Spatial analysis of *Maja squinado* larval dispersal: implications for conservation in a changing Mediterranean Sea

C. Barrier*[1], T. Beneteau[1], M-C Raffalli[1,2], N. Barrier[3], C. Lett[3], V. Pasqualini[1,2], E.D.H. Durieux[1,2]

1 : Université de Corse, UMR CNRS 6134 Sciences pour l'Environnement, Corte, France

2 : Université de Corse, UAR CNRS 3514 Stella Mare, Biguglia, France

3 : MARBEC, Université de Montpellier, CNRS, Ifremer, IRD, Sète, France

Corresponding authors: Céline Barrier (BARRIER_C@univ-corse.fr) and Éric Durieux (durieux_e@univ-corse.fr)

Abstract

The Mediterranean spinous spider crab, *Maja squinado* (Herbst, 1788), plays a pivotal role in Mediterranean fisheries, significantly contributing to local economies and culinary traditions. While stocks have declined in some areas, others continue to support fishing activities despite declines. Understanding the species' demography is crucial for future management. A biophysical model was developed to explore the larval dispersion dynamics of *M. squinado* in the Mediterranean. This model incorporated data on the biology and ecology of the species, including larval duration and spawning habitats. The tool Ichthyop, designed to study ichthyoplankton dynamics, was used for simulations conducted from 2010 to 2020. These simulations were analyzed considering global surface water warming trends. The analysis generated maps illustrating trajectory density, system connectivity, and density and distance over time. Comparisons between scenarios highlighted the impact of environmental variations, identifying the Tunisia-Sardinia-Corsica complex as having strong connectivity, while the Balearic Islands remained isolated due to the crab's short pelagic larval duration (PLD). The study demonstrated the effectiveness of biophysical models in hypothesizing population declines in isolated areas and emphasized the importance of diverse modelling approaches at varying resolutions. Kernel density estimates (KDE) maps revealed interannual changes and temporal shifts in particle density, suggesting that global changes, including surface water warming, should be considered in future simulations to predict dispersal routes and connectivity more effectively in a changing Mediterranean.

Keywords: *Maja squinado*, larval dispersal, Mediterranean Sea, biophysical models, regional connectivity

1. Introduction

The Mediterranean Sea is a biodiversity hotspot, representing 4 to 18% of global marine species (Bianchi & Morri, 2000). This reservoir has been under increasing pressure for several decades due to habitat degradation, marine and atmospheric pollution, invasive species, and climate change. Fishing is a major activity in the Mediterranean Sea, with catches reaching 1.19 million tons in total in 2020. The majority of fisheries are industrial, with an annual catch of 1 million tons. Yet, this activity represents only 17% of the total number of boats, with the remaining 83% engaged in artisanal fishing (FAO, 2020). The lack of regulation of artisanal vessels, illicit fishing practices, the discard of unwanted catch, and the overfishing of fish stocks have collectively led to the overexploitation of marine resources and an irreversible decline in fish stocks (Carlson et al., 2016; Zaimen et al., 2021). Besides, the majority of specific fish stocks have not yet been assessed, making it difficult for political decision-makers to apply and establish regulations (Marengo et al., 2016). As a locally important fishing resource, the Mediterranean spinous spider crab *Maja squinado* (Herbst, 1788) has experienced a significant decline in its population in recent years, likely due to overexploitation (Abello et al., 2014; Durán et al., 2013; Martín et al., 2012; Rotllant et al., 2014).

In areas such as the Balearic Islands or the Columbretes Islands, the species appears to be nearly extinct for approximately a decade, prompting research and reintroduction initiatives (Garcia, 2007; Torres et al., 2013). Given this decrease in stocks, *Maja squinado* is internationally recognised as a species of ecological interest within the United Nations Environment Programme's Action Plan for the Mediterranean (UNEP/MAP). Additionally, it was included as a protected species in the Bern Convention for the Conservation of European Wildlife and Natural Habitats and was added to Appendix III of the Barcelona Convention in 2009. In France, the IUCN has not yet concluded on the species' status, however regional decrees are already applied in order to limit and regulate catches by recreational fishing. In Corsica, populations continue to support exploitation by small-scale fisheries (Bousquet et al., 2022) but, a notable decline in CPUEs (Catches per unit effort) has been observed in recent years (Marengo et al., 2023).

The spinous spider crab *Maja squinado*, a member of the Majidae family, was initially described as inhabiting both the Atlantic and the Mediterranean Sea. In 1998, Neumann proposed a distinction between *Maja squinado* and *Maja brachydactyla* (Balss, 1922) based on morphological characteristics identified by Balss in 1922, with the respective distribution areas assigned to the Mediterranean and the Atlantic (Neumann, 1998). This differentiation was further supported by a genetic study that analyzed mitochondrial gene variations in Atlantic (*Maja brachydactyla*) and Mediterranean (*Maja squinado* and *Maja crispata*) spider crab populations (Sotelo et al., 2008). Given that a significant proportion of the studies conducted on *Maja squinado* were, in fact, based on the Atlantic species *Maja brachydactyla*, our understanding of the biology of *Maja squinado* in the Mediterranean is somewhat limited and varies

according to different authors and geographic areas. Nevertheless, studies consistently agreed that these crabs undertake seasonal migrations, descending to depths of up to 150 meters in winter and ascending to shallower waters (10 to 15 m) in summer (Gualtieri et al., 2013; Rotllant et al., 2015). Mating typically occurs during the autumn migration. Gravid females, those carrying at least fertilized eggs, ascend in summer to spawn, while males remain at deeper levels. These females possess a spermatheca, enabling them to spawn multiple times from winter matings. The number of egg clutches and larvae varies according to authors, geographical areas, and water temperatures. Each female produces approximately three clutches of 30,000 to 200,000 larvae (Calado et al., 2013; Durán et al., 2012). Gravid females incubate the eggs under their abdomen before releasing the larvae at the zoea I stage, which then progress through three stages: zoea I (ZI), zoea II (ZII), and megalopa. *Maja squinado* eggs and larvae are carried by currents and drift in the environment to complete their lifecycle, a process known as larval dispersion (Okubo, 1994). This process involves biological and physical mechanisms that facilitate the movement of larvae from breeding to recruitment sites (Begon et al., 2005). Hence, the transport of larvae is influenced by physical oceanic factors such as currents and turbulence (Power, 1984). In addition, larval behaviours, such as larval vertical migration or free swimming, also play a role in dispersal (Adams et al., 2012; Gary et al., 2020). On a larger scale, exchanges between subpopulations are vital for understanding larval connectivity and the state and connections between marine metapopulations (Pineda et al., 2007).

Understanding the population dynamics of *Maja squinado* is crucial for developing effective management and conservation strategies. Although biophysical models are not often used for population dynamics, they are frequently employed to investigate pelagic larval dispersal and connectivity (Swearer et al., 2019). By integrating biophysical modeling, we can gain insights into the species' larval stages, aiding in the prediction of dispersal patterns and connectivity, which are essential for informed management and conservation efforts. This approach offers numerous benefits for predicting and visualising the dynamics of population dispersal and for hypothesising species vulnerabilities. For example, it can highlight isolated habitats or a lack of connectivity between populations, which are critical for effective conservation strategies (Jahnke & Jonsson, 2022; Lett et al., 2010). Individual-based models (IBMs) are designed to include detailed information about the life history traits of species for which researchers intend to model spatial and/or temporal dynamics (DeAngelis & Mooij, 2005). Each individual in the model is defined by a set of state variables and behaviours, which are determined according to available information on the species and the model's desired level of precision. These include geographical location, physiological traits, and certain behavioural traits such as reproduction and habitat selection. In a biophysical model, the trajectories of particles representing larvae are influenced by ocean currents and other environmental factors. By incorporating larval behaviours and physiological processes, the model becomes more precise, allowing for refined predictions that align more closely with other scientific approaches studying the species of interest.

In many Brachyura species, larval dispersion and migration are influenced by dominant ocean currents, as well as seasonal variations, water temperature, and food availability (Anger et al., 2015; Anger, 1991; Bryars & Havenhand, 2006; Epifanio & Garvine, 2001b). Significant environmental shifts in the Mediterranean were observed in 2014, particularly in the Northwestern region, with increased temperature and salinity, contrasting with a decline in these parameters in the offshore Ligurian Levantine Intermediate Water (LIW) during the same period (Margirier et al., 2020). This marked the start of an accelerated warming trend in the Mediterranean Sea (Margirier et al., 2020; Pastor et al., 2020), reflecting global patterns (Yin et al., 2018).

Maja squinado has significantly declined in some Mediterranean areas, such as the Balearics, but continues to be exploited in others, like Corsica, despite its "non-evaluated" IUCN status. The species' ecology and population dynamics remain poorly understood, posing challenges for future predictions. Biophysical modeling, however, offers valuable insights into larval dispersal and connectivity. This study investigates the dispersal trajectories of *Maja squinado* larvae in the Mediterranean from 2010 to 2020, focusing on connectivity between spawning and nursery areas and analysing changes over time and environmental variations.

2. Material and Methods

2.1 Mediterranean's surface circulation

The Mediterranean Sea is divided into two main basins, the Western and Eastern, separated by the Sicily-Tunisia Strait. The Western Basin extends from the Alboran Sea to the Tyrrhenian Sea, with the Atlantic Ocean connected to it via the Strait of Gibraltar. The Eastern Basin extends from the Adriatic to the Levantine Sea, including the Ionian and Libyan Seas. The Mediterranean Sea's intricate surface circulation, influenced by its segmented geography and complex seabed, predominantly exhibits anticyclonic movement. Fresh Atlantic waters enter the Mediterranean through the Strait of Gibraltar, increasing in density due to evaporation before exiting, typically taking 50 to 100 years to circulate. Surface currents are influenced by wind and topography, forming stable gyres and up to one-kilometre-wide eddies. However, some areas exhibit instabilities over time (Millot & Taupier-Letage, 2005; Pinardi et al., 2015) (Fig. 1A).

Surface currents in the northwestern Mediterranean are primarily influenced by thermohaline circulation, with cyclonic currents observed near the continental slopes. Notable currents include the Liguro-Provençal-Catalan Current, which flows in an east-to-west direction, and various gyres such as the Gulf of Lion Gyre and the Northern Tyrrhenian Gyre, which exhibit distinct circulatory patterns. Furthermore, the Tyrrhenian Sea's connectivity with the Corsican and Sardinian shores is characterised

by the presence of various currents and gyres, which collectively contribute to the formation of a dynamic marine environment (Pinardi et al., 2015) (Fig. 1B).

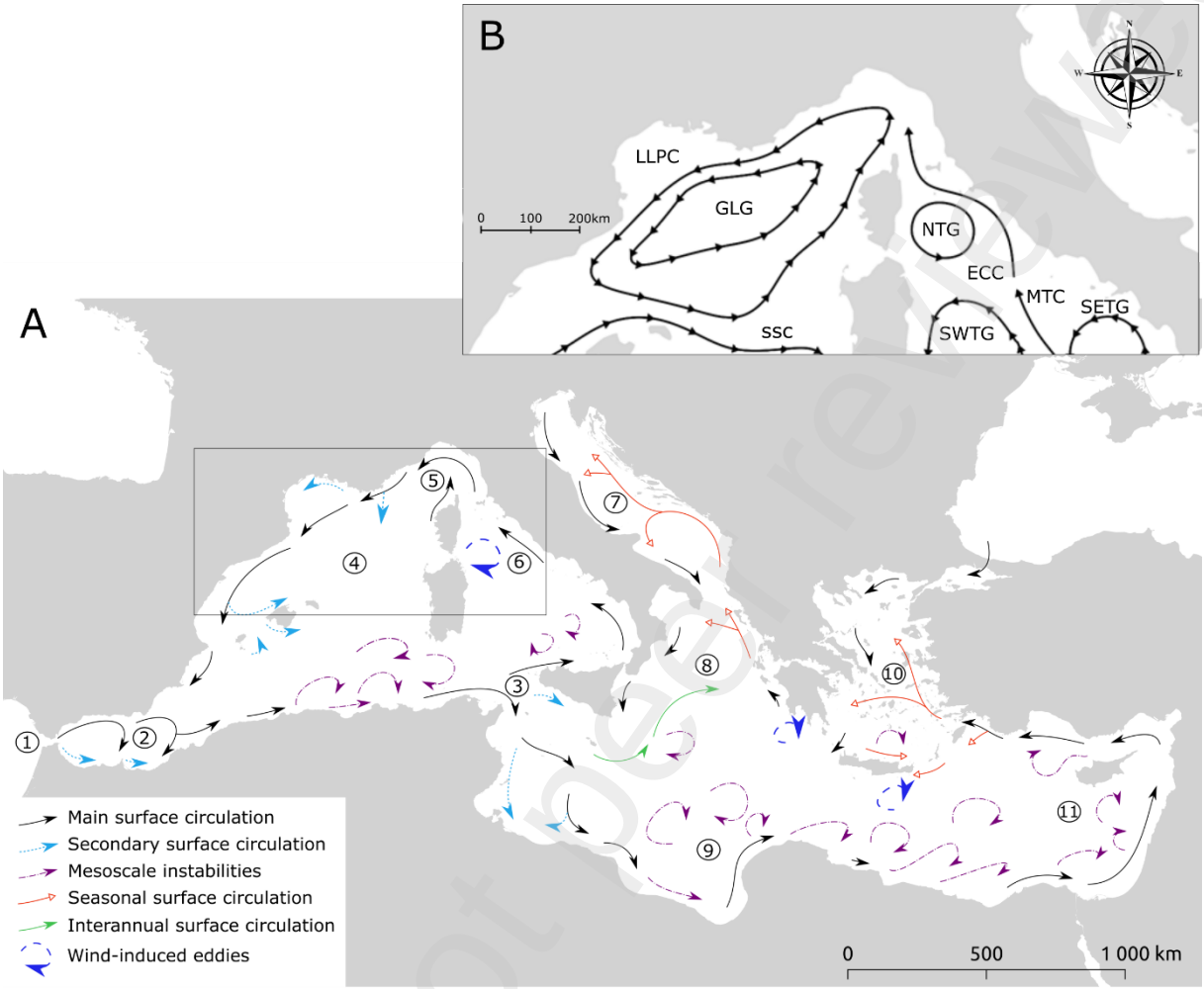


Figure 1: **Map of the general circulation currents in the Mediterranean (A)**, covering all basins (adapted from Millot and Taupier-Letage, 2005). 1: Strait of Gibraltar, 2: Alboran Sea, 3: Sicilia-Tunisia Strait, 4: Algero-Provençal Basin, 5: Ligurian Sea, 6: Tyrrhenian Sea, 7: Adriatic Sea, 8: Ionian Sea, 9: Libyan Sea, 10: Aegean Sea, 11: Levantine Sea. **Focus on the Northwestern Mediterranean Sea (B)** adapted from the study by Pinardi et al. (2015). LPCC: Liguro-Provençal-Catalan Current, GLG: Gulf of Lion Gyre, NTG: Northern Tyrrhenian Gyre, ECC: Eastern Corsica Current, SSC: Southern Sardinia Current, MTC: Middle Tyrrhenian Current, and SETG: South-Eastern Tyrrhenian Gyre.

2.2 Hydrodynamical models

The simulations for this study were performed using two hydrodynamic models. The first one, MEDSEA_MULTIYEAR_PHY_006_004 (MedMFC), was used to carry out simulations encompassing the entirety of particle release polygons representing larvae in the Western Mediterranean. This model, which presents a daily temporal resolution, integrates a hydrodynamic model contributed by the Nucleus for European Modelling of the Ocean (NEMO). It is further enhanced by a variational data assimilation approach known as OceanVAR, which processes vertical profiles of temperature and salinity, along

with satellite-derived sea level anomaly data. The dataset includes a comprehensive reanalysis segment, as well as an interim segment that extends from the end of the reanalysis to one month prior to the current date. The model operates on a finely calibrated horizontal grid with a resolution of 1/24°, equivalent to approximately 4-5 km (Escudier et al., 2021). A second hydrodynamic model, MARS3DMed, was employed for focused analyses and to attempt observing phenomena at a finer scale. This model, derived from the MARS3D (Model for Application at Regional Scales 3D) code and developed by Ifremer, has a temporal resolution of three hours, a horizontal resolution of about 1.2 kilometers, and 60 vertical levels using a generalized sigma coordinate system on an Arakawa-C grid, extending from the seabed to the surface, and is adapted for fine graphical resolutions (Arakawa & Lamb, 1977; Lazure & Dumas, 2008).

2.3 The Lagrangian transport tool

The model employed for larval dispersal is Ichthyop v.3.3.16, an offline Java Lagrangian tool (Lett et al., 2008). This tool has been extensively utilised in marine ecology studies, including those by Rojas-Araos et al. (2024) and Flores-Valiente et al. (2023), as well as in the broader field of physical oceanography, including work by Al-Qattan et al. (2023) and de Mello et al. (2023). This model is biophysical as it assesses the influence of physical and biological factors on the dynamics of ichthyoplankton. It follows the water masses or drifting entities from oceanic models ROMS, MARS, NEMO, or SYMPHONIE (Imzilen et al., 2023). The particle trajectories are calculated using a fourth-order Runge-Kutta method with a constant time step (van Sebille et al., 2018). The time step used in time integration of motion was defined according to the Ichthyop configuration editor to ensure that the Courant-Friedrichs-Lewy (CFL) condition is met, 720 seconds for the MARS3DMed outputs and 2880 seconds for the MedMFC outputs. Data recordings are made at regular intervals (every 60th and 15th timestep for the respective models), capturing the position of the particles every 12 hours. Horizontal diffusion was set according to the standard parameters of Ichthyop based on Peliz et al. (2007), with a dissipation rate of 10^{-9} $m^2.sec^{-3}$, while vertical migration follows a daily cycle depending on the depth and the sunrise and sunset times (Table 1). Buoyancy is added to the vertical velocity, determined by the density differences between the egg and the water, depending on temperature and salinity (Table 1). The particle release sub-model depends on the number, depth, and release dates, with parameters assigned to specific sites (Table 1). Particle retention at these sites depends on the minimum number of days before a particle can be considered as retained (Table 1). After this period, if a particle is found at a site, it stops moving. If a particle exceeds a certain pelagic larval duration (PLD) and is not found at any site, it is considered dead. The schedule for particle releases corresponds to spawning events for *Maja squinado* in the Western Mediterranean as documented in the literature, particularly using data available for Corsica and Catalonia (Calado et al., 2013, and Duran et al., 2012 in Corsica; Rotllant et al., 2014 in Corsica and Catalonia). Thus, each simulation year includes eight release dates, as detailed

in Table 1. Each release site disperses 40,000 particles at depths ranging from 0m to 50m (Gualtieri et al., 2013). The maximum duration of particle dispersal is 20 days, and particles are considered as competent for settlement from 17 days, corresponding to the juvenile stage of *Maja squinado* (Durán et al., 2012; Rotllant et al., 2014). Each particle undergoes daily vertical migration at sunrise and sunset, within the depths defined by the photic zone at 1.10^{-7} m^{-2} for these larvae, averaging about 30 meters deep during the day and about 1 meter at night (Anger et al., 2015; Ospina-Alvarez et al., 2018). No horizontal migration or free swimming is included, as the swimming appendages of the early zoeae stages are primarily for vertical movement, before being replaced by walking and feeding appendages at the megalopa and first juvenile stages. The buoyancy of the particles is determined by a density of 0.9 g/cm^3 (Epifanio & Garvine, 2001a). Finally, a rebound behavior upon contact with physical barriers is attributed to the particles, with a force equivalent to that required to overcome these barriers.

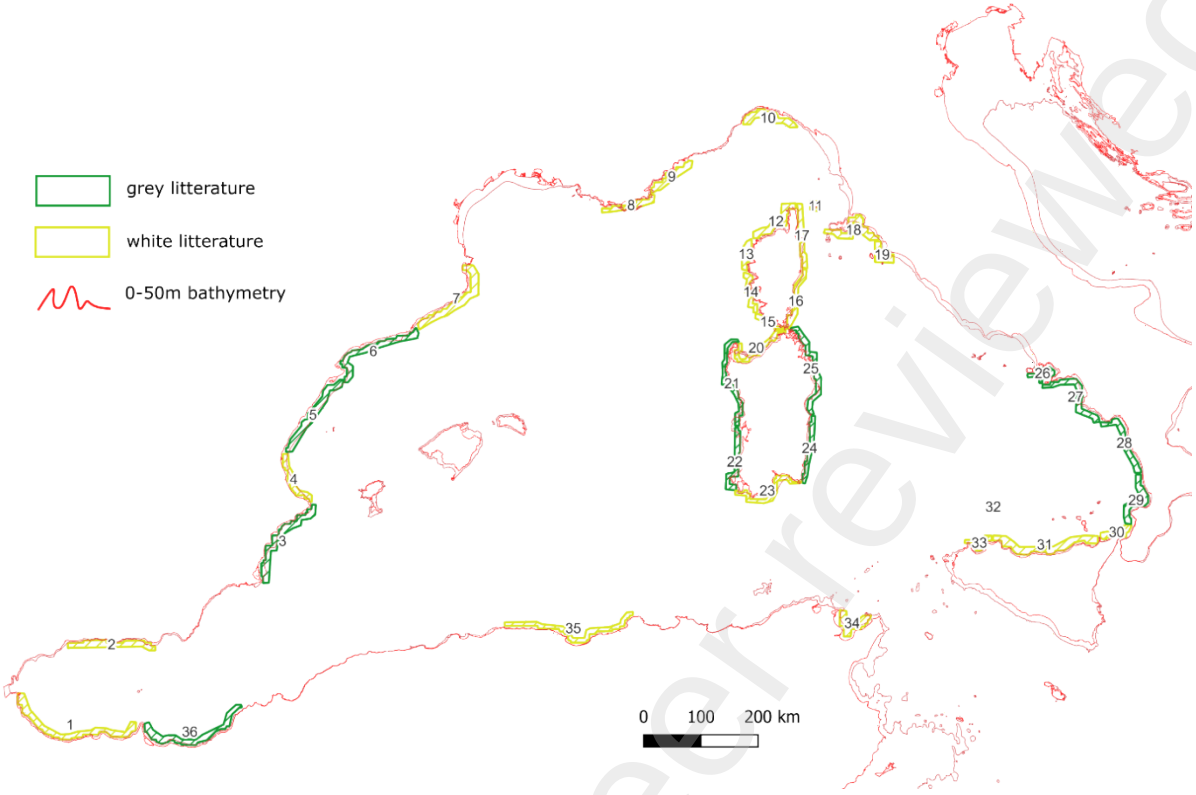
Table 1. Biological parameters of the simulations applied to the dispersion of *Maja squinado*.

Parameter	Value	Reference
Pelagic larval duration (PLD)	20 days	Durán et al., 2012
Release date (per year)	April 15 - Start of the laying period. April 22 - One week after the start. April 29 - Two weeks after the start. May 6 - Three weeks after the start. May 13 - Four weeks after the start. May 20 - Five weeks after the start. May 27 - Six weeks after the start. May 31 - End of the laying period.	
Particles number	MedMFC: 50000 particles were released on each release day (8 days in total), amounting to 400000 particles per simulation. This equates to 4400000 particles over the 11-year study period, distributed evenly across 36 zones. MARS3DMed: in order to maintain proportional relationships, 31250 particles were released each day of the release period (8 days in total), resulting in a total of 250000 particles per simulation, or 2750000 particles over the 11-year study period, distributed evenly across 23 polygons in the Northwestern Mediterranean.	
Release depth	0 – 25m	Gualtieri et al., 2013
Release polygons	See Figure 2 for geographical localization: 1: MA1, 2: SP2, 3: SP5, 4: SP6, 5: SP7, 6: SP8, 7: SP9, 8: FR2, 9: FR3, 10: FR-I, 11: CAPi, 12: NWCO The following codes correspond to the polygon numbers: 13: WCO, 14: SWCO, 15: SCO, 16: SECO, 17: NECO, 18: IT3, 19: IT4, 20: NSA, 21: NWSA, 22: SWSA, 23: SSA, 24: SESA, 25. The following abbreviations are used in this document:	Rotllant et al. 2014, Guerao & Rotllant 2010, Guerao et al. 2016, Seytre et al. 2013, Modena et al. 2001 and Durán et al. 2012 and grey littérature.

	NESA, 26: IT7, 27: IT8, 28: IT9, 29: IT10, 30: SIC1, 31: SIC2, 32: USTi, 33: SIC3, 34: TUN, 35: AL3, 36: MA-AL.	
Ideal habitat for recruitment polygons	See Figure 3 for geographical localization: 1:MA1, 2:ALB, 3:SP1, 4:SP2, 5:SP3, 6:SP4, 7:SP5, 8:SP6, 9:COLUI, 10:SP7, 11:BA2, 12:BA1, 13:BA3, 14:BA4, 15:BA8, 16:BA5, 17:SP8, 18:BA7, 19:SP9, 20:BA6, 21:SP-FR, 22:FR1, 23:FR2, 24:FR3, 25:FR4, 26:FR-I, 27:IT1, 28:CAPi, 29:NWCO, 30:WCO, 31:SWCO, 32:SCO, 33:SECO, 34:NECO, 35:IT2, 36:IT3, 37:PIAI, 38:IT4, 39:IT5, 40:NSA, 41:NWSA, 42:SWSA, 43:SSA, 44:SESA, 45:NESA, 46:IT6, 47:IT7, 48:IT8, 49:IT9, 50:IT10, 51:SIC1, 52:EOLI, 53:SIC2, 54:USTi, 55:SIC3, 56:TUN, 57:ALTUN, 58:GALI, 59:AL4, 60:AL3, 61:AL2, 62:AL1, 63:MA-AL.	Rotllant et al. 2014, Guerao & Rotllant 2010, Guerao et al. 2016, Seytre et al. 2013, Modena et al. 2001 and Durán et al. 2012 and grey littérature.
Minimum retention age	17 days	Rotllant et al., 2014
Buoyancyy	0.9g/cm3	Epifanio & Garvine, 2001a
Vertical migration depth	day: 30m – night: 1m	Ospina-Alvarez et al., 2018
Coastal particles behaviour	Bouncing	

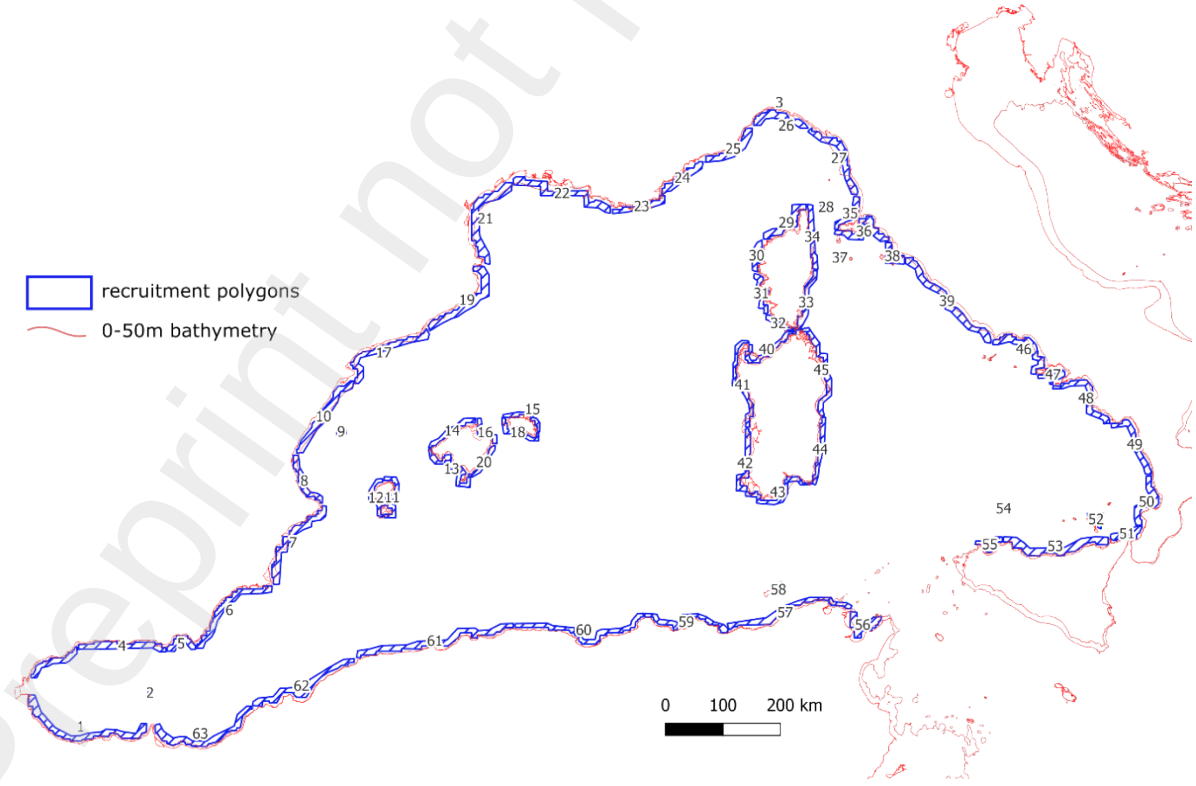
2.4 Delimitation of release and recruitment sites

The sites used for the release of particles were designed based on the presence of *Maja squinado* as documented in the literature (Rotllant et al. 2014, Guerao & Rotllant 2010, Guerao et al. 2016, Seytre et al. 2013, Modena et al. 2001) Durán et al. 2012) Rotllant et al. 2015, Angeletti et al. 2014), Gualtieri et al. 2013, Durán et al. 2013, Calado et al. 2013, Sotelo et al. 2008, Vignoli et al. 2004) Rocklin 2010) Mura & Corda 2011, and Pipitone & Arculeo 2003; Fig. 2). Using the same body of literature, the recruitment sites were approximated by coastal areas in proximity to documented catch of *M. squinado*, taking into account bathymetry (< 50 m, Fig. 3).



228

229 Figure 2: The 36 polygons used for particle release within the MedMFC model domain as identified in white (dark
230 green polygons) and grey (light green) literature. See Table 1 for the detailed names of the acronyms.



231

232 Figure 3: The 63 ideal habitat for recruitment polygons within the MedMFC model domain. See Table 1 for the
233 detailed names of the acronyms.

2.5 Environmental trends visualization and data analysis

The Ichthyop simulation outputs are files in netcdf format, which were analyzed with R (version 4.0.4; R Core Team 2021) and Python (version 3.11) scripts. Firstly, particle density maps were produced over the entire period (2010-2020). Trajectory densities were calculated through the following steps: the final positions of particles were extracted from simulation outputs. The coordinates (longitude and latitude) of these particles were used to create spatial line objects, which were then converted into spatial vectors. These vectors were rasterized onto a background map grid, where each raster cell contained the sum of trajectories passing through that cell. Mathematically, this entails enumerating the number of particles present in each grid cell at the conclusion of the simulation. A coefficient of variation (CV) was calculated in each map in order to compare the relative variability between different trajectories or periods, even if the absolute densities differ. Connectivity matrices between release zones and recruitment zones, as well as local retention and self-recruitment at each site, and distribution of traveled distances and directions followed from release to recruitment were also computed. On connectivity matrices, a Gini coefficient (Hixon & Jones, 2005) was also shown on connectivity matrices in order to assess disparities between years and sites.

The sea surface temperature data extracted from the Copernicus Marine Environment Monitoring Service (CMEMS) satellite product over the western Mediterranean Sea demonstrated a temperature increase trend of 0.034 ± 0.002°C per year, with a 95% confidence interval (Appendix Figure A1). To analyse trends spatially and focus on the last decade, data from the MedMFC model were examined at all points in the Western Mediterranean (focusing on our study window), providing a more spatially detailed view of regional temperature variations. Linear regression was used to calculate a linear temperature trend for each grid point, with a color gradient from blue (indicating a decrease in temperature) to red (indicating an increase in temperature) used to map these trends. A comprehensive examination of these findings is provided in the appendix section.

The simulation results were divided into two groups: 2010-2014 and 2015-2019, in order to contrast periods of different average temperatures while maintaining an equal number of simulations for comparison. Firstly, an overall visualization was carried out, with the calculation of KDE's (kernels density estimates). The KDE calculation is based on a symmetric function centered around each data point. The most commonly used kernel is the Gaussian kernel (normal function), which is selected based on the bandwidth, which determines the extent of the smoothing. A smaller bandwidth leads to a more detailed estimate, while a larger bandwidth results in a smoother estimate. In the context of particle position simulations modelling larvae, KDE can be employed to estimate the spatial density of particle positions at different times, thereby enabling the visualization of areas of high particle concentration and the identification of any differences between the two scenarios. Secondly, a subsampling of two

zones was employed to analyse the distribution of travelled distances and directions followed from release to recruitment. The distances were calculated using the Haversine formula, which accounts for the Earth's curvature by calculating the great-circle distance between points. The presented plots illustrate the distribution and density of data points, comparing the density of particles based on the distance travelled from spawning areas in the pre- and post-warming scenarios of the Western Mediterranean. Furthermore, wind roses were constructed to examine the typical orientations assumed by the particles following their arrival at a recruitment zone for each year. The orientations were calculated by determining the angle of each trajectory segment and averaging these angles, with the weights being proportional to the distances.

3. Results

3.1 Exploring multi-scale trends over the entire temporal period (2010-2020)

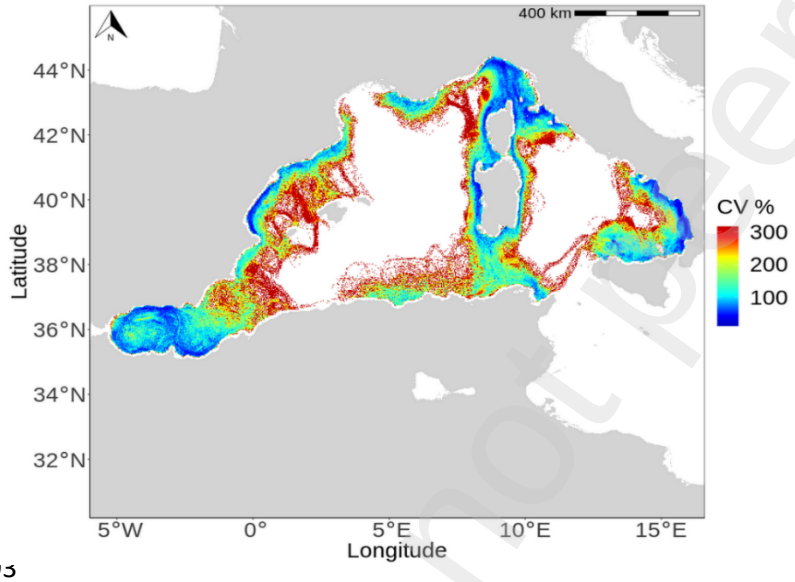


Figure 4: Density map of particles that successfully reach a recruitment zone averaged for the period 2010 to 2020, based on simulations carried out with the MedMFC model in the Western Mediterranean. The interannual variability of these trajectories is expressed by a coefficient of variation (CV).

Maps of particle density's coefficient of variation (CV) computed over the entire study period and domain covered by the MedMFC model highlight the principal simulated routes and their temporal variability for larvae transported from spawning to recruitment zones (Fig. 4). We note a continuity in the simulated larval dispersal pattern of *Maja squinado* between the North and South around Corsica and Sardinia, with low CV values, indicating that this pattern is recurrent along the study period. In contrast, other areas, such as the Balearic Islands, have less connection with the coastlines, or at least less regularly along the study period. Lastly, the Alboran Sea emerges as a significant exchange hub for larvae along its various coastlines, yet it has limited connection with the rest of the Western Mediterranean.

The MARS3DMed model (Fig. 5) reveals that trajectories with low coefficients of variation primarily connect nearby coastal areas, at times forming interconnected sets over the course of the eleven considered years. This is exemplified by the routes appearing on both sides along Corsica and Sardinia.

The broader geographic window used with MedMFC allows for the identification of routes in the southern Western Mediterranean, particularly in the Alboran Sea, which is minimally or not connected to the rest of the sub-basins. Furthermore, the Balearic Islands are geographically isolated, although a few trajectories (with very high coefficients of variation) exhibit weak connectivity to the Spanish coastlines over the studied period. The southern coastlines of Sardinia are connected with the Tunisian coastlines on a regular basis over time. This creates a group with probable larval exchanges between Tunisia, Sardinia, and then Corsica moving northward.

The Gulf of Lion is also a site of significant exchanges, with distinct routes emerging: one arriving from the east and another departing towards the west. Notwithstanding the high CV (panel C of Fig. 5) of these routes, they play a pivotal role in regional connectivity. In the easternmost part of the Western Mediterranean, there is also a coastal route along the Sicilian-Italian coastline with minimal connectivity to the rest of the basin, with the exception of a few trajectories (with high CV) connecting to the Tunisian coasts.

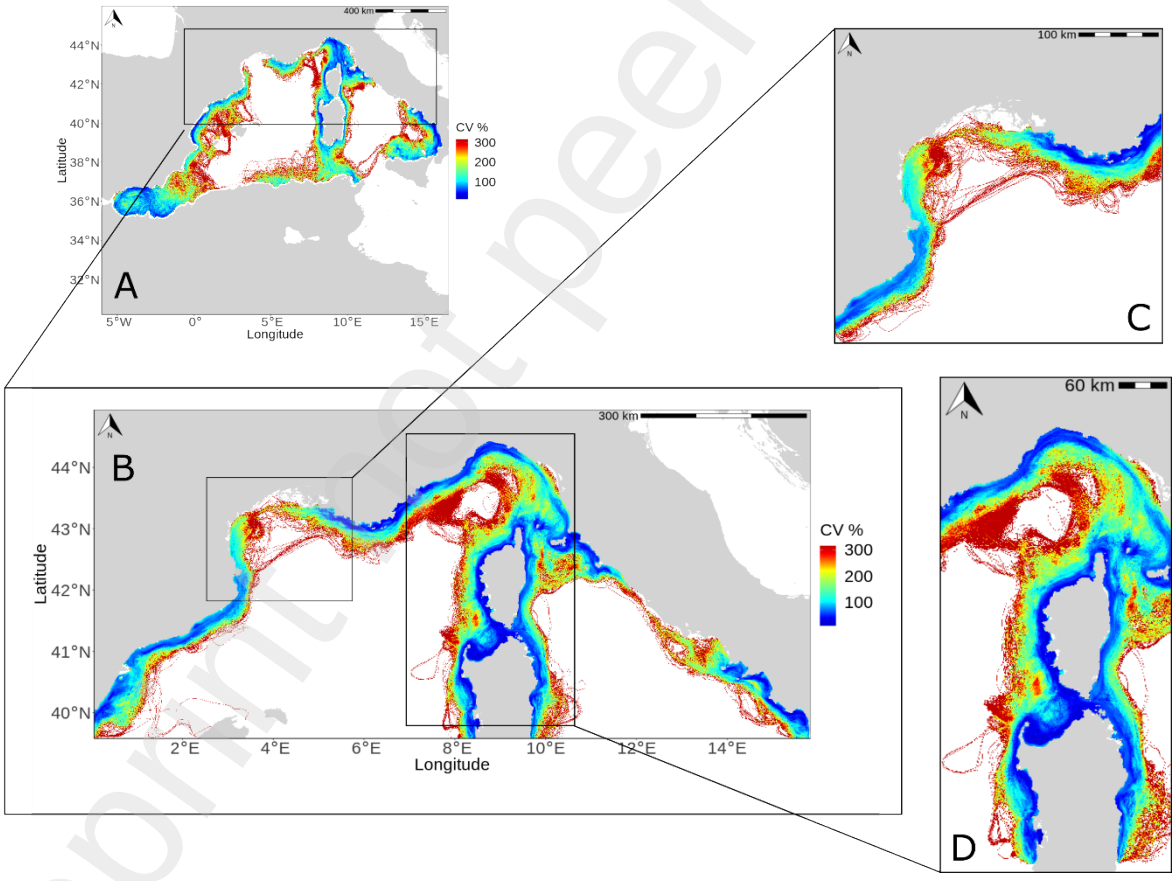


Figure 5: Trajectory densities for the entire period from 2010 to 2020 generated using two hydrodynamic models with different geographical windows and foci. A: Simulations carried out with the MedMFC model in the western Mediterranean. B: Simulations carried out with the MARS3DMed model in the north-western Mediterranean, allowing finer resolution focuses in C (Gulf of Lion) and D (Sardinia-Corsica ensemble). The variability of the trajectories over time is expressed by the coefficients of variation (CVs).

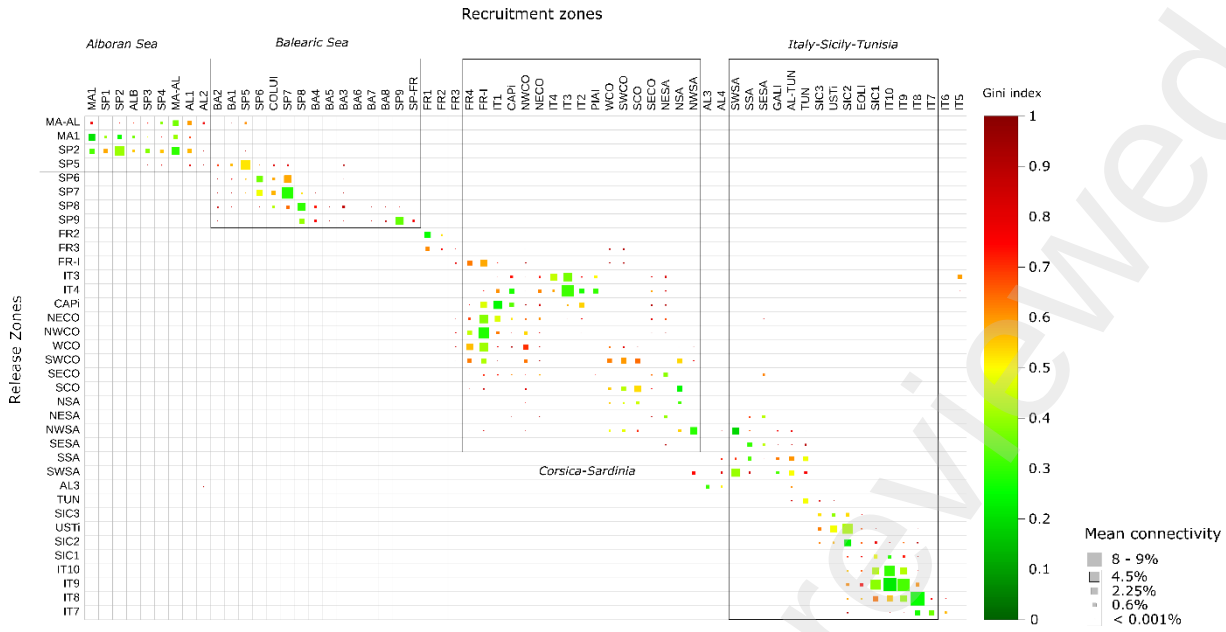


Figure 6: The connectivity matrix was constructed on the basis of simulations conducted with the MedMFC model in the Western Mediterranean, spanning the period from 2010 to 2020. The release zones are displayed on the vertical axis, while the recruitment zones appear on the horizontal axis.

The connectivity matrix (Fig. 6) was organized in a manner consistent with the Mediterranean sub-basins. The maximum connectivity values of approximately 9% were obtained in the cluster Italy-Sicily-Tunisia, between the IT8 and IT9 zones in the southern Tyrrhenian Sea. In the Alboran Sea, we observe regular connectivity relationships (as indicated by low Gini index) and remarkably high local retention values for MA1 and SP2. In the Balearic Sea, the most notable elements are the high local retention within SP7, SP8 and SP9, all with low Gini indices. The Balearic Islands BA1 to BA9 are connected by small amount of particles and with Gini indices higher than 0.5. The Corsica-Sardinia area and the coasts of the Ligurian Sea have connections close to the maximum of obtained connectivity values (e.g., IT3 with IT4, NWCO with FR-I, WCO with FR-I) with low Gini indices.

Local retention values in Corsica can reach high percentages, as for the NWCO, but with an intermediate Gini index. In the same way, we observe an intermediate level of connectivity between the Corsican and Sardinian zones. Thus, in general, we observe relatively regular exchanges between Corsica, Sardinia and the Ligurian coasts. Finally, the last remarkable group is that of the Italian, Sicilian and Tunisian coasts, where we obtain strong connectivity between zones IT7 to IT10 with strong local retention within each of these zones as well, and low Gini indices. The Tunisian zone is connected to the Sardinian ones, and the Sicilian zones are connected to both the Aeolian Islands and the Italian zones south of the Tyrrhenian Sea.

3.2 Analysis of trends in light of global change signals in the Western Mediterranean

3.2.1 Warming signals and comparison of larval recruitment kernels

The kernel density estimates (KDE) map for the period 2010-2014 (Fig. 7A) shows higher maximum density values than for the 2015-2019 scenario (Fig. 7B). However, the areas of highest concentration remain similar, i.e., the Ligurian Sea, the southern Tyrrhenian Sea, the Balearic Sea, and to a lesser extent the area between Tunisia and southern Sardinia. The map of differences between the two time periods (Fig. 7C) shows areas where the density has decreased in blue, such as the northern region of Italy, particularly Liguria and Tuscany, and parts of the Balearic Sea, Alboran Sea and Tyrrhenian Sea. On the other hand, an increase in density is observed in the southern Tyrrhenian Sea, particularly around Sicily and Tunisia, and in areas off the northwestern coast of Italy and northeastern coast of Spain.

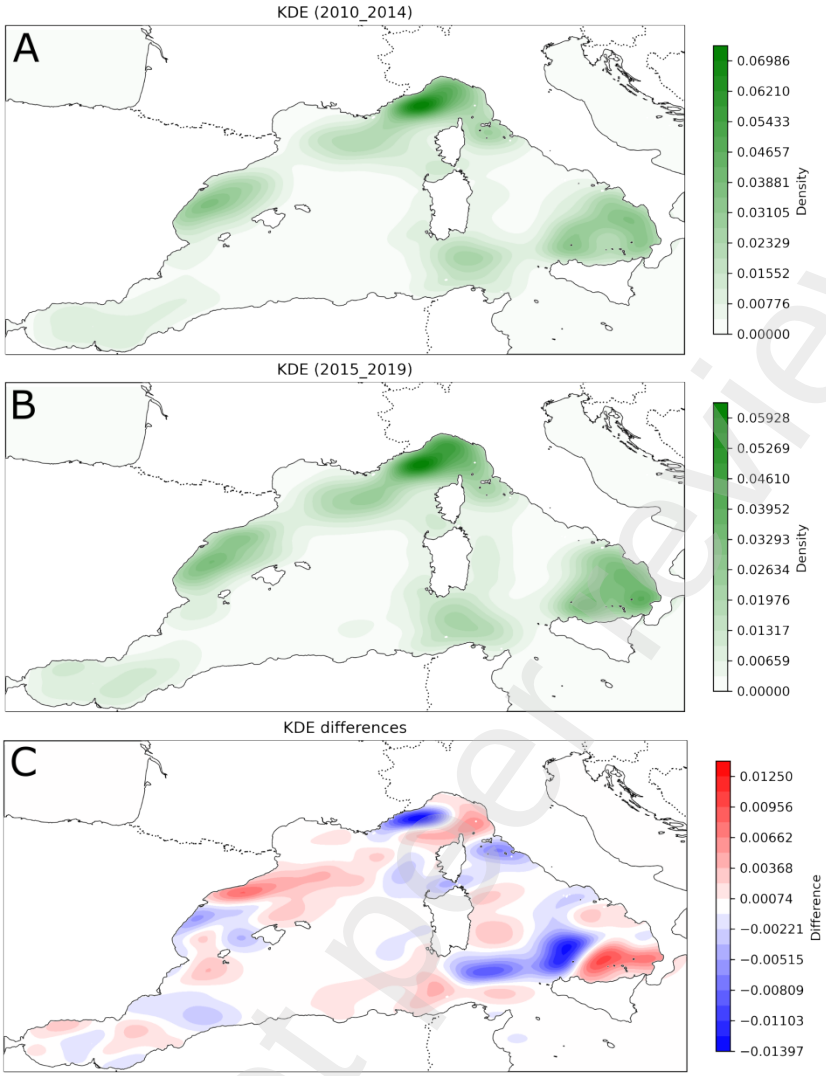


Figure 7: Kernel density estimates (KDEs) of particle locations at the end of the PLD obtained using the MedMFC configuration for (A) 2010-2014 (B) 2015-2019 (C) shows the differences between the two time periods.

3.2.3 Dispersal distances and orientations in a changing Mediterranean Sea

The following analyses and results present two contrasting areas from the perspective of simulated connectivity and the status of *Maja squinado* in the Mediterranean. The Catalan coast (SP9; Figure 2) is the area that connects the largest number of recruitment areas in the Balearic Islands, but with low connectivity percentages and high Gini indices (Fig. 6). Furthermore, the literature and supplementary approaches have demonstrated that *M. squinado* has almost disappeared from the Balearic Islands, rendering this area a primary focus of interest. This area contrasts with the Corsica-Sardinia zones were the spinous spider crab is still exploited. Consequently, it was decided to compare it in this analysis with the southwestern Corsica zone (SWCO; Fig. 2). The latter exhibits in the matrix a number of significant connections with other zones (Fig. 6). It is also included in what appears to be a cluster of larval

exchange between Tunisia, Sardinia, Corsica, and the Ligurian Sea, in connection with other areas such as those in southern Corsica (SCO and SECO in Fig. 2).

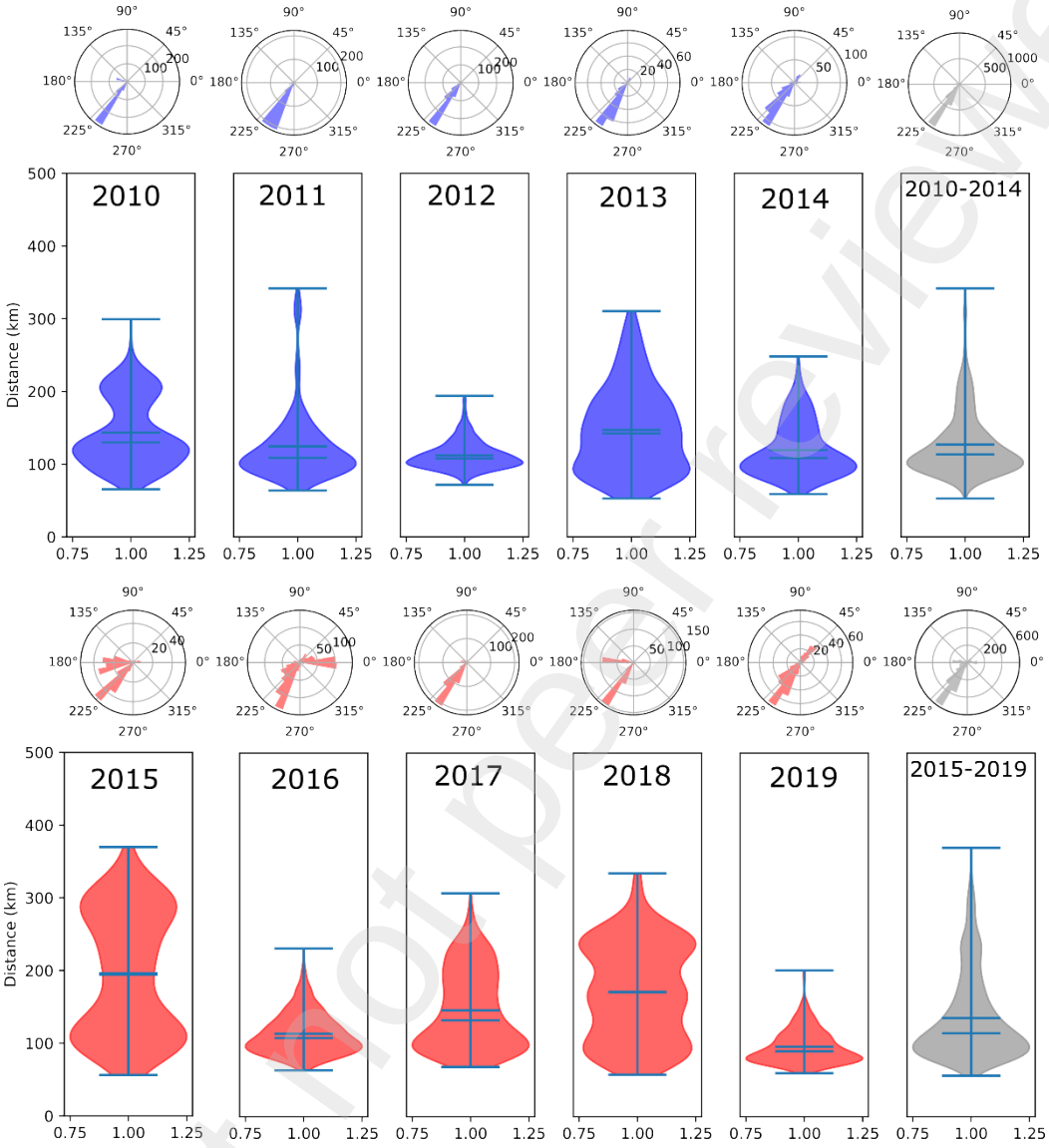


Figure 8: Violin plots showing the distribution of distances traveled by larvae that have successfully reached a recruitment area from the Catalan coast release zone (SP9; Figure 2) for different time periods. Wind roses show the distribution of directions traveled by these larvae.

The mean distance travelled by larvae from SP9 exhibited a slight increase from 127.06 km (2010-2014) to 135.60 km (2015-2019). Furthermore, the standard deviation of the distance increased from 44.35 km to 58.82 km, indicating greater variability in the distances travelled. The standard deviation of the direction of travel also increased, from 57.59° to 83.01°, indicating greater variability in the dispersal directions. Indeed, the distribution of directions was bimodal in 2015, 2016, 2018, and 2019, as opposed to being unimodal in all years from 2010 to 2014 (Fig. 8).

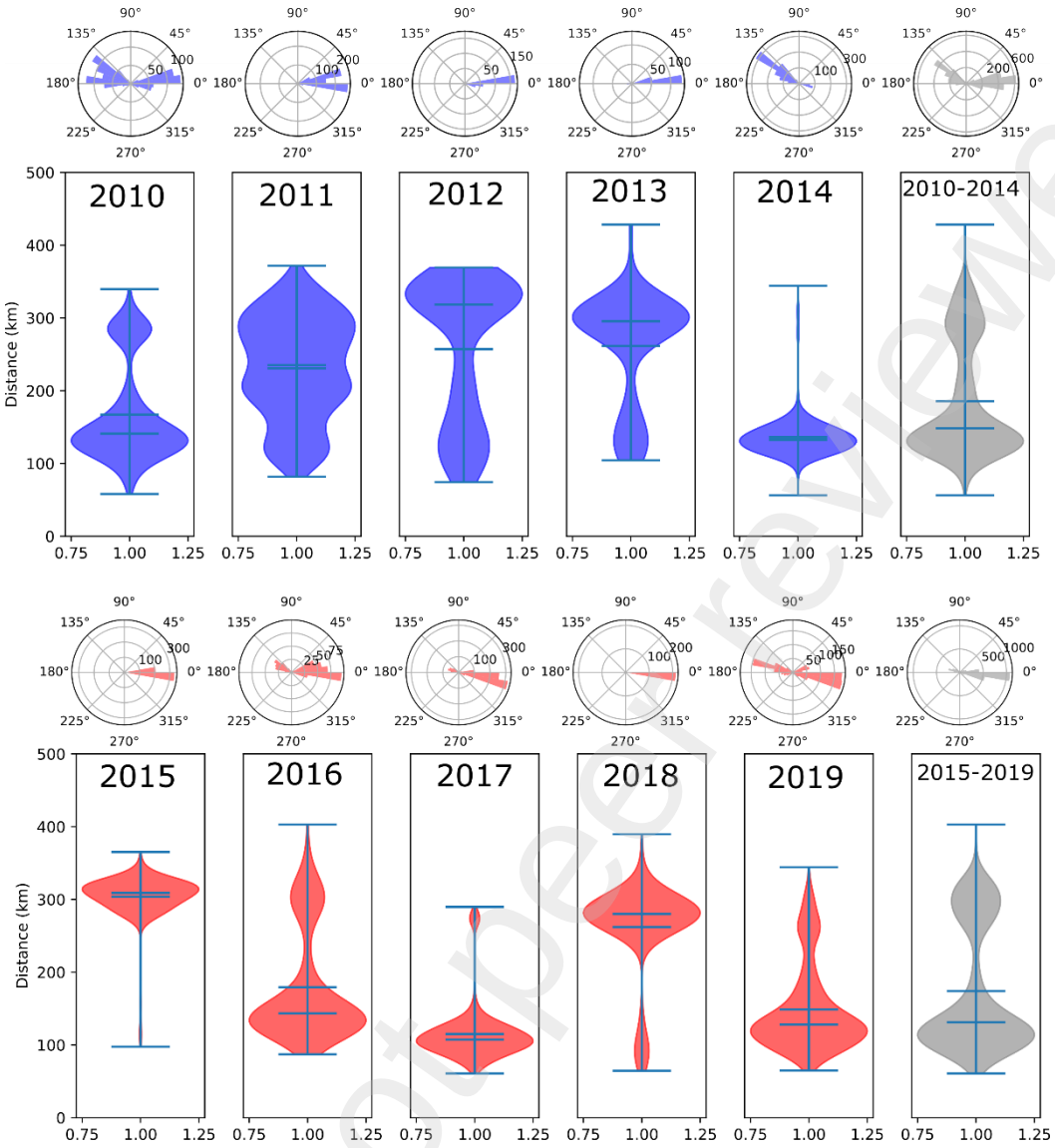


Figure 9: Violin plots showing the distribution of distances traveled by larvae that have successfully reached a recruitment area from the Southwestern Corsican zone (SWCO; Figure 2) for different time periods. Wind roses show the distribution of directions traveled by these larvae.

The mean distance travelled by larvae was found to be slightly shorter in the 2015-2019 period (174.07 km) compared to the 2010-2014 period (185.60 km), according to data from SWCO. However, the variability in distances travelled in the 2015-2019 period was greater than in the 2010-2014 period (standard deviation 85.23 km and 77.93 km, respectively). The mean direction of movement exhibited a notable shift, from 58.51° to 1.10°, and the variability of directions also increased during the 2015-2019 period. Indeed, the mean direction of dispersal averaged over the 2010-2014 period exhibited two peaks, at approximately 135° and 0°, respectively. In contrast, only the 0° peak was observed from 2015 to 2019 (Fig. 9).

4. Discussion

The simulations generated by the MARS3DMed model are intended to reinforce and refine the findings observed in the MedMFC model simulations. This was made possible by meticulously delineating specific coastal exchanges, which could only be discerned with a higher level of detail. Consequently, the simulations are more closely aligned with field reality in the MARS3DMed model than in MedMFC, despite the broader geographic scope being essential to encompass pertinent release and recruitment sites. It is crucial to acknowledge that a model with a higher resolution will yield results that are more reflective of reality than a model with a less precise resolution. This is because the latter is prone to underestimating particle dispersion (Saint-Amand et al., 2023).

The results of simulations conducted in the Western Mediterranean have demonstrated, for the first time with a biophysical modelling approach at this spatiotemporal scale, that *Maja squinado*, with its relatively short PLD, exhibits limited dispersal capabilities. In general, the dispersion paths taken by the organism exhibit minimal variation over time, both in terms of distance and direction. These paths align with the predominant current patterns of the region and can be dispersed to distances exceeding eight times the average observed distance. Medium-scale oceanographic features, such as fronts and eddies, have been identified as key mechanisms affecting dispersion in these specific areas (Alcaraz et al., 2007). Although vertical migration is commonly accepted in crustaceans of the Brachyurans group, its effects were not tested in this study and were parameterised as active in our simulations. However, in other species, this migration has been demonstrated in the literature to constrain the distance and speed of dispersion (Zakardjian et al., 1999). As with other Brachyurans, larval dispersion and migration may be defined here by the dominant current patterns of the location (Anger et al., 2015), as well as the presence or absence of suitable habitats for spawning and recruitment.

In the presented study, observations were made in the context of the warming of surface waters in the Mediterranean, with particular attention paid to the acceleration observed between 2014 and 2015 (Margirier et al., 2020; Pastor et al., 2020). The graphical observations indicate differences between the two scenarios in the Mediterranean for the two subsampled areas, SP9 and SWCO. While statistical analysis would have been relevant, the limited quantity of data and the low number of trajectories, combined with their irregularity, did not permit a statistically robust analysis. A recommendation for future studies attempting to hypothesise about the synergy of causes of changes in dispersal dynamics, involving global change, would be to collect more data to improve the robustness of the analyses, particularly for areas where the number of observations is currently limited, such as the Balearic Islands and their connectivity with the closest coastlines, where reports of *M. squinado* are still made (the Spanish coasts, for example, notably SP9). Consequently, although statistical analysis is constrained by the quantity and variability of the data, the graphical observations indicate potential changes in the

dispersal behaviours of *Maja squinado* larvae in response to global warming. This finding warrants further investigations and increased attention to these dynamics. The KDE results reinforce the hypothesis that the acceleration of global warming, in particular the increase in the temperature of surface waters, could affect the dispersal trajectories of *Maja squinado* larvae predicted by the simulations. The observed changes in particle densities indicate that traditionally favourable areas may become less conducive to larval concentration, while other areas may see an increase in density. These kinds of observations, when considered in conjunction with the population dynamics of an exploited species with an IUCN status of non-evaluated, could prove crucial for the development of future management measures. Another crucial link to be considered between global change and larval dispersion dynamics in *Maja squinado* is the biological model itself. Indeed, temperature could be a significant factor conditioning spawning schedules, thus affecting the quality and quantity of eggs laid. For example, studies have demonstrated the effects of ovarian mutations in the freshwater shrimp (*Penaeus merguiensis*, Hoang et al., 2002), and a meta-analysis has highlighted the impact of temperature on various stages in brachyuran crabs, indicating that spawning is advanced as temperatures rise (Azra et al., 2019). Furthermore, another study indicates a correlation between temperature evolution and crab population dynamics. This study demonstrates that environmental temperature variations correlate with the spatial and temporal variation of the crab *Portunus armatus* during the breeding period (Johnson and Yeoh, 2021). To date, no study has specifically focused on *Maja squinado* in the Western Mediterranean and examined the evolution of its thermal tolerances and spawning schedule in light of global change and surface water warming. Nevertheless, it would be beneficial to observe the results of forthcoming studies with a view to enhancing the calibration of models that could shed light on the dynamics of its populations in a changing Mediterranean.

It is therefore inaccurate to draw a direct cause-and-effect relationship between global change and changes in larval dispersal and connectivity in species with a biphasic life cycle. Therefore, we prefer to discuss the interaction of environmental and biological traits parameters as a "synergy". Nevertheless, since current patterns are the primary driver of larval dispersion in larvae incapable of swimming, there is a correlation between minor or major changes in current regimes and global changes, which in turn result in cascading effects on zooplankton species and their dispersion. Further in-depth studies are warranted. Indeed, a number of factors have been identified as being of crucial importance for the survival and dispersion of crustacean larvae, including seasonal variations in currents, water temperature, and the availability of food resources. These factors have been demonstrated to be of importance in a number of studies, including those by Anger (1991), Bryars & Havenhand (2006), and Epifanio & Garvine (2001b). In the absence of warming scenarios, our findings indicate that interannual variability in connectivity between sites is the most significant factor. This may be attributed to the impact of current global warming on surface temperatures and, consequently, on currents on an annual basis. A more detailed analysis of these parameters and their implementation in future models could

provide a better understanding of the observed dispersion patterns, while explaining the contribution of water warming to the interannual variability (Corrochano-Fraile et al., 2022; Šargač et al., 2022).

The findings of this study enable the prediction of large-scale and long-term trends in *Maja squinado*, a species whose ecology and population dynamics remain poorly understood. Along the coasts where areas favorable to the spawning of the spinous spider crab have been parameterized, connectivity over multiple sites can occur between relatively distant locations through various intermediaries. It is likely that these coastal zones exhibit small-scale circulation dynamics that trap larvae near the release site, influenced by interactions with eddies and seafloor topography. Sites with high local retention can maintain significant local recruitment, supporting a population over time and reducing the risk of larval loss or recruitment failure due to phenotype-environment mismatches (King et al., 2023). Based on the selected release sites, larval exchanges in the Mediterranean appear to be confined within distinct basins. For instance, there is a scarcity of larval exchanges between the Algero-Provençal basin and the Tyrrhenian Sea via the Ligurian Sea. Similarly, the Alboran Sea and the Balearic Islands appear isolated from the rest of the coastlines. With the exception of the Northwestern Mediterranean, where connectivity between Corsica, Italy, and the French coastlines is consistent and regular over the study period, it is challenging to estimate links between more distant sites due to the relatively short larval duration of the spider crab. There is almost no observable connection between Catalonia and the Balearic Islands, suggesting low connectivity with these islands. This isolation can be attributed to the hydrodynamically complex nature of the Balearic Sea, resulting from interactions between different water masses and the island's topography, which limits species exchange between these areas and other regions (López-Jurado et al., 1995; Pinot et al., 2002). This research contributes to our understanding of the exploitation and preservation challenges of *M. squinado* in the Mediterranean by offering initial observations on connectivity and population dynamics, highlighting the constraints on larval exchanges within the Mediterranean's distinct basins.

The reliability and significance of predictions derived from biophysical models are becoming increasingly evident when compared to alternative scientific methodologies. Consequently, it can be postulated that population genetic studies on *M. squinado* may offer invaluable insights that could facilitate more accurate parameterisation of future simulations. For instance, they could provide further understanding of the species' dispersal patterns by identifying specific sub-populations around these islands and on a broader scale. Nevertheless, the findings of these studies elucidate the behaviour of *Maja squinado* larvae and the potential for dispersion from a known population location. This study focuses on larval dispersion, and it is important to note that several factors affect larval recruitment, including predation, competition, and ontogenetic traits (Anger et al., 2015). For instance, some species may benefit from the presence of larvae as food, while others may act as potential predators (Anger et al., 2015; Torres et al., 2013). The present model does not include the factors affecting larval mortality,

which are influenced by interspecific relationships. Future simulations could therefore benefit from further studies in order to refine the parameters. For example, it would be beneficial to be able to specify the quality and quantity of spawning, as well as the factors influencing the survival of larval flows from one year to the next.

It is evident that the results of the study largely depend on the ability to identify source and sink sites within the dispersion system. For the purposes of management, the dispersion characteristics of sites can be considered in order to assess their importance in a small-scale system. Sites that release more larvae than they retain may be vulnerable to population collapse due to fishing, resulting in a decrease in the number of potentially recruitable larvae at another site (Cowen et al., 2002; Steneck et al., 2006). This may be particularly pertinent to the Balearic Islands, which have limited larval recruitment from Spain and possibly the Maghreb, while also being subject to overfishing (Garcia, 2007). The prevalence of short-distance dispersal, in comparison to other species that pose invasion concerns, raises questions about the role of islands in large-scale species dispersal.

Areas with high connectivity, such as the Corsican and Sardinian coastlines, along with Sicily, Tunisia, and southern Sardinia, could be the subject of studies on the benefits of establishing a network of protected areas. This would favor and protect the exchange of larvae and the pools of breeding individuals. Such measures could help to prevent scenarios where potentially overly isolated areas cut off from exchanges have experienced population collapses and consequently the cessation of fishing activities, as seen in the Balearic Islands due to depleted stocks. These results could be supported by genetic and phylogenetic studies, which would show genetic differentiation or proximity between different areas, indicating the existence of several sub-populations. Such studies have been conducted on the sister species *Maja brachydactyla* in the Atlantic, which have highlighted the importance of the Strait of Gibraltar in defining species boundaries (Abello et al., 2014). Identifying genetic barriers and gene flows would be useful indicators for assessing dispersion and differentiation between populations (Gilg & Hilbish, 2003). This information is crucial for establishing protected areas for the species and identifying nursery zones.

5. Conclusion

This study represents the first larval dispersal model of *Maja squinado* on a Western Mediterranean scale. Our analyses, combining graphical observations, have provided insights into the dispersal patterns and potential impacts of climate change on the larval stages of this commercially exploited species. The relatively short pelagic larval duration (PLD) of *Maja squinado* likely explains the observed relationship between the disappearance of the species in heavily fished areas and poorly connected zones. For example, the Balearic Islands, which are geographically isolated, do not consistently connect with other

coastal areas due to the limited pelagic larval duration of the spinous spider crab. This isolation could be a primary factor in the species' decline in these regions. However, this hypothesis requires further investigation, including genetic analyses, to better understand the level of population isolation. The predictions from our simulations allow us to observe interannual changes, especially in the context of post-warming acceleration shifts. It is of the utmost importance to incorporate these climatic considerations into future models, as global changes not only affect the dynamics of ocean currents, which are crucial for larval dispersal, but also directly impact the physiology of the modelled organisms. Our results emphasise the necessity to integrate biophysical modelling approaches with other methodologies, particularly genetic studies. For instance, it is of the utmost importance to determine whether the populations within the Sardinia-Corsica cluster are homogeneous or exhibit significant genetic differentiation. Such combined approaches will provide a more comprehensive understanding of the population dynamics and connectivity of *Maja squinado*. In conclusion, while the current study provides valuable insights, it also highlights the necessity for multidisciplinary research to address the complex interactions between environmental changes, species physiology, and population connectivity.

6. References

Abelló, P., Guerao, G., Salmerón, F., & Raso, J. E. G. (2014). *Maja brachydactyla* (Brachyura: Majidae) in the western Mediterranean. *Marine Biodiversity Records*, *7*, e77.

Adams, D. K., Arellano, S. M., & Govenar, B. (2012). Larval dispersal: vent life in the water column. *Oceanography*, *25*(1), 256-268.

Alcaraz, M., Calbet, A., Estrada, M., Marrasé, C., Saiz, E., & Trepat, I. (2007). Physical control of zooplankton communities in the Catalan Sea. *Progress in Oceanography*, *74*(2-3), 294-312.

Al-Qattan, N., Herbert, G. S., Spero, H. J., McCarthy, S., McGeady, R., Tao, R., & Power, A. M. (2023). A stable isotope sclerochronology-based forensic method for reconstructing debris drift paths with application to the MH370 crash. *AGU Advances*, *4*(4), e2023AV000915.

Angeletti, R., Binato, G., Guidotti, M., Morelli, S., Pastorelli, A. A., Sagratella, E., ... & Stacchini, P. (2014). Cadmium bioaccumulation in Mediterranean spider crab (*Maja squinado*): Human consumption and health implications for exposure in Italian population. *Chemosphere*, *100*, 83-88.

Anger, K. (1991). Effects of temperature and salinity on the larval development of the Chinese mitten crab *Eriocheir sinensis* (Decapoda: Grapsidae). *Marine ecology progress series. Oldendorf*, *72*(1), 103-110.

Anger, K., Queiroga, H., & Calado, R. (2015). Larval development and behaviour strategies in Brachyura. In *Treatise on Zoology-Anatomy, Taxonomy, Biology. The Crustacea, Volume 9 Part C (2 vols)* (pp. 317-374). Brill.

Arakawa, A. (1977). Computational design of the basic dynamical processes of the UCLA general circulation model. Methods in Computational Physics. Advances in Research and Application, Vol. 17: General circulation models of the atmosphere, 337.

Azra, M. N., Chen, J. C., Hsu, T. H., Ikhwanuddin, M., & Abol-Munafi, A. B. (2019). Growth, molting duration and carapace hardness of blue swimming crab, *Portunus pelagicus*, instars at different water temperatures. *Aquaculture reports*, *15*, 100226.

Balss, H., Crustacea VII: Decapoda Brachyura (Oxyrhyncha und Brachyrhyncha) und geographische Übersicht über Crustacea Decapoda. Beitr. Kennt. Meeresfauna Westafr., 3 (1922) 71–110.

Begon, M., ownsend, C., arper, J. (2005). Ecology: rom Individuals to Ecosystems. In Freshwater Biology—FRESHWATER BIOL (Vol. 51).

Bianchi, C. N., & Morri, C. (2000). Marine biodiversity of the Mediterranean Sea: situation, problems and prospects for future research. *Marine pollution bulletin*, *40*(5), 367-376.

Bousquet, C., Bouet, M., Patrissi, M., Cesari, F., Lanfranchi, J. B., Susini, S., ... & Durieux, E. D. (2022). Assessment of catch composition, production and fishing effort of small-scale fisheries: The case study of Corsica Island (Mediterranean Sea). *Ocean & Coastal Management*, *218*, 105998.

Bryars, S. R., & Havenhand, J. N. (2006). Effects of constant and varying temperatures on the development of blue swimmer crab (*Portunus pelagicus*) larvae: Laboratory observations and field predictions for temperate coastal waters. *Journal of Experimental Marine Biology and Ecology*, *329*(2), 218-229.

Calado, R., Guerao, G., Gras, N., Cleary, D. F., & Rotllant, G. (2013). Contrasting habitats occupied by sibling spider crabs *Maja squinado* and *Maja brachydactyla* (Brachyura, Majidae) can influence the biochemical variability displayed by newly hatched larvae. *Journal of plankton research*, *35*(3), 684-688.

Carlson, A., Maynou, F., Basurco, B., & Bernal, M. (2016). Chapitre 2-Gestion des ressources marines vivantes. In Mediterra 2016 : Zéro gaspillage en Méditerranée (pp. 51-70). Presses de Sciences Po.Coll et al., 2014.

Corrochano-Fraile, A., Adams, T. P., Aleynik, D., Bekaert, M., & Carboni, S. (2022). Predictive biophysical models of bivalve larvae dispersal in Scotland. *Frontiers in Marine Science*, *9*, 985748.

Cowen, R. K. (2002). Larval Dispersal and Retention and Consequences for. *Coral reef fishes: dynamics and diversity in a complex ecosystem*, 149.

Cowen, R. K., Gawarkiewicz, G., Pineda, J., Thorrold, S., & Werner, F. (2002, November). Population connectivity in marine systems. In *Report of a workshop to develop science recommendations for the National Science Foundation* (Vol. 84, pp. 119-119).

de Mello, C., Barreiro, M., Hernandez-Garcia, E., Trinchin, R., & Manta, G. (2023). A Lagrangian study of summer upwelling along the Uruguayan coast. *Continental Shelf Research*, *258*, 104987.

Durán, J., Palmer, M., & Pastor, E. (2013). Growing reared spider crabs (*Maja squinado*) to sexual maturity: the first empirical data and a predictive growth model. *Aquaculture*, *408*, 78-87.

Durán, J., Pastor, E., Grau, A., & Valencia, J. M. (2012). First results of embryonic development, spawning and larval rearing of the Mediterranean spider crab *Maja squinado* (Herbst) under laboratory conditions, a candidate species for a restocking program. *Aquaculture Research*, *43*(12), 1777-1786.

Epifanio, C. E., & Garvine, R. W. (2001a). Larval Transport on the Atlantic Continental Shelf of North America: A Review. *Estuarine, Coastal and Shelf Science*, *52*, 51-77. https://doi.org/10.1006/ecss.2000.0727.

Escudier, R., Clementi, E., Cipollone, A., Pistoia, J., Drudi, M., Grandi, A., Lyubartsev, V., Lecci, R., Aydogdu, A., Delrosso, D., Omar, M., Masina, S., Coppini, G., & Pinardi, N. (2021). A High Resolution

Reanalysis for the Mediterranean Sea. *Frontiers in Earth Science*, *9*. https://www.frontiersin.org/articles/10.3389/feart.2021.702285.

FAO. (2020). *La situation mondiale des pêches et de l'aquaculture 2020 : La durabilité an action*. FAO. https://doi.org/10.4060/ca9229fr.

Flores-Valiente, J., Lett, C., Colas, F., Pecquerie, L., Aguirre-Velarde, A., Rioual, F., ... & Brochier, T. (2023). Influence of combined temperature and food availability on Peruvian anchovy (*Engraulis ringens*) early life stages in the northern Humboldt Current system: A modelling approach. *Progress in Oceanography*, *215*, 103034.

Garcia, L. (2007). *Garcia Ll (2007) Els crancs de les Balears. Quaderns de Natura de les Balears. Ed Documenta Balear SL, Palma de Mallorca, 104 pp*.

Gary, S. F., Fox, A. D., Biastoch, A., Roberts, J. M., & Cunningham, S. A. (2020). Larval behaviour, dispersal and population connectivity in the deep sea. *Scientific Reports*, *10*(1), Article 1. https://doi.org/10.1038/s41598-020-67503-7.

Gilg, M. R., Hilbish, J. (2003). The Geography of marine larval dispersal: coupling genetics with fine-scale physical oceanography. *Ecology*, *84*(11), 2989-2998. https://doi.org/10.1890/02-0498.

Gualtieri, J.-S., Aiello, A., Antoine-Santoni, T., Poggi, B., & DeGentili, E. (2013). Active tracing of *Maja squinado* in the Mediterranean Sea with wireless acoustic sensors: Method, results and prospectives. *Sensors (Basel, Switzerland)*, *13*(11), 15682-15691. https://doi.org/10.3390/s131115682.

Guerao, G., & Rotllant, G. (2010). Development and growth of the early juveniles of the spider crab *Maja squinado* (Brachyura: Majoidea) in an individual culture system. *Aquaculture*, *307*(1-2), 105-110.

Guerao, G., Rotllant, G., Gisbert, E., Uyà, M., & Cardona, L. (2016). Consistent habitat segregation between sexes in the spider crabs *Maja brachydactyla* and *Maja squinado* (Brachyura), as revealed by stable isotopes. *Scientia Marina*, *80*. https://doi.org/10.3989/scimar.04236.23B.

Herbst, J.F.W., 1788. Versuch einer Naturgeschichte der Krabben und Krebse nebst einer systematischen Beschreibung ihrer verschiede-nen Arten. Lange, G.A., Berlin and Stralsund, pp. 207–238.

Hixon, M. A., & Jones, G. P. (2005). Competition, Predation, and Density-Dependent Mortality in Demersal Marine Fishes. *Ecology*, *86*(11), 2847-2859. https://doi.org/10.1890/04-1455.

Hoang, T., Lee, S. Y., Keenan, C. P., & Marsden, G. E. (2002). Effect of temperature on spawning of Penaeus merguiensis. *Journal of Thermal Biology*, *27*(5), 433-437.

Imzilen, T., Kaplan, D. M., Barrier, N., & Lett, C. (2023). Simulations of drifting fish aggregating device (dFAD) trajectories in the Atlantic and Indian Oceans. *Fisheries Research*, *264*, 106711. https://doi.org/10.1016/j.fishres.2023.106711.

Jahnke, M., & Jonsson, P. R. (2022). Biophysical models of dispersal contribute to seascape genetic analyses. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *377*(1846), 20210024. https://doi.org/10.1098/rstb.2021.0024.

Johnston, D. J., & Yeoh, D. E. (2021). Temperature drives spatial and temporal variation in the reproductive biology of the blue swimmer crab *Portunus armatus* A. Milne-Edwards, 1861 (Decapoda: Brachyura: Portunidae). *Journal of Crustacean Biology*, *41*(3), ruab032.

King, S., Saint-Amand, A., Walker, B. K., Hanert, E., & Figueiredo, J. (2023). Larval dispersal patterns and connectivity of Acropora on lorida's Coral Reef and its implications for restoration. *Frontiers in Marine Science*, *9*. https://www.frontiersin.org/articles/10.3389/fmars.2022.1038463.

Lazure, P., & Dumas, F. (2008). An external–internal mode coupling for a 3D hydrodynamical model for applications at regional scale (MARS). *Advances in Water Resources*, *31*(2), 233-250. https://doi.org/10.1016/j.advwatres.2007.06.010.

Lett, C., Ayata, S.-D., Huret, M., & Irisson, J.-O. (2010). Biophysical modelling to investigate the effects of climate change on marine population dispersal and connectivity. *Progress In Oceanography*, *87*, 106-113. https://doi.org/10.1016/j.pocean.2010.09.005.

Lett, C., Verley, P., Mullon, C., Parada, C., Brochier, T., Penven, P., & Blanke, B. (2008). A Lagrangian tool for modelling ichthyoplankton dynamics. *Environmental Modelling and Software*, *23*(9), 1210. https://doi.org/10.1016/j.envsoft.2008.02.005.

López-Jurado, J. L., García-Lafuente, J. M., & Cano-Lucaya, N. (1995). Hydrographic conditions of the Ibiza Channel during November 1990, March 1991 and July 1992. https://digital.csic.es/handle/10261/317533.

Marengo, M., Pere, A., Marchand, B., Lejeune, P., & Durieux, E. (2016). Catch variation and demographic structure of common dentex (Sparidae) exploited by Mediterranean artisanal fisheries. *Bulletin of Marine Science*, *92*. https://doi.org/10.5343/bms.2015.1041.

Marengo, M., Vanalderweireldt, L., Horri, K., Patrissi, M., Santoni, M.-C., Lejeune, P., & Durieux, E. (2023). Combining indicator trends to evaluate a typical Mediterranean small-scale fishery: a case study of Corsica. *Regional Studies in Marine Science*, *65*, 103087. https://doi.org/10.1016/j.rsma.2023.103087.

Margirier, F., Testor, P., Heslop, E., Mallil, K., Bosse, A., Houpert, L., ... & Taillandier, V. (2020). Abrupt warming and salinification of intermediate waters interplays with decline of deep convection in the Northwestern Mediterranean Sea. *Scientific Reports*, *10*(1), 20923.

Martín, P., Maynou, F., Stelzenmüller, V., & Sacanell, M. (2012). A small-scale fishery near a rocky littoral marine reserve in the northwestern Mediterranean (Medes Islands) after two decades of fishing prohibition. *Scientia Marina*, *76*. https://doi.org/10.3989/scimar.03471.07F.

Millot, C., & Taupier-Letage, I. (2005). Circulation in the Mediterranean Sea. In A. Saliot (Éd.), *The Mediterranean Sea* (p. 29-66). Springer. https://doi.org/10.1007/b107143.

Modena, M., Mori, M., & Vacchi, M. (2001). Note su alcuni crostacei malacostraci raccolti in aree adiacenti alla M/C Haven (Mar Ligure). *Biologia Marina Mediterranea*, *8*, 675-679.

Mura, M., & Corda, S. (2011). Crustacea Decapoda in the Sardinian Channel: a checklist. *Crustaceana*, *84*(5-6), 667-687.

Neumann V., (1998). A review of the *Maja squinado* (Crustacea: Decapoda: Brachyura) species-complex with a key to the eastern Atlantic and Mediterranean species of the genus. *Journal of Natural History*, *32*(10-11), 1667-1684. https://doi.org/10.1080/00222939800771191.

Okubo, A. (1994). The role of diffusion and related physical processes in dispersal and recruitment of marine populations. In *The Bio-Physics of Marine Larval Dispersal* (p. 5-32). American Geophysical Union (AGU). https://doi.org/10.1029/CE045p0005.

Ospina-Alvarez, A., Weidberg, N., Aiken, C., & Navarrete, S. (2018). Larval transport in the upwelling ecosystem of central Chile: he effects of vertical migration, developmental time and coastal topography on recruitment. *Progress In Oceanography*, *168*. https://doi.org/10.1016/j.pocean.2018.09.016.

Pastor, F., Valiente, J. A., & Khodayar, S. (2020). A warming Mediterranean: 38 years of increasing sea surface temperature. *Remote sensing*, *12*(17), 2687.

Peliz, A., Marchesiello, P., Dubert, J., Marta-Almeida, M., Roy, C., & Queiroga, H. (2007). A study of crab larvae dispersal on the estern Iberian Shelf: Physical processes. *Journal of Marine Systems*, *68*(1), 215-236. https://doi.org/10.1016/j.jmarsys.2006.11.007.

Pinardi, N., Zavatarelli, M., Adani, M., Coppini, G., Fratianni, C., Oddo, P., ... & Bonaduce, A. (2015). Mediterranean Sea large-scale low-frequency ocean variability and water mass formation rates from 1987 to 2007: A retrospective analysis. *Progress in Oceanography*, *132*, 318-332.

Pineda, J., Hare, J., & Sponaugle, S. (2007). Larval Transport and Dispersal in the Coastal Ocean and Consequences for Population Connectivity. *Oceanography*, *20*(3), 22-39. https://doi.org/10.5670/oceanog.2007.27.

Pinot, J.-M., López-Jurado, J., & Riera, M. (2002). The CANALES experiment (1996-1998). Interannual, seasonal, and mesoscale variability of the circulation in the Balearic Channels. *Progress In Oceanography*, *55*, 335-370. https://doi.org/10.1016/S0079-6611(02)00139-8.

Pipitone, C., & Arculeo, M. (2003). The marine Crustacea Decapoda of Sicily (central Mediterranean Sea): a checklist with remarks on their distribution. *Italian Journal of Zoology*, *70*(1), 69-78.

Power, J. (1984). *Advection, Diffusion, and Drift Migrations of Larval Fish* (p. 27-37). https://doi.org/10.1007/978-1-4613-2763-9_2.

Power, J. H. (1984). Advection, diffusion, and drift migrations of larval fish. In *Mechanisms of Migration in Fishes* (pp. 27-37). Boston, MA: Springer US.

Rojas-Araos, F., Rojas-Hernández, N., Cornejo-Guzmán, S., Ernst, B., Dewitte, B., Parada, C., & Veliz, D. (2024). Population genomic and biophysical modeling show different patterns of population connectivity in the spiny lobster *Jasus frontalis* inhabiting oceanic islands. *Marine Environmental Research*, *193*, 106253.

Rotllant, G., Aguzzi, J., Sarria, D., Gisbert, E., Sbragaglia, V., Río, J. D., Simeó, C. G., Mànuel, A., Molino, E., Costa, C., & Sardà, F. (2015). Pilot acoustic tracking study on adult spiny lobsters (*Palinurus mauritanicus*) and spider crabs (*Maja squinado*) within an artificial reef. *Hydrobiologia*, *742*(1), 27-38. https://doi.org/10.1007/s10750-014-1959-5.

Rotllant, G., Guerao, G., Gras, N., & Estevez, A. (2014). Larval growth and biochemical composition of the protected Mediterranean spider crab *Maja squinado* (Brachyura, Majidae). *Aquatic Biology*, *20*, 13-21. https://doi.org/10.3354/ab00540.

Saint-Amand, A., Lambrechts, J., & Hanert, E. (2023). Biophysical models resolution affects coral connectivity estimates. *Scientific Reports*, *13*(1), Article 1. https://doi.org/10.1038/s41598-023-36158-5

Šargač, Z., Giménez, L., González-Ortegón, E., Harzsch, S., Tremblay, N., & Torres, G. (2022). Quantifying the portfolio of larval responses to salinity and temperature in a coastal-marine invertebrate: A cross population study along the European coast. *Marine Biology*, *169*(6), 81. https://doi.org/10.1007/s00227-022-04062-7.

Seytre, C., Vanderklift, M. A., Bodilis, P., Cottalorda, J. M., Gratiot, J., & Francour, P. (2013). Assessment of commercial and recreational fishing effects on trophic interactions in the Cap Roux area (north-western Mediterranean). *Aquatic Conservation: Marine and Freshwater Ecosystems*, *23*(2), 189-201.

Sotelo, G., Morán, P., & Posada, D. (2008). Genetic Identification of the Northeastern Atlantic Spiny Spider Crab as *Maja Brachydactyla (*Balss, 1922). *Journal of Crustacean Biology*, *28*(1), 76-81. https://doi.org/10.1651/07-2875R.1.

Steneck, R. S. (2006). Possible demographic consequences of intraspecific shelter competition among American lobsters. *Journal of Crustacean Biology*, *26*(4), 628-638.

Swearer, S., Treml, E., & Shima, J. (2019). *A Review of Biophysical Models of Marine Larval Dispersal* (p. 325-356). https://doi.org/10.1201/9780429026379-7.

Torres, A., Dos Santos, A., Alemany, F., & Massutí, E. (2013). Larval stages of crustacean species of interest for conservation and fishing exploitation in the western Mediterranean. *Scientia Marina*, *77*, 149-160. https://doi.org/10.3989/scimar.03749.26D.

van Sebille, E., Griffies, S. M., Abernathey, R., Adams, T. P., Berloff, P., Biastoch, A., Blanke, B., Chassignet, E. P., Cheng, Y., Cotter, C. J., Deleersnijder, E., Döös, K., Drake, H. F., Drijfhout, S., Gary, S. F., Heemink, A. W., Kjellsson, J., Koszalka, I. M., Lange, M., … i a, J. D. (2018). Lagrangian ocean analysis : undamentals and practices. *Ocean Modelling*, *121*, 49-75. https://doi.org/10.1016/j.ocemod.2017.11.008.

Vignoli, V., Caruso, T., & Falciai, L. (2004). Decapoda Brachyura from Monte Argentario (Mediterranean Sea, central Tyrrhenian). *Crustaceana*, *77*(2), 177-186.

Yin, J., Overpeck, J., Peyser, C., & Stouffer, R. (2018). Big jump of record warm global mean surface temperature in 2014–2016 related to unusually large oceanic heat releases. *Geophysical Research Letters*, *45*(2), 1069-1078.

Zaimen, F., Ghodbani, T., & Vermeren, H. (2021). L'activité de pêche artisanale au sud de la Méditerranée : Gouvernance, dynamique socio-économique et enjeux environnementaux dans le port algérien de Jijel (Boudis). VertigO-la revue électronique en sciences de l'environnement, 21(1).

Zakardjian, B. A., Runge, J. A., Plourde, S., & Gratton, Y. (1999). A biophysical model of the interaction between vertical migration of crustacean zooplankton and circulation in the Lower St. Lawrence Estuary. *Canadian Journal of Fisheries and Aquatic Sciences*, *56*(12), 2420-2432. https://doi.org/10.1139/f99-095.

Appendices

The sea surface temperature data extracted from the Copernicus Marine Environment Monitoring Service (CMEMS) satellite product over the western Mediterranean Sea demonstrated a temperature increase trend of 0.034 ± 0.002°C per year, with a 95% confidence interval. To analyse trends spatially and focus on the last decade, data from the Med MFC physical multiyear product (Mediterranean Sea Physics Reanalysis) were examined at all points in the Western Mediterranean (focusing on our study window). A linear temperature trend was calculated for each grid point based on time series data through linear regression. A color gradient from blue (indicating a decrease in temperature) to red (indicating an increase in temperature) was used to map these trends. The detailed analysis is presented in the figure A1 below.

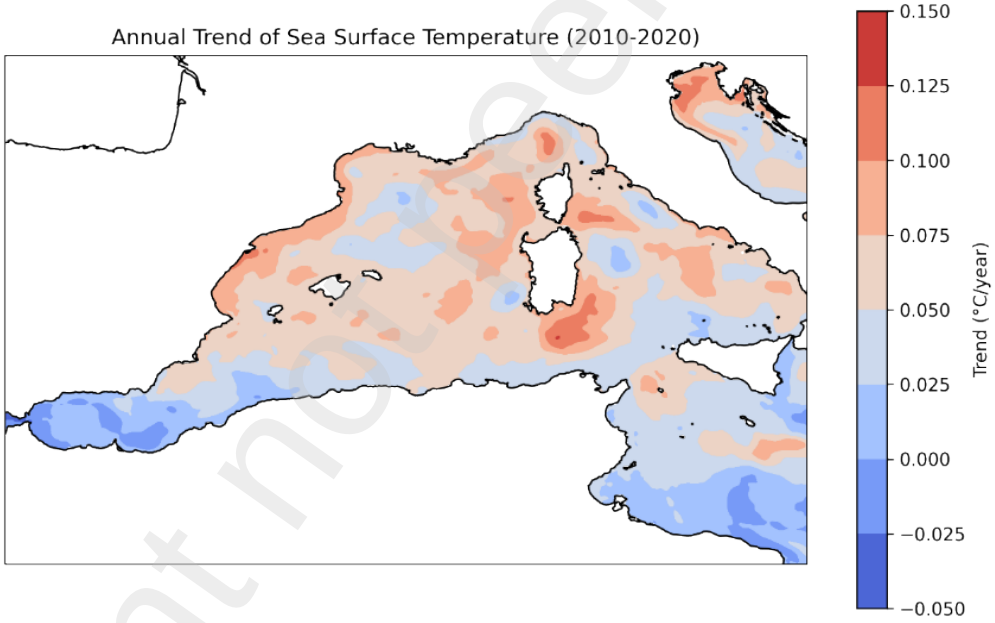


Figure A1: Sea Surface Temperature Trends in the Western Mediterranean from 2010 to 2020. This map illustrates the decadal trend in sea surface temperatures, with the color scale ranging from -0.050°C (blue) to +0.150°C (red), highlighting areas of temperature decrease and increase relative to the period average.