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# Larval connectivity of the invasive blue crabs *Callinectes sapidus* and *Portunus segnis* in the Mediterranean Sea: A step toward improved cross border management

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## ABSTRACT

The two invasive blue crabs, *Callinectes sapidus* and *Portunus segnis* have spread rapidly in the Mediterranean and no data exists on the connectivity of populations. Determining the source and recruitment areas is crucial to prioritize where population control measures should be put into immediate action. We simulated the dispersal of blue crab larvae using a Lagrangian model coupled at high resolution to estimate the potential connectivity of blue crab populations over a 3-year period. Our results reveal that the main areas at risk are the Spanish, French, Italian Tyrrhenian and Sardinian coasts for *Callinectes sapidus* with high populations connectivity. Tunisia and Egypt represent high auto recruitment zones for *Portunus segnis* restricted to the central and western basins. This study provides an overview of the connectivity between populations and will help define priority areas that require the urgent implementation of management measures.

## 1. Introduction

Understanding connectivity and the processes it involves can help us to make predictions on the likelihood Non-Indigenous Species (NIS) is an important point to explore to define international management plan of these species at diverse spatial scales: global, regional and local level (Cowen et al., 2000, 2006). In the case of NIS, studying larval planktonic exchange and the consequent movement between populations is crucial to determine the connections and the risk associated with larval dispersal of NIS. Yet the underlying mechanisms of larval exchange and movement between populations remain poorly understood for most species. Understanding these underlying mechanisms is a key focus of modern ecology (Cowen and Sponaugle, 2009). Dispersal, usually termed ‘connectivity’, is one of the most important ecological processes of larval exchange between distinct populations, and when assessing its ecological role in shaping local biodiversity (Cowen and Sponaugle, 2009; Wood et al., 2014). High connectivity can enhance a species resilience to exploitation (Jones et al., 2015; Marchessaux et al., 2020; Strathmann et al., 2002); climate change (Peterson, 2002); and genetic

diversity (Garant et al., 2007; Reynes et al., 2021; Thibaut et al., 2016). However, studying larval dispersal in the field can be a major challenge (Kinlan and Gaines, 2003). This is because small planktonic larvae (often <1 mm) incur high rates of natural mortality and sampling methods to identify their migrations have some limitations. Direct estimates of larval connectivity rely on mark-recapture of artificially marked larvae or by analyzing geochemical signatures in calcified structures (Thorrold et al., 2002). However, the results yielded are not generalizable due to the reduced sampling effort. For some taxa these methods are difficult or impossible to apply, for example crustacean larvae, do not contain calcified parts and frequently molt (Anger, 2001). In these cases indirect estimates of connectivity using genetic markers often remain too expensive (Hedgecock et al., 2007). There is therefore a clear need to adopt affordable, feasible, and effective solutions to understand larval dispersal.

The increased power of computer-based systems and the availability of high-resolution hydrodynamic datasets that allow the implementation of Lagrangian particle tracking models, means that, when applied at the correct biogeographic scale, effective estimates of the potential

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connectivity among distant populations. Lagrangian particle tracking models allow us to simulate the movement of individual particles, that in this context represent “larvae”, through hydrodynamic current fields. These models are being used in numerous studies with varied applications including: stock management of commercially valuable species (Criales et al., 2019), creation of marine protected areas (Hinrichsen et al., 2009), conservation of protected species (Reynes et al., 2021), and to research invasive species (Marchessaux et al., 2020). These models could provide credible and salient knowledge, that proves fruitful when assessing the invasive potential of an alien species. Larval dispersal models therefore provide an optimal tool for determining connections between populations and areas of larval stage retention in Early Detection and Rapid Response (EDRR) programs (Reaser et al., 2020). The early detection of invasive species is one of the first measures to prevent an invasion (Reaser et al., 2020). Surprisingly, these connectivity models are not being extensively applied to biological invasions, even though, in marine ecosystems, species do not have borders and understanding the connections among populations in the same biogeographical area could be crucial to the design and implementation of effective management measures for these species. Identification of source and recruitment areas could be useful to disrupt the connectivity dynamics.

For species such as the two invasive blue crabs in the Mediterranean, *Callinectes sapidus* (Rathbun, 1896) and *Portunus segnis* (Forskål, 1775), collecting such information is critical for its management. Native to the American coast and Indo-Pacific Ocean, respectively, these blue crab species have both recently shown a large expansion in the Mediterranean Sea (Mancinelli et al., 2021; Marchessaux et al., 2022; Shaiek et al., 2021). Their biological traits, such as: early maturity, rapid growth rates, opportunist diet, high reproductive rates, generalist habitat use, long-range larval dispersal, and effective physical and aggressive behavior (Castriota et al., 2022; Mancinelli et al., 2017), facilitate their invasiveness and boost their successful spread across regions (Mancinelli et al., 2021; Shaiek et al., 2021). Despite local observations of competitive interactions with native species (Gennaio et al., 2006; Mancinelli et al., 2013) and impacts on the artisanal fishery (Fuentes et al., 2019; Kampouris et al., 2019; Marchessaux et al., 2023), the ecological and economic consequences of these two blue crabs remains theoretical (Mancinelli et al., 2017; Suaria et al., 2017).

The implementation of effective cross-border management measures to limit the impacts of blue crabs in the Mediterranean basin is urgently needed. Several authors have proposed the development of specific blue crab fisheries to be the only possible effective management measure to control populations (Ennouri et al., 2021). However, these strategies remain localized at the regional level (Ayas and Ozogul, 2011; Ennouri et al., 2021; Kevrekidis et al., 2013). Therefore, identifying the source and recruitment areas for these two species would allow for prioritization of the areas where population control measures would be most effective. Creating population control in source areas (capture of vulnerable life stages such as ovigerous females for example) would limit the arrival of new individuals in recruitment areas (Barbour et al., 2011; Hussner et al., 2017; Ramula et al., 2008). Thus, this type of measure could be an effective strategy for the cross-border management of these invasive blue crabs. We therefore simulated the dispersal of blue crab larvae using a Lagrangian particle tracking model coupled with a high-resolution hydrodynamic model to estimate the potential connectivity of blue crab species *C. sapidus* and *P. segnis* at the Mediterranean scale. Our results provide an overview of the connectivity between populations and can be used to help define priority areas where management measures should focus and be rapidly implemented.

## 2. Materials and methods

The Mediterranean Sea, a semi-enclosed basin with its own physical circulation and ecological functioning, is under significant human pressure (de Madron et al., 2011). It represents a natural laboratory for

connectivity studies as it is subject to various pressures from invasive species such as the blue crabs *C. sapidus* and *P. segnis* (Mancinelli et al., 2021; Shaiek et al., 2021). We partitioned the Mediterranean sea surface into hydrodynamic provinces, i.e., a set of oceanic sub-regions in which larvae/particles are much more likely to disperse efficiently between, rather than, among themselves on a given time scale (Rossi et al., 2014).

The Lagrangian approach gives a natural perspective that characterizes the potential transport patterns affecting free-swimming larvae (Dell’Amico et al., 2012; Rossi et al., 2014). Presence data were extracted from Mancinelli et al. (2021) for *C. sapidus*, and from Shaiek et al. (2021) for *P. segnis*, and projected on to QGIS software (version 3.10) to determine the release or source areas for the larval stages of the two species. Given the strong capacity of these species to move and occupy large geographical areas, and the lack of information on the precise spawning areas, the full species distribution range was used. But it was not appropriate to use all the points where blue crabs have been recorded at the Mediterranean scale, as some have high geographic proximity (i.e., several points present within a radius of 5 km). A 10 km<sup>2</sup> grid was projected on to QGIS software and each mesh containing points of presence were kept as source areas within our study (release areas of 10 km<sup>2</sup>). In total, 125 source areas were determined for *C. sapidus* and 40 source areas for *P. segnis* (Fig. 1) including known spawning areas and areas where populations are supposed to reproduce (Cilenti et al., 2015; Gaber et al., 2021; Safaie et al., 2013; Sumer et al., 2013). The recruitment areas were defined according to the distribution of the 27 fisheries subareas from the FAO in the Mediterranean Sea (FAO, 2013). These subareas are often used in management, and are generally specific to each country, making them an advantageous point of reference. Our study objective is to present an useful tool for managers to show how the existing populations of blue crabs are currently connected. The study was restricted to the coastline with a maximum bathymetry of 100 m, which corresponds to the maximum depth for blue crabs (Hines et al., 1995; Safaie et al., 2013) (Fig. 1).

Hydrodynamic data were extracted from the Copernicus Marine Project database (<https://marine.copernicus.eu>, MEDSEA\_MULTITYEAR\_PHY\_006\_004) with a spatial resolution grid of 1/24° (~4.4 km) and 141 vertical levels with higher resolution at the surface. Particle tracking simulations to study blue crab larval transport were performed using the free Java tool Ichthyop/Roms3D (Version 3.3.3) (<http://www.ichthyop.org/>). Ichthyop is an individual-based Lagrangian particle tracking model that can be used to study biological and physical factors that may influence fish eggs and larvae (Lett et al., 2008). The Ichthyop software has been used extensively in a number of studies on ichthyoplankton dynamics (Deschepper et al., 2020; Martins et al., 2020), population genetic studies (Reynes et al., 2021), and invasive species studies (Marchessaux et al., 2020). Ichthyop simulates Lagrangian particle transport using velocity fields from ocean models such as ROMS (Regional Ocean Modeling System). The software uses a standard 4th order Runge-Kutta equation to implement differentiation of the advection/diffusion equations. Oceanographic connectivity was assessed at the Mediterranean scale. We expected oceanographic connectivity to be variable depending on the year of simulation, as such, Lagrangian modeling was performed over three years using ocean circulation models from 2017 to 2019.

There are very few data available regarding the reproduction periods for both blue crab species in the Mediterranean Sea. Ovigerous females of *C. sapidus* were observed in Trapani (Sicily, Italy) between August and September 2021-2022 (pers. obs.). For *C. sapidus* and *P. segnis*, the breeding periods have generally been observed between April and September in the Mediterranean (Cilenti et al., 2015; Gaber et al., 2021; Safaie et al., 2013; Sumer et al., 2013). In contrast, data on the length of the life cycle of blue crabs is very sparse, with some studies indicating a growth time of 27 days (Zmora et al., 2005) and others 47 days (Costlow and Bookhout, 1959), dependent to temperature with optimum conditions occurring at 25–30 °C for *Portunus armatus* (Hewitt et al., 2022) and food availability (Schilling et al., 2022; Steele and Neuheimer,

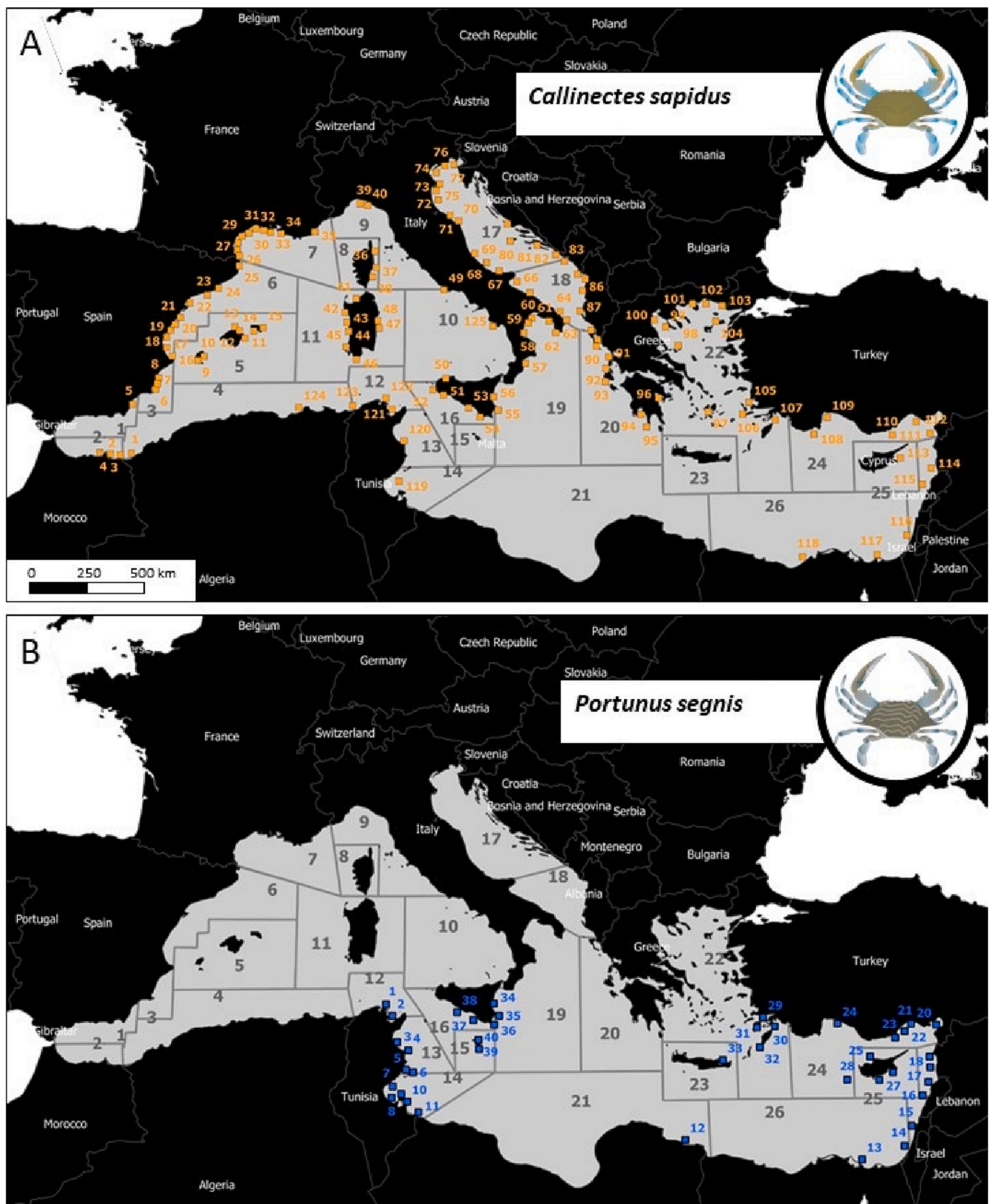


Fig. 1. Distribution of the release zones for *Callinectes sapidus* (n = 125) and *Portunus segnis* (n = 40) in the Mediterranean Sea and, the FAO fisheries areas (n = 27, numbers in gray) defined as recruitment zones.



2022). Based on the data available in the literature, 3 growth rates scenarios were simulated in this study: (1) a short life cycle of 30 days, (2) a medium life cycle of 40 days, and (3) a slow life cycle of 50 days. For each species, a total of 100,000 particles were released every day between April, 1st and September 30th in 2017, 2018 and 2019 for each source area. Particles were evenly distributed between 10 m and 40 m deep simulating egg release events by female blue crabs. For both species, the same larval behavior was used: each particle was passively advected with a vertical migration behavior (30–40 m during the night and 0–1 m during the day; Ospina-Alvarez et al., 2018; and a buoyancy at  $0.9 \text{ g cm}^{-3}$ ; Epifanio, 1995). A total of 549 simulations for each scenario (30 days, 40 days and 50 days) were performed. The computational time step was set to 400 s and the particle position was recorded in the NetCDF output files every 24 h.

Here, we define “source” areas as corresponding to the particle release areas (blue crab populations), and the “recruitment” areas which correspond to areas receiving particles from source areas. We will define the “Index of Connectivity (IC)” as the value of connectivity between 2 release areas (between 0 and 1). The Pairwise IC was calculated as  $IC_{ij} = \frac{N_{i-j}}{N_i}$  where  $IC_{ij}$  is the probability of connectivity,  $N_i$  is the total number of released particles from site  $i$  and  $N_{i-j}$  the total number of released particles from site  $i$  arriving in site  $j$  after 30 days, 40 days and 50 days of transport time. The IC was calculated between the release and the

recruitment areas. These probabilities were computed in MATLAB (version R2021a) and the connectivity matrix was calculated for each day or release and for each growth scenario. Finally, the probabilities of connectivity between all pairs of sites were averaged over 3 years of simulation to obtain the mean connectivity matrix and the mean time of transport for each growth scenario. To create the connectivity maps showing the connections (Index of connectivity  $< 0.8$  excluding self-recruitment) between each blue crab population (*Callinectes sapidus* and *Portunus segnis* respectively) at the Mediterranean Sea scale, a shortest-path analysis was performed using the script “seaConnect—spatialGraph” performed by (Boulanger et al., 2020) using R Studio (version 2021.09.0).

To propose a prioritization of invasion risks related to the connectivity of blue crab populations at the Mediterranean scale, we defined the invasion risk 3 scale levels from the local to the global scale based on the index of connectivity (IC). The first level corresponds to the scale of a crab population (source areas) where we calculate the number of recruitment areas reached and the mean connectivity for each source area. The second level corresponds to the calculation of the mean connectivity for each source area. The last, and most important is at the proportion of the self-recruitment areas in each of the FAO districts (recruitment areas) and the frequency of distance covered (in km) by particles. The results obtained were mapped using QGIS software (version 3.16.3). The mean ( $\pm$  standard error) distance covered by

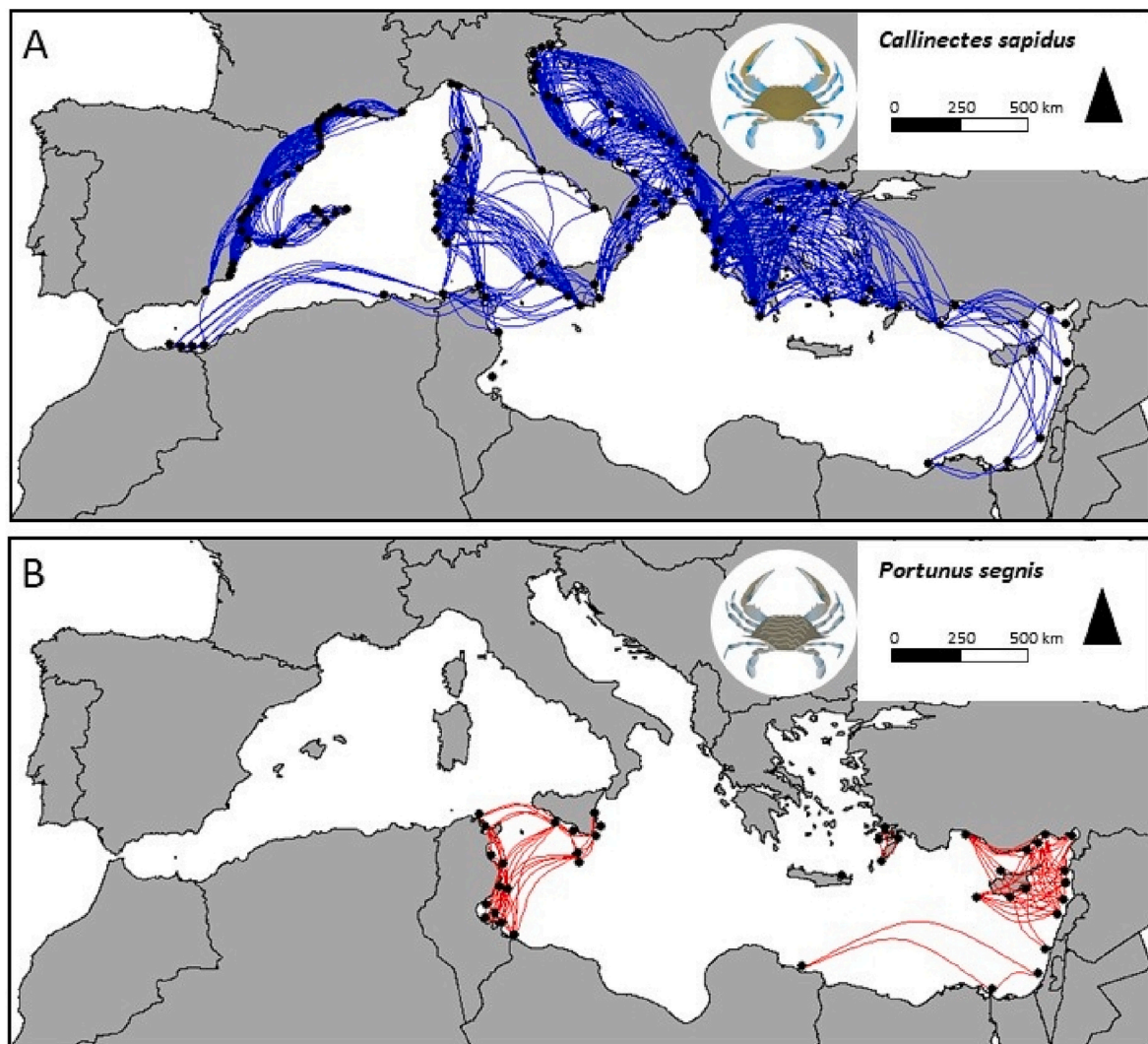


Fig. 2. Network of larval exchanges between the populations for (A) *Callinectes sapidus* and (B) *Portunus segnis* in the Mediterranean Sea (average on the 3 durations scenarios, 549 simulations, strict self-recruitment excluded), the colored curved lines represent the exchange of particles/larvae between the release zones.

particles was calculated for the 549 simulations and plotted using R Studio (version 2021.09.0).

### 3. Results

Particle dispersal dynamics for *Callinectes sapidus* showed little variability regardless of the simulation time (Fig. 2A, Supplementary Figs. 1–2). For the remainder of the study, we will present the results of the 40-day scenario, the intermediate larval growth time. The Moroccan populations were connected with Southern Spain (Table 1A). The southern Spanish populations exported larvae to the northern Spanish coasts. Northern Spanish populations exported larvae to France where a self-recruitment was observed (Table 1A). A self-recruitment in *C. sapidus* larvae was observed for the main islands (e.g., the Balearic Islands, Corsica, Sardinia and Sicily) in the western Mediterranean basin. A small proportion of the particles were exported from the islands: a connection between Corsica and Sardinia island; and between Sardinia island and Tunisian island (e.g. Kerkennah islands) populations was identified. In Tunisia 50 % of the larvae was auto-recruited (Table 1A) but a small part was exported to Sicily. In the Adriatic Sea, the populations of the west and east coasts were connected to each other with >70 % of the populations having an IC > 0.8, and no export of larvae was observed outside. Finally, in the western Mediterranean basin, the Aegean Sea populations were auto recruited, and the southern Turkish populations were connected with the Cypriot populations (Table 1A).

*Portunus segnis* showed little dispersion and variability regardless of the simulation time (Fig. 2B, Supplementary Figs. 3–4). Larvae from a given source area in the Mediterranean remained contained in that same area. For example, the source populations from the central basin were retained in this same area with a high index of connectivity (IC > 0.8) (Table 1B). It appeared that all the populations present in Tunisia were auto-recruited. Moreover, a low index of connectivity was observed between Tunisia and Sicily for larvae coming from Tunisia. The central basin areas had high connectivity. In the Eastern Mediterranean, the index of connectivity between source and recruitment areas was low (Table 1B, Fig. 2B). Only Egypt and Turkey appeared to be source areas for the Eastern Mediterranean (Table 1B).

At the local scale the most connected populations and the number of recruitment areas reached could give important information about the populations that disperse the most and reach multiple recruitment areas (Fig. 3). The populations of greatest concern in terms of connectivity for *Callinectes sapidus* in the western basin were the populations present on the Spanish coast (IC = 1) (Fig. 3A) but were only connected with one

recruitment area. The populations on the French and Sardinian coasts showed ICs between 0.1 and 0.4, dispersing their larvae to several recruitment areas (between 2 and 4 areas). In the central part of the Mediterranean, the Tunisian populations were the most connected (IC = 1) but only with 1 area, in contrast to the Sicilian populations which connected with 2 recruitment areas (IC between 0.2 and 0.4). Finally, it appeared that almost all the populations of the Adriatic Sea showed an IC > 0.5. The Northern Adriatic populations were only connected with 1 recruitment area unlike the southern populations which were connected with 1 or 2 recruitment areas. For *P. segnis*, almost all the Tunisian populations had an IC between 0.8 and 1 but were connected with 1 recruitment area (Fig. 3B). The Sicilian populations were connected with 1 and/or 3 recruitment areas, but with an average index of connectivity of  $0.36 \pm 0.02$  (Fig. 3B). In the Eastern Mediterranean basin, only the populations of Egypt and South-East Turkey showed high IC.

Characterizing the average connectivity of recruitment areas allow to classify the areas most at risk of invasion (index of connectivity, IC > 0.4) at the Mediterranean scale (Fig. 3A). For *C. sapidus*, the main areas at risk in the Western Mediterranean were the Spanish coast (IC = 0.5) and the Italian Tyrrhenian coast (IC = 0.4) and Sardinia (IC = 0.4). In the central Mediterranean, the Tunisian east coast was the area most at risk (IC = 1). Also, the Adriatic Sea as a whole was a recruitment area at high risk of invasion with an IC between 0.5 and 0.8. Finally, in the Eastern Mediterranean, the Aegean Sea was an area at high risk of invasion (IC = 0.5). As *P. segnis* was restricted to the central and eastern Mediterranean areas, the risk of invasion in the western part is zero (Fig. 3B). Like *C. sapidus*, the eastern Tunisian coasts were particularly at risk (IC > 0.7) and the risk of invasion extended from Tunisia to the Egyptian coasts which constituted the second recruitment area at risk of invasion (IC = 0.6).

Finally, on a basin scale, the index of connectivity of self-recruitment for the release areas presented in each recruitment area was considered (Fig. 4). In the Western Mediterranean, the areas of greatest concern for *C. sapidus* were Spanish coasts and southern Italian coasts which had a high proportion of release areas (IC > 0.5) with an IC > 0.4 (Fig. 4A). In the Central basin, the Tunisian coasts were the areas of greatest concern in the Mediterranean, with 100 % of the release areas having an IC = 1, as well as the areas of the Adriatic Sea, which occupied >50 % of the areas with an IC > 0.4. In the eastern basin, only a few areas were important for connectivity, except for the Aegean Sea, which included 40 % of the release areas with an IC > 0.4. Concerning *P. segnis*, few areas were of concern but had a high proportion of release areas with an IC between 0.8 and 1 (Fig. 4B). This was the case for the Tunisian,

**Table 1**

Resume of the main important results on the connectivity for (A) *Callinectes sapidus* and (B) *Portunus segnis*.

Country of release	Release areas ID	Country of recruitment	Recruitment areas ID	Index of connectivity (IC) value
<b>A   <i>Callinectes sapidus</i></b>				
Morocco	1–4	Spain (South)	2,3	0.2
Spain (South)	5–8	Spain (North)	6	0.8
Spain (Balearic)	5	Spain (Balearic)	5	0.3
Spain (North)	17–25	France	7	0.3
France	26–35	France	7	0.4
		Spain	6	0.2
France (Corsica)	36–38	France (Corsica)	8	0.2
France (Corsica)	36–38	Sardinia	11	0.2
Sardinia	41–48	Sardinia	11	0.6
Sardinia	41–48	Tunisia	12–13	0.2
Tunisia	119–123	Tunisia	12–14	0.8
Tunisia	119–123	Italy (Sicily)	16	0.3
Aegean Sea	95–107	Aegean Sea	22	0.6
Turkey	100–101	Cyprus	25–26	0.8
<b>B   <i>Portunus segnis</i></b>				
Tunisia	1–11	Tunisia	12–14	0.7
Tunisia	1–11	Italy (Sicily)	16	0.2
Egypt	13	Egypt	26	1
Turkey	29–33	Lebanon-Israel	22	0.3

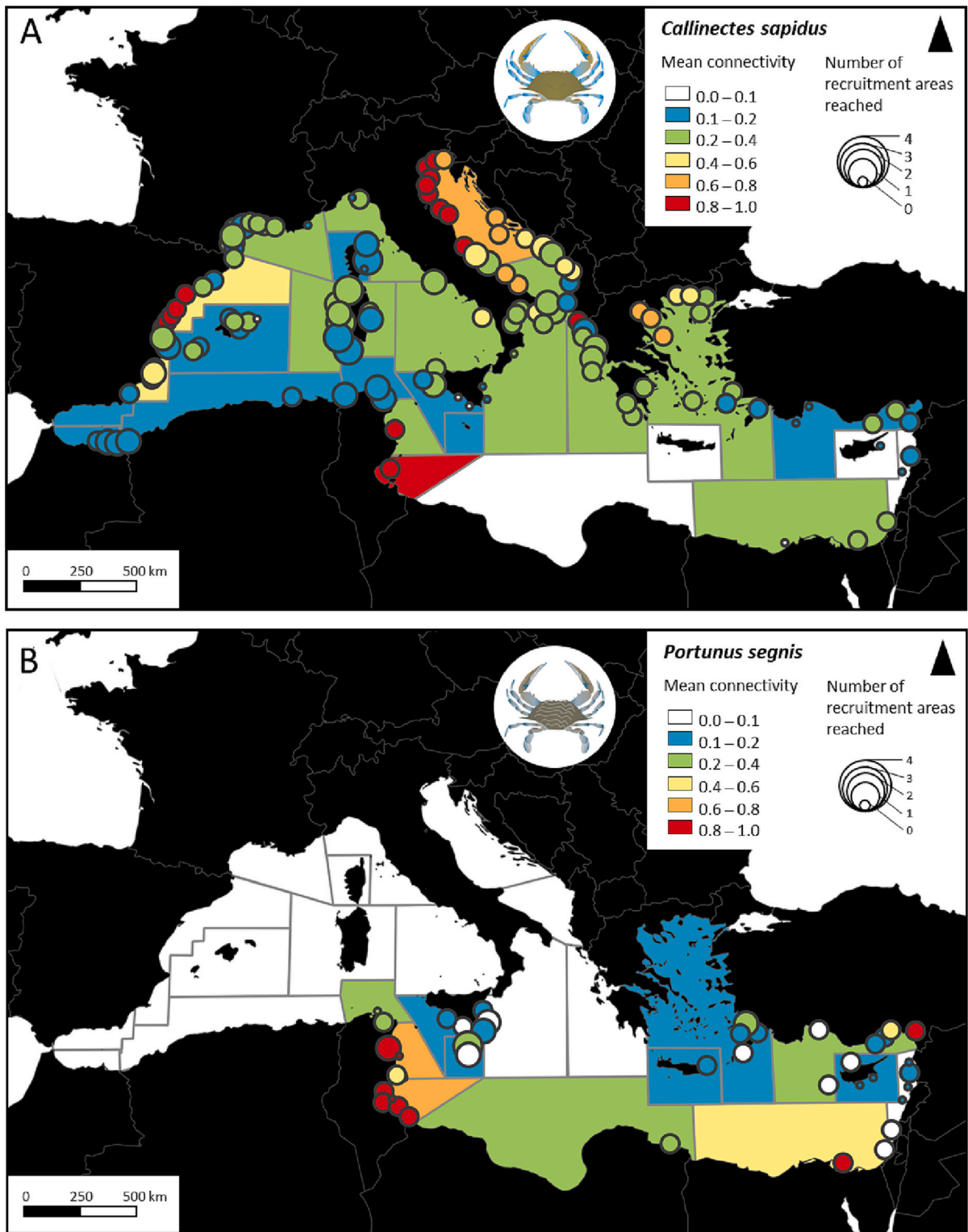


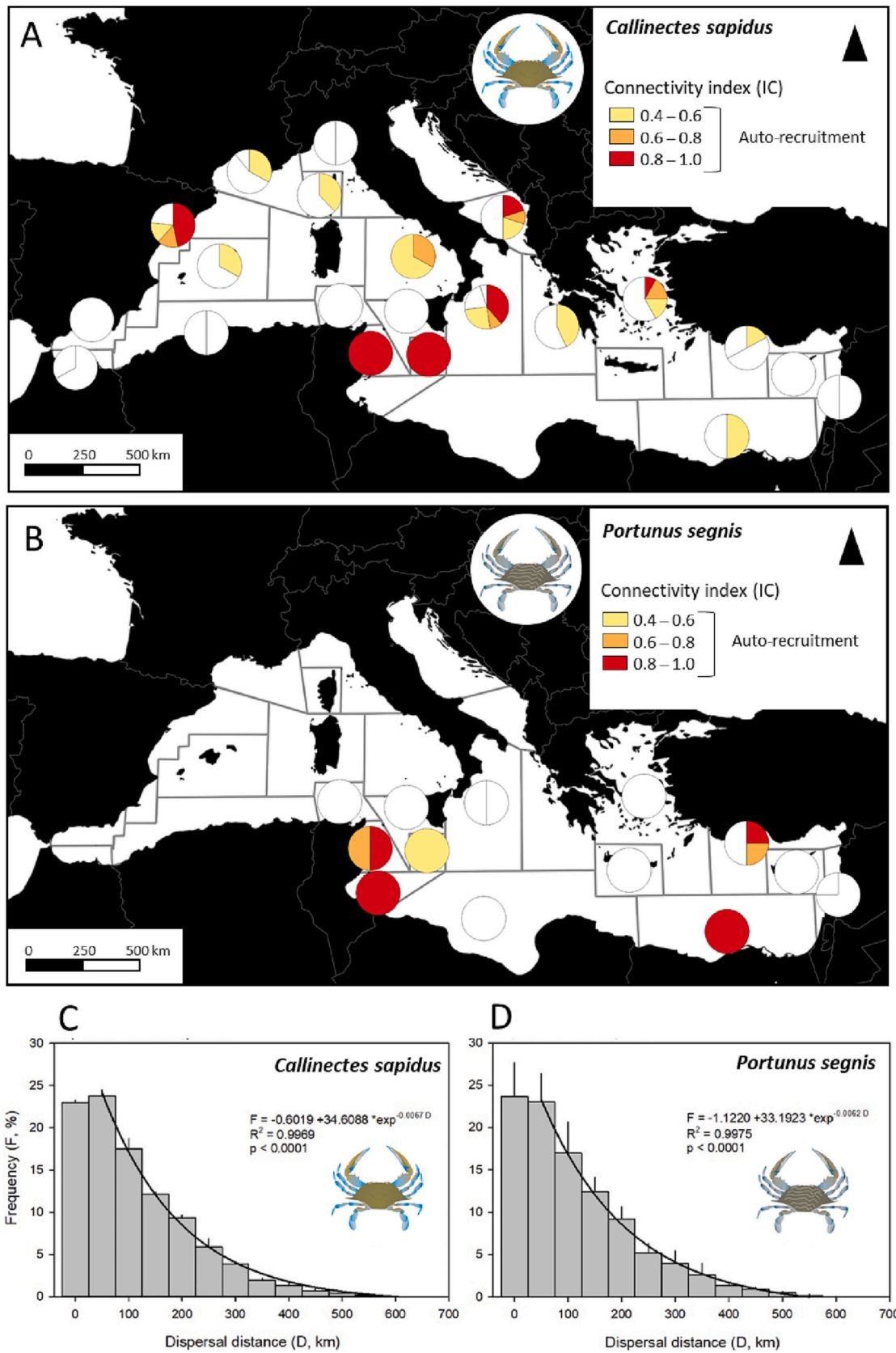
Fig. 3. Distribution of the average connectivity and the number of recruitment areas reached of the different recruitment populations, and mean connectivity index of recruitment areas, for (A) *Callinectes sapidus* and, (B) *Portunus segnis* in the Mediterranean. The color represents the connectivity index, and the circles' size the number of recruitment areas reached.

Turkish and Egyptian coasts which were the main source areas in the Mediterranean for this species. For both species the distance covered by the particles ranged from 0 km to 600 km and decreased exponentially (Fig. 4C & D). The highest frequencies were observed for distances <100 km (64.2 % for *C. sapidus* and 63.6 % for *P. segnis*) illustrating a recruitment close to the release areas.

#### 4. Discussion

The high-resolution, multi-scale biophysical model, based on spatial population distribution data and habitat colonization at the Mediterranean scale, developed in this study provides much needed insight to support successful cross-border management of Non-Indigenous Species





**Fig. 4.** Proportion of self-recruitment (or auto-recruitment; connectivity index IC > 0.4) for the release areas for (A) *Callinectes sapidus*, and (B) *Portunus segnis*, and mean ( $\pm$  SD) distance covered by particles (average on the 549 simulations) for (C) *Callinectes sapidus*, and (D) *Portunus segnis*.



(NIS). This was the first study on the connectivity of invasive blue crab species in the Mediterranean Sea. Having applied our models to the invasive blue crabs, *Callinectes sapidus* and *Portunus segnis*, we have improved the knowledge base on the complexity of population dynamics and larval connectivity which will help in the design and implementation of effective management strategies (Botsford et al., 2009; Cowen et al., 2006; Criales et al., 2019). Specifically, our results (i) suggest that there is a high degree of local retention mainly in the western and central basins for *C. sapidus* and in the central basin for *P. segnis* (Fig. 4); and (ii) identified large-scale connected areas. We showed that dispersal is, in line with the current ecological theories based on functional traits (thermal and salinity tolerance, ingestion rates, growth rates, etc.), life histories (Schoener, 1986), and species-specific processes. This finding was demonstrated by the fact that most *C. sapidus* populations (~99 %) were connected to at least one recruitment area, and about 22 % for *P. segnis*. Larval dispersion did not show significant variability between the 3 years simulated which illustrated the power of the models used. The information yielded here can reinforce and complete the picture for phylogeographical studies currently performed in the Mediterranean Sea (unpublished data, pers. com.). Larval dispersal pathways provide new insights into the connectivity and connectivity mechanisms that facilitate natural populations (Criales et al., 2019). Linking this to population dynamics (i.e., growth, survival, reproduction) could be useful to estimate the impact of dispersal on population demographic structure (Lowe and Allendorf, 2010; Reynes et al., 2021).

Our study provides an initial overview of the connectivity among invasive blue crab populations in the Mediterranean. In our study, there was no impact from the duration of simulations on connectivity. Our results, although highly informative, may be limited by the current gap in knowledge on all the possible biological factors that are able to influence larval connectivity, such as, egg production, larval growth and mortality (Pineda et al., 2007). However, while the biophysical model provided predictions of larval distribution prior to colonization and the potential recruitment, to understand the real success at local level it is necessary to have information on post-colonization processes such as predation and competition that play a role in recruitment success (Criales et al., 2019; Doherty et al., 2004; Hunt and Scheibling, 1997; Reynes et al., 2021). Future studies will need to be conducted, particularly on the temperature-food dependence of blue crab larvae in experimentally measured growth and mortality (Everett et al., 2017; Schilling et al., 2020), which can be included in future connectivity models. Additionally, based on the aforementioned information, future connectivity studies should include pelagic larval duration (PLD) combined with environmental data (e.g., temperature, salinity, food availability) (Shropshire et al., 2022), which is lacking in our study due to the limitation of data available on the both Portunidae specie biology. Also, including studies on adults blue crabs movement and migrations could be a very important information to define the specific zones of larval release by females (Aguilar et al., 2005; Oesterling, 1976).

Nonetheless, the information gathered through our modeling exercise will offer insight when selecting management options for invasive species and will help to ensure all the steps, namely, prevention, eradication and containment are fully addressed with the correct choice of mitigation measures (Packer et al., 2017; Pyšek et al., 2020; Pyšek and Richardson, 2010). Among them, Early Detection and Rapid Response (EDRR) programs (Harvey and Mazzotti, 2019) are one of the best management options to prevent invasive species colonization (Larson et al., 2020; Meyers et al., 2020; Reaser et al., 2020; Xiong et al., 2016). Yet, this measure represents the ultimate phase of the management action and the most expensive (Alvarez and Solís, 2018; Genovesi, 2007; Prior et al., 2018; Simberloff, 2009). The recognized economic value of both blue crabs seems to foster the 'adoption' of a control program, promoting fishing exploitation. This has led to disagreements between citizens and scientists during the implementation of management programs (i.e., control vs eradication) (Crowley et al., 2017; Loss and Marra, 2018). For a species control plan to be effective, it is necessary to

ensure the removal of a sufficient number of individuals at vulnerable life stages to initiate a significant population decline (decrease in population growth and size) (Barbour et al., 2011; Hussner et al., 2017; Ramula et al., 2008). In the Chesapeake Bay (USA), native area of *C. sapidus*, overfishing induced a drastic population decline (Lipcius et al., 2005; Stagg and Whilden, 1997), overfishing the blue crab in the Mediterranean Sea could be an effective management plan. To do this, it is important to know the precise geographic distributional trajectories of the species as well as the factors that support its life cycle, growth and populations' connectivity. Studies based on connectivity validate that tailored local and/or regional management plans offer the best solution to firstly, reduce the ecological costs, and secondly, the economic and social costs that result from a large invasion, such as the one we are seeing with blue crabs in the Mediterranean Sea. Some recent studies also showed that gathering mechanistic based information, akin to that presented here, facilitates the design of tailored temporal and/or spatial management measures of anthropogenic pressures on ecosystems such as NIS invasion or fisheries (e.g. (Mangano et al., 2020)).

Most current management programs are based on long-term and fixed solutions, however in an era of rapid environmental change due to pervasive anthropogenic actions, innovative NIS management plans that are flexible, tailored, and that incorporate adaptive tools and strategies need to be designed and implemented. Model predictions promote more flexible management plans and facilitate more appropriate and specifically tailored monitoring plans (sensu Mangano et al., 2020). Larval connectivity is a key element to study to support the implementation of effective management measures. Using this tool, we are able to prioritize the most at-risk areas that require urgent implementation of management measures (Boschetti et al., 2020; Hidalgo et al., 2017; Marchessaux et al., 2020). In the case of *Callinectes sapidus*, which is widely distributed throughout the Mediterranean, the western basin seems to be the main area of larval production and aggregation. For example, we observed through our modeling that Moroccan populations were connected with Spanish populations, that in turn exchange larvae with the French coast. Following the ideas of speciation and in agreement with some ecological theories (MacArthur, 1955), islands such as the Balearic Islands, Corsica and Sardinia appeared to auto-recruit their own larvae which can explain the presence of populations that have lasted over time (Box et al., 2020; Culurgioni et al., 2020; Mancinelli et al., 2021) and can lead us to hypothesize the possible development of different genetic sub-units with respect to continental populations. Tunisia and Sicily exchanged larvae on both sides of the Strait of Sicily, but in Tunisia the presence of large sustainable populations (Mancinelli et al., 2021) could also be explained by the self-recruitment of larval stages, especially in the Gulf of Gabes. Finally, the semi-enclosed seas such as the Adriatic Sea and the Aegean Sea were auto-recruited and exported little or no larvae to other regions. For *Portunus segnis*, the main area at risk was the central basin. Indeed, the Tunisian populations and Sicily were connected in both directions. Moreover, as for *C. sapidus*, the Tunisian populations were auto-recruited at the larval stage, promoting sustainable populations (Shaiek et al., 2021). In the eastern part of the Mediterranean, the Egyptian populations were auto-recruited and the Lebanese and Turkish populations were connected.

It appears from this study that the Spanish/French coasts, the Strait of Sicily, the Adriatic Sea, and the Aegean Sea should be the priority areas for the design and implementation of specific management measures for *C. sapidus* populations. These areas, which were highly connected, were source areas for larvae on a Mediterranean scale. For *P. segnis*, the Gulf of Gabes, the mouth of the Suez Canal in Egypt and the southern coasts of Turkey were identified as priority areas. Although the Egyptian populations exported few larvae, the mouth of the Suez Canal and the arrival of new individuals could maintain a regular supply of larvae and a higher genetic diversity. The risk areas identified in this study should be prioritized for management. Furthermore, controlling the larval stages seemed to be the most effective measure to control the populations.

In the Mediterranean, there is a serious lack of data on the genetic connectivity of blue crab populations. The range and scale of physical and genetic connections need to be defined more precisely. Once defined, an assessment that integrates immigration and emigration rates across currently defined boundaries can be used to adequately represent population structure and form the basis of a regional blue crab invasion management strategy for the Mediterranean. A comprehensive study of hydrological data, particle movements, genetic datasets (Feng et al., 2017a, 2017b; Reynes et al., 2021) and correction for natural mortality and habitat suitability would also aid in understanding the dynamics involved.

In conclusion, this study is a step toward the identification of broader connectivity of blue crab stocks throughout the Mediterranean biogeographical range and aims to encourage more comprehensive approaches that will elucidate the population dynamics of the two species studied. Taken together, these results challenge the appropriateness of the current state-based assessment structure and highlight the need for cooperative assessment and management of blue crab in Mediterranean waters. Based on our results, our recommendations would be to implement control plans for blue crab populations at local and regional scales in order to disrupt connections between populations at a larger scale. This could be achieved, for example, by intensively fishing gravid females before they release larvae into the sea. Doing this, this method could limit the production of new generations for both blue crab species and decrease in the following years the recruitment and the populations densities.

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## CRedit authorship contribution statement

G.M and C.C. contributed to the conception and design of the study, performed the simulations and the statistical analyses. G.M. wrote the first version of the manuscript. M.C.M. and G.S. conceived the project. M.C.M., C.C. and G.S. contributed to the data analyses and revised the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

## 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.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2023.115272>.

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