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Salinity tolerance of the invasive blue crab *Callinectes sapidus*: From global to local, a new tool for implementing management strategy

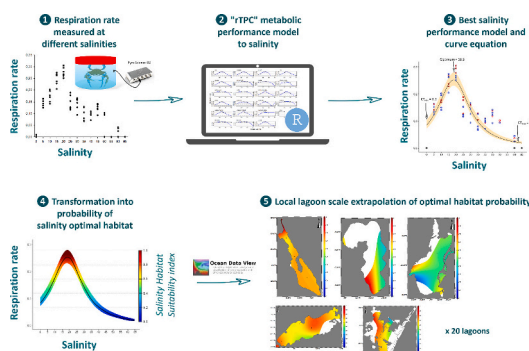
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HIGHLIGHTS

- We measure the salinity tolerance of the blue crab *Callinectes sapidus*.
- Physiological response curves for potential suitable habitat conditions.
- Lagoons with salinities between 5 and 30 psu are identified as the most favorable environments for blue crab populations.
- Enhanced Management Strategies determined by the salinity regimes of invaded lagoons.
- Physiological tool in decision-making for the management of invasive species.

GRAPHICAL ABSTRACT



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ABSTRACT

The latest report from the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) raises concerns about the global proliferation of non-native species (NIS) driven by increasing temperatures. In 2023, the invasive blue crab *Callinectes sapidus* experienced a significant range expansion in the French Mediterranean lagoons, now present in over 20 lagoons and numerous estuaries with different invasion gradients. It has been established that this species is eurytherm (tolerates a wide range of temperatures; 0–40 °C), rendering temperature a non-limiting factor for its proliferation. On the other hand, salinity is a critical factor to consider, as *C. sapidus* requires brackish water for copulation and saline water for egg maturation. In this study, we present the salinity tolerance of *C. sapidus* using the metabolic performance to define the tolerance of the species to a large range of salinities (13 levels from 0 to 65 psu). Results showed that *C. sapidus* tolerates a large range of salinities with a minimum critical threshold (CT_{min}) at 0 psu, an optimum at 18.5 psu, and a CT_{max} at 62.4 psu.

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Using the performance curve equation, we applied the curve to real salinity data measured each month in 2023 in 20 lagoons invaded. Using this approach, we were able to map, on a fine spatial scale, the distribution of suitable habitats for *C. sapidus* in the year 2023. Additionally, we have developed a tool to prioritize the lagoons based on their suitability, thereby providing a decision-making framework for management measures in each lagoon. It emerged that 50 % of lagoons were priority areas, 10 % were intermediate and 40 % required monitoring. On the basis of this approach, we can respond to European regulations to help decision-makers implement action plans and/or early detection programs for invasive species management.

1. 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, 3500 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, or tropicalization (González-Ortegón et al., 2020), exacerbates changes in species distribution, indirectly facilitating the spread of IAS, often to the detriment of native species. Monitoring both indigenous and invasive species is crucial for understanding climate change impacts and implementing effective conservation measures (DeLong et al., 2018). Habitat characteristics and geographic origin can predict the success of invasions, particularly in aquatic environments where salinity tolerance plays a key role.

The blue crab *Callinectes sapidus* Rathbun (1896) is a native species of the western Atlantic Ocean, and has been introduced to several regions of the world, including the Mediterranean Sea (Galil et al., 2017; Goren et al., 2020) and the Eastern Atlantic Ocean (Chairi and González-Ortegón, 2022; Chaouti et al., 2022; González-Ortegón et al., 2022). The first record of *C. sapidus* in the Mediterranean was reported in 1949 in the Venice Lagoon (Nehring, 2011), in 1962 in the Berre Lagoon (South France) and its expansion on the French Mediterranean coast has only been confirmed since 2016 (Labruno et al., 2019), spreading in many lagoons, becoming one of the most common invasive species in several locations (Labruno et al., 2019). The presence of *C. sapidus* in Mediterranean lagoons has raised concerns about its potential impacts on native biodiversity and artisanal fisheries (Marchessaux et al., 2023c) inducing declines in commercial species and local biodiversity (Clavero et al., 2022). In France, the *C. sapidus* has been proliferating firstly in 2019 in the Canet Lagoon, and in 2021 in the Biguglia and Palo Lagoons (Corsica island). Currently *C. sapidus* has established populations in some brackish lagoons on the French west Mediterranean coast and in Corsica, and is currently extending its range eastwards. *Callinectes sapidus* is a generalist thermal species presenting a large thermal performance curve (0–40 °C) with an optimal temperature at 24 °C, allowing it to not be limited by temperature (Marchessaux et al., 2022); but it appears that salinity is the key environmental factor influencing its distribution (Costa et al., 2023) and reproduction (Herrera et al., 2024). *Callinectes sapidus* is an euryhaline species found mostly in estuaries and brackish lagoons allowing it to tolerate a wide range of salinity levels (Epifanio, 2019). Salinity is the key factor in *C. sapidus*' reproduction, since copulation takes place in brackish and desalinated water (Anderson et al., 2017; Forward et al., 2003). One perfect example on high salinity tolerance is that females *C. sapidus* migrate for hundreds kilometers from the desalinated waters of estuaries and lagoons where they mated with males (Epifanio, 2019), to the waters with high salinity where that the eggs can hatch and the larvae can complete their development cycle offshore at higher salinities (> 20 psu) (Costlow Jr and Bookhout, 1959). Eggleston (1990) found that adult *C. sapidus* exhibited a strong preference for areas with moderate salinity levels, as they tend to avoid areas with very low or very high salinity. *Callinectes sapidus* has also been described in very low salinity or even fresh water (Churchill, 1919). In lagoons, estuaries, and low-salinity environments, juveniles *C. sapidus*

predominate, while adult males remain in the brackish waters, adult ovigerous females migrate to saltier waters to release larvae in the open sea (Aguilar et al., 2005; Ortiz-Leon et al., 2007; Ramach et al., 2009).

Callinectes sapidus is able to osmoregulate efficiently and can tolerate extreme salinities (Guerin and Stickle, 1997; Herrera et al., 2024). Metabolism is highest at intermediate salinity levels and decreased at both lower and higher salinity levels (Tagatz, 1971). Adult blue crabs exhibited a strong preference for areas with moderate salinity levels, avoiding regions with very low or very high salinity (Eggleston, 1990; Johnson and Eggleston, 2010). Regarding its feeding behavior, *C. sapidus*, being omnivorous, requires access to both freshwater and saltwater sources to feed and regulate their ion balance (Ortega-Jiménez et al., 2024). Salinity impacts the blue crab's protein metabolism and growth as well as juvenile blue crabs that are exposed to low salinity conditions had reduced protein synthesis rates and slower growth rates than those reared in higher salinity conditions (Costlow, 1967; Henry and Wheatly, 1992). Changes in salinity can affect the lipid metabolism of adults *C. sapidus*, which could impact their energy balance and survival (Havird et al., 2016; Kinsey et al., 2003). Additionally, low salinity levels can affect the osmoregulatory ability, leading to reduce ion uptake and nutrient absorption (Guerin and Stickle, 1997). These findings highlight the importance of considering the effects of salinity on *C. sapidus* metabolism, as well as growth, survival, behavior, reproduction, as well as distribution of blue crabs (Aguilar et al., 2005; Costa et al., 2023; Eggleston et al., 1992; Ramach et al., 2009), in the context of their natural environments and the potential impacts of environmental changes on their survival and fitness (Rome et al., 2005).

As such, understanding the effects of salinity on *C. sapidus* in the Mediterranean Sea is important for the management and the implementation of control measures directed toward this invasive species in brackish Mediterranean lagoons they mainly inhabit (Labruno et al., 2019). The importance of considering salinity in the context of biological invasions has become increasingly clear in the light of recent studies. Invasive species can have a remarkable ability to adapt to environments subject to salinity fluctuations (D'Amen et al., 2023) and these changes in salinity in coastal ecosystems can favor the establishment and spread of invasive species (González-Ortegón et al., 2006; Occhipinti-Ambrogi and Savini, 2003). Interactions between native and invasive species can be promoted or limited by salinity, affecting population dynamics and community structure. (González-Ortegón et al., 2010; Marchessaux et al., 2023b; Mrozińska et al., 2021). By integrating salinity into the assessment and management of biological invasions, it becomes possible to better predict and mitigate the impacts of these invasions on aquatic and terrestrial ecosystems.

The objective of this study was to determine the salinity tolerance of *C. sapidus* by evaluating the species' performance response, as indicated by its relationship with oxygen consumption, which is commonly used as a proxy for metabolic activity. Based on the metabolic performance response curve of *C. sapidus*, our study aimed to develop a predictive tool for identifying favorable habitats for the blue crab and to classify the lagoons to identify priority sites for implementing control measures across 20 lagoons on the French Mediterranean coasts. We hypothesize that *C. sapidus* exhibits high salinity tolerance and that the French coastal lagoons may serve as optimal habitats for the expansion and establishment of *C. sapidus* in France.

2. Materials and methods

2.1. Sampling and respirometry measurements

This study was part of a one-year and a half study on blue crabs invasion in the Biguglia Lagoon (France; latitude: 42.597, longitude: 9.481) in collaboration between the University of Palermo (Italy), the Environmental Agency of Corsica and the Laboratory Stella Mare (France). This project was divided in 3 different aspects: (i) measure the blue crab's population dynamics (Marchessaux et al., 2024), (ii) determine the trophic network between blue crabs and autochthones species, (iii) and measure the salinity tolerance of *Callinectes sapidus* in the Biguglia Lagoon to implement management measures.

In May 2023, 78 specimens of blue crabs *C. sapidus* (46 males; 32 females; wet weight: 166 ± 54 g; carapace width: 13.7 ± 2.2 cm) were collected in the Biguglia Lagoon, using fyke nets, in collaboration with local fishers. Organisms were placed in coolers filled with lagoon's water for transportation from the sampling area (10 min by car) to the Stella Mare Platform (University of Corsica, CNRS). Only mature males and females were used for the experiment.

To investigate the salinity tolerance of *C. sapidus*, individual respiration rate (RR, $\text{mgO}_2 \text{ h}^{-1} \text{ gWW}^{-1}$) was estimated as a proxy of the metabolism (Angilletta et al., 2010; Gould et al., 2021; Sokolova et al., 2012) at 13 different salinities: 0, 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 60 and 65 psu. The lowest $S = 0$ (freshwater) and the highest $S = 65$ (hypersaline) corresponded to the extreme conditions to determine the species resistance/survival to these stressful conditions.

The specimens' good morphological conditions (whole organisms, no missing organs [e.g. claws, legs]) were checked. Specimens were randomly divided in 13 groups ($n = 6$) according to the number of experimental salinities. The salinity tolerance experiments were performed starting from the sampling water salinity ($S = 18$ psu in Biguglia Lagoon). The salinity was gradually decreased for lowest salinities or increased for highest salinities by 5 psu per 2 h, corresponding to the probable salinity ranges to which the crabs are exposed in the lagoon (individuals migrations between freshwater mouth (~ 5 psu) to marine areas (between 10 and 40 psu) in few hours). Individuals were acclimatized for 24 h after reaching the experimental salinities. Acclimatization and experiments were performed at 24°C , optimal temperature for *C. sapidus* metabolism (Marchessaux et al., 2022).

After the acclimatization to the experimental salinity, oxygen consumption measurements were performed. The six individuals from each salinity set were individually placed within a respirometric chamber (2300 ml) containing filtered (Whatman GF/C $0.1 \mu\text{m}$) air-saturated seawater. Two other respirometric chambers were filled only with filtered seawater and used as controls. To ensure the constant mixing of the water, each chamber was stirred with a magnet bar and an individual stirring device (Bosch-Belmar et al., 2021, 2022; Marchessaux et al., 2022). The respirometric chambers were then randomly distributed in two temperature-controlled circulated stable water baths at 24°C (Grant Optima TX150) to maintain stable experimental temperatures. The dissolved oxygen concentration was measured simultaneously using the Pyro Science Firesting O2 system consisting of 3 optical oxygen meters for specimens, and 1 optical oxygen meter for control. Oxygen consumption was measured every second for 1 h. Temperature was recorded throughout a HOBO Pendant® logger (mod. MX2201, $\pm 0.5^\circ\text{C}$ accuracy) and with a probe included in the Pyro Science Firesting O2 system.

At the end of respiration rate measurements, the individual wet weight (WW, in g), and the carapace width (CW, as the widest point behind the posterior anterolateral spines, in cm) of all organisms were measured using a ruler (accuracy ± 0.1 cm). Respiration rate was calculated according to Sarà et al. (2013a): $RR = (C_{t_0} - C_{t_1}) \text{Vol}_r / 60 (t_1 - t_0)^{-1}$ where “ C_{t_0} ” is the oxygen concentration at the beginning of the measurement, “ C_{t_1} ” the oxygen concentration at the

end of the measurement, and “ Vol_r ” the volume of water in the respirometric chamber. The respiration rate was reported to the individuals' wet weight to avoid the effect of the body mass on the respiration rate. The differences in respiration rates between males and females for each salinity were tested using an ANOVA and a Bonferroni post-hoc test (significant difference = $p < 0.05$) using R (version 2021.09.0).

2.2. Metabolic model regressions

To identify the salinity metabolic performance curve of *C. sapidus*, the “rTPC” R package (Padfield and O'Sullivan, 2020) was used, launching and comparing a total of 24 different non-linear least-squares performance curve models (Padfield and O'Sullivan, 2020). The “best” fitting model was identified based of the lowest AIC scores (Padfield and O'Sullivan, 2020; Bosch-Belmar et al., 2022; Marchessaux et al., 2022). The Salinity Performance Curve (SPC) was drawn, a bootstrapping was performed to calculate 95 % prediction limits for the selected SPC model and confidence intervals around its salinity optimum. The metabolic model parameters were used to predict the current potential occurrence of *C. sapidus* based on the adaptation of metabolic performance to lagoon's salinity conditions (Di Biagio et al., 2020; Sakalli, 2017). Parameters related to the maximum respiration rate (r_{max}), the optimal salinity (S_{opt}) and the full curve width (a) were extracted from the Salinity Performance Curve model and used in the Salinity Habitat Suitability (SHS) maps.

2.3. Mapping the salinity habitat suitability

Before applying the performance curve to environmental salinity data, we converted the respiration rate into Salinity Habitat Suitability (SHS) probability (between 0 and 1) at each in situ salinities following formula according to Marchessaux et al. (2022): $SHS = RR_S / RR_{\text{Opt}}$ where SHS was the occurrence probability (comprised between 0: unfavorable and 1: favorable), RR_t the respiration rate value at salinity S , and RR_{Opt} the value of respiration rate at the optimal salinity predicted by the best SPC model chosen.

We considered 20 French Mediterranean lagoons where the presence of *C. sapidus* is proven, with established populations but not with the same invasion dynamics. For each lagoon, we retrieved salinity data monthly or continuously measured by the managers of these natural areas or as part of monitoring programs (such as the Corsican Managers Forum (FOGEC) coordinated by the Environmental Agency of Corsica, the Interregional Forum of Mediterranean Lagoons (FILMED) led by the Pôle-Relais Lagunes Méditerranéennes (Mediterranean Lagoons Pole-Relay), and monitoring carried out under the Water Framework Directive (2000/60/CE).

Using the lagoons' salinity values for the year 2023 (Fig. 1), monthly distributions of the SHS values were mapped using the software OceanDataView (version 5.1.7.; DIVA kriging mode; Schlitzer, 2022) applied to monthly measured salinity values. Additionally, density plots were used to determine the distribution of SHS probabilities (for each season, and throughout the year) using the package “ggridges” in R Studio (version 2021.09.0).

To help prioritize management efforts, we also calculated for each lagoon the frequency (%) of SHS with favorable ($SHS_{\text{fav}} > 0.5$) and unfavorable ($SHS_{\text{unfav}} < 0.5$) values and plotted the $SHS_{\text{fav}} - SHS_{\text{unfav}}$ relationship using R Studio. The position of each lagoon along a linear regression on the plot determined the priority gradient for management efforts (lagoons with $> 50\%$ of SHS_{fav} were considered as “priority”, on the contrary, lagoons with SHS_{unfav} were considered as “surveillance”).

3. Results

Based on the respiration (RR) data, the best performance curve (lowest AICc values) was the Flinn (1991) regression and the equation obtained was:



Fig. 1. Distribution of the French lagoons studied ($n = 20$) to determine the distribution of the salinity habitats of the blue crab *Callinectes sapidus*. All lagoons' characteristics (area, connection to the sea) are available in the Supplementary Table 1.

$$RR = \frac{1}{[1 + 10.77076 + (-0.84421 \times \text{Salinity}) + (0.02282 \times \text{Salinity}^2)]}$$

All organisms died after 24 h of exposure to freshwater, corresponding to the CT_{\min} determined by the model (Fig. 2A). However, metabolism increased from $0.15 \pm 0.02 \text{ mgO}_2 \text{ h}^{-1} \text{ gWW}^{-1}$ at $S = 5$ to a maximum rate at $S = 20$ ($0.28 \pm 0.02 \text{ mgO}_2 \text{ h}^{-1} \text{ gWW}^{-1}$). Beyond this optimum, metabolism decreased from $0.15 \pm 0.03 \text{ mgO}_2 \text{ h}^{-1} \text{ gWW}^{-1}$ at $S = 25$ to $0.04 \pm 0.01 \text{ mgO}_2 \text{ h}^{-1} \text{ gWW}^{-1}$ at $S = 60$, with the death of all organisms at $S = 65$ (Fig. 2A). The model showed a CT_{\max} at $S = 62.5$ and an optimum at $S = 18.5$. No significant differences (ANOVA analysis; Supplementary Table 2) were observed between males and females. The Fig. 2B presents the correspondence of metabolism with Salinity Habitat Suitability probability (SHS).

On the basis of the *C. sapidus*' tolerance curve to salinity variations (Fig. 2A) and the curve equation converted into a probability of favorable habitat (Fig. 2B), we mapped the monthly distribution of suitable habitats for the year 2023 for the 20 lagoons considered. For each one, SHS distribution showed monthly and seasonal variations at local lagoon scales. All maps and interpretations are presented in the supplementary materials (Supplementary Figs. 2–20).

In addition to the mapping approach carried out on all lagoons on a monthly basis, we were also able to determine the density of SHS values for each season and for the year 2023 as a whole, enabling us to determine whether or not the lagoons were predominantly favorable for *C. sapidus* (Fig. 3). The winter and spring seasons were the most favorable for *C. sapidus*, with 52 % (for example Pisciu-Cane, Balistra, Santa-Ghjulia, Arasu, Palo, Biguglia, Berre, Or) and 47 % (for example Pisciu-Cane, Santa-Ghjulia, Biguglia, Berre) of lagoons respectively showing high densities of SHS > 0.5 (Fig. 3A–B). During summer 42 % of lagoons presented high densities for SHS > 0.5 and in autumn 32 % (Fig. 3C–D). For the year as a whole, the distribution of SHS value densities showed that only 2 lagoons (e.g. Urbinu, Diana) had SHS densities < 0.5 (Fig. 3E). For the other lagoons, the SHS densities distribution was variable but was high for the Biguglia and Berre lagoons, consistently presenting SHS > 0.5 throughout the year.

Based on the results obtained, we proposed a hierarchy of priorities in terms of control measures or early detection by relating the frequency of SHS values > 0.5 and < 0.5 for each lagoon (Fig. 4). The results obtained enable us to determine the distribution of the lagoons (between 0 and 100 %) and thus showed that Berre, Biguglia, Or, Vendres, Villepey, Camargue Gardoise, Santa-Ghjulia, Arasu, Palo and Méjean

lagoons were the sites most likely to host persistent *C. sapidus*' populations, and/or could in the future host the species that would find favorable conditions there. On the other hand, the lagoons of Bages-Sigean and Pisciu-Cane, where SHS probabilities were favorable 50 % of the time and unfavorable 50 % of the time, were considered as intermediate lagoons that deserve to be monitored (Fig. 4). Finally, the other lagoons, where SHS were > 50 % unfavorable, were considered of lower priority but where surveillance is needed.

4. Discussion

4.1. Salinity, a critical factor for *Callinectes sapidus*

The metabolic response of the blue crab *Callinectes sapidus* to varying salinity levels revealed a typical curve's shape of specialist species. In freshwater, all specimens perished within 24 h, aligning with the critical threshold minimum (CT_{\min}) at 0 psu determined by the model. Metabolic activity peaked at a salinity level of 18.5 psu, optimal salinity condition for *C. sapidus*, and declined slowly beyond this optimum. The model indicated a maximum critical threshold $CT_{\max} = 62.5$ in accordance with the death of all organisms recorded at $S = 65$ psu. These findings align with previous literature, which highlights the significant impact of salinity on the survival and development of *C. sapidus* (Costlow, 1967). Our study highlights no significant difference in salinity preference between mature males and females, in contrast to the literature, which demonstrates that mature female *C. sapidus* exhibit specific salinity preferences, influencing their movement between habitats (Eggleston et al., 1992). This consistency across studies underscores the critical role of salinity in *C. sapidus* physiology and habitat selection. Although salinity plays a crucial role in the survival of *C. sapidus*, it is important to specify that this is possible because the thermal conditions of the lagoons studied are optimal for *C. sapidus* (Marchessaux et al., 2022), so as long as populations remain in the Mediterranean thermal zone, their distribution can persist. Temperature and salinity therefore play a dual role in the persistence and success of *C. sapidus*.

Osmoregulation is a critical physiological process that allows a species to survive and thrive in environments with varying salinity levels. As an euryhaline organism, *C. sapidus* can adapt to a wide range of salinities, making it a particularly resilient species in estuarine and lagoon ecosystems (Herrera et al., 2024). This adaptability is largely due to its ability to regulate the balance of salts and water in its body, a process governed by specialized mechanisms in its gills playing a central

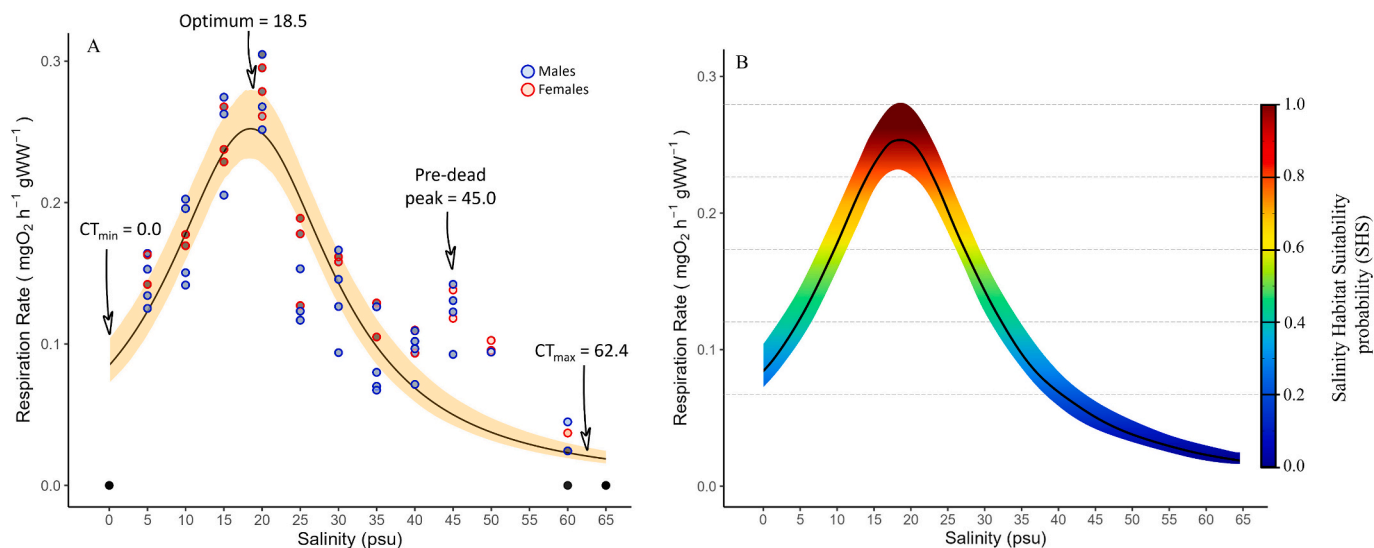


Fig. 2. (A) Salinity Performance Curve (SPC) of *Callinectes sapidus* based on the species metabolism (RR, $\text{mgO}_2 \text{ h}^{-1} \text{ gWW}^{-1}$). CT_{\min} : critical threshold minimum; CT_{\max} : critical threshold maximum. (B) Salinity Habitat Suitability (SHS) probability.

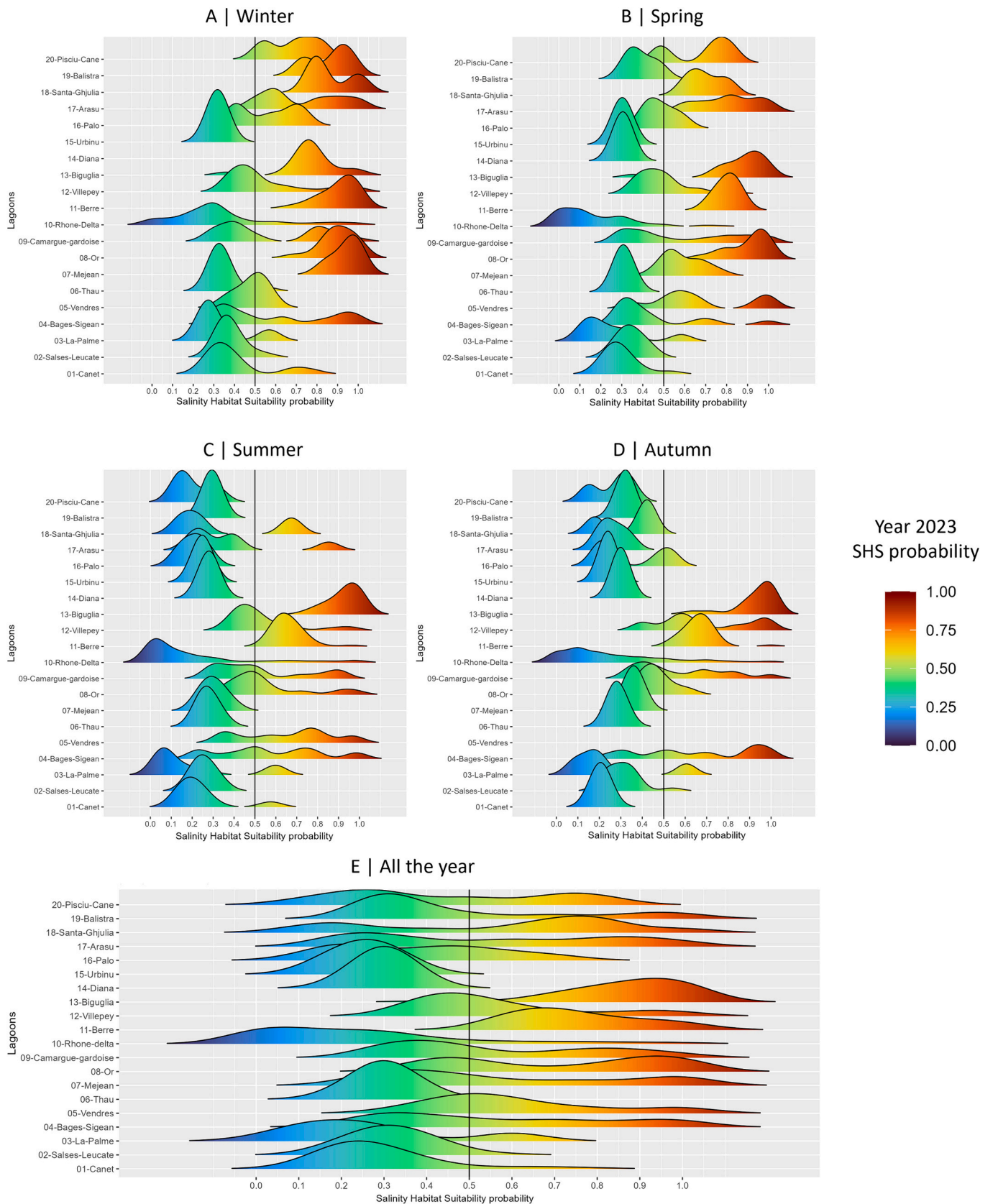


Fig. 3. Density of the number of stations as a function of SHS (Salinity Habitat Suitability probability) values for each season: (A) winter, (B) spring, (C) summer, (D) autumn, and (E) for the whole year 2023 in all seasons for the 20 lagoons studied. The color gradient is based on the gradient shown in Fig. 3 corresponding to the SHS probability values (dark red: favorable (=1), blue: unfavorable (=0)).

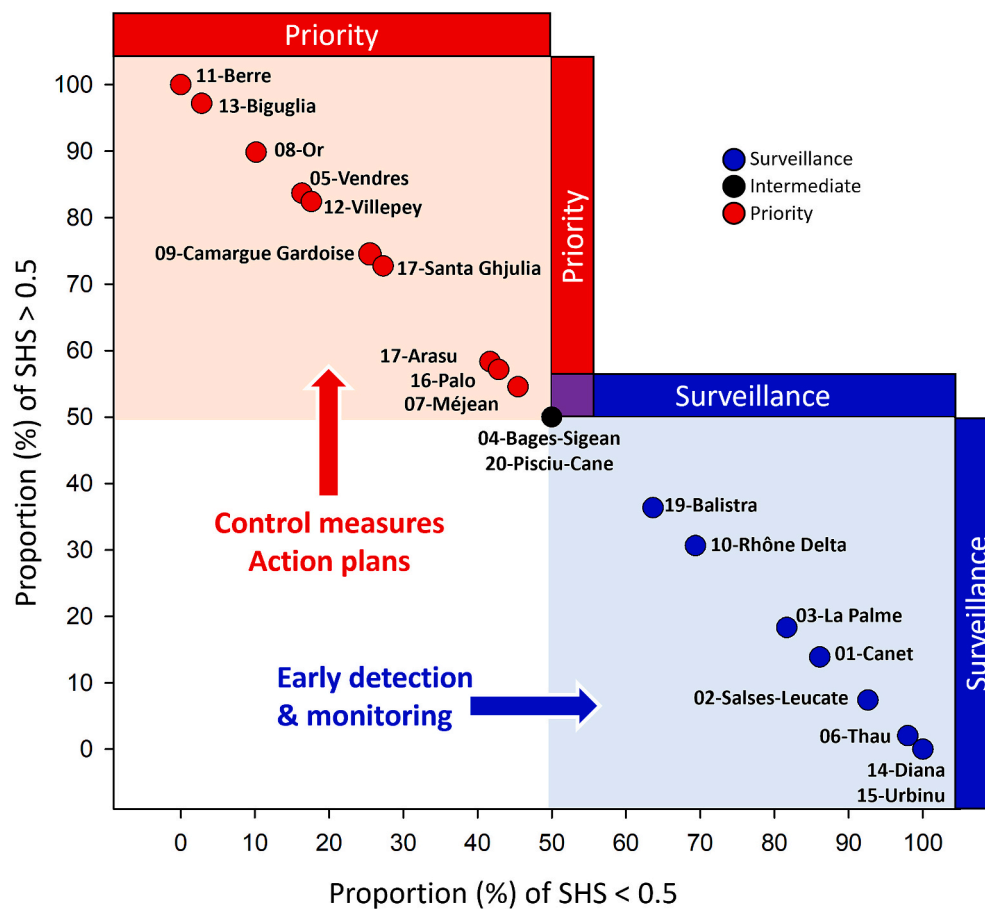


Fig. 4. Prioritization of lagoons for blue crab management actions *Callinectes sapidus* based on the salinity conditions for the year 2023. The graph shows the relationship between the proportion of SHS (Salinity Habitat Suitability probability) < 0.5 (unfavorable) and > 0.5 (favorable) and allows us to determine the distribution of lagoons and prioritize the implementation of management actions for the species along a linear regression. Red dots indicate priority lagoons, blue dots non-priority lagoons to be monitored, and black dots intermediate lagoons to be monitored.

role in osmoregulation (Henry and Wheatly, 1992; Towle and Burnett, 2007). In contrast to other portunid crab species, *C. sapidus* is highly efficient at osmoregulation, and can be considered a “strong regulator” due to its ability to constantly maintain hemolymph composition, whatever the salinity of the environment (Pequeux, 1995). In the Chesapeake Bay, its native area, *C. sapidus* keeps its hemolymph hyperosmotic compared to the external environment at salinities <25 psu, and isosmotic at salinities >25 psu (Lynch et al., 1973). *Callinectes sapidus* is equipped with ion transporters that actively regulate the movement of ions such as sodium and chloride between the crab's body and the surrounding water. These ion transporters help maintain internal homeostasis by either absorbing salts in low salinity conditions or excreting excess salts when the blue crab is in high salinity environments (Henry and Wheatly, 1992), by adapting its behavior to support osmoregulation (Eggleston et al., 1992). For instance, they often seek out habitats with optimal salinity levels that require minimal energy expenditure for osmoregulation (Ramach et al., 2009). This behavior is crucial for their survival and reproductive success. In low salinity environments, *C. sapidus* tends to be more active in regulating ion intake to compensate for the dilution of bodily fluids (Eggleston et al., 1992). Conversely, in high salinity environments, they focus on excreting excess salts to avoid hyperosmotic stress (Eggleston et al., 1992). The metabolic rate of *C. sapidus* increased significantly as they work to maintain ionic balance, especially when specimens were exposed to salinity levels outside their optimal range (Guerin and Stickle, 1992). Our study showed that the metabolic performance of *C. sapidus* followed a Gaussian regression curve, where metabolism peaked at an optimal salinity (18.5 psu) and declined at higher levels. These results differ

from those published by Bauer and Miller (2010) who measured respiration rates of juvenile blue crabs and showed that specimens consumed more oxygen at lower salinities. Our results obtained on adult provide new information on the ability of adults to tolerate greater variations in salinity indicating that *C. sapidus* is highly adaptable.

The upregulation of specific ion transporter proteins occurs in response to changes in environmental salinity (Guerin and Stickle, 1992). This molecular adaptation is a key aspect of *C. sapidus*' ability to thrive in fluctuating salinity conditions, providing a genetic basis for its physiological resilience. Understanding the salinity tolerance of *C. sapidus* is not only important for comprehending its ecological success but also for managing its populations, especially in regions where it is invasive. By mapping the salinity tolerance of *C. sapidus*, we can predict their potential spread on invaded ecosystems. This information is valuable for developing targeted conservation strategies and for making informed decisions about habitat management and invasive species control.

Our study investigated the habitat suitability for *C. sapidus* in 20 Mediterranean lagoons. In the Mediterranean Sea, as in its native area, brackish environments (e.g. lagoons, estuaries) are important for *C. sapidus* especially for its reproduction occurring in lowest salinities (Gandy et al., 2011). Our study, showed that mesohaline and polyhaline lagoons (salinity comprised between 5 and 30) were identified as the most favorable environments, supporting blue crab populations effectively. The spatial variability and the presence of salinity gradients observed each month in the lagoons could contribute to the establishment of populations within a broader range, from 5 to 35 psu, as *C. sapidus* could find at least one favorable site each month. Using this

data, we mapped the monthly small-scale distribution of based salinity suitable habitats across lagoons based on the metabolic performance of *C. sapidus*. This mapping is crucial in identifying potential areas of invasion, and present an important tool to help decision-makers in prioritizing control measures and early detection efforts at a local scale. This approach is also supported by the study of Aguilar et al. (2005), who studied the movement and habitat use of *C. sapidus* in different salinity zones, emphasizing the need for strategic management in high-salinity environments.

Moreover, the relationship between salinity and species invasions has been well-documented in the literature. Some studies have highlighted how high-salinity river mouth can influence the habitat use and population dynamics of *C. sapidus* (Ramach et al., 2009). These insights highlight the importance of understanding salinity gradients particularly when implementing management actions against an invasive species such as *C. sapidus* or in guiding the strategic choices to be made. Furthermore, salinity has a critical influence on the early life stages of *C. sapidus* (Costlow, 1967), a finding showing that the physiological mechanisms underlying salinity tolerance indicated that salinity stress can have profound effects on development and survival. Although we have no data on the spatio-temporal variability of blue crab numbers caught in the lagoons considered in our study. It would be interesting to compare the distribution of blue crab numbers with the distribution of SHS to determine whether salinity is the driver conditioning the distribution of individuals in each lagoon, or whether salinity combined with prey availability could play a role. Our study and the information available in the literature highlight the importance of salinity as a key driver of habitat preference and distribution, impacting both individual fitness and population dynamics. By integrating these perspectives, our research offers a comprehensive view of how salinity influences *C. sapidus*' ecology and provides valuable insights into the metabolic

responses and habitat suitability of *C. sapidus* in relation to salinity. By integrating these findings with existing literature, we can enhance our strategies for managing *C. sapidus* populations and mitigate the risks of invasion of new environments.

4.2. The metabolic performance as a management tool

In the context of the scenario of continued expansion and explosion of *C. sapidus* populations within the Mediterranean basin, and more specifically within Mediterranean lagoons, it is crucial to keep studying its impact on biodiversity and the functioning of lagoon ecosystems, as well as on local artisanal fisheries or more broadly on economic losses (including monetary expenses associated with management) (Marchessaux et al., 2023c). Furthermore, in a context of climate change, it is important to ask what the consequences of rising temperatures and salinities (and extreme climatic events) will be on the response and expansion of *C. sapidus*. There is an urgent need to raise awareness of this issue among the general public and decision-makers. The regulatory framework and its implementation are often too limited to effectively slow the flow of Non-Indigenous Species (NIS) introductions. Integrated knowledge is crucial for developing effective conservation and management strategies, ultimately aiding in the preservation of biodiversity in lagoon ecosystems.

Our study classified French Mediterranean lagoons into three categories—priority, intermediate, and surveillance—based on their suitability for *C. sapidus* persistence. This classification prioritized risk, guiding decision-makers to focus efforts in 2023, with 50 % of lagoons deemed priority, 10 % intermediate, and 40 % requiring monitoring (Fig. 5). However, given the inter-annual variability of salinity conditions in lagoons (e.g. hydrometry, droughts, etc.), this work should be reviewed by the managers and/or scientists in charge of control actions

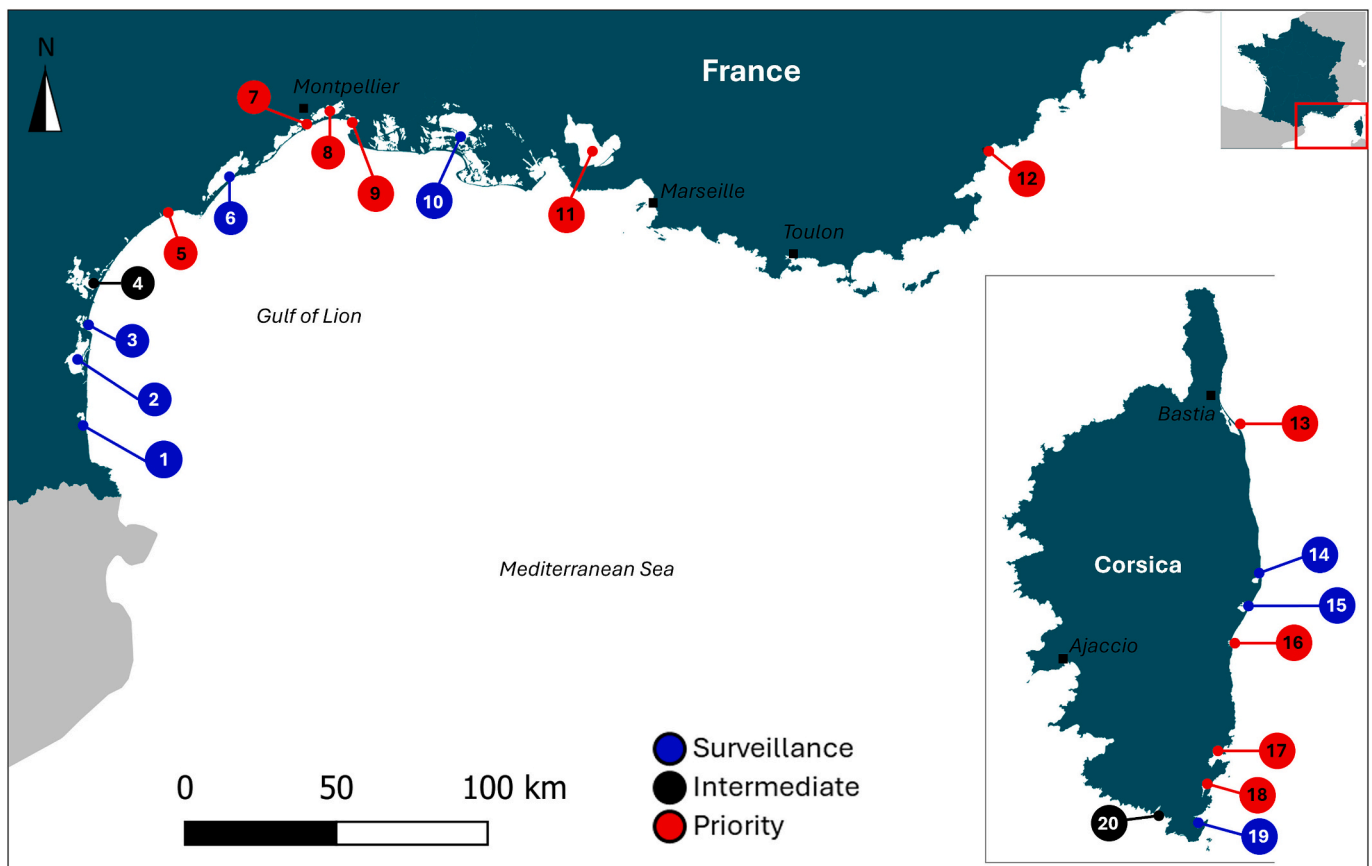


Fig. 5. Distribution of lagoon prioritization for locally adapted management based on the salinity conditions for the year 2023.

to check whether their lagoon has not become a favorable/unfavorable habitat in a changing climatic context. For example, the Canet Lagoon (ID: 01-Canet), which until the end of the year 2022 was a lagoon that was particularly affected by *C. sapidus* (~15 tons caught in 2022, Pôle-Relais Lagunes Méditerranéennes, unpublished data), showed favorable salinity conditions for *C. sapidus* (annual salinity mean in 2022: 31.9 ± 12.1 (SHS: 0.5 ± 0.3). Since 2023, however, the region has been affected by severe drought and a lack of rainfall, which have contributed to a significant increase in salinity levels up to 45 psu (annual salinity mean in 2023: 40.9 ± 5.9) unfavorable values for *C. sapidus* (SHS: 0.3 ± 0.1). The example of the Canet Lagoon shows the importance of considering drought scenarios, which could become increasingly significant and impact all the lagoons under consideration. In fact, some of the lagoons considered in our study are connected to the sea all year round (e.g. Berre Lagoon for example) and others are connected occasionally, mainly in autumn and winter (Biguglia Lagoon for example). In the first case, drought scenarios would certainly result in an increase in salinity, which would approach that of the sea for lagoons connected all year round. For lagoons partially connected to the sea, drought episodes will, via evaporation, lead to over-salting of the lagoons, as observed for Canet Lagoon in 2023. In fact, global change could have significant effects on salinity variations in coastal lagoons, making them less optimal for blue crabs, but also for all species living in these lagoon systems.

Based on this categorization, we now have concrete data to help decision-makers manage *C. sapidus* in French Mediterranean lagoons. European regulations on invasive species management are mainly governed by Regulation (EU) No. 1143/2014 of the European Parliament and of the Council of October 22, 2014 on the prevention and management of the introduction and spread of invasive species. Our study is part of two categories (Figs. 4–5):

- **Prevention of the invasion risk and early detection and rapid action (lagoons in the “surveillance” category):** with the implementation of surveillance and monitoring systems to rapidly detect invasive species. When such a species is detected, rapid action must be taken to eradicate or contain the population
- **Management of established species and implementation of action plans (“priority” and “intermediate” lagoons):** action plans to address the threats posed by invasive alien species must be put in place, including specific management strategies, measures to manage, control or, if possible, eradicate the species in order to minimize its impact on biodiversity and ecosystems.

This cartographic approach and the evaluation of the probability of salinity suitable habitat (SHS) have been provided to the managers of each lagoon. In addition to providing management support, this work and the tools generated will contribute to territorial action plans against *C. sapidus* (e.g. Territorial Action Plan in Corsica or Regional Action Plan in Occitanie) and provide valuable support for decision-making and prioritization of actions. Regarding the interannual salinity variability in lagoon systems (Erostate et al., 2022; Garrido et al., 2016; Gavini et al., 2013; Ligorini et al., 2022; Marchessaux et al., 2020), it is essential for lagoon managers to have a tool that allows them to determine if the salinity conditions are optimal or not for *C. sapidus*. To this end, we gave to the managers a spreadsheet where they can enter, each month, their salinity measurements and thus determine whether the conditions (optimal or non-optimal). Based on these findings and the potential to use the metabolic performance of blue crabs (or more generally invasive species) as a tool for the management of this species, it would be interesting to create an interactive online platform where managers can enter their data and identify optimal areas for *C. sapidus* on lagoon maps. Additionally, the tool developed in our study on spatial priority alternation between lagoons along the coast, based on salinity data, could also be used to implement control measures on favorable (priority) lagoons so that they do not become source populations for other lagoons considered to be non-priority and thus reduce the probability of larval

connectivity between lagoons (Marchessaux et al., 2023a).

To conclude, our study presented a combination of approaches on the metabolic performance of an invasive species and the mapping of favorable habitats, a tool applied to the management of invasive species. The creation of this tool was made possible by long-term data monitoring of the physicochemical conditions of lagoon systems. This approach was conducted on 20 French Mediterranean lagoons and represents a case study that can be widely applicable to other species and areas in the world. Our study highlights the importance of assessing the metabolic performance of NIS in response to salinity, but it also suggests that other factors, such as temperature and prey availability, can influence NIS distribution. Therefore, considering multiple stressors could significantly enhance our understanding of the complexity of environmental stressors on NIS distribution.

In the context of biological invasions, it is crucial to understand how the invasive species responds to local environmental conditions to implement management and control measures. Moreover, it appears that long-term monitoring of the environmental conditions of lagoon systems — important habitats for many species and providers of numerous ecosystem services (Rodrigues-Filho et al., 2023) — is necessary and useful at a local scale to address the challenges associated with biological invasions. In addition to the importance of long-term monitoring, it is necessary to focus our efforts on developing small-scale climate models (e.g., within lagoons) to predict the future distribution of invasive species like *C. sapidus* and then improve the early detection and rapid response (EDRR) actions.

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CRedit authorship contribution statement

Guillaume Marchessaux: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Nathalie Barré:** Writing – review & editing, Resources. **Virginie Maclert:** Writing – review & editing, Resources. **Katia Lombardini:** Writing – review & editing, Resources. **Eric D.H. Durieux:** Writing – review & editing, Resources. **Dimitri Veysiere:** Writing – review & editing, Investigation. **Jean-José Filippi:** Writing – review & editing, Resources. **Jérémy Bracconi:** Writing – review & editing, Resources. **Antoine Aiello:** Writing – review & editing, Resources. **Marie Garrido:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.176291>.

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Corrigendum

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The authors regret that the printed version of the above article omitted a co-author from the list of contributors to this study. The correct version of the list of authors corresponds to the one mentioned above, and the CRediT authorship contribution statement as described below.

CRediT authorship contribution statement

Guillaume Marchessaux: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Nathalie Barré: Writing – review & editing, Resources. **Virginie Mauclet:** Writing – review & editing, Resources. **Katia Lombardini:** Writing – review & editing, Resources. **Eric D.H. Durieux:** Writing – review & editing, Resources. **Dimitri Veysiere:** Writing – review & editing, Investigation. **Jean-José Filippi:** Writing – review & editing, Resources. **Jérémy Braconi:** Writing – review & editing, Resources. **Antoine Aiello:** Writing – review & editing, Resources. **Gianluca Sarà:** Funding acquisition, Conceptualization. **Marie Garrido:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

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