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Assessing Habitat Suitability and Distribution Patterns of the Invasive Brachyuran Crabs *Callinectes sapidus* and *Portunus segnis* in the Mediterranean Basin

Chiara SIDDILOLO^{1,2}, Valeria PALUMMO^{3,4}, Giacomo MILISENDA³, Carlo PIPITONE^{5,6}, Antonietta ROSSO², and Renato CHEMELLO⁷

¹ University School for Advanced Studies IUSS Pavia, Pavia, Italy

² Department of Biological, Geological and Environmental Sciences, University of Catania, Catania, Italy

³ Stazione Zoologica Anton Dohrn, Department of Integrative Marine Ecology (EMI), Sicily Marine Centre, Palermo, Italy

⁴ Stazione Zoologica Anton Dohrn, Department of Integrative Marine Ecology, CRIMAC, Calabria Marine Centre, Amendolara (CS), Italy

⁵ CNR-IAS, Lungomare Cristoforo Colombo 4521, 90149 Palermo, Italy

⁶ National Biodiversity Future Centre (NBFC), Piazza Marina 61, 90133 Palermo, Italy

⁷ Department of Earth and Marine Sciences, University of Palermo, 90128 Palermo, Italy

Corresponding author: Chiara SIDDILOLO; chiara.siddiolo@iusspavia.it

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Abstract

In this study, we investigate the habitat suitability and distribution patterns of two invasive alien crab species, *Callinectes sapidus* and *Portunus segnis*, in the Mediterranean basin. Using a comprehensive dataset compiled from multiple sources, including bibliographic records, online databases, and online informal sources, we mapped the occurrences of these species and overlaid them with environmental variables obtained from the Copernicus Marine Service. We employed MaxEnt species distribution models to predict habitat suitability, considering variables such as sea surface temperature, salinity, chlorophyll, and oxygen. Our results indicate widespread distribution of *C. sapidus* across the basin, with notable concentrations in certain areas, while *P. segnis* exhibits a predominantly southern distribution. Model evaluations demonstrate high predictive performance, with average AUC (area under the receiver operating characteristic curve) values exceeding 0.85. Additionally, we assessed potential habitat overlap between the two species at different probability thresholds, revealing regions where coexistence is likely. Our findings provide valuable insights into the spatial dynamics of invasive alien crab species in the Mediterranean and contribute to ongoing efforts in biodiversity conservation and management.

Keywords: Blue crab; species distribution model; non-indigenous species; Mediterranean; climate change; ecology.

Introduction

Biological invasions in the Mediterranean Sea are a focal point within the scientific community due to the significant impact of alien species on native biodiversity and ecosystems. In the past few decades, the introduction and establishment of non-indigenous species (NIS) through the Suez Canal and the Strait of Gibraltar have increased by 40% (Zenetos *et al.*, 2022). Climate change and the increase in commercial and tourist shipping play a key role in facilitating the entry of NIS (Pinsky *et al.*, 2020). Among the alien decapods in the Mediterranean, the Atlantic blue crab *Callinectes sapidus* Rathbun, 1896 and the African blue crab *Portunus segnis* (Forskål, 1775) are among the most widespread and have an increasingly dramatic impact on Mediterranean

ecosystems and the economy associated with fishery and aquaculture industry (Kampouris *et al.*, 2019). *Callinectes sapidus* – coming from the western Atlantic Ocean from Nova Scotia to northern Argentina (Millikin & Williams, 1984) - is one of the most invasive crab species (Streftaris & Zenetos, 2006) due to its great adaptability to different environmental conditions. Typically considered a predator (Mancinelli *et al.*, 2016), it is a generalist omnivorous that mainly feeds on algae, fish, mollusks, and other small invertebrates, depending on availability (Hines, 2007; Aslan & Polito, 2024; Prado *et al.*, 2024; Vivas *et al.*, 2025). *Callinectes sapidus* colonizes multiple habitats, mainly in shallow waters, from seagrass to soft bottoms and estuarine habitats, depending on its life stage and needs (Millikin & Williams, 1984; Mancinelli *et al.*, 2016). Females spawn several times during

summer, with multiple clutches of eggs in each spawning event (Dickinson *et al.*, 2006). Its invasiveness is further worsened by current rising sea temperatures (Nehring, 2011; Mancinelli *et al.*, 2017; Marchessaux *et al.*, 2022). First recorded in the Mediterranean in 1949 (as *Neptunus pelagicus*: Giordani Soika, 1951), its presence is now widely documented throughout the basin (Deidun *et al.*, 2022). *Callinectes sapidus* likely went through several independent introductions from the Atlantic Ocean, mainly with ballast water as a vector (Nehring, 2011). The Lessepsian migrant *P. segnis* is considered the first crustacean to have approached the Mediterranean, where it arrived shortly after the opening of the Suez Canal (as *N. pelagicus*: Fox, 1924; Galil, 2011). Since then, it has expanded its range significantly, colonizing vast areas of the central Mediterranean basin (Katsanevakis *et al.*, 2020) and, more recently, the Sicilian Strait (Shaiek *et al.*, 2021; Castriota *et al.*, 2022). It usually inhabits coastal waters, especially seagrass beds and mangroves (Giraldes *et al.*, 2016), feeding mainly on fish, invertebrates, and algae (Zainal, 2013; Giraldes *et al.*, 2016; Mancinelli *et al.*, 2022; Vivas *et al.*, 2025). *Portunus segnis* has at least two seasonal spawning events per year, one between December and March and the other between August and October (Giraldes *et al.*, 2016; Hadj Hamida *et al.*, 2022). Previous studies on the distribution of invasive species, such as the blue crabs *C. sapidus* and *P. segnis* (Mancinelli *et al.*, 2021; Shaiek *et al.*, 2021), and on larval connectivity (Marchessaux *et al.*, 2023) have been carried out.

Monitoring the distribution of alien species, particularly crustaceans such as *C. sapidus* and *P. segnis*, whose larval stages exhibit complex mechanisms of dispersion over time and space (Criales *et al.*, 2019), is crucial for a better understanding of their ecology, in order to mitigate the impact of invasive NIS on the native biota and its linked economy in the Mediterranean. It is crucial to detect any connections between the occurrence of these

species and environmental factors, particularly those associated with ongoing climate change. The main purpose of this study is to understand the current distribution ranges of *C. sapidus* and *P. segnis* and how environmental variables connected to climate change may affect their spreading and establishment in the Mediterranean Sea. The use of species distribution models for the development of habitat suitability maps allows, among other things, the identification of areas where the two species have not yet been found but would potentially encounter ideal conditions for their survival.

Materials and Methods

Dataset

The records of *C. sapidus* and *P. segnis* have been organized into a database from multiple sources: a) bibliographic sources, particularly collective articles and first records in the Mediterranean (Suppl. Data S1). b) online databases, specifically inaturalist.org and GBIF (last accessed on 07/02/2024); and c) Facebook pages and groups, especially “Oddfish” and “Mediterranean Marine Fauna” (last accessed on 07/02/2024). The records used to populate our database always include geographical coordinates, year of occurrence, country of occurrence, and references. In most records coming from Facebook groups and inaturalist.org, photos and the date of the occurrence are also included. The data were collected in spreadsheets where, if available, additional information such as the number of observed individuals, habitat, and depth were added. Subsequently, the data were processed using R studio, standardizing coordinates from different databases when in different formats. Finally, they were represented on a shapefile of the Mediterranean basin (Fig. 1).

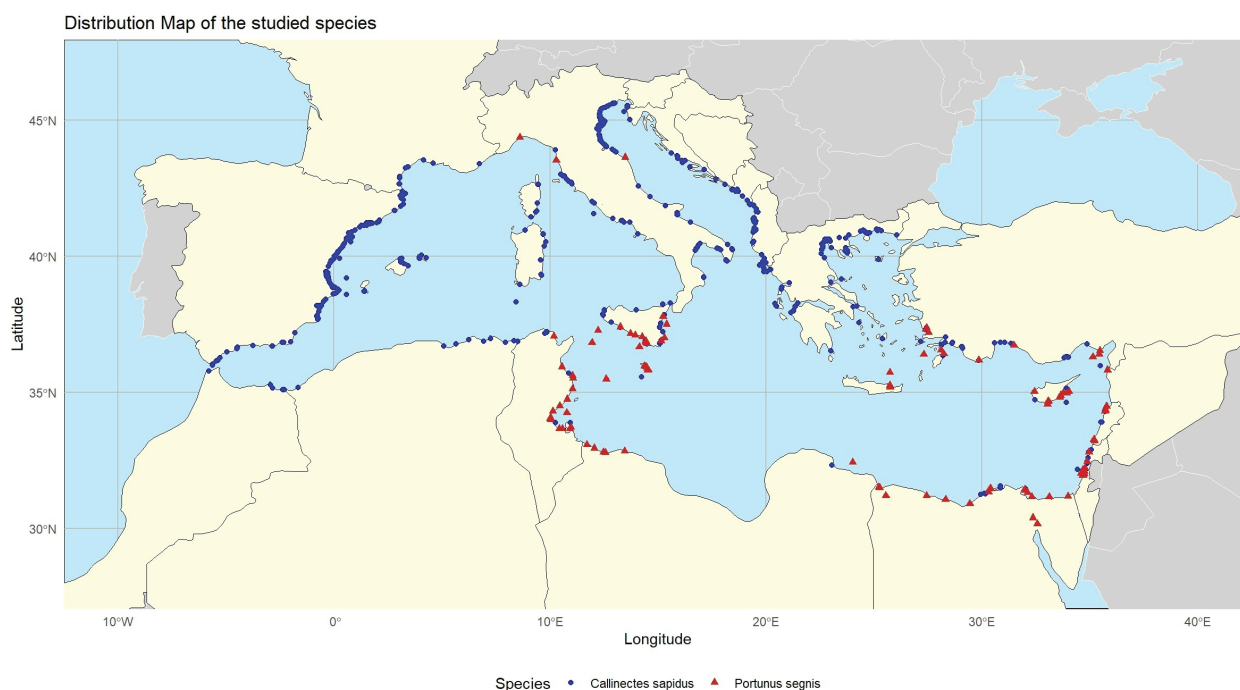


Fig. 1: Distribution map of *Callinectes sapidus* (in blue) and *Portunus segnis* (in red) in the Mediterranean Sea.

Environmental Variables

Environmental variables were downloaded from the Copernicus Marine Service in raster files with a resolution of $0.042^{\circ} \times 0.042^{\circ}$ (MEDSEA_MULTIYEAR_PHY_006_004; MEDSEA_MULTIYEAR_BGC_006_008), over a time span of 20 years, from 2001 to 2021, according to data availability. The selection of environmental variables considers the physiology of the species in larval and adult stages. Sea surface temperature (SST), salinity, chlorophyll, and oxygen raster files were processed, and for each variable, a 20-year mean was calculated, obtaining a single value per pixel using the R studio library *Raster*. During the initial selection of environmental variables, phytoplankton was also included, but it was later excluded due to its strong correlation with chlorophyll (0.99). The coordinates of the occurrences for the two species under consideration were overlaid to the raster of environmental variables. Data related to the averages of environmental variables were then graphically represented along with the species distribution, allowing an initial overview of the correlation between the presence of individual species and the single environmental variable.

Species Distribution Models

Habitat suitability maps for the two species were performed using the maximum entropy model (MaxEnt; Elith *et al.*, 2006; Phillips *et al.*, 2006; Merow *et al.*, 2013), allowing us to process only presence data to calculate the probability distribution for *C. sapidus* and *P. segnis* in the Mediterranean. MaxEnt was employed to develop a model linking each georeferenced observation with a series of predictor variables to forecast habitat distribution based on the probability of suitability for species distribution. We assessed the level of intercorrelation using R Studio by calculating pairwise Pearson's correlation coefficient. Therefore, we identified the most significant factors among variable pairs with a Pearson correlation coefficient $|r| > 0.85$. Variables exhibiting strong correlations were omitted to avoid misshaped outcomes. Weakly correlated environmental variables were then analyzed to determine the percentage contribution of each. To assess the importance of each variable, we performed a jack-knife test by running the model multiple times, each time excluding an environmental variable, and comparing the performance of the model with and without that variable. The performed MaxEnt model – trained using batch files – maintained several parameters as default, such as a convergent threshold of 10^{-5} , a maximum interaction value of 500, and a maximum of 10,000 randomly selected background points, as recommended by previous studies (Phillips *et al.*, 2006; Phillips & Dudík, 2008; Anderson *et al.*, 2016; Bargain *et al.*, 2017). For the modeling evaluations, we considered the area under the receiver operating characteristic (ROC) curve (AUC) values, the standard deviation, and the true skill statistic (TSS) mean, as used in previous studies (Phillips *et al.*, 2006; Liu *et al.*, 2016;

Palummo *et al.*, 2023). The ROC curve displays the true positive rate (sensitivity) in relation to the false positive rate ($1 - \text{specificity}$) at different thresholds. The AUC identifies the total performance of the model (**AUC ≥ 0.9** : Excellent model performance, with a very high ability to distinguish between positive and negative cases; **0.7 \leq AUC < 0.9** : Good performance, the model has some misclassifications; **0.6 \leq AUC < 0.7** : Fair performance; **AUC < 0.6** : Poor performance; Bargain *et al.*, 2017). TSS measures the accuracy of the model by combining both sensitivity and specificity. The range spans from -1 to $+1$ (**TSS ≥ 0.8** : Excellent performance, the model has high accuracy; **0.6 \leq TSS < 0.8** : Good performance, the model provides useful predictions; **0.4 \leq TSS < 0.6** : Fair performance, the model requires improvements; **TSS < 0.4** : Poor performance. The model's predictions are not reliable; Li *et al.*, 2023).

Response Curves

The response curves delineate the influence of each environmental variable on the MaxEnt predictions for both species. They demonstrate how the predicted probability of presence changes as each environmental variable is varied while keeping others at their average sample value. The curves provide insight into variable marginal effects and their impact on model predictions.

The records for the two species were overlaid on their respective maps in order to detect any possible areas where habitat suitability indicates the presence of the species. The two resulting maps – one for *C. sapidus* and one for *P. segnis* – were then cropped by applying a bathymetric filter ranging from 0 to 100 meters in depth in order to define habitat suitability areas likely to support the presence of both species. At last, the maps were overlaid to underline areas with the potential presence of both species. Then, the degree of potential competition was assessed using different approaches. Each model aimed to delineate areas where there is a specific likelihood threshold of habitat overlap. Specifically, we created maps highlighting regions where there is a 40%, 60%, and 80% probability of habitat overlap between the two species (highlighted in red) and areas where only one species can be found (highlighted in yellow).

This approach offers important insights into the spatial dynamics of the species distributions within the Mediterranean environment and provides an understanding of potential coexistence between the species.

Results

Distribution

Data collection on both species, using multiple sources, yielded 1378 occurrences for *C. sapidus* and 125 occurrences for *P. segnis* (Fig. 1) in the Mediterranean basin. The distribution maps reveal that the presence of *C. sapidus* extensively covers the entire basin, while

P. segnis maintains a predominantly southern distribution, primarily centered in North Africa, the southern Italian peninsula, and Greece.

Callinectes sapidus

The provided results from the MaxEnt model analysis offer comprehensive insights into the predictive performance and variable contributions of the species model. Response curves (Fig. 2) highlight how individual environmental variables influence MaxEnt predictions, while the analysis of variable contributions quantifies the relative importance of each variable. Notably, chlorophyll-a (chl) emerges as the most influential variable for *C. sapidus*, contributing 81.1% to the model, while oxygen also

plays a significant role, particularly in distinguishing the species from background data (Table 1). The jackknife test further underscores variable importance, with oxygen and chl identified as the variables with the highest gain when used in isolation, emphasizing chl predictive power. The provided command line offers a means to replicate the species model, outlining the specific parameters and data sources used in the MaxEnt analysis. The resulting habitat suitability map (Fig. 3) shows a wide range along the Mediterranean coasts for this species. In the Western Mediterranean, the most suitable areas for the species, depicted in red, correspond to the Alboran Sea and to several areas, particularly along the North-West African coasts. Along the northern coast of the Mediterranean, the areas deemed most suitable by the MaxEnt model are homogeneous from the coasts of Spain to those

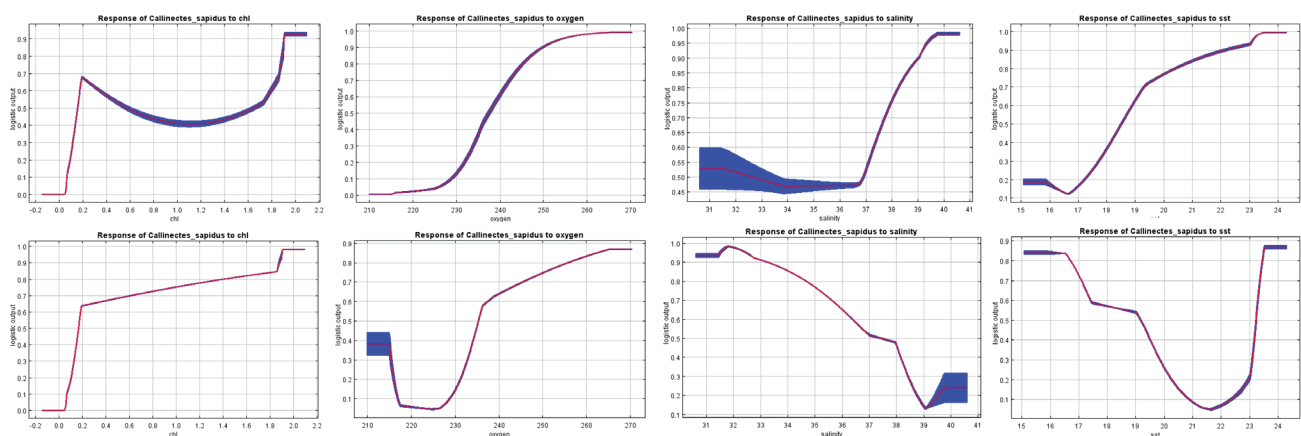


Fig. 2: Curves of predicted probability of presence for *Callinectes sapidus*. The curves in the top row show changes as each environmental variable is varied, keeping all other environmental variables at their average sample value. The curves in the bottom row derive from the MaxEnt model using only the corresponding variable. These plots reflect the dependence of predicted suitability both on the selected variables and on dependencies induced by correlations between the selected variable and other variables.

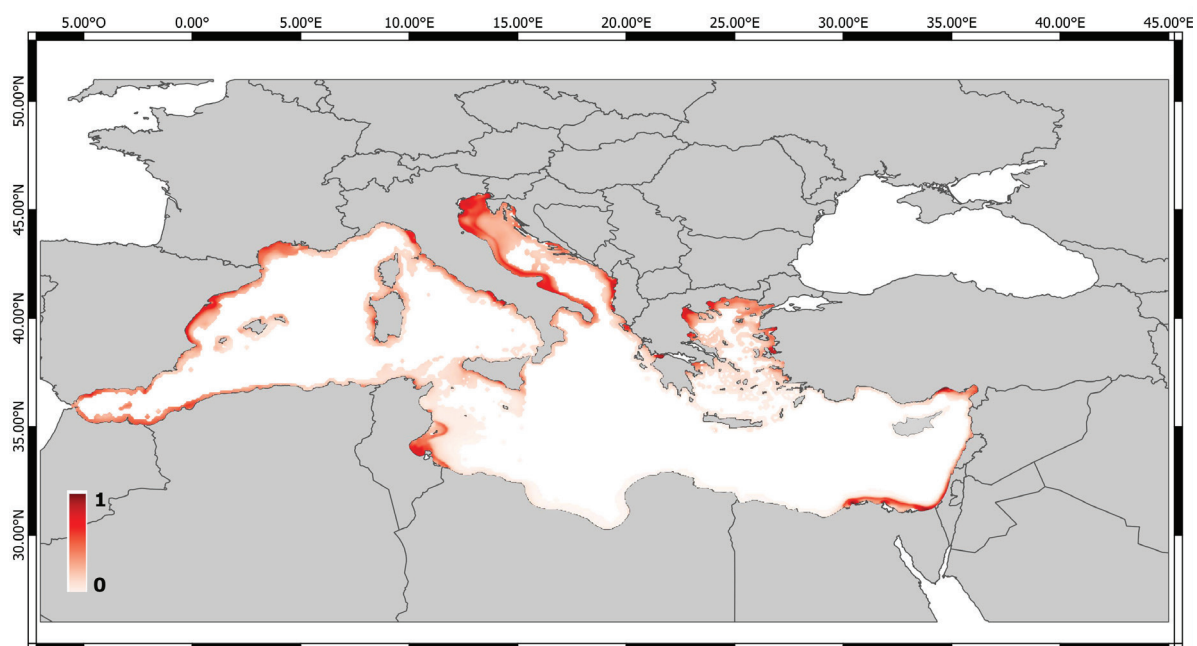


Fig. 3: Habitat suitability map for *Callinectes sapidus* in the Mediterranean Sea. The increasingly dark shades, from 0 (white) to 1 (red), indicate areas where the chance of encountering the species is increasingly higher according to the environmental variables tested with the MaxEnt model.

Table 1. Estimate of relative contributions of environmental variables to the MaxEnt model for *Callinectes sapidus*.

Variable	Percent contribution	Permutation importance
chl	81.1	40.9
oxygen	10.2	44.2
salinity	4.9	6.6
sst	3.8	8.3

of northern Italy, with greater adaptability in areas with a high concentration of river mouths and brackish zones. The Adriatic coast features areas more suitable for the species' presence in the entire coastal area until the Gulf of Taranto, as well as along the coastal areas of Montenegro and Albania. Proceeding along the Aegean Sea, the suitable areas embrace Greece and Turkey. Further south, the most suitable areas are between Israel and Egypt (especially along the mouth of the Nile) on the east side and between the Gulf of Gabes in Tunisia and Morocco.

Portunus segnis

Table 2 presents the estimate of the relative contributions of environmental variables to the MaxEnt model. Response curves (Fig. 4) show how each environmental variable shapes the MaxEnt predictions, while the analy-

sis of variable contributions quantifies the relative importance of each variable. SST emerges as the most influential variable, contributing 64.6% to the model, followed by chlorophyll-a (chl), salinity, and oxygen. The jack-knife test confirms SST as the variable with the highest gain when used in isolation and the most significant decrease in gain when omitted. The suitability map for this species (Fig. 5) remarks an imaginary border between the north of the basin, where *P. segnis* meets less suitable areas, remarked with light red, and the central-south basin, where we see more suitable habitats. The Italian peninsula shows good suitability in its southern part, and the same is true for the entire Sicilian and Maltese coasts. The coasts of Greece, in the Aegean Sea, are suitable for the presence of the species, together with the entire coastal areas of Turkey, Cyprus, Syria, Lebanon, and Israel. The same high suitability is displayed in the entire Mediterranean African coast from Egypt to Morocco.

Table 2. Estimate of relative contributions of environmental variables to the MaxEnt model for *Portunus segnis*.

Variable	Percent contribution	Permutation importance
sst	64.6	46.5
chl	16.8	19.1
salinity	11.4	13.3
oxygen	7.2	21.2

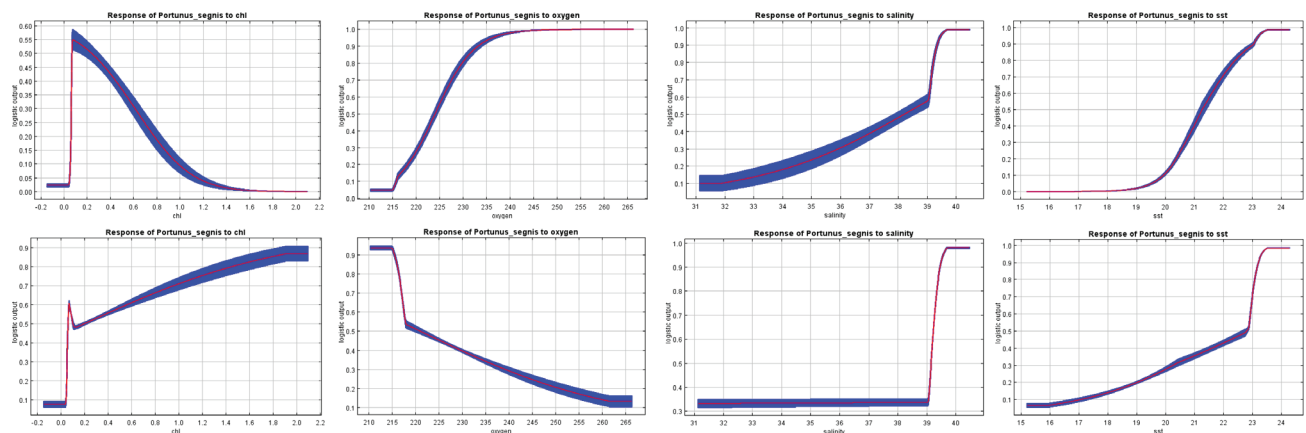


Fig. 4: Curves of predicted probability of presence for *Portunus segnis*. The curves in the top row show changes as each environmental variable is varied, keeping all other environmental variables at their average sample value. The curves in the bottom row derive from the MaxEnt model using only the corresponding variable. These plots reflect the dependence of predicted suitability both on the selected variables and on dependencies induced by correlations between the selected variable and other variables.

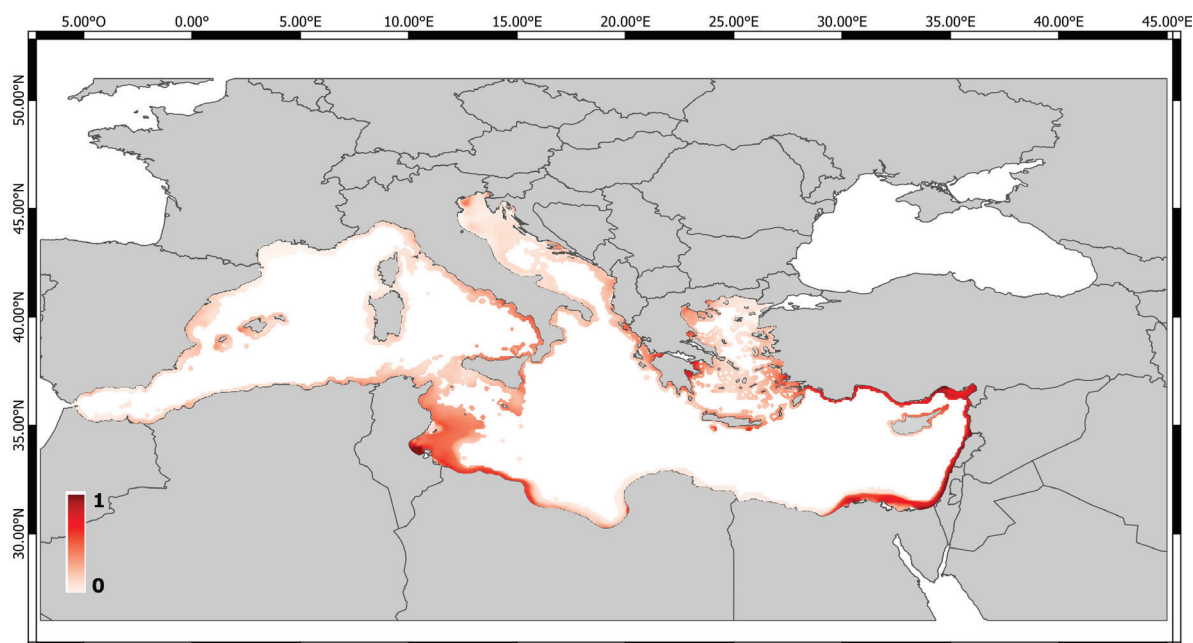


Fig. 5: Habitat suitability map for *Portunus segnis* in the Mediterranean Sea. The increasingly dark shades, from 0 (white) to 1 (red), indicate areas where the chance of encountering the species is increasingly higher according to the environmental variables tested with the MaxEnt model.

Modeling Evaluation

Both MaxEnt models underwent cross-validation, resulting in an average AUC value exceeding 0.85 and a standard deviation ranging from 0.014 to 0.044. This indicates a significant improvement over random prediction. Table 1 displays the AUC values, standard deviations, and mean TSS for both models, serving as indicators of model accuracy.

Coexistence

In the first model (Fig. 6), where the probability of finding habitat suitability for both *C. sapidus* and *P. segnis* is set at 40%, the areas affected by a possible overlap are many. These include the area around the Strait of Gibraltar, a significant portion of the Spanish and French coasts, almost the entire Italian peninsula, part of northern Sicily and the Strait of Sicily, and all the coasts of the Eastern Mediterranean. However, the areas highlighted in

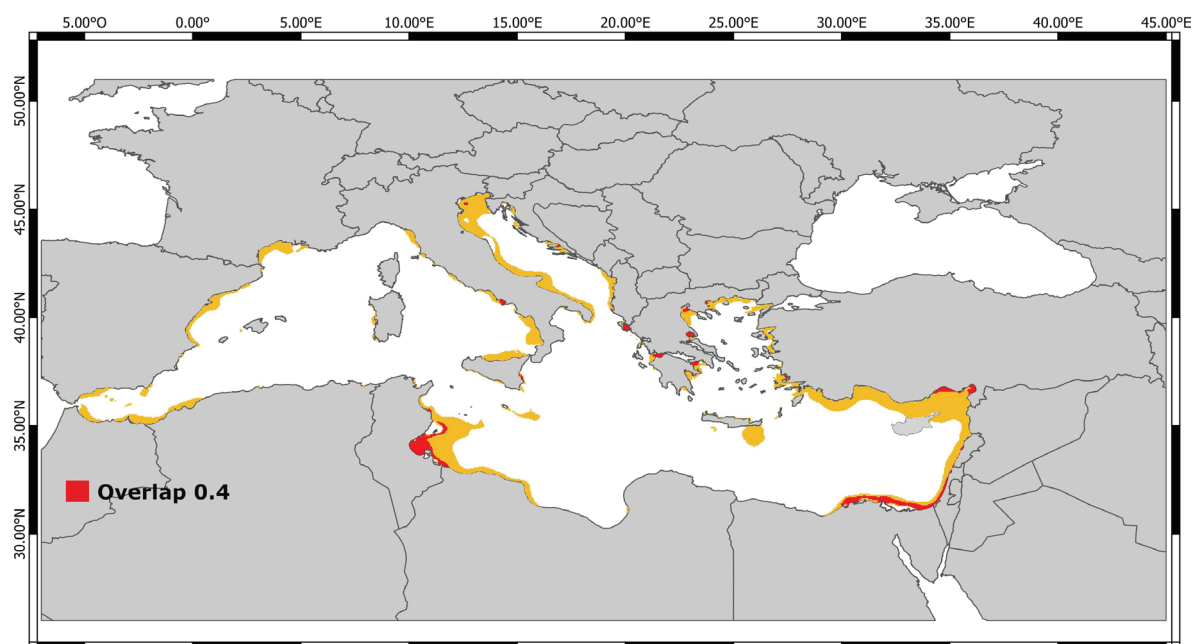


Fig. 6: Habitat suitability maps for *Callinectes sapidus* and *Portunus segnis* with overlap at 40% possibility. Areas with 40% opportunity to find both crab species are highlighted in red; those with 40% chance of finding only one of the two species are highlighted in yellow.

red represent the regions where the probability of coexistence of the two species is higher. On the Tyrrhenian side, the area of overlap is limited to the Italian Gulf of Naples. On the Ionian side, a localized red area is highlighted on the eastern coast of Sicily, between Catania and Siracusa. On the Adriatic coast, only some enclosed areas are affected by this overlap: a part of the Gulf of Venice, a portion of south Croatia, and a wider area within the border of Albania and Greece, which includes the eastern side of Corfu Island. Lastly, in the Eastern Mediterranean, several other gulfs in Greece are contained in the overlap, along with the eastern coasts of Turkey, part of the coast of Lebanon, and the entire coasts of Israel, as well as the entrance of the Suez Canal and the eastern coast of Egypt. The Tunisian coast is almost entirely highlighted in red, especially in the whole area of the Gulf of Gabes.

The second model (Fig. 7) displays the areas where the probability of coexistence is higher than 60%, and the areas affected by the possibility of coexistence between the two species are reduced throughout the entire Mediterranean basin. The highlighted areas along the Spanish, French, and Italian coasts almost disappear, with no red areas for the Northern and Western coasts. The only remarked area is a small portion of the coast in Greece, between the main Island and Zante. Moving to the Eastern Mediterranean, the Gulf of Antalya in Turkey is still marked in red. Israel and Egypt show again a high possibility of overlapping, but the red areas are more limited. The Gulf of Gabes, in Tunisia, is the only remarkable spot along the North African coast.

Finally, the third model (Fig. 8) depicts the areas where the probability of coexistence is greater than 80% and highlights only a few areas throughout the entire basin. The areas that were highlighted in red in the previous models are now less frequent and yellow, marking the

same areas. However, the red areas are limited to a small portion of the Turkish coast, in the Gulf of Antalya, a few areas in Egypt, between the Suez Canal and the Nile, and a tiny portion of the Gulf of Gabes, in Tunisia.

Discussion

The Mediterranean Sea is witnessing increasing concern within the scientific community due to the escalating impact of biological invasions, particularly from NIS, on native biodiversity and ecosystems. The introduction and establishment of NIS, facilitated by human activities and global environmental changes, pose significant threats to the region's ecological balance and socio-economic stability. The invasion dynamics of NIS, such as *C. sapidus* and *P. segnis*, highlight the challenges posed by biological invasions in the Mediterranean. Both species have rapidly expanded their ranges, with *C. sapidus* displaying extensive coverage across the entire basin, while *P. segnis* maintains a predominantly southern distribution, concentrated in regions such as North Africa, southern Italy, and Greece. The spread of these species is attributed to various factors, including the widening connectivity facilitated by the Suez Canal – for *P. segnis* – alongside climate change-induced alterations in marine environments (Harley *et al.*, 2006; Pecl *et al.*, 2017; Santojanni *et al.*, 2023).

The implementation of MaxEnt modeling techniques provided insights into the habitat suitability and potential distribution patterns of *C. sapidus* and *P. segnis* across the Mediterranean basin. The points indicating every occurrence for *C. sapidus* and *P. segnis* (collected data) are overlaid to the suitability distribution models (MaxEnt) to highlight how most of the red areas, where the environ-

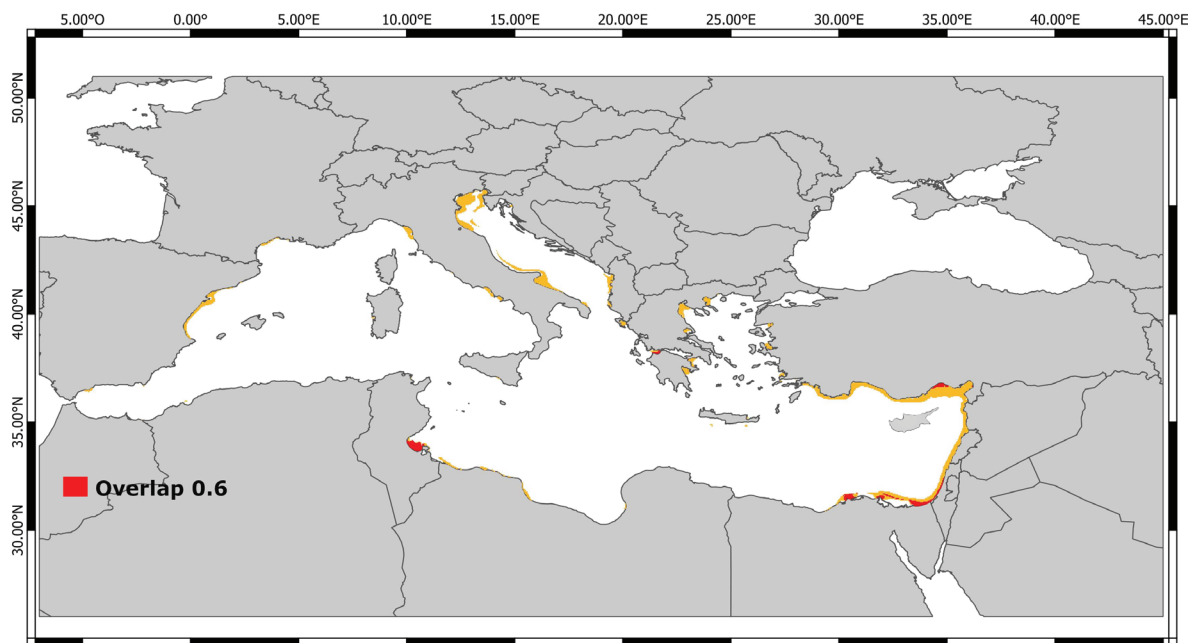


Fig. 7: Habitat suitability maps for *Callinectes sapidus* and *Portunus segnis* with overlap at 60% possibility. Areas with 60% opportunity to find both crab species are highlighted in red; those with 60% chance of finding only one of the two species are highlighted in yellow.

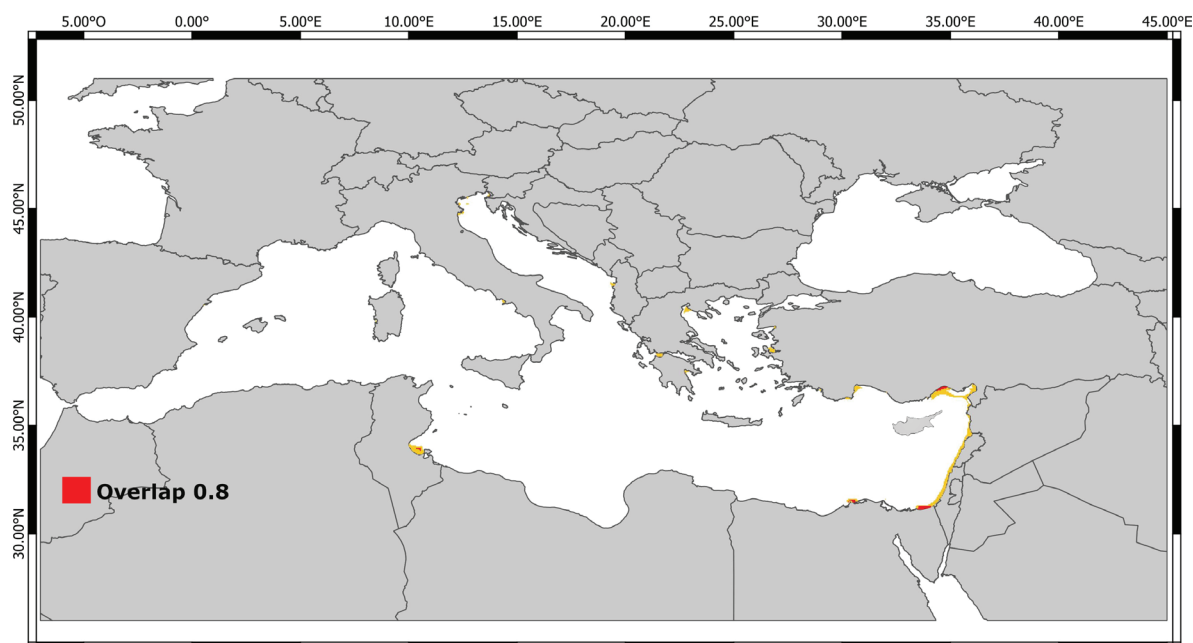


Fig. 8: Habitat suitability maps for *Callinectes sapidus* and *Portunus segnis* with overlap at 80% possibility. Areas with 80% opportunity to find both crab species are highlighted in red; those with 80% chance of finding only one of the two species are highlighted in yellow.

mental conditions are ideal, already have several occurrences of each species (Fig. 9; Fig. 10).

The habitat suitability map provided by MaxEnt also highlights some areas where the two species have not yet been found but where the environmental conditions suggest their possible presence. *C. sapidus* is spread in most of the areas highlighted by the suitability map: the only areas highlighted in red where the species does not show occurrences are on the western coast of Algeria and in Syria. For *P. segnis*, the red areas where the species does

not occur include the western coast of Lybia, the Syrian coast, some areas in Turkey, and some portions of southern Greece.

Through the integration of species occurrence data and environmental variables, our study developed robust predictive models capable of accurately forecasting the current species distributions across varying temporal and spatial scales. The achievement of consistently high average AUC values exceeding 0.85, coupled with minimal standard deviations, attests to the effectiveness of the

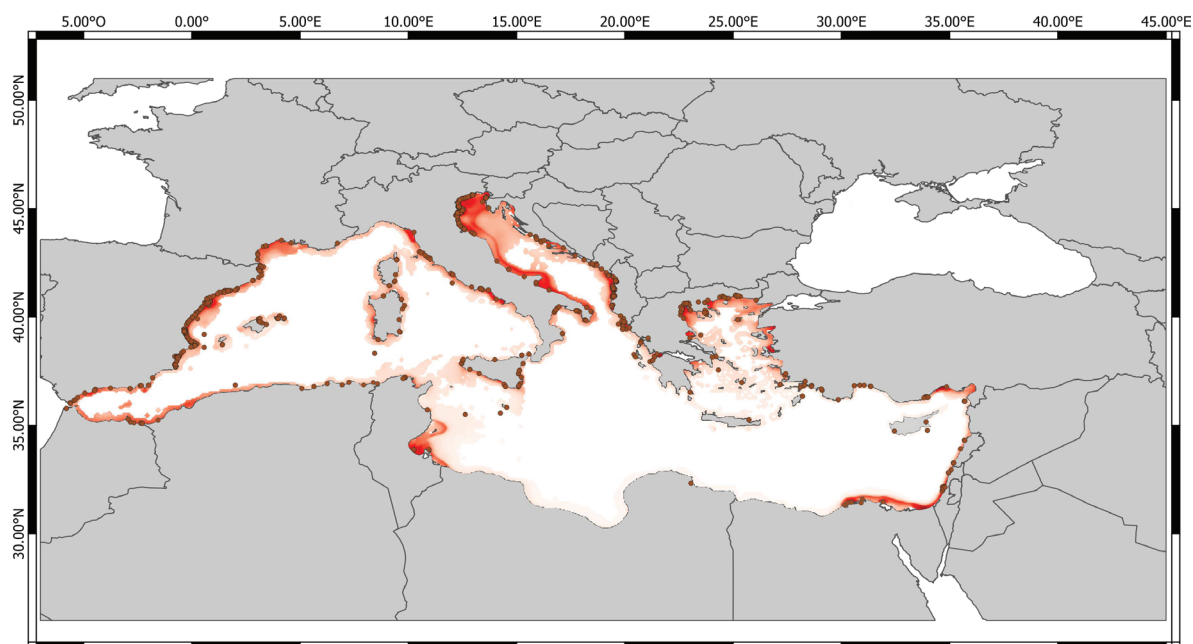


Fig. 9: Occurrences of *Callinectes sapidus* collected from the Mediterranean Sea and used to build the MaxEnt model, overlaid to the habitat suitability map, to emphasize areas where the species has not yet been reported, but which have suitable environmental conditions for its occurrence.

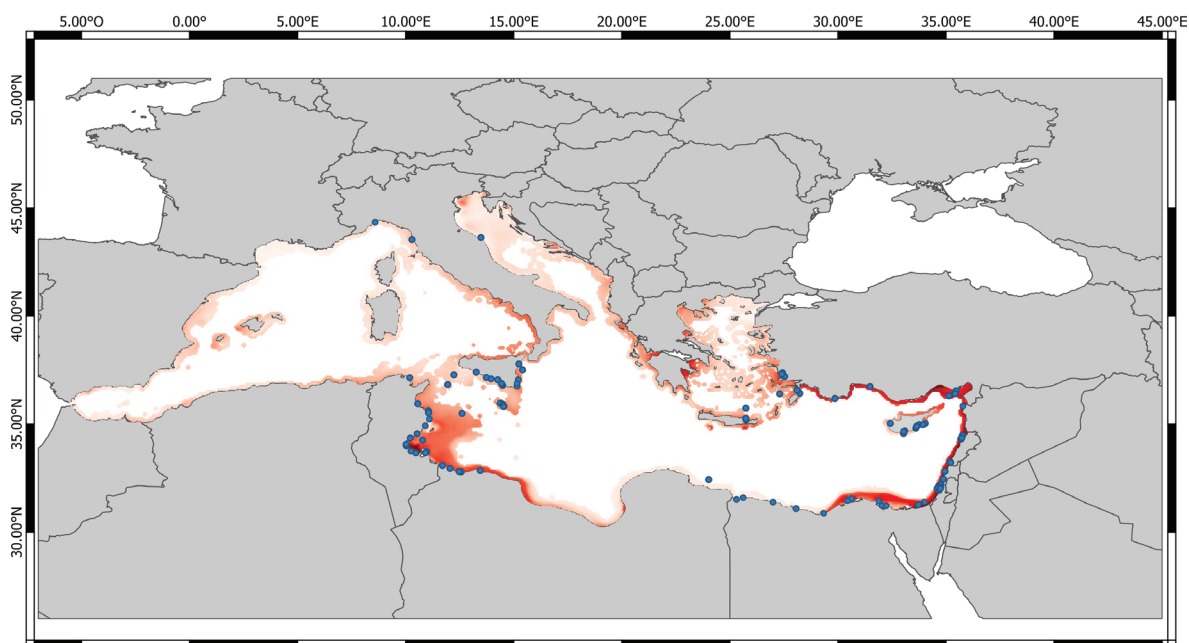


Fig. 10: Occurrences of *Portunus segnis* collected from the Mediterranean Sea and used to build the MaxEnt model, overlaid to the habitat suitability map, to emphasize areas where the species has not yet been reported, but which have suitable environmental conditions for its occurrence.

MaxEnt models in discerning suitable habitat conditions from unsuitable ones. These results underscore the reliability of our models in capturing the intricate relationships between species occurrences and environmental factors. These findings highlight the effectiveness of the models and the accuracy of their predictions regarding the habitat distribution of *C. sapidus* and *P. segnis* in the Mediterranean region (Table 3).

An in-depth analysis of the contribution from different variables revealed the pivotal environmental drivers shaping the habitat suitability of both *C. sapidus* and *P. segnis*. Variables such as chlorophyll-a and oxygen emerged as significant predictors for *C. sapidus*, reflecting the species' preference for nutrient-rich and thermally suitable habitats. However, SST exhibited the highest influence on the habitat suitability of *P. segnis*, underscoring its critical role as an environmental determinant for the species' distribution. Moreover, response curves provided nuanced insights into the marginal effects of individual environmental variables on species distributions, elucidating how changes in environmental conditions influence habitat suitability probabilities. These findings contribute to a deeper understanding of the ecological niche requirements of invasive decapod species, thereby informing targeted conservation efforts and management strategies aimed at mitigating their impacts.

The assessment of habitat overlaps between *C. sapi-*

idus and *P. segnis* unveiled intriguing spatial dynamics with profound implications for species coexistence and potential interspecific competition. By delineating areas of high probability of habitat overlap, our study identified regions where interspecific interactions may occur, thereby influencing community dynamics and ecosystem functioning. In the first model, depicting a 40% probability of habitat overlap, extensive areas across the Mediterranean basin were identified as potential hotspots for both species' coexistence. Particularly noteworthy were regions around the Strait of Gibraltar, the Spanish and French coasts, the Italian peninsula, and the Eastern Mediterranean, suggesting widespread opportunities for interspecific interactions and ecological niche overlap. As the probability threshold for habitat overlap increased to 60% in the second model, the extent of overlapping areas decreased, indicating a more constrained range of potential coexistence. This reduction in overlap was particularly pronounced in Greece and Turkey, as well as in Israel, Egypt, and Tunisia, suggesting a decreased likelihood of interspecific interactions in these regions. In the third model, where the probability of habitat overlap exceeded 80%, only a few localized areas throughout the basin exhibited significant overlaps, highlighting specific regions of increased potential for coexistence. Despite the overall reduction in overlapping areas, certain hotspots of coexistence persisted along the Egyptian and Tunisian

Table 3. Modelling evaluation showing the Threshold, TSS, AUC and Dev/st values for both species, highlighting the accuracy of the MaxEnt models.

Species	Threshold	TSS	AUC	Dev/st
<i>Callinectes sapidus</i>	0.2455	0.7512	0.901	0.014
<i>Portunus segnis</i>	0.2857	0.6811	0.891	0.044

coasts, underscoring areas of elevated interspecific interaction potential and ecological significance. These maps confirm expectations indicating that areas with a chance of a high coexistence of *C. sapidus* and *P. segnis* are the ones where the environmental conditions are suitable for both species, allowing their presence. However, it is important to consider not only the presence of a suitable habitat but also their biology and ecology. A key ecological factor at the base of coexistence is competition. The two species are both predators, so they might compete for food resources. Habitat is another aspect of paramount importance. Although *C. sapidus*, unlike *P. segnis*, needs brackish-water environments to complete its life cycle, they could co-occur in the open sea because they can inhabit coastal sandy bottoms at least for a part of their life cycle. Lastly, temperature, which we have already identified as a key parameter, especially for *P. segnis*, may help explain the current and future distribution of the two species. On the one hand, *P. segnis*, which comes from the Red Sea and the western Indian Ocean, tends to prefer the warmer areas of the Mediterranean; on the other hand, the temperate west-Atlantic origin of *C. sapidus* might have favored its wide spreading throughout the Mediterranean basin (Marchessaux *et al.*, 2022; 2024).

Our study offers comprehensive insights into habitat suitability and potential coexistence dynamics of invasive decapod species within the Mediterranean basin. By integrating MaxEnt modeling techniques with habitat overlap analysis, we have provided a holistic understanding of species distributions and ecological interactions, thereby informing targeted conservation efforts and invasive species management strategies. Future research endeavors should prioritize the refinement and validation of predictive models, the inclusion of additional environmental variables, and the integration of spatiotemporal dynamics to enhance the accuracy and applicability of habitat suitability assessments. Continued monitoring efforts and collaborative initiatives are imperative for addressing the ongoing challenges posed by biological invasions and safeguarding the ecological integrity of the Mediterranean ecosystem. The possibility that *C. sapidus* and *P. segnis* may coexist in certain areas of the Mediterranean is made plausible not only by the environmental conditions of the entire basin and their evolution but also by the ecology of the two species. Along the Atlantic coast of America, *C. sapidus* has been observed competing with the lady crab, *Ovalipes ocellatus* (Herbst, 1799), and the Atlantic rock crab, *Cancer irroratus* (Say, 1817), at the mouths of several rivers (Stehlik *et al.*, 2004). Dietary overlap has been identified with *Callinectes similis* (Williams, 1966) and *Callinectes ornatus* (Ordway, 1863). In general, the genus *Callinectes* is particularly competitive and aggressive (Ben Abdallah-Ben Hadj Hamida *et al.*, 2019). The future coexistence of *C. sapidus* and *P. segnis* in certain areas of the Mediterranean could result in significant ecological interactions. Given the competitive nature of *C. sapidus*, known for its aggressive behavior and dietary overlap with other species, it is likely that both species will compete for similar resources. Both species are carnivores and feed on a wide variety of prey items

(Mancinelli *et al.*, 2017; Hamida *et al.*, 2019). Moreover, the introduction of these crabs might affect the local biodiversity and ecosystem dynamics, potentially leading to unforeseen consequences for the marine environment. To fully understand the implications of their coexistence, comprehensive studies are necessary, focusing on their ecological roles, competition mechanisms, and potential impacts on native species and habitats in the Mediterranean.

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References

- Aslan, H., Polito, M.J., 2021. Trophic ecology of the Atlantic blue crab *Callinectes sapidus* as an invasive non-native species in the Aegean Sea. *Biological Invasions*, 23 (7), 2289-2304.
- Bargain, A., Marchese, F., Savini, A., Taviani, M., Fabri, M.-C., 2017. Santa Maria di Leuca province (Mediterranean Sea): identification of suitable mounds for coldwater coral settlement using geomorphometric proxies and maxent methods. *Frontiers in Marine Science*, 4, 338.
- Ben Abdallah-Ben Hadj Hamida, O., Ben Hadj Hamida, N., Ammar, R., Chaouch, H., Missaoui, H., 2019. Feeding habits of the swimming blue crab *Portunus segnis* (Forskål, 1775) (Brachyura: Portunidae) in the Mediterranean. *Journal of the Marine Biological Association of the United Kingdom*, 99 (6), 1343-1351.
- Castriota, L., Falautano, M., Maggio, T., Perzia, P., 2022. The

- blue swimming crab *Portunus segnis* in the Mediterranean Sea: invasion paths, impacts and management measures. *Biology*, 11 (10), 1473.
- Criales, M.M., Chérubin, L., Gandy, R., Garavelli, L., Ali Ghannami, M. *et al.*, 2019. Blue crab larval dispersal highlights population connectivity and implications for fishery management. *Marine Ecology Progress Series*, 625, 53-70.
- Deidun, A., Galdies, J., Marrone, A., Sciberras, A., Zava, B. *et al.*, 2022. The first confirmed record of the Atlantic blue crab *Callinectes sapidus* Rathbun, 1896 (Decapoda, Brachyura) from Maltese waters. *BioInvasions Records*, 11 (1), 238-243.
- Dickinson, G., Rittschof, D., Latanich, C., 2006. Spawning biology of the blue crab, *Callinectes sapidus*, in North Carolina. *Bulletin of Marine Science*, 79 (2), 273-285.
- Fox, H.M., 1924. The migration of a Red Sea crab through the Suez Canal. *Nature*, 113 (2846), 714-715.
- Galil, B.S., 2011. The alien crustaceans in the Mediterranean Sea: an historical review. *In the wrong place-alien marine Crustaceans: distribution, biology and impacts*, 377-401.
- Giordani Soika, A., 1951. Il *Neptunus pelagicus* (L.) nell'Alto Adriatico. *Natura*, 42 (1-2), 18-20.
- Giraldes, B.W., Al-Maslamani, I., Al-Ashwel, A., Chatting, M., Smyth, D., 2016. Basic assessment of *Portunus segnis* (Forskål, 1775). A baseline for stock management in the Western Arabian Gulf. *Egyptian Journal of Aquatic Research*, 42 (1), 111-119.
- Hadj Hamida, O. B. A. B., Hadj Hamida, N. B., Chaouch, H., Nafkha, B., Ben Ali *et al.*, 2022. Reproductive biology of the blue swimming crab *Portunus segnis* (Forskål, 1775) (Brachyura: Portunidae) in the Gulf of Gabes (southeastern Tunisia, central Mediterranean Sea). *African Journal of Marine Science*, 44 (1), 11-20.
- Harley, C.D., Hughes, A.R., Hultgren, K.M., Miner, B.G., Sorte, C.J. *et al.*, 2006. The impacts of climate change in coastal marine systems. *Ecology letters*, 9 (2), 228-241.
- Hines, A.H., 2007. Ecology of juvenile and adult blue crabs. Biology of the blue crab. *Bulletin of Marine Science*, 72 (2), 423-433, 2003.
- Kampouris, T.E., Porter, J.S., Sanderson, W.G., 2019. *Callinectes sapidus* Rathbun, 1896 (Brachyura: Portunidae): an assessment on its diet and foraging behaviour, Thermaikos Gulf, NW Aegean Sea, Greece: evidence for ecological and economic impacts. *Crustacean Research*, 48, 23-37.
- Katsanevakis, S., Poursanidis, D., Hoffman, R., Rizgalla, J., Rothman, S.B. *et al.*, 2020. Unpublished Mediterranean records of marine alien and cryptogenic species. *BioInvasions Records*, 9 (2), 165-182.
- Li, S., Wang, Z., Zhu, Z., Tao, Y., Xiang, J., 2023. Predicting the potential suitable distribution area of *Emeia pseudosauteri* in Zhejiang Province based on the MaxEnt model. *Scientific Reports*, 13 (1), 1806.
- Liu, C., Newell, G., White, M., 2016. On the selection of thresholds for predicting species occurrence with presence-only data. *Ecology and Evolution*, 6 (1), 337-348.
- Mancinelli, G., Bardelli, R., Vizzini, S., 2022. Functional response and prey preference of the Atlantic blue crab *Callinectes sapidus* from a recently established population in a coastal Mediterranean lake. *Aquatic Invasions*, 17, 104-116.
- Mancinelli, G., Bardelli, R., Zenetos, A., 2021. A global occurrence database of the Atlantic blue crab *Callinectes sapidus*. *Scientific data*, 8 (1), 111.
- Mancinelli, G., Glamuzina, B., Petrić, M., Carrozzo, L., Glamuzina, L. *et al.*, 2016. The trophic position of the Atlantic blue crab *Callinectes sapidus* Rathbun 1896 in the food web of Parila Lagoon (South Eastern Adriatic, Croatia): a first assessment using stable isotopes. *Mediterranean Marine Science*, 17 (3), 634-643.
- Mancinelli, G., Chainho, P., Cilenti, L., Falco, S., Kapiris, K. *et al.*, 2017. The Atlantic blue crab *Callinectes sapidus* in southern European coastal waters: Distribution, impact and prospective invasion management strategies. *Marine pollution bulletin*, 119 (1), 5-11.
- Marchessaux, G., Bosch-Belmar, M., Cilenti, L., Lago, N., Mangano, M.C. *et al.*, 2022. The invasive blue crab *Callinectes sapidus* thermal response: Predicting metabolic suitability maps under future warming Mediterranean scenarios. *Frontiers in Marine Science*, 9, 1055404.
- Marchessaux, G., Chevalier, C., Mangano, M. C., Sarà, G., 2023. Larval connectivity of the invasive blue crabs *Callinectes sapidus* and *Portunus segnis* in the Mediterranean Sea: A step toward improved cross border management. *Marine Pollution Bulletin*, 194, 115272.
- Marchessaux, G., Ghanem, R., Chaffai, A., Bahri, W.R., Marsiglia, N. *et al.*, 2024. The use of thermal performance analysis to improve conservation management: The case of the invasive Red Sea swimming blue crab *Portunus segnis*. *Global Ecology and Conservation*, 54, e03071.
- Millikin M.R., Williams A.B., 1984. Synopsis of Biological Data on the Blue Crab, *Callinectes sapidus* Rathbun. *FAO Fisheries Synopsis*, 138, 32-39.
- Nehring, S., 2011. Invasion history and success of the American blue crab *Callinectes sapidus* in European and adjacent waters. In: *In the wrong place-alien marine crustaceans: distribution, biology and impacts* (pp. 607-624). Dordrecht: Springer Netherlands.
- Palummo, V., Milisenda, G., Canese, S., Salvati, E., Pica, D. *et al.*, 2023. Effect of environmental and anthropogenic factors on the distribution and co-occurrence of cold-water corals. *Frontiers in Marine Science*, 10, 1272066.
- Pecl, G.T., Araújo, M.B., Bell, J.D., Blanchard, J., Bonebrake, T. *et al.*, 2017. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, 355 (6332), eaai9214.
- Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190 (3-4), 231-259.
- Phillips, S.J., Dudík, M., 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography* 31 (2), 161-175.
- Pinsky, M. L., Selden, R. L., Kitchel, Z. J., 2020. Climate-driven shifts in marine species ranges: scaling from organisms to communities. *Annual review of marine science*, 12 (1), 153-179.
- Prado, P., Baeta, M., Mestre, E., Solis, M.A., Sanhauja, I. *et al.* 2024. Trophic role and predatory interactions between the blue crab, *Callinectes sapidus*, and native species in open waters of the Ebro Delta. *Estuarine Coastal and Shelf Science*, 298, 108638.
- Santojanni, F.B., Miner, H., Hain, H., Sutton, G., 2023. The

- Impact of Climate Change on Biodiversity in Coastal Ecosystems. *Jurnal Ilmu Pendidikan dan Humaniora*, 12 (3), 167-182.
- Shaiek, M., El Zrelli, R., Crocetta, F., Mansour, L., Rabaoui, L., 2021. On the occurrence of three exotic decapods, *Callinectes sapidus* (Portunidae), *Portunus segnis* (Portunidae), and *Trachysalambria palaestinensis* (Penaecidae), in northern Tunisia, with updates on the distribution of the two invasive portunids in the Mediterranean Sea. *BioInvasions Records*, 10 (1), 158-169.
- Streftaris, N., Zenetos, A., 2006. Alien marine species in the Mediterranean-the 100 'Worst Invasives' and their impact. *Mediterranean Marine Science*, 7 (1), 87-118.
- Vivas, M., Garcia-Rodriguez, E., Munoz-Vera, A., Barcala, E., Guijarro-Garcia, E., 2025. Effect of the Invasive Blue Crab (*Callinectes sapidus* Rathbun, 1896) in a Protected Coastal Lagoon. *Estuaries and Coasts*, 48 (1), 1-13.
- Zenetos, A., Tsiamis, K., Galanidi, M., Carvalho, N., Bartilotti, C., *et al.*, 2022. Status and Trends in the Rate of Introduction of Marine Non-Indigenous Species in European Seas. *Diversity*, 14 (12), 1077.

Supplementary Data

The following supplementary information is available online for the article:

Table S1. References of *Callinectes sapidus* and *Portunus segnis* occurrences in the Mediterranean Sea.