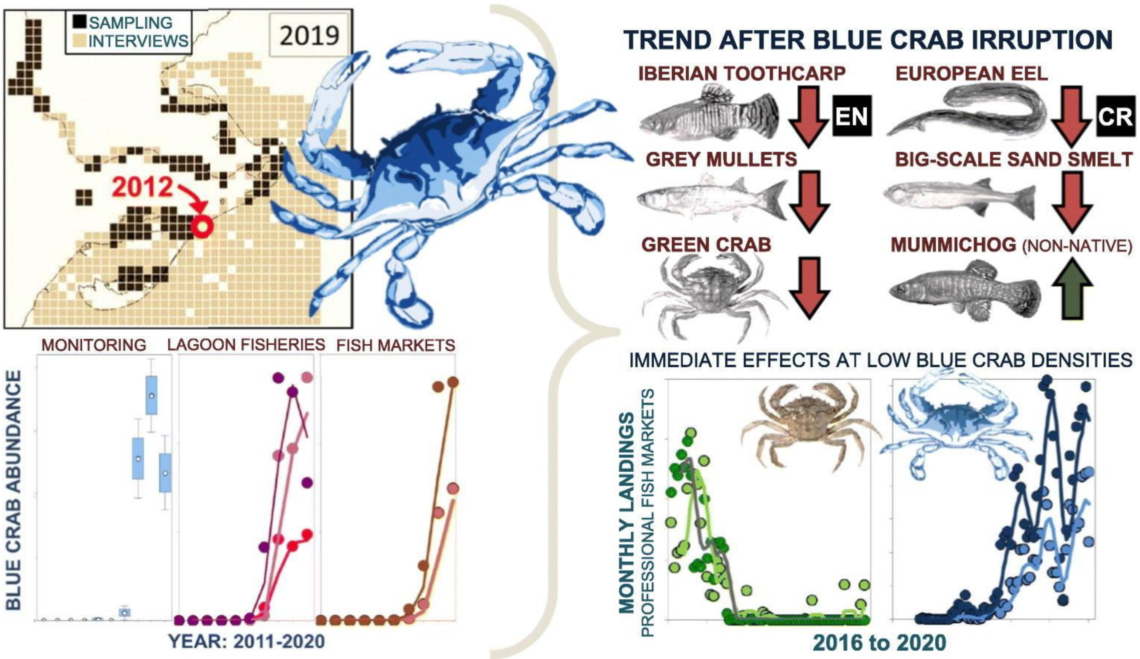


Figure 12. Summary of impacts of *Callinectes sapidus* on Mediterranean biodiversity (Spain). Figure extracted from Clavero *et al.* (2022).

The dietary diversity of *Callinectes sapidus* **causes significant impacts on Mediterranean biodiversity**, with local species extinctions observed in areas invaded by *Callinectes sapidus*. In Spain for example the increase in *C. sapidus* abundances has caused a decline in apple snail stocks in the Elbro delta (Céspedes et al., 2024). In the Po Delta (Italy), the explosion of populations of *C. sapidus* in summer 2023 has caused the drastic decline of clams up to 100%, clam shells showing signs of blue crab predation up to 56%, and the absence of seed in natural recruitment areas (Chiesa et al., 2025).

Predators of *Callinectes sapidus*

The predators of the American blue crab (*Callinectes sapidus*) in its native range are well-documented and numerous. They include:

- **Starfish**: For example, the Forbes Sea star (*Asterias forbesi*) (Auster and DeGoursey, 1994).
- **Marine Turtles**: Such as the olive ridley sea turtle (*Lepidochelys olivacea*) (Wildermann and Barrios-Garrido, 2012).
- **Fish**: Including the red drum (*Sciaenops ocellatus*), the Atlantic croaker (*Micropogonias undulatus*) (Overstreet and Heard, 1978), the black drum (*Pogonias cromis*), and the American eel (*Anguilla rostrata*) (Jaworski, 1972). An observation of predation of *Dicentrachus labrax* on juveniles of *C. sapidus* was recorded in Corsica by fishermen (pers. Com.)

- **Seabirds**: Including the herring gull (*Larus argentatus*) (Kent, 1981), the double-crested cormorant (*Phalacrocorax auritus*), and various heron species (Kent, 1986).
- **Other Crabs**: The green crab (*Carcinus maenas*) is known to dominate *C. sapidus* in direct competition at equal size (MacDonald *et al.*, 2007; Seed, 1980).
- **Cephalopods**: Potential predators that can include squids and octopuses. In the Mediterranean, few studies have been conducted on the predators of the American blue crab. However, a recent study (Prado *et al.*, 2024) demonstrated that Mediterranean octopuses are capable of consuming *Callinectes sapidus* in aquariums (Figure 13). These observations were further corroborated in Corsica at the end of 2024, where underwater photographers documented octopuses preying on blue crabs.

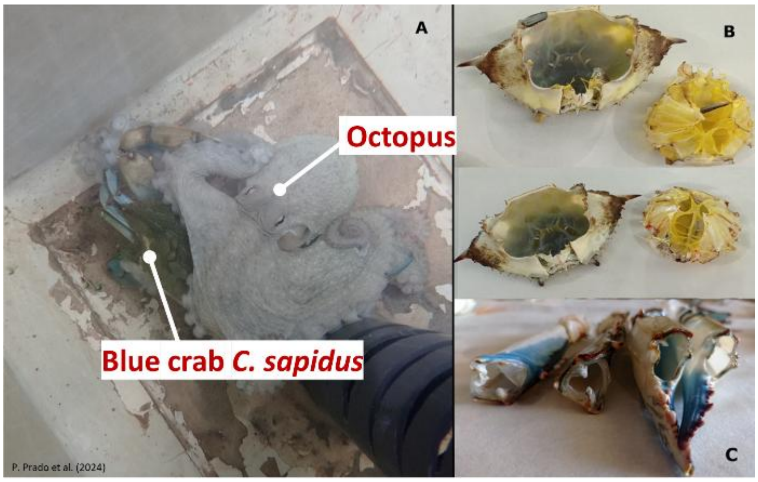
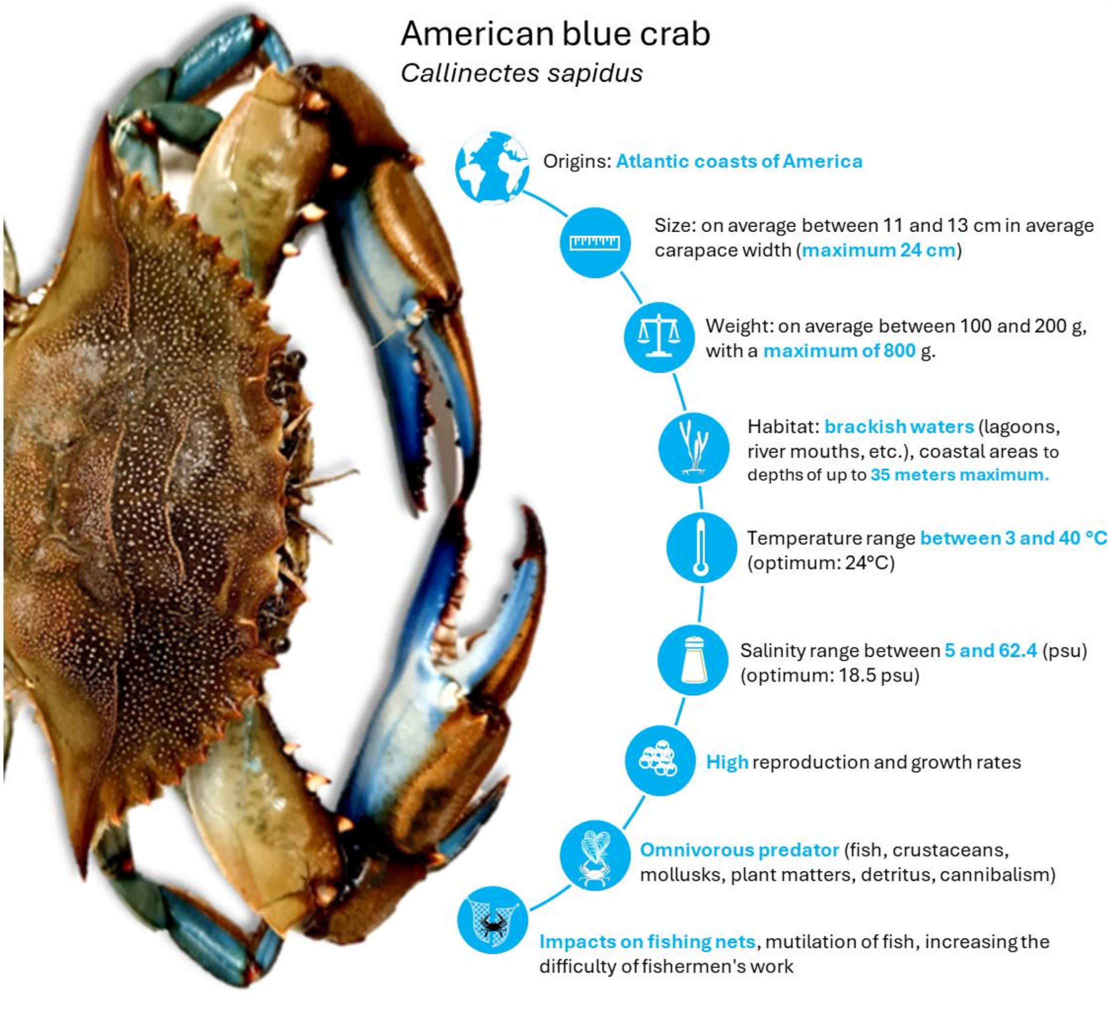


Figure 13. Pictures of a Mediterranean octopus feeding on *Callinectes sapidus*. Pictures extracted and modified from Prado *et al.*, (2024).

- **Cannibalism**: Particularly on juvenile stages, is well-documented (Hines and Ruiz, 1995; Peery, 1989).

2.5 Summary of information on *Callinectes sapidus*



3 Current knowledge of the swimming blue crab *Portunus segnis*

3.1 General characteristics of the species

The blue swimming *Portunus segnis* (Forskål, 1775) crab is generally recognizable by its oval carapace, which is twice as wide as it is long (Figure 14). The carapace surface is rough to finely granular, with 9 marginal spines or spines symmetrically arranged along each side of the anterior lateral edge, and a more pronounced median spine known as the frontal spine. The other legs are laterally flattened, with the last two segments of the posterior pair shaped like paddles for swimming.

Male coloration is dark blue with subtle white spots on the carapace, sometimes merging into a network of fine lines. **Females have similar coloration, but their claws are red instead of blue, with spots on the posterior third of the carapace** (Figure 15). Males are generally larger and more colorful than females, with bright blue legs and claws.

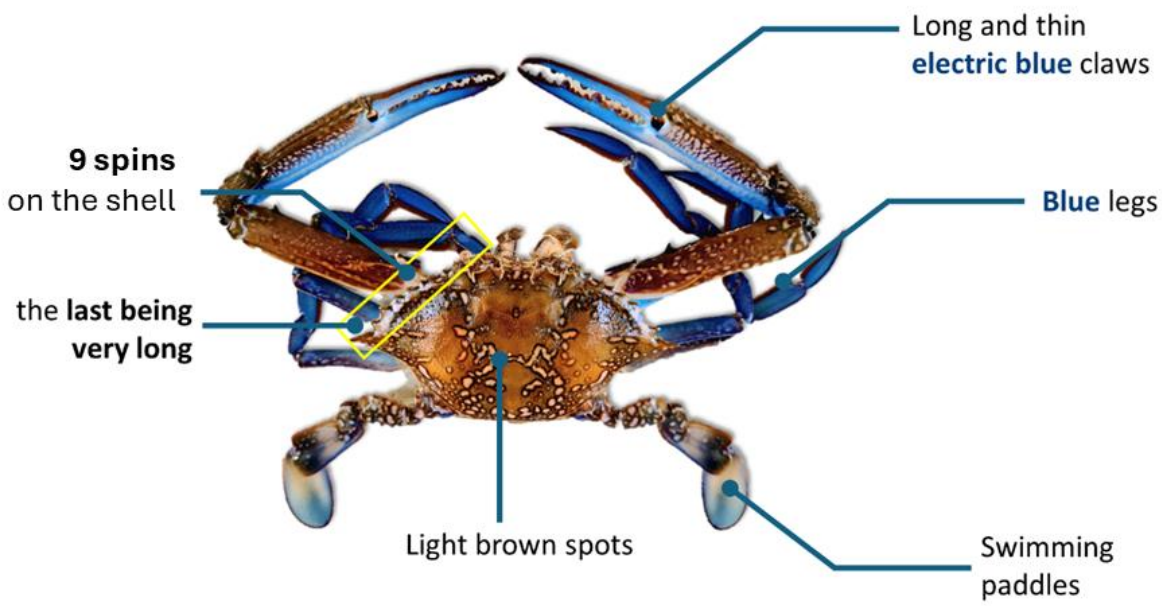


Figure 14. Morphological characteristics of the Swimming blue crab *Portunus segnis*. Photography: Guillaume Marchessaux.

Although females tend to have red claw tips, the difference between males and females is identifiable on the ventral side of the abdomen (Figure 15). In **males**, the **abdomen is triangular**, **T-shaped** and tapered with only 3 segments. In females, the abdomen is wider and rounded, with several segments. In **females**, the shape of the abdomen is a **key indicator for differentiating mature from immature females**. In **immature females,** the **abdomen is triangular**, **narrow** and **pointed**, and **fused with the plastron** (underside of the carapace). In **mature females**, the abdomen is **rounded or broadly dome-shaped**, often **compared to a horseshoe**. The abdomen is wider and more pronounced to accommodate eggs during reproduction (egg sac or sponge). These differences are linked to the morphological evolution of females as they reach sexual maturity, a change essential to their reproductive role.

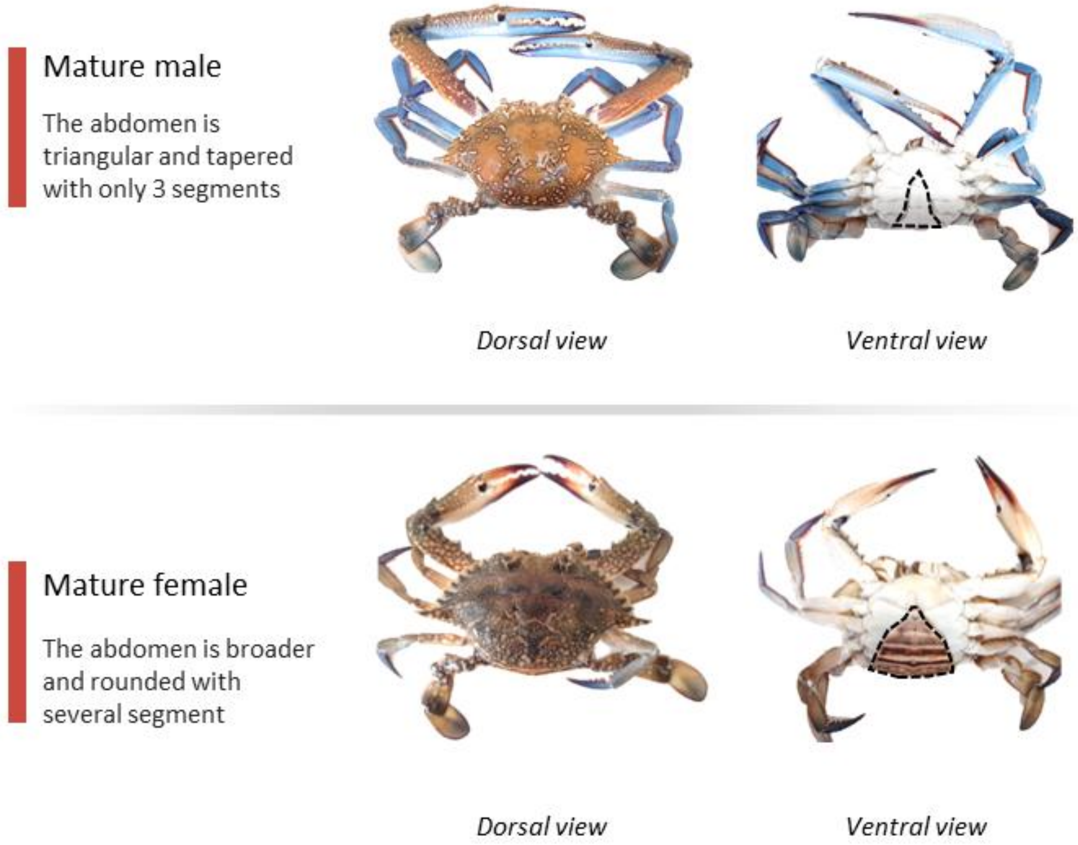


Figure 15. Morphological characteristics of males and females of the blue crab *Portunus segnis*. Photography: Guillaume Marchessaux for males, Jamila Ben Souissi for females.

3.2 Distribution and invasion history

Portunus segnis is **native to the western Indian Ocean**, west of the Indian subcontinent, including the East African coast, the Red Sea, the Arabian Gulf, and the Gulf of Oman. *Portunus segnis* is **one of the first Lessepsian species reported in the Mediterranean** (Fox, 1924; Lai *et al.*, 2010). Initially, *P. segnis* was incorrectly described as *Portunus pelagicus* (Linnaeus, 1758). According to Lai *et al.* (2010), morphological, genetic, and biogeographical studies have identified four distinct species: *Portunus pelagicus* (Linnaeus, 1758), *Portunus reticulatus* (Herbst, 1799), *Portunus armatus* (Milne-Edwards, 1861), and *Portunus segnis* (Forskål, 1775). Some authors refer to these species collectively as the "Portunus complex." In fact, interspecific hybridizations within the *Portunus* genus are frequently observed.

As early as 1898, just a few years after the opening of the Suez Canal, *P. segnis* was reported almost everywhere in the Mediterranean. In Tunisia, it was first observed in the Gulf of Gabès (Rabaoui *et al.*, 2015; Rifi *et al.*, 2014) and more recently in the southern Gulf of Hammamet (Bdioui, 2016). The species was certainly present in southern Tunisia before 2014. In fact, a sample of *Portunus sp.* (incorrectly identified as another genus) was preserved in formalin in the INSTM crab collection, with records dating back to the 1990s. This aligns with the conclusions proposed by Lai *et al.* (2010) regarding interspecific hybridizations within the *Portunus* genus.

After its first report in Egypt in 1898 (Castriota *et al.*, 2022), *P. segnis* was gradually documented in various areas of the Mediterranean, extending from the Levantine Basin to the **eastern Aegean Sea, eastern Sicily, and the northern Tyrrhenian Sea** (Figure 16). The species is known from Cyprus, Egypt, Syria, Palestine, Israel, Turkey, Tunisia, Lebanon, Italy, Greece, and Albania. In 2023, it **has also been reported along the Adriatic coasts** of Italy (Grati *et al.*, 2023) and in **Spain** (Gulf of Cadiz) (de Carvalho-Souza *et al.*, 2023).

Portunus segnis likely entered the Mediterranean via the Suez Canal. The study by Castriota *et al.* (2022) identified **significant hotspots in Tunisia** (Gulf of Gabès) and **in the Eastern Mediterranean** (from Egypt to southern Turkey). Furthermore, Castriota *et al.* (2022) showed that the invasion of *P. segnis* in the Mediterranean, which has been ongoing for a long time, is **currently considered to be expanding**.

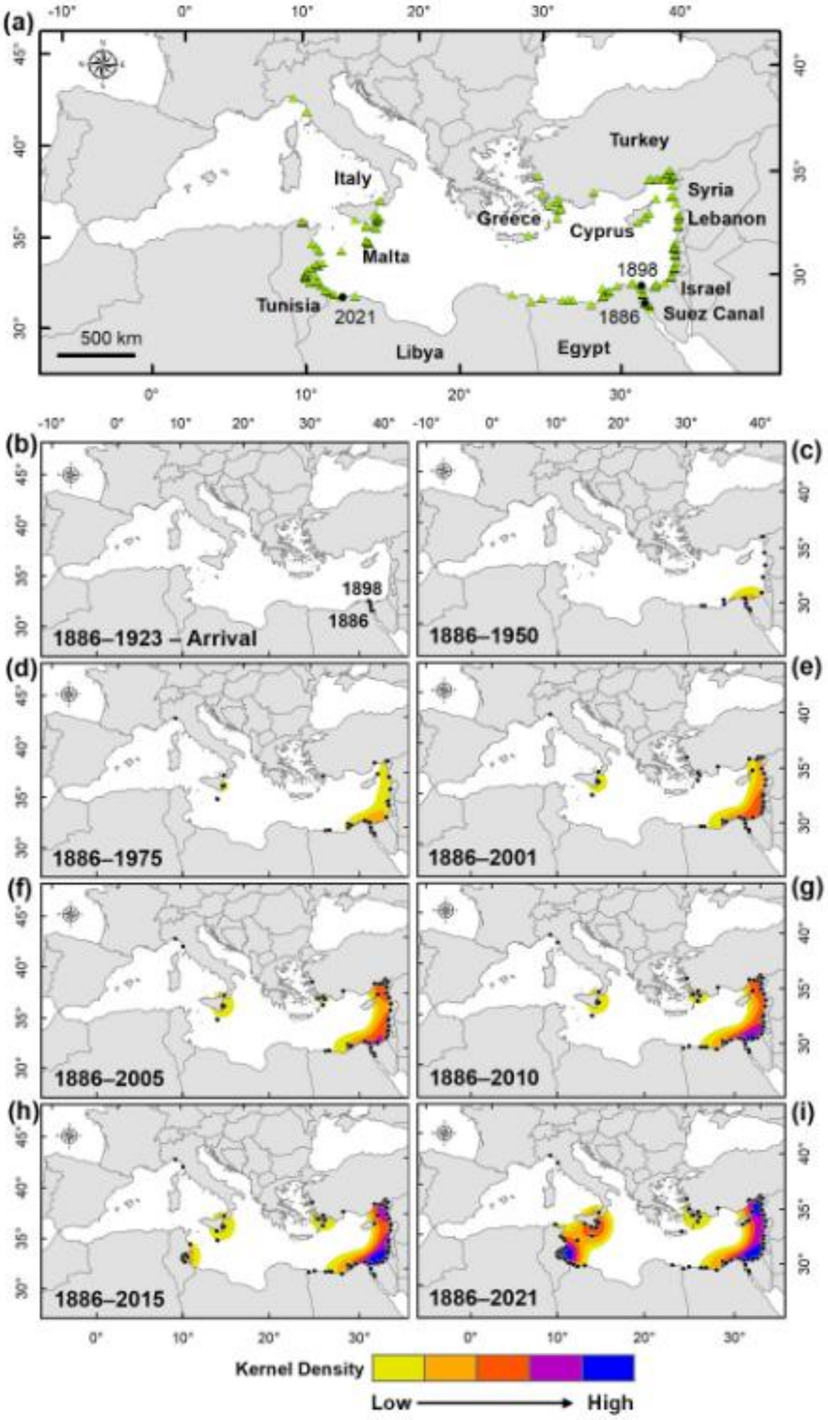


Figure 16. Distribution of *Portunus segnis* in the Mediterranean Sea and history of invasion. Figure extracted from Castriota *et al.* (2022).

3.3 Population dynamics and life cycle of *Portunus segnis*

3.3.1 Population dynamics and size spectra

The populations of *Portunus segnis* are **generally dominated by adults during the winter and spring months**, while **juveniles are more abundant in summer and autumn**. This reflects a seasonal dynamic where reproduction and recruitment strongly influence size composition (Mohsen Safaie *et al.*, 2013; Safaie *et al.*, 2015).

Carapace widths typically range between 38 and 168 mm. Adults (> 100 mm) predominate in winter and spring, while smaller size classes (< 100 mm) increase in summer (Safaie *et al.*, 2015). **The average size at sexual maturity is between 115 and 120 mm** carapace width for females and between 113 and 125 mm for males, depending on the region (Tureli and Yesilyurt, 2017).

The growth pattern follows an allometric relationship, with von Bertalanffy parameters indicating rapid growth rates in the warm, saline waters of the Mediterranean (Yeşilyurt *et al.*, 2022). This observed allometry generally shows faster growth in males. This allometric difference reflects distinct energy strategies between the sexes (O. B. A. H. Hamida *et al.*, 2019). As observed for *Callinectes sapidus*, **each *P. segnis* population is unique**, and **size-weight relationships vary from one area to another**, primarily due to environmental conditions (e.g., temperature, salinity) that influence these relationships. Table 3 highlights the differences in size-weight relationship coefficients reported in the literature, showing significant variations between males and females as well as between sites. The allometric relationships differ across regions, influenced by environmental parameters such as temperature and salinity, as well as prey availability, for instance.

Table 3. Allometric parameters of *Portunus segnis.* Source: https://www.sealifebase.se

a	b	Doubtful?	Sex	Length (cm)	Length type	No.	Country	Locality
0.0062	2.443	No	female	7.0 - 16.5	CW		Iran	Persian Gulf/2011-2012
1.6873	2.511	No	female	5.1 - 7.2	CL	24	Tunisia	Gulf of Gabes
0.1108	2.743	No	female	3.4 - 14.9	CW	299	Tunisia	Gulf of Gabes/2015-2016
0.6418	2.904	No	female	1.8 - 7.5	CL	299	Tunisia	Gulf of Gabes/2015-2016
0.0735	2.980	No	mixed	3.4 - 15.6	CW	634	Tunisia	Gulf of Gabes/2015-2016
0.5268	3.023	No	mixed	1.8 - 7.9	CL	634	Tunisia	Gulf of Gabes/2015-2016
0.0643	3.030	No	female	8.5 - 16.3	CW	154	Iran	Bandar Abbas/2012-2013
0.0587	3.033	No	male	4.0 - 8.0	CL		Iran	Persian Gulf/2011-2012
0.5849	3.068	No	male	2.0 - 7.9	CL	335	Tunisia	Gulf of Gabes/2015-2016
0.0558	3.144	No	male	3.9 - 15.6	CW	335	Tunisia	Gulf of Gabes/2015-2016
0.0491	3.214	No	male		CW	1839	Iran	Persian Gulf and Gulf of Oman/2010-2011
0.0341	3.232	No	mixed		CW	3608	Iran	Persian Gulf and Gulf of Oman/2010-2011
0.0199	3.299	No	female		CW	1769	Iran	Persian Gulf and Gulf of Oman/2010-2011
0.0240	3.380	No	female	11.8 - 15.6	CW	24	Tunisia	Gulf of Gabes
0.0074	3.443	No	female	3.5 - 8.0	CL		Iran	Persian Gulf/2011-2012
0.0254	3.450	No	male	8.1 - 14.9	CW	148	Iran	Bandar Abbas/2012-2013
0.2306	3.552	No	male	7.5 - 17.5	CW		Iran	Persian Gulf/2011-2012

***Portunus segnis* prefers shallow areas (< 10 m) with high biomass and density**. The catch per unit effort (CPUE) is **highest in October**, **making this month the optimal period for fishing**. Biomass shows an increasing trend from June to October, reflecting seasonal recruitment and rapid growth. Adult crabs contribute the most to the total biomass (Safaie *et al.*, 2015).

3.3.2 Sexual maturity and reproduction

The life cycle of the blue swimming crab *Portunus segnis*, includes several characteristic stages typical of brachyuran crustaceans. **Its life cycle is therefore similar to that of *Callinectes sapidus*** (described in section II.3.2.). The primary difference between the two species is that ***Portunus segnis* mates and reproduces in marine environments**, whereas *Callinectes sapidus* mates in brackish waters.

In *Portunus segnis*, **adults reach sexual maturity at approximately 93 mm carapace width** (Hadj Hamida *et al.*, 2022). **Males and females mate after the female's molt** (pre-copulatory molt). The male transfers spermatophores into the female's spermathecae. Fertilized females lay eggs, which they carry on their abdomen in the form of an egg mass. A single female can carry between **142,000 and 2.6 million eggs**, depending on her size (Hadj Hamida *et al.*, 2022). In its native range, the Persian Gulf and the Gulf of Oman, ovigerous females are present year-round, with the highest proportion observed in autumn; spawning occurs throughout the year, peaking in winter (Kamrani *et al.*, 2010; Safaie *et al.*, 2013). Interestingly, two regional studies provide different data on fecundity: between **277,421 and 1,114,348 eggs, with an average fecundity of 662,978 eggs** (Kamrani *et al.*, 2010), and between 521,027 and 6,656,599 eggs, with an average fecundity of **2,397,967 eggs** (Safaie *et al.*, 2013). In the Mediterranean, the average number of eggs (fecundity) observed in 12 ovigerous females (with an average carapace width of 143.3 ± 6.2 mm) was 777,642 ± 80,684 (Rabaoui *et al.*, 2015).

The eggs change color as they develop, transitioning from yellow-orange (immature eggs) to dark brown just before hatching (Figure 17). In *Portunus segnis*, development takes approximately 10 to 15 days, depending on the water temperature.

Figure 17. Photographs of ovigerous females of *Portunus segnis* at different stages of egg maturation. Figure taken from (Safaie *et al.*, 2013).

After hatching, the larvae go through several stages:

- **Zoea**: Zoea larvae feed on plankton. They have a distinct carapace with long dorsal and lateral spines. Growth occurs through several molts.
- **Megalopa**: This is an intermediate stage between larva and juvenile, where the larvae begin to resemble crabs. They migrate to shallow coastal areas, often in seagrass meadows or muddy bottoms, to undergo metamorphosis.

The blue swimming crab can reproduce multiple times a year, with spawning peaks varying by region. For example**, in the Gulf of Gabès (Tunisia),** three main spawning periods have been identified: **May, July, and October-November** (Hadj Hamida *et al.*, 2022).

3.3.3 Larval connectivity

Portunus segnis showed little dispersion and variability regardless of the simulation time (Figure 18) (Marchessaux *et al.*, 2023b). ***Portunus segnis* is less widely distributed than *Callinectes sapidus* in the Mediterranean**, resulting in fewer connectivity clusters. Currently, **two major clusters** are identified: one **between Sicily and Tunisia**, and another in the **Eastern Mediterranean**, **spanning from Turkey to Egyp**t. Additionally, a smaller cluster exists in southern Turkey, connecting populations from mainland Turkey to the islands. The highest frequencies of distances traveled by *Portunus segnis* **larvae were observed for distances <100 km** (63.6%), highlighting recruitment near release areas and indicating a **medium-scale dispersal** challenge (Marchessaux *et al.*, 2023b).

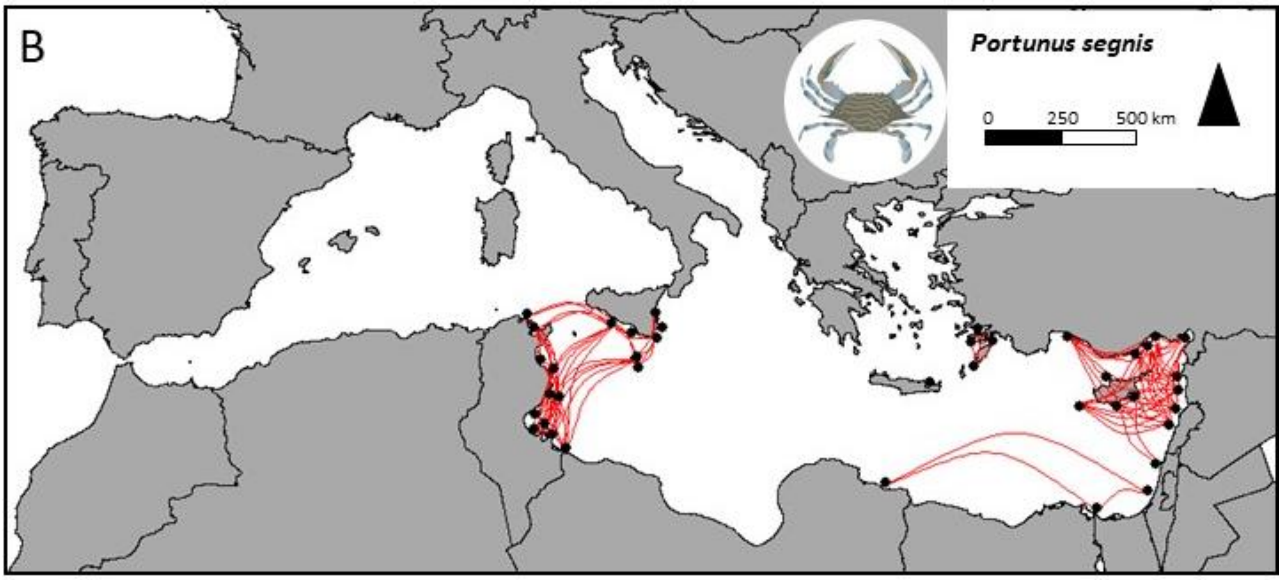


Figure 18. Clusters of larval connectivity identified in the Mediterranean Sea for *Portunus segnis.* Figure extracted from Marchessaux *et al.*, (2023a).

3.4 Ecology of *Portunus segnis*

3.4.1 Habitat

The blue swimming crab inhabits **coastal areas**, **ranging from rocky or stony intertidal zones to depths of up to 65 meters** (Naderloo and Tuerkay, 2012), primarily on sandy and muddy substrates near reefs, in mangroves, seagrass beds, and algal mats. It is an **active nocturnal predator**, **buried during the day** with only its eyes, antennae, and gill openings visible. When disturbed, it burrows into the sand but is a **fast swimmer** and an **opportunistic predator**, primarily carnivorous, voraciously feeding on a variety of benthic animals and to a lesser extent on marine plants and seagrasses. Juveniles tend to remain in shallow intertidal zones.

3.4.2 Environmental tolerance

Portunus segnis is **euryhaline** (adaptable to a wide range of salinities), moving between brackish estuaries, marine environments, and even hypersaline waters (e.g., the Bitter Lakes, Suez Canal). In Tunisia, for instance, the blue swimming crab is observed in the Bizerte Lagoon, a brackish lagoon. It appears that *Portunus segnis* tolerates salinity ranges between 20 and 33 psu.

Regarding the temperature tolerance of *Portunus segnis*, a recent study showed that the species is a **tropical specialist** (Marchessaux *et al.*, 2024c). Its invasive success in the Mediterranean is explained from its physiological plasticity and ability to adapt to global temperatures.

Portunus segnis thermal tolerance discloses a **thermal optimum at 33.64°C**, **CT_{min} at 11.33∘C, and CT_{max} at 41.13°C**, and contributing to understanding its distribution dynamics in response to temperature changes.

The Thermal Habitat Suitability (THS) probability of *P. segnis*, based on its thermal performance, revealed a North-South division in Mediterranean Sea thermal habitats (Figure 20) (Marchessaux *et al.*, 2024c). Throughout winter and early spring (January to May), THS were unfavorable (THS < 0.2) across the Mediterranean. However, in summer-autumn (June to October), particularly in the Gulf of Gabès, Tunisia, southern Mediterranean coasts became suitable (THS > 0.6).

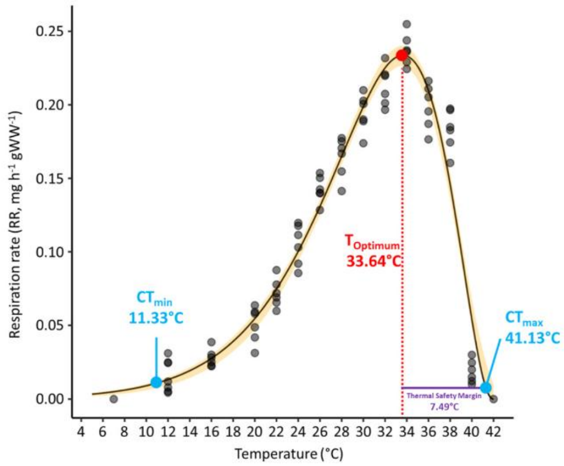


Figure 19. Thermal Performance Curve (TPC) of the Red Sea swimming blue crab *Portunus segnis.* Figure and legend extracted from (Marchessaux *et al.*, 2024c)

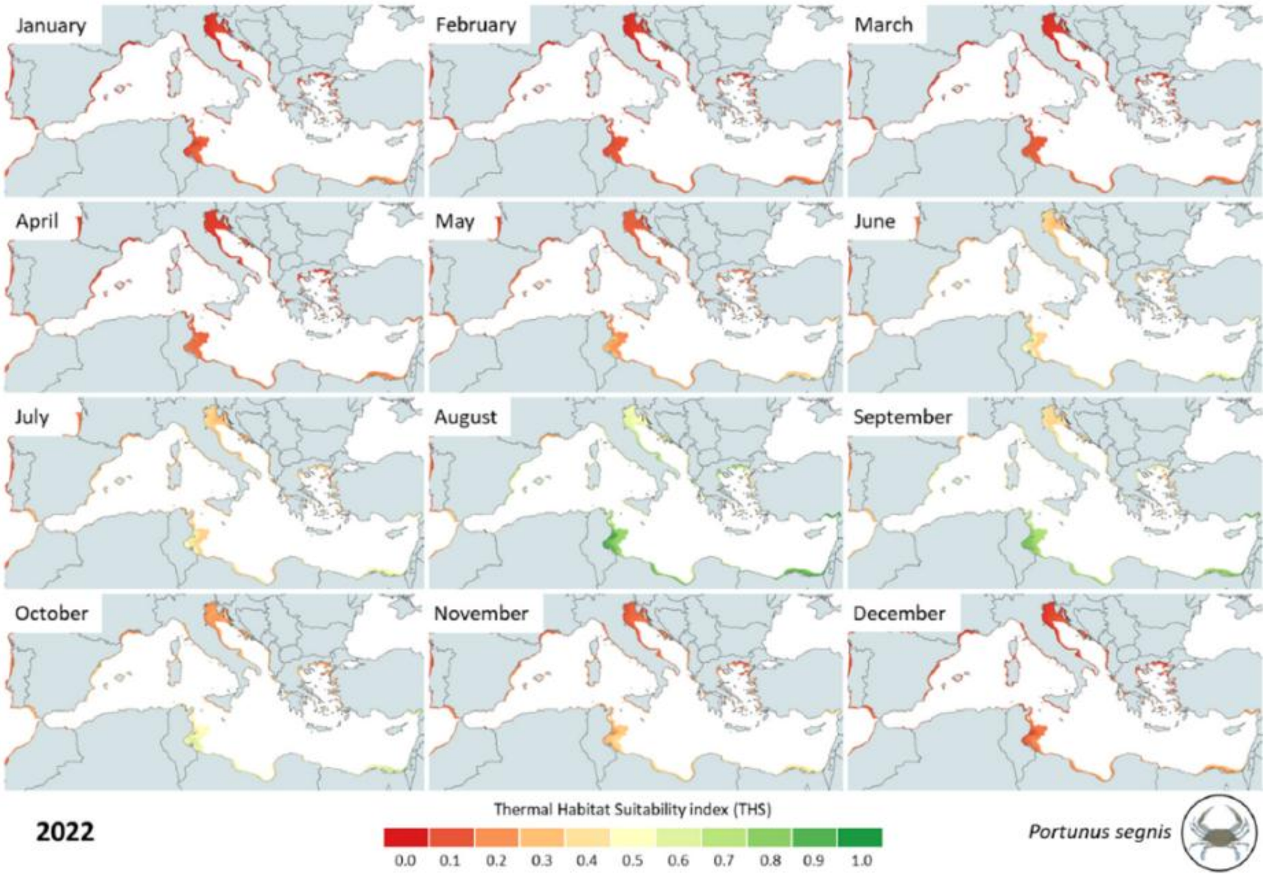


Figure 20. Current predicted Thermal Habitat Suitability (THS) of *Portunus segnis* in the Mediterranean Sea based on the species metabolic performance. THS values at 0 = not favorable; and THS at 1 = favorable). Different colors (representing the species THS) would correspond to: optimum temperature range (THS > 0.8; green colored), lower and upper *pejus* ranges (0.5 < THS < 0.8; light green and yellow colored), *pessimum* (0.2 < THS < 0.5; orange colored), and lethal ranges (THS < 0.2; red colored). Figure and legends extracted from Marchessaux *et al.*, (2024c).

During summer (June to September), all southern Mediterranean coasts provided favorable thermal habitats. In the North, THS were favorable along Spanish, Tyrrhenian and Adriatic Italian coasts to Greek Aegean coasts. For both future scenarios, an increase of THS was observed earlier in the year in the North-Western Mediterranean (Marchessaux *et al.*, 2024c).

The change in Thermal Habitat Suitability (THS) probability between the 2050 RCP 4.5 scenario and the situation in 2022 varied across countries. In the Eastern Mediterranean (Israel, Egypt, Lebanon, Syria), THS was negative, indicating a decrease. Tunisia and Cyprus showed stability (THS ~ 1) with minor changes. Increases in THS were observed in Greece, Malta, and Italy. At the Mediterranean Sea level, 2050 RCP 4.5 showed-0.7 ± 8.9 %, contrasting with +0.1 ± 8.7 % for the 2050 RCP 8.5 scenario. In 2050 RCP 8.5, Cyprus, Italy, and Malta decreased in THS, while Syria, Greece, Turkey, Lebanon, Tunisia stabilized. Egypt, Libya, and Israel had positive THS changes for this scenario (Marchessaux *et al.*, 2024c). Generally, **at the Mediterranean Sea level, the species distribution will increase.**

3.4.3 Diet and feeding ecology of *Portunus segnis*

The blue swimming crab is **carnivorous, scavenging, and a voracious predator** that can compete with local fauna. *Portunus segnis* is an **opportunistic omnivore**, with **dietary variations depending on seasons, developmental stages, and habitats.** This species demonstrates **ecological flexibility**, which significantly contributes to its invasion success. The main dietary categories consumed include:

- **Crustaceans** including shrimps, crabs and benthic copepods (Hosseini *et al.*, 2014). Crustaceans**, such as shrimp and other crab species** (Hosseini *et al.*, 2014), **dominate its diet throughout the year**, representing more than 65% of stomach contents (Hamida *et al.*, 2019; Hosseini *et al.*, 2014).
- **Fish**, although less frequent in the diets of juveniles, become an important component as the crab reaches adulthood.
- **Mollusks** like *Cardita bicolor, Cerithium erythraeonense, Circenita callipyga, Marcia hiantina* (Hosseini *et al.*, 2014)). Primarily bivalves such as *Tellina sp.* and *Cardita bicolor*, as well as gastropods like *Cerithium erythraeonese*, are also common prey, particularly during winter and spring (Hamida *et al.*, 2019).
- **Polychaetes** (Zainal, 2013).
- **Unidentified organic matter and detritus** (Zainal, 2013).

Studies have also revealed **significant seasonal variations in the diet of *Portunus segnis***. For instance, **crustaceans dominate during the summer**, **while mollusks and fish become more prevalent in stomach contents during autumn and winter**, respectively, due to changes in prey availability. According to studies of stomach contents, juvenile crabs (< 90 mm CW) prefer crustaceans (48.6 %) to mollusks (21.5 %) and fish (17.5 %), adults (CW 111-150 mm) shift their diet to a higher proportion of fish (26.7 %), though crustaceans and mollusks remain principal components (40.5 %, 24.5 %, respectively), and the largest adults (CW 151-170 mm) consume more fish (29.4%), and reduce the proportions of crustaceans and mollusks (37.5 %, 21.6 %, respectively) (Hosseini *et al.*, 2014; Pazooki *et al.*, 2012)

Furthermore, the presence of unidentified organic matter and plant debris in the diet indicates the ability of *P. segnis* to exploit unconventional resources when animal prey is scarce. (Tadi Beni *et al.*, 2018). In ovigerous females, a significant increase in food consumption has been observed, likely to meet the high energy demands associated with reproduction. Moreover, *P. segnis* has demonstrated dietary flexibility in the presence of introduced species, which could amplify its ecological impact in Mediterranean ecosystems (Mancinelli *et al.*, 2022).

This dietary plasticity highlights the ability of *P. segnis* to **occupy different trophic levels and adapt to a wide range of environments**. Its varied diet, combined with the continuous availability of prey in Mediterranean ecosystems, reinforces its role as an effective invasive species and contributes to its demographic success. However, this flexibility can also lead to significant ecological impacts, including exerting predation pressure on local species and disrupting trophic networks (Hamida *et al.*, 2019; Mancinelli *et al.*, 2022; Tadi Beni *et al.*, 2018).

The impact of *Portunus segnis* on benthic fauna in the Mediterranean is not well understood. It is likely that *P. segnis* exerts **significant pressure on local ecosystems by altering trophic dynamics and directly competing with native species for food resources and habitat** (Mancinelli *et al.*, 2022). Through its diverse diet, *P. segnis* may reduce the populations of many local species, causing imbalances in trophic chains. In Tunisia, the **consumption of mollusks species particularly impacts populations of bivalves and other benthic invertebrates, which play a crucial role in maintaining the ecological balance of coastal zones** (Hamida *et al.*, 2019).

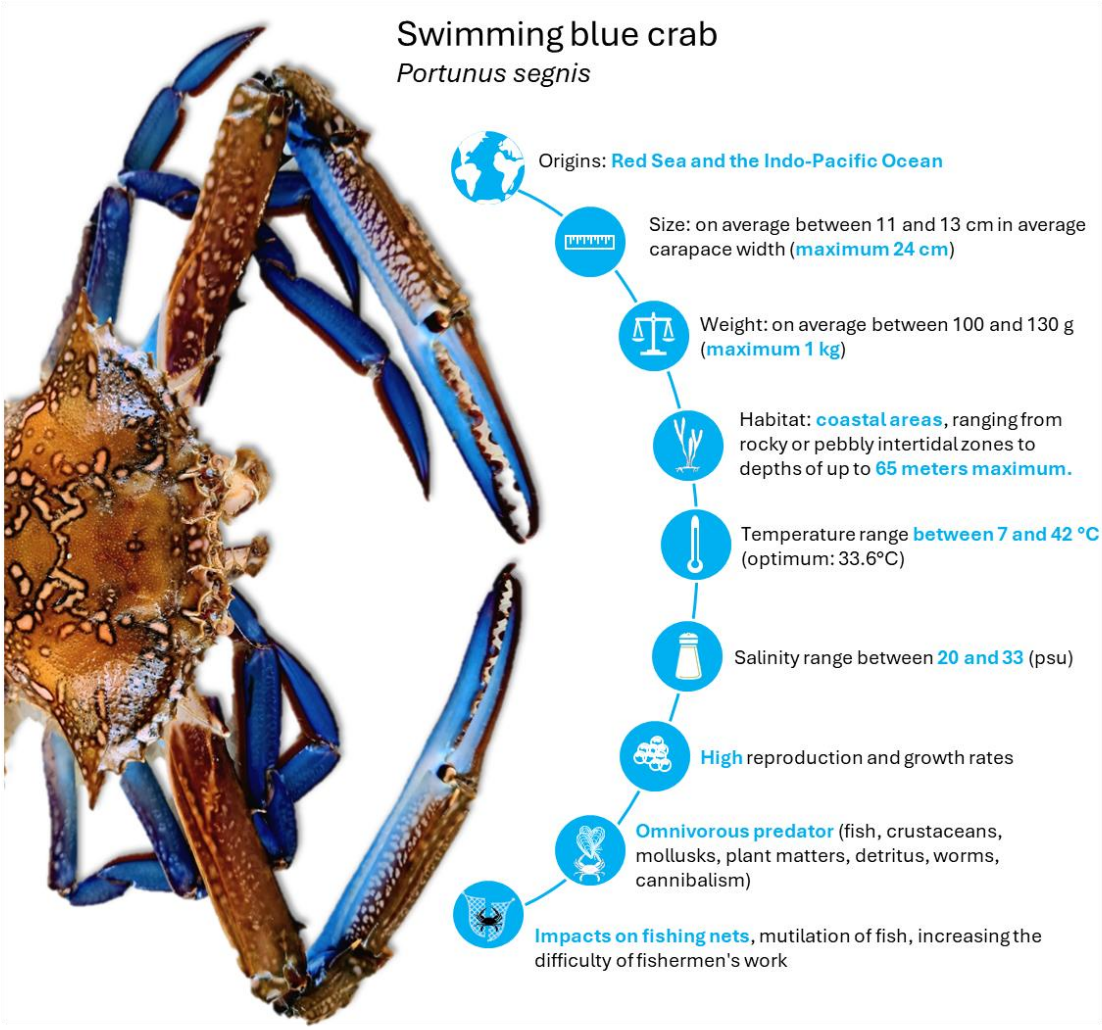
Furthermore, *P. segnis* demonstrates a **high trophic niche and significant dietary flexibility**, enabling it to rapidly adapt to varied environments and efficiently colonize new habitats, often at the expense of less competitive native species. For instance, in Elounda Bay, Greece, its occupation of a h**igh trophic position has been associated with increased competition with other native predators, potentially contributing to their decline** (Mancinelli *et al.*, 2022).

Another concerning aspect is the **indirect impact of *P. segnis* on human activities**, particularly fishing. By exploiting the same resources as some commercial species, this crab can negatively affect stocks of economically important fish and mollusks, leading to conflicts with local fishers. For instance, in Turkey, *P. segnis* catches are often associated with a decline in native fish catches, indicating increased interspecific competition in these already stressed environments (Yeşilyurt *et al.*, 2022).

Predators of *Portunus segnis*

In its native habitat, this crab is often **preyed upon by carnivorous fish** such as groupers (*Epinephelus spp.*) and barracudas (*Sphyraena spp.*), which occupy higher trophic niches in tropical marine ecosystems. In the Mediterranean, where *P. segnis* is a recent invader, its trophic network is still being structured. Isotopic analyses conducted in Crete have shown that it occupies a **high trophic position, making it vulnerable to certain local predators such as large carnivorous fish**. However, these interactions remain limited due to the lack of co-evolution with these species (Annabi *et al.*, 2018).

3.5 Summary of information on *Portunus segnis*



4 *Callinectes sapidus* vs. *Portunus segnis*: Many similarities

Morphological Similarities

- **Swimming adaptations**: both species have specialized fifth legs modified into swimming paddles, making them efficient swimmers. They can cover 15 km per day.
- **Broad carapace**: both crabs have a wide, flattened carapace with lateral spines, aiding in hydrodynamics.
- **Coloration**: while *C. sapidus* is known for its distinct blue claws, *P. segnis* exhibits a more variable coloration, often greenish or brownish.

Habitat Preferences

- **Brackish and marine waters**: both species thrive in estuaries, brackish lagoons, and coastal marine environments.
- **Tolerance to temperature**: both species are capable of surviving in a wide range of temperature: *Callinectes sapidus*: 0 to 40°C ; *Portunus segnis*: 7 to 42°C.
- **Tolerance to salinity**: both are euryhaline, capable of surviving in a wide range of salinities, from nearly freshwater to hypersaline conditions.
- **Depth range**: both species can inhabit shallow waters and extend to deeper zones (up to ~50 meters for *P. segnis* and 35 meters for *C. sapidus*).

Diet and Feeding Ecology

- **Omnivorous predators**: both crabs are omnivores, feeding on a mix of mollusks, crustaceans, fish, algae, and detritus.
- **Cannibalistic and aggressive behavior**: both species exhibit cannibalism, especially during molting stages.
- **Trophic impact**: both are opportunistic feeders, capable of preying on a wide range of species and altering local food webs
- **Competition with native species**: both crabs compete with native crustaceans for food and habitat, impacting local biodiversity

Reproductive Strategies

- **High reproductive potential**: both species produce a large number of eggs per reproductive cycle, contributing to their rapid population growth.
- **Planktonic larvae**: their larvae are planktonic, allowing long-distance dispersal via ocean currents, which supports their invasive potential. Larvae can cover > 100 km.

Invasive Success

- **Environmental adaptations**: both species are highly adaptable, with broad tolerances to temperature and salinity fluctuations.
- **Human-mediated introduction**: both species were introduced to the Mediterranean through human activities, including ballast water discharge and the Suez Canal (*P. segnis*).

5 Blue crabs and artisanal fisheries: what challenges?

5.1 Socio-economic impacts

These two Portunidae species, due to their **many similarities**, **cause significant socio-economic impacts**. Through their **aggressive behavior and high abundances**, the two blue crabs **exert considerable socio-economic pressures, particularly on artisanal fisheries**. Marchessaux *et al.* (2023c) studied the impact of *Callinectes sapidus* and *Portunus segnis* on artisanal fisheries in France, Italy, and Tunisia, interviewing 102 fishermen.

Artisanal small-scale fishermen were the social component and economic sector to be most affected by the presence of blue crabs and considerable negative effects on fishing activities are recognized by local populations (Mancinelli *et al.*, 2017; Marchessaux *et al.*, 2023c). The invasion of blue crab species affects **3 aspects** of artisanal fisheries: **fishing activities**, the **number and quality of catches in nets**, and the associated **economic revenues** (Figure 21).

The primary impact caused by the presence of blue crabs is the **damage to fishing nets**, followed by an **increase in the labor intensity** required for net maintenance and **physical injuries** sustained by fishermen (Figure 21A). **The clogging nets can be huge and can represent 150 kg per day in Tunisia** (Khamassi *et al.*, 2019) increasing the frequency of net hauling to avoid clogging (Culurgioni *et al.*, 2020; Khamassi *et al.*, 2019). Blue crabs are capable of **shredding nets** (Öndes and Gökçe, 2021) and in Tunisia, ***P. segnis* damages the catches in the nets reducing fish catches resulting in a 37 % loss of catch** (Khamassi *et al.*, 2019).

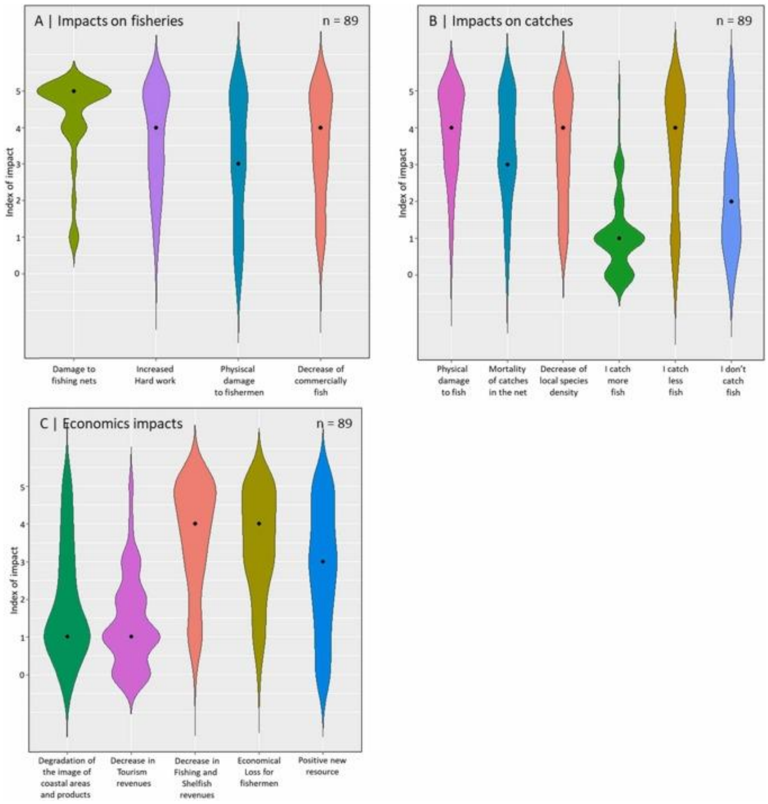


Figure 21. Distribution of perceived impacts of blue crabs (*C. sapidus* and *P. segnis*) on (A) artisanal fisheries activities, (B) on catches, and (C) economics impacts. Black dots represent the median. Figure and legend extrated from Marchessaux *et al.* (2023c).

The **prey caught in fixed nets were also damaged** by the presence of blue crabs (Figure 21B), which are highly voracious and active scavengers that attack other dead species, in this case, those entangled in the nets (Figure 21B). Small-scale fishers specifically reported catching fewer fish and noted that blue crabs caused significant damage to fish, leading to **high mortality rates among fish caught in fyke nets**, a type of net commonly used in coastal and lagoon systems (Figure 21B). This results in a **decrease in the quantity of captures** and, more generally, a **reduction in the density of local species**, according to the artisanal fishers.

The combination of these impacts on fishing gear and catches has led to economic losses for small-scale fishers (Figure 21C), representing a major disruption in the supply chain of small-scale artisanal fishing. The proliferation of blue crab species **results in decreased revenues from fishing and aquaculture and significant economic losses for small-scale artisanal fishers**.

The combination of the time and financial costs of mending and changing nets (Khamassi *et al.*, 2019; Öndes and Gökçe, 2021) imply a significant economic loss for the fishing sector. In **Tunisia the average annual income *per* fisherman decreased from 73,000 € to 20,500 € after the invasion of *P. segnis*** (Khamassi *et al.*, 2019). **In Croatia, the cost of damages on the nets caused by *C. sapidus* represented $20 per week per artisanal small-scale fishermen** (Glamuzina *et al.*, 2021).

In general, to address the economic loss associated with the invasive species, the artisanal small-scale fishermen deployed different strategies showing a true professional culture of adaptation (Deldrève, 2000; Marchessaux *et al.*, 2022b). Indeed, this profession had always been exposed to environmental hazards, leading to develop a culture that "manage" the problems that may arise with a strong capacity to adapt (Andersen, 2011; Bataille and Deldrève, 2009; Candau *et al.*, 2015; Deldrève, 2000; Marchessaux *et al.*, 2022b). But, in the case of the blue crabs, these temporary adaptations (e.g. reduced net setting time, change of nets or fishing technique) tend to be costly and restrictive. The main solution for the management of blue crabs' populations in the Mediterranean Sea would be represented by **exploitation as also reported by 72 % of the artisanal small-scale fishermen** interviewed in Marchessaux *et al.*, (2023c).

5.2 Can we control blue crabs by eating them?

Consuming blue crabs is a highly anticipated measure among artisanal fishers (Marchessaux *et al.*, 2023c). Despite the significant impacts on fishing activities and nets, **fishers sometimes perceive blue crabs as both negative and positive** (Figure 22A). This is not the case in France, where the species (*Callinectes sapidus* specifically) is still expanding. However, in Italy and particularly in Tunisia, both blue crab species are viewed as having both negative and positive aspects (Figure 22B).

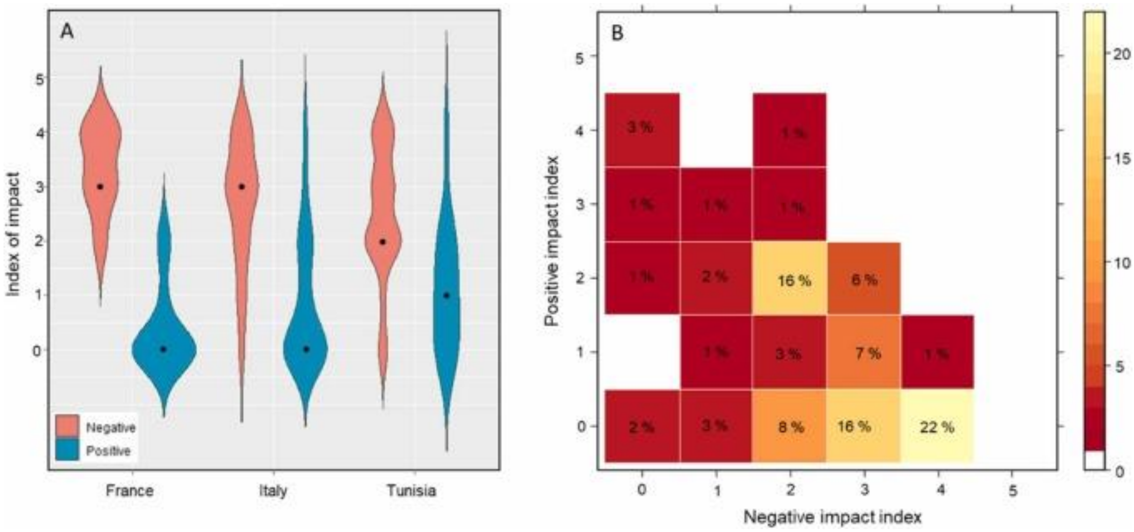


Figure 22. A) Positive and/or negative impacts of blue crabs (*C. sapidus* and *P. segnis*) as perceived by stakeholders, and (B) a comparison of the percentage of responses in each impact index category (positive vs. negative). The black dots on plot A represent the median. Figure and legend extracted from Marchessaux *et al.* (2023c).

The valuable meat and commercial potential of blue crabs are seen as a new source of income for small-scale artisanal fishers. In this context, it is clear that the **creation of a blue crab industry seems to be necessary**, but it is equally important for the general public to be willing to consume blue crab. Two large-scale studies were conducted in 2023 in Italy and France (Azzurro *et al.*, 2024; Marchessaux *et al.*, 2024b).

In Italy | The population explosion of *Callinectes sapidus* in 2023 in the northern Adriatic had significant impacts on the Italian shellfish industry (Azzurro *et al.*, 2024). This invasion garnered considerable media attention and raised questions about the management and commercial exploitation of this species. The survey, named **UseIt**, interviewed 2,466 Italian participants to assess consumer perceptions, their acceptance of *C. sapidus* as a food product, and their willingness to pay.

Interest in *C. sapidus* increased significantly after the media coverage in August 2023 (Azzurro *et al.*, 2024). A majority of participants discovered the species through social media (59% via Facebook) and traditional media. However, only 38% of respondents had observed blue crabs available for sale in Italy. A majority (69.5 %) had never tasted the species, but those who had largely approved of its organoleptic qualities (Azzurro *et al.*, 2024). Participants positively rated *C. sapidus* for its taste, smell, and ease of preparation. Pric**es dropped by €2.62/kg after the population explosion, reflecting an increased supply** (Azzurro *et al.*, 2024) (Figure 23).

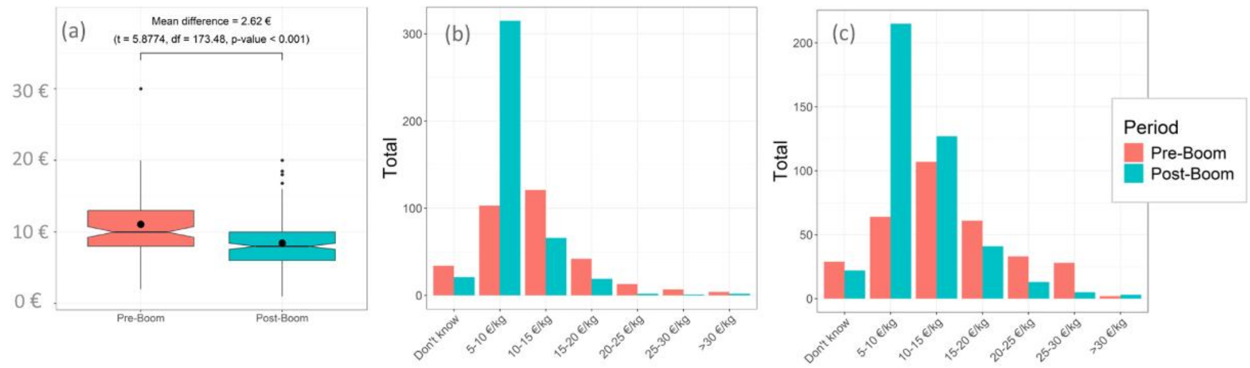


Figure 24. Consumer perception of blue crab price: (a) Boxplots showing the current distribution of reported market prices for 1 kg of *Callinectes sapidus* in Italy, black dots represent the mean values; (b) Distribution of optimal and (c) maximum price ranges the respondents would pay for 1 kg of blue crab. Pre-boom period (in red) and post-boom (in green). Figure and legend extracted from Azzurro *et al.* (2024).

In France | The study by Marchessaux *et al.* (2024b) addresses the management of the American blue crab (*Callinectes sapidus*) invasion in France and explores the possibility of managing it through its consumption as a food resource. A national survey was conducted in France with 2,040 participants between March and May 2023 to assess their perception of blue crab consumption and their willingness to pay for this product.

A total of 96% of respondents were willing to consume blue crab, with motivations including the discovery of a new product (68%), its exotic appeal (11%), and its taste (10%) (Marchessaux *et al.*, 2024b). Respondents were willing to **pay €15–19 for a dish at a restaurant** and **€8–10 per kilogram at fish markets** (Figure 24). Consumption was perceived as a civic and ecological act by the majority, particularly among younger generations.

Restaurants were the preferred place for consumption (78% positive responses), while fish markets and supermarkets generated moderate interest (Figure 24). Blue crab consumption is perceived as a solution to mitigate its ecological impact while supporting local fishers.

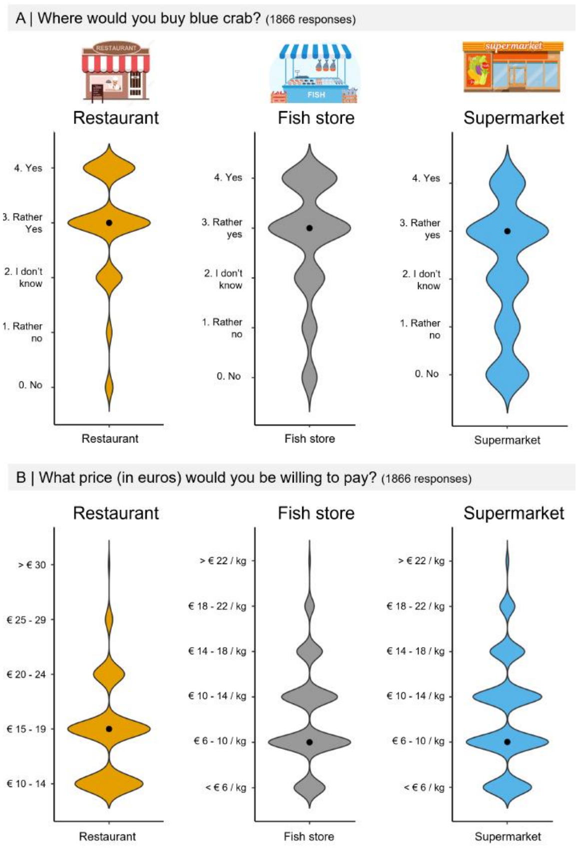


Figure 23. People's perception of the place where they are able to buy blue crabs for consumption (on the top) and how much they are able to pay (on the bottom). Figure and legends extracted from Marchessaux *et al.* (2024b).

The two studies highlights a gap between consumer interest and the actual availability of the product on the market . **Italian and French respondents expressed a willingness to integrate this species into their diets, which could represent an effective strategy to manage the invasion while supporting local fisheries**. These studies emphasize the potential of *C. sapidus* as a new commercial resource in Italy and in France. However, efforts are needed to harmonize the supply chain, improve market access, and develop sustainable exploitation and management strategies.

5.3 Fishing gear to catch the blue crabs

The commercialization of blue crabs in the Mediterranean appears to be the best option to control populations and limit ecological and socio-economic impacts. However, it is clear that to implement effective commercialization of blue crabs, it is necessary to **determine which fishing gears to use for their efficient and selective capture**.

Castriota *et al.* (2024) reviewed the scientific literature to identify the types of fishing gears used in the Mediterranean to capture the American blue crab, *Callinectes sapidus* (Figure 25). The authors found that **traps** were the most commonly used fishing gear in the Mediterranean (31.6%) and were widely adopted across many countries. **Gillnets and entangling nets** were also extensively used (24.2%), primarily along Mediterranean coasts.

Regarding *Portunus segnis*, the FAO proposed a specific type of trap for its capture (Bdioui *et al.*, 2020). Similar to *Callinectes sapidus*, several types of fishing gears are also used to catch *Portunus segnis*. For instance, **gillnets** are commonly employed by artisanal fishers to capture a variety of species, including the blue swimming crab (Khamassi *et al.*, 2019). **Traps, such as specific pots or baited devices**, are also used to target crabs, allowing for selective capture and reducing bycatch (Khamassi *et al.*, 2019). **Bottom trawls** are additionally utilized, particularly in Tunisia and Turkey, although these are primarily intended for other species; they frequently capture blue swimming crabs as bycatch (Yeşilyurt *et al.*, 2022). It appears that bottom trawls are the most frequently used fishing gear to catch *Portunus segnis* specially in Tunisia (O. B. A. H. Hamida *et al.*, 2019). These capture methods have been documented in various scientific studies, particularly those conducted in the Gulf of Gabès, Tunisia, where the species is notably prevalent.

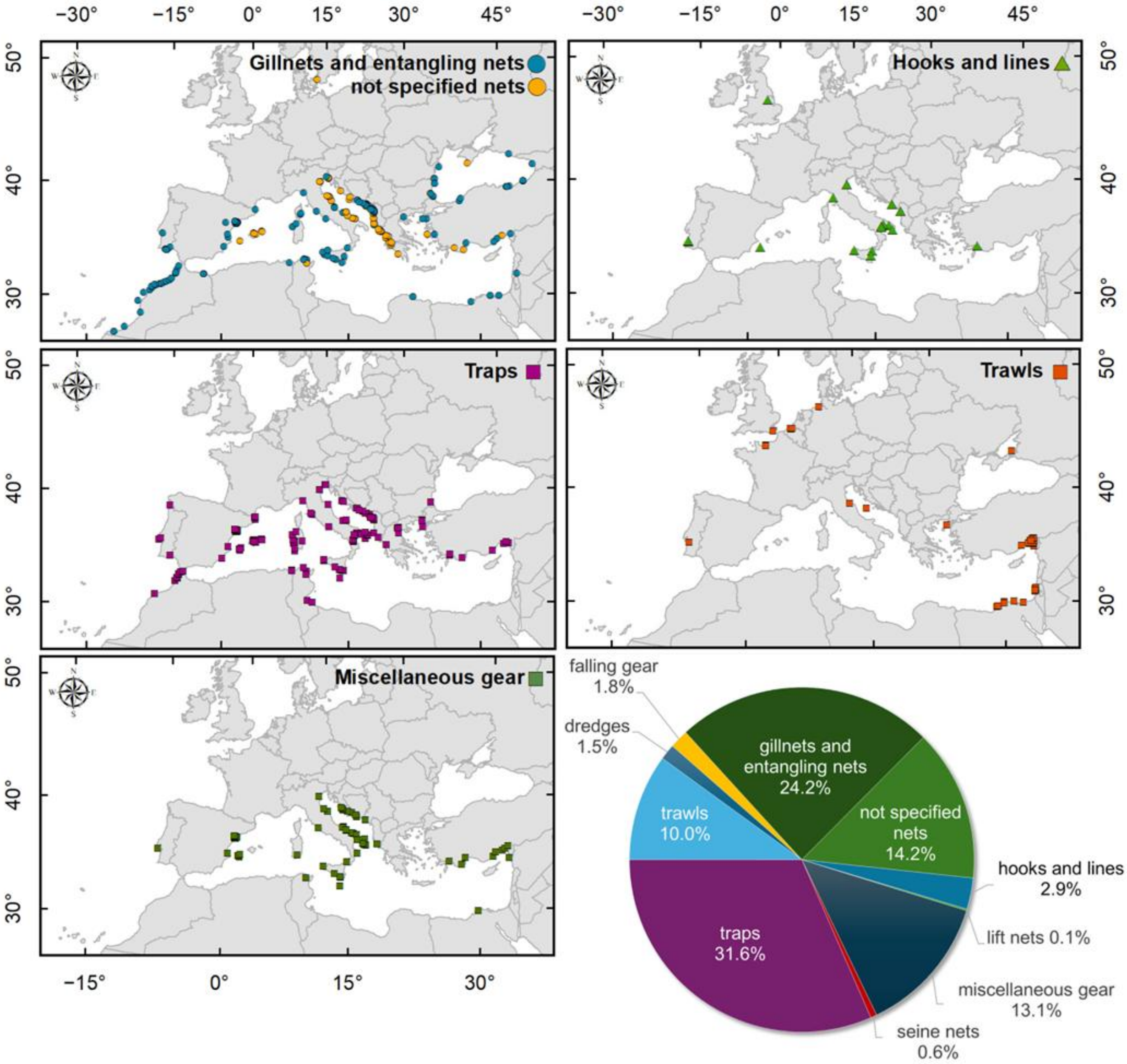


Figure 25. Fishing gear categories used to catch the American blue crab *Callinectes sapidus* and frequency. Figures extracted and modified from Castriota *et al.* (2024).

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