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Edible Sea urchin (*Paracentrotus lividus*) larval dispersal and connectivity modelling in the northwestern Mediterranean Sea



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ABSTRACT

The edible sea urchin (Paracentrotus lividus) is of significant economic importance due to high demand for its consumption in various Mediterranean countries. This echinoderm plays a crucial ecological role by regulating the dynamics of seaweed and seagrass through its grazing behaviour. The abundance of sea urchin is variable in time and space, but it is currently potentially declining in the Mediterranean Sea, and likely to be negatively affected by global change. Therefore, gaining a more comprehensive understanding of sea urchin larval dispersal patterns over an extended period could contribute to our understanding of how their dynamics relate to population connectivity. To investigate the trajectories of larval dispersal of this sea urchin in the Northwestern Mediterranean Sea, we combined a Lagrangian model (Ichthyop) with a hydrodynamic model (MARS3D). This study covered the years 2010-2018 and aimed to quantify the connectivity between the preferred habitats of the sea urchin (seagrasses and rocky substrates). The present study explores seasonal variations in dispersal routes and habitat connectivity relationships for two spawning scenarios identified in the literature (spring and autumn). The results enable us to identify dispersal routes, and their regularity over time. They highlight a consistent connection between Sardinia, Corsica, and the coastlines of the Ligurian and Tyrrhenian Seas, indicating a lack of genetic structuring within the edible sea urchin population in this area, particularly in Corsica. The connectivity matrices confirm the observed dispersal trajectories and highlight certain areas of significant and enduring local retention over time. The results also reveal minimal seasonal variability. Conversely, interannual variability appears pronounced, particularly in relation with trends in the warming of surface waters in the Mediterranean, which seem to impact the dispersal routes taken by P. lividus larvae. Lastly, a connectivity map was created to explore spatial resource management perspectives, aiming to identify frequent connections over an extended time period and assign varying levels of intensity to them. This approach can provide guidance with regard to resource management issues for different coastal areas that can be connected by larvae.

1. Introduction

In species with benthopelagic lifecycles and, consequently, planktonic larvae, dispersion processes play a crucial role by facilitating connectivity between distant areas and supporting the colonization of new habitats (Cowen and Sponaugle, 2009; Pineda et al., 2007). The dispersal of larvae is significantly influenced by ocean currents (White et al., 2010) and the biological characteristics of the species. Depending on the species, larvae might lack the ability to actively swim, as observed in sea urchins (Boudouresque and Verlaque, 2013), or they could perform vertical migrations, similar to crustaceans (Queiroga and Blanton, 2005; Anger et al., 2015), or they may possess the capacity for active oriented swimming, as seen in fish during their late larval stages (Leis, 2006; Faillettaz et al., 2018). Their recruitment and survival also hinge on their success in reaching suitable habitats, success that is greatly influenced by ocean currents (Sánchez and Gil, 2000) and the species' abilities. Substantial interannual variability in oceanic conditions can result in significant fluctuations in larval recruitment,

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retention and connectivity among populations from one year to the next (Siegel et al., 2008; Ospina-Alvarez et al., 2015). The abundances of larvae in *P. lividus* can vary considerably in time and space, as do the processes of settlement and recruitment, within a single year and between years, as shown by some studies conducted in the Mediterranean Sea (López et al., 1998; Hereu et al., 2004; Tomas et al., 2004). Understanding this interannual variability is especially critical for appropriately managing commercially exploited species (Wilderbuer et al., 2002; Churchill et al., 2011).

The edible sea urchin (*Paracentrotus lividus*) (Lamarck, 1816) is found throughout the Mediterranean Sea and to a lesser extent in the Northeastern Atlantic. This species plays a significant role in Mediterranean coastal waters in relation with its ecological (Boudouresque and Verlaque, 2013) and economic (Ceccherelli et al., 2011) importance. The sea urchin is not only fished and consumed, but it also holds a prominent position as a primary consumer of primary producers in food webs, capable of transforming habitats (Steneck, 2013).

P. lividus follows a benthopelagic life cycle, consisting of pelagic larval development and benthic juvenile and adult stages. In general, both males and females release gametes into the water column for external fertilization. This process leads to egg production, followed by three successive larval stages. Subsequently, the larvae become competent and have the ability to metamorphose into juvenile sea urchins in their benthic form (Duchaud et al., 2018). Abundances of P. lividus exhibit high variability in both time and space (Turon et al., 1995; Sala et al., 1998) and are influenced by various local factors, including seawater temperature, salinity, intra- and interspecific interactions (Fernandez and Pergent, 1998; Gianguzza et al., 2006; Guidetti, 2004), and habitat heterogeneity (Prado et al., 2012). For instance, in the Northwestern Mediterranean Sea, a primary spring spawning season is characterized by a larger quantity and higher quality of offspring, followed by a fall spawning season of lesser significance (Duchaud et al., 2021). Despite their importance for understanding the mechanisms that impact population dynamics (Hereu et al., 2012), there are a limited number of studies investigating the long-term abundance fluctuations of *P. lividus* sea urchins across extensive geographical scales.

P. lividus is a highly prized resource, consumed exclusively for its gonads. Consequently, intensive and targeted fishing quickly led to population collapses in the Atlantic (for instance, in Brittany and Ireland, Hannon et al., 2017) and in the Mediterranean (as observed in Sardinia), with an almost complete disappearance of individuals over 4 cm in diameter, the legal size for commercial purposes at this time (Guidetti, 2004). Conversely, certain populations and stocks appear to be preserved, such as in the Cantabria region of Spain (Guinda et al., 2017) and in Corsica (Duchaud et al., 2018), as demonstrated by the relatively high densities of individuals over 5 cm in those areas. In response to these observations, management measures have been implemented with regional adaptations. The main management tools include imposing size limits for capture, fishing quotas and capture seasons, and conducting monitoring surveys (Couvray, 2014). For example, along most Mediterranean coastlines, including Corsica, French fishermen must respect quotas and capture seasons. Only free diving fishing is allowed, and only individual specimens with a test diameter greater than 5 cm can be harvested. The authorized fishing period extends from autumn to early spring in order to respect the reproductive and growth periods of sea urchins, and is subject to potential changes over time (Duchaud et al., 2018). Alongside these management measures, marine protected areas (MPAs) and no-take zones (NTZs) have been established to attempt to restore stocks. Paradoxically, in some of these zones, edible sea urchin abundances remain low or are even non-existent. Several hypotheses can be considered to explain the low biomass levels observed. These may involve factors such as the increased abundance of sea urchin predators resulting from fishing regulations (such as Diplodus sargus) or ocean currents (Sala and Zabala, 1996; Guidetti, 2006).

hosted relatively stable populations of edible sea urchins, this is no longer the case today, with signs of decline (Duchaud et al., 2021). Despite regulatory measures in place to govern its exploitation, concerns persist among managers and scientists regarding the future of this resource due to the limited understanding of its demographic dynamics thus far (Duchaud et al., 2021). Given the scarcity of studies covering relatively extended time periods and large scales, numerical approaches and computer modelling emerge as suitable tools for tracing the larval dispersal in of this exploited species. The simulations carried out with this methodology necessitate data modelled or collected on-site on variables such as currents, and biological parameters for achieving the desired accuracy in the model. These data will be integrated with specific characteristics of the model species (Swearer et al., 2019).

Furthermore, studies have demonstrated that seawater temperature has a significant impact on the life cycles, reproductive periods, and overall metabolism of planktonic organisms, including echinoderms (Edmunds et al., 2005), influencing larval development and dispersion (O'Connor, 2008). These observations are consistent with findings regarding the warming trend in surface waters of the global ocean (Yin et al., 2018), particularly in the Mediterranean Sea (Margirier et al., 2020).

The main objective of the approach proposed here is to focus on the echinoderm *P. lividus* and investigate the larval dispersal routes taken over an extended period of time, as well as the interactions among coastal rocky habitats favored by this species within the Northwestern Mediterranean, particularly in the coastal areas of Corsica, Sardinia, and the Ligurian and Tyrrhenian coasts. Through a biophysical modelling approach, this study aims to investigate the dispersion dynamics of the edible sea urchin over a nine-year period (2010 to 2018) in relation to the two spawning seasons identified in the literature. Furthermore, in order to consider the context of global change and sea surface warming that could potentially influence larval dispersion, the simulations conducted were analysed by dividing the period into two sub-periods (2010 to 2014 and 2015 to 2018), corresponding to the warming signals identified by climatologists, to determine whether this trend impacts the dispersion routes of *P. lividus* larvae.

2. Materials & methods

2.1. Study area

The large-scale water circulation in the Mediterranean is characterized, in its Northern regions, by cyclonic current patterns generated by the shape of the continental slopes (Millot and Taupier-Letage, 2005). A recent overview of the general circulation pattern in the Mediterranean, at both the overall scale and the sub-basin level, has been provided by Pinardi et al. (2015). Concerning surface currents (0-15 m), from east to west, the Liguro-Provençal-Catalan Current (LPCC) flows between the Ligurian Sea, the Gulf of Lion, and the Northern areas of the Balearic Islands. The Gulf of Lion Gyre (GLG) circulates counter to the prevailing Gulf of Lion current. The Eastern Corsica Current (ECC) flows to the east of the Corsican coast, and the Northern Tyrrhenian Gyre (NTG) circulates southeast of Corsica. The South-Western Tyrrhenian Gyre circulates to the south of the Tyrrhenian Sea and passes close to the eastern coasts of Sardinia. In addition, flowing from west to east, the Southern Sardinia Current (SSC) circulates north of the Balearic Islands before flowing south of Sardinia, and the Middle Tyrrhenian Current (MTC) continues from the Southern Sardinia Current (SSC), flowing northward in the Tyrrhenian Sea (Fig. 1). The Corsica Channel connects the Tyrrhenian Sea located east of Corsica to the NW Mediterranean. To the east of the Strait of Bonifacio - between Sardinia and Corsica - the west winds are channelled and intensified, resulting in cyclonic circulation to the north. Finally, to the north of the island, the East Corsican Current is joined by the West Corsican Current, accompanied by the presence of eddies, to form the northward current.

While in the past shallow waters and coastal habitats in Corsica



Fig. 1. Map of the Northwestern Mediterranean surface circulation, 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. Larval dispersion model and simulation parameterization

The ocean current fields were extracted from the MARS3DMed (Ifremer), the regional configuration of the MARS3D model described in Lazure and Dumas (2008), and validated using observational data (Pairaud et al., 2011; Gatti and Pairaud, 2010). The current fields used here are available at 3-h intervals, on a $1/64^{\circ}$ grid (approximately 1.2) km), with 60 sigma layers, covering a large portion of the NW Mediterranean Sea, from 0° to 15°E and 39.5° to 44.5°N. Spatial discretization is performed using an Arakawa C type grid (Arakawa and Lamb, 1977), with sigma coordinates on the vertical axis. To simulate the larval dispersal of P. lividus, MARS3DMed was coupled with a Lagrangian tool (Ichthyop v3.3.12; Lett et al., 2008). Particle trajectories are tracked at a constant time step using a fourth-order Runge-Kutta model, which is commonly used as it enables trajectory tracking with adaptive time steps while restricting computational costs (Van Sebille et al., 2018). The biological parameters necessary to configure larval dispersion simulations primarily involve the pelagic larval duration (PLD), the presence or absence of specific larval behaviours, particle buoyancy, setting release and recruitment areas, and modelling of spawning dates/periods (summarized in Table 1). For this study, the transport duration was set to 37 days based on the work of Duchaud et al. (2021), with larvae considered competent (capable of settling in an area) from 30 days onwards. Release dates were configured in the Ichthyop tool by extracting all dates within the study period (2010 to 2018) for which sea surface temperatures ranged between 17 °C and 18 °C, the optimal temperature range for spawning as identified in the literature (Duchaud et al., 2021). Particle buoyancy has been described in the literature as a function of larval density, compelling particles to remain close to the surface, and is set at a value of 0.9 g.cm-3 (Epifanio and Garvine, 2001). Regarding specific larval behaviours, P. lividus larvae, while capable of some limited holding movement, are deemed unable to contend with the force of currents. Consequently, they will passively follow these currents within the framework of this model (Boudouresque and Verlague, 2013). Release and recruitment areas were pre-defined using QGIS software version 3.24.0. Polygons were drawn to encompass both seagrass and seagrass on rocky substrate habitats, which were identified as favourable to sea urchin spawning and settlement. These polygons were situated within a realistic bathymetric context, considering the presence of sea urchins (0-20 m), as informed by biological parameters documented in the species literature (Boudouresque and Verlague, 2013, 2020), and utilizing GIS data available on the EMODnet Portal (www. emodnet.eu). Thus, for each simulated year, batches of particles were

released from 25 predefined zones (Fig. 2). Finally, the "bouncing" option was selected in Ichthyop to return particles to the water when they encountered the coastline. This choice was made because sea urchin larvae, unlike other pelagic organisms such as large jellyfish, are not considered to be significantly affected by currents as they approach the coast.

2.3. Visualization and analysis of results

The simulation outputs were analysed using R Statistical Software (v.4.0.4; R Core Team 2021). Dispersion statistics were calculated for all 9 years combined, while distinguishing between the two distinct seasons. From these 9 years, the proportions of particles retained at the release site, those settling at a site other than the release site, or those not retained were calculated. These dispersion proportions were averaged, and a Gini coefficient was calculated and associated to measure the disparity between years and sites. It ranges from 0 (perfect equality) to 1 (extreme inequality). Between 0 and 1, inequality becomes stronger as the Gini index increases. It equals 0 in a situation of perfect equality where the variable takes an identical value across the entire population. At the other extreme, it equals 1 in the most unequal situation possible, where the variable is 0 for the entire population except for a single individual (Dorfman, 1979; He et al., 2004; Hixon and Jones, 2005). Trajectory density maps, connectivity matrices and comprehensive connectivity mapping analysis were subsequently performed for particles retained at any site. These analyses involved the following R packages: netcdf4 (v1.21; Pierce and Pierce, 2019), ggplot2 (v3.4.2; Wickham, 2016), and corrplot (v0.92; Wei and Simko, 2017). Permutation tests were conducted to evaluate differences in the proportions of local retention, distant settlement, and non-retained particles (abbreviated as NRP for non-retained particles, which means particles that have neither been retained within a distant zone nor within the same spawning zone), computed for the 25 release stations. They were executed using the R package coin (v1.4-2; Hothorn et al., 2008). The p-values for these tests are interpreted as follows: if they are less than 0.05, the observed differences are significantly distinct; conversely, if the p-value exceeds 0.05, the observed differences are not significantly distinct.

Table 1

Compilation of the parameters used to create the larval dispersion model for *Paracentrotus lividus* in the Northwestern Mediterranean using the Lagrangian transport tool Ichthyop.

Parameter	Value	Reference/Comments
Tool used for simulations Advection	Ichthyop v.3.3.16	Lett et al., 2008
numerical method	4th order Runge-Kutta	Van Sebille et al., 2018
Turbulence	Horizontal dispersion is implemented natively in Ichthyop following the literature.	Peliz et al., 2007
Number of simulations	2 per year – total: 18 simulations	
Release/ recruitment zones	25 release/recruitment zones	Release/recruitment parameterized using QGIS, based on the identification of habitats and depths favourable for the spawning/ development of <i>P. lividus</i> populations (Boudouresque and Verlaque, 2013).
Pelagic larval duration	37 days	Duchaud et al., 2018
Release dates	Release dates extracted for the period studied (2010 to 2018) corresponding to surface temperatures ranging from 17 °C to 18 °C (temperatures estimated as a favourable window for spawning). Please refer to Appendix A for more details.	Duchaud et al., 2021
Number of particles	2.106 per year	
Release depth	0–20 m	Boudouresque and Verlaque, 2013
Minimum age for particles retention	30 days	Duchaud et al., 2018
Buoyancy	0.9 g/cm3	Epifanio and Garvine, 2001
Vertical migration	Not applicable/negligible strength compared to the currents.	Boudouresque and Verlaque, 2013
Swimming behaviour	Not applicable/negligible strength compared to the currents. In Ichthyop, a rebound behaviour upon contact with	Boudouresque and Verlaque, 2013
Particles coastal behaviour	a physical barrier is imparted to particles, with an equivalent force to the force the particle would exert in order to penetrate the coastline).	Lett et al., 2008

3. Results

3.1. Connectivity matrices and fate of particles

The connectivity matrices (Fig. 3) allow us to highlight the average connectivity percentages over the studied period between source sites (on the ordinate) and sink sites (on the abscissa). The matrices are square and organized in such a way that the diagonal indicates local retention rates, i.e., the proportion of larvae retained in their original production site. Local retention is relatively high at most sites for both spring and fall releases. There is little variability in local retention over the studied period in western Corsica (WC1 and WC2), the Balearic Islands (BA1 and BA2), and the north and west of Sardinia (NSA and

WSA), for example (Gini index close to zero). On the other hand, Gini indices between 0.5 and 1 indicate an uneven contribution of years to local retention, as seen, for example, at CAP (Cap Corse), illustrating an irregular phenomenon over the nine-year study period. Aside from the local retention relationships within a site itself, the average connectivity percentages are lower. However, there are some relatively significant connectivity relationships observed, notably between Sardinia and Corsica (ESA and ECO, DBO and NSA), which remain consistent over time with a low Gini index. Connectivity exists between relatively distant areas, such as the Corsican stations (CAP, WC1, and WC2), and the Balearic Islands stations (BA1 and BA2), but the high Gini index suggests that these events are rare or even exceptional over the studied time period. Regarding the seasonal comparison, most relationships are observed both on the diagonal and in long-distance connections. However, some connectivity relationships only appear in the spring, such as between Corsican and Spanish stations (CAP, CW2, and WC1 with SP1), and even Spanish and Sardinian stations (SP2 and NSA). These relationships exist but have a low Gini index, indicating their rarity over the nine-year study period.

The particle fate, which represent numerical sea urchin larvae, is analysed in Tables 2 and 3. The term non-retained particles (NRP) refers to particles that do not reach any settlement zone by the end of the PLD. On the other hand, particles that reach a settlement zone different from, or the same as, the zone where they were initially released are categorized as "distant settlement" and "local retention", respectively. The results of the permutation test are presented in Table 2. According to these results, it appears that only the year 2015 shows significant differences between the fall and spring scenarios, specifically in terms of the proportion of particles lost at sea (p-value = 0.01) and the proportion of local retention (p-value = 0.0341). For the other values, there were no significant differences based on this test in relation to the season.

For further analysis, the proportions of local retention, distant settlement, and NRP were averaged annually to observe differences at the release stations over time (Table 3). Regarding the average NRP percentages (larval mortality) for both seasons, the 25th percentile is higher than 66%. Similarly, for both seasons, 25% or more of the stations have their 75th percentile higher than 80%. The minimum average percentages are all above 48%. Thus, it appears evident that regardless of the station and the seasonal scenario considered, the majority of dispersed larvae will be dispersed outside the favourable zones for their settlement. Regarding the distant settlement values, some differences can be observed between the spring and fall scenarios. For the Spanish stations (SP1 and SP2), the values are 6% to 10% higher in the fall scenario compared to the spring scenario. The same phenomenon is observed for the Ligurian Sea stations, particularly FR1, which shows a 12% higher dispersion percentage in the fall compared to the spring. The same observation applies to the Corsican stations, which, despite similar trends for both seasons, exhibit a higher average distant settlement percentage in the fall. For example, the average percentage is 7.89% higher in the fall for the ECO station (east Corsica) compared to the spring. Similar observations can be made for the Sardinian and Tyrrhenian Sea stations, albeit to a lesser extent. For the average percentages of local retention, over 25% of the stations have an average percentage higher than 10%. Seasonal differences are observed, with significantly higher values of local retention in the fall compared to the spring: for example, 40.42% in the fall versus 26.73% in the spring for the Spanish coast, or values higher than 30% for the coastal stations in the Tyrrhenian Sea in the fall (IT3, IT4), while they range from 15% to 20% in the spring. It is also noted that the percentages of local retention are higher by 10% in the fall compared to the spring for the Corsican stations ECO and DBO (east Corsica and Strait of Bonifacio). For all other stations, the average percentages in the fall scenario are 1% to 4% higher than the observed local retention percentages in the spring. The overall trend resulting from these average percentages of larval fate after 37 days of PLD is that the observed percentages are higher for the fall scenario compared to the spring scenario.



Fig. 2. The 25 zones utilized for the spawning and settlement habitats of sea urchins in the NW Mediterranean Sea are as follows: The polygons were strategically positioned within depths ranging from 0 to 20 m, in areas colonized by *P. lividus* (such as rocky regions and seagrass beds on rocky substrates). The designated zones include CAP Corsican Cape, ECO East Corsica, DBO Bonifacio Strait, WC1/WC2 West Corsica, NSA North Sardinia, ESA East Sardinia, WSA West Sardinia, BA1 to BA2 Balearic Islands, SP1 to SP3 Spanish coast, IT1 to IT10 Italian coast, and FR1/FR2 French coast. The blue line on the map indicates the 20-m depth isobath, while the source/sink polygons are marked in red and the habitats conducive to the growth of *P. lividus* are highlighted in green. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2. Larval trajectories in a changing Mediterranean Sea

Density maps of particles for spring (Fig. 4A) and autumn (Fig. 4B) releases illustrate the prevalent pathways taken by particles that eventually reach a settlement zone and their consistency over the years. The primary routes align with the general circulation in the NW Mediterranean Sea, connecting Corsica to the Ligurian Sea coasts and the entire Tyrrhenian Sea coastline. Pathways between Corsica and Sardinia, particularly through the Strait of Bonifacio, are also clearly visible. These routes correspond to the lowest coefficient of variation (CV) values in particle density (Fig. 5), indicating their yearly occurrence. Particles released north of Corsica tend to be transported to the Ligurian Sea regardless of the season. The central area of the basin is rarely crossed by particles, except sporadically, such as in spring 2013 (Fig. 4A) and autumn 2012 (Fig. 4B), explaining the high CV values observed in this region (Fig. 5). A similar pattern is observed in the central Tyrrhenian Sea, where particles seldom pass through, except in spring 2013. The Gulf of Lion falls between these two extremes, with particles passing through it in approximately half of the cases (spring 2010, 2012, 2014, 2015, 2016, 2018; autumn 2015 to 2018; Fig. 4), resulting in the average CV values observed there (Fig. 5). In summary, for both seasons examined, it is evident that from 2010 to 2014, trajectories traversed the basin from east to west, albeit infrequently (dark blue in Figures Fig. 4A and B, particularly in the years 2012, 2013, and 2014). Conversely, these occurrences, although rare, were no longer observed from 2015 to 2018. Thus, these maps suggest an apparent difference of dispersal from 2010 to 2014 and from 2015 to 2018, trends which will be explored in the remainder of this study.

To explore whether the consequences of global change, specifically the trend of increasing surface water temperatures, can influence dispersion trajectories, two temporal sub-periods were investigated. The study focused on the Northwestern Mediterranean and examined the changes in the rise in surface temperatures extracted from the MARS3DMed model during this period (Fig. 5). A trend line slope of 0.18, in the context of MARS3DMed temperature data, signifies that the average temperature increases each year between 2010 and 2018, resulting in a change in average temperature from 2010 to 2018 of $1.68~^{\circ}$ C according to the MARS3DMed data. In addition, the MARS3DMED data indicates a trend line slope of 0.43 for the period from 2010 to 2014 and 0.45 for the period from 2015 to 2018.

A study of variations in trajectory densities was conducted for the springtime spawning season, which appears to be the primary season according to the literature, covering two distinct time periods: 2010 to 2014 (Fig. 6A). and 2015 to 2018 (Fig. 6B). This mapping confirms a difference in the trajectories followed during these two temporal periods. While the main channels regularly traversed (such as those between Corsica and Sardinia or between Corsica and the coastlines of the Ligurian and Tyrrhenian Seas) remain highly prominent, some patterns appear to decrease or even vanish from 2015 onwards. For instance, connections that used to occur between the Balearic Islands and the Spanish coast seem to have significantly decreased since 2015, in addition to a reduction in the frequency and intensity of connections that appeared to take place between Northern Corsica and the Ligurian Sea coastline.

3.3. Graphic representations for management purposes

To make the current modelling work available in the context of spatial resource management perspectives, a conceptual map was created (Fig. 7). Its purpose was to highlight the primary connectivity relationships (excluding local retention) between release and parameterized retention measurement zones near the NW Mediterranean coastlines. This map was specifically crafted for the spring spawning season, as it is considered as the principal spawning season according to existing literature. On the map green arrows represent connectivity relationships with Gini index values ranging from 0 to 0.5. This indicates a tendency towards regular or systematic connectivity relationships throughout the study period (2010 to 2018). In contrast, paths represented in red denote rarer relationships over time. The thickness of the green arrows reflects the average percentage of connectivity between stations, referring to values calculated in the connectivity matrices previously presented in this study. This map thus provides a spatial perspective on frequent connectivity relationships over time, consequently highlighting displaying larval exchanges. It validates the cluster



Fig. 3. Connectivity matrices for the NW Mediterranean Sea stations between spawning areas (y-axis) and settlement habitats (x-axis) for the spring (A) and the fall (B) releases over the 2010–2018 period.

formed by Sardinia and Corsica, as well as connections among the Balearic Island stations and Spanish stations. In terms of the regularity and intensity of exchanges, some stations appear isolated from others, such as those in the Balearic Islands, despite a relatively long PLD of 37 days during the study period. Finally, along the coastlines of the Tyrrhenian and Ligurian Seas, it can be observed that the direction vectors of the green arrows align as might be expected with the main currents.

Table 2

Summary table of *p*-values calculated in conjunction with permutation tests conducted on the proportions of particle fates, for all combined stations and each year (NRP = non-retained particles, DS = distant settlement, and LR = local retention).

Year	NRP*	DS*	LR*
2010	0.797	0.8685	0.575
2011	0.6191	0.3668	0.5081
2012	0.9774	0.9713	0.926
2013	0.3181	0.6428	0.9004
2014	0.528	0.0738	0.261
2015	0.01	0.1723	0.0341
2016	0.5123	0.9948	0.6946
2017	0.3	0.1105	0.4574
2018	0.3144	0.729	0.234

4. Discussion

We used currents from a regional configuration of the MARS3D hydrodynamic model covering the Northwestern Mediterranean Sea in order to investigate the pelagic phase of the sea urchin life cycle, especially around Corsica. MARS3D focuses on coastal oceanography, encompassing regional scales spanning a few tens of kilometers to coastal scales within a few hundred meters (Lazure and Dumas, 2008), enabling the study of the effects of spatial and temporal variability on sea urchin larval dispersal.

Knowledge of demographic connectivity is crucial to the understanding of spatiotemporal dynamics of fragmented populations (Kool et al., 2013) and essential in fisheries management to define sustainable yields (Legrand, 2022). For this species with limited larval behaviour, i. e. reduced swimming movements and migration compared to current speeds (Boudouresque and Verlaque, 2013, 2020), the primary factor influencing dispersal is indeed the seasonal and inter-annual variability of ocean currents. We identified years and seasons that appeared more suitable for larval local retention, whereas others allowed a wider dispersal of larvae across the basin and thereby connectivity to distant sites. Notably, local retention was globally high in the coastal areas considered as suitable habitats for P. lividus.

It is necessary to distinguish between the often-confused indices local retention and self-recruitment (Burgess et al., 2014; Lett et al., 2015). Only individuals that establish themselves in their population of origin after the larval dispersal process can be considered as "self-recruited" offspring. The self-recruitment process is often considered predominant in the demographic maintenance of populations, such as tropical fish (Teske et al., 2016). However, self-recruitment does not inform on population dynamics and persistence as much as local retention does (Burgess et al., 2014; Lett et al., 2015). Besides, the demographic interdependence between populations depends on the number of selfrecruits and propagules exchanged during dispersal, not the proportion, in order to compensate for mortality (Lowe and Allendorf, 2010). The influx of individuals from other populations is often crucial for its potential maintenance (Sanz-Aguilar et al., 2016) and may represent a significant fraction of the total number of recruits. A population is considered demographically interdependent when at least 10% of recruited individuals come from other populations (Waples and Gaggiotti, 2006). The results of the present study show success rates of dispersal approaching 10%, for example, in the spring scenario of the Balearic Islands (BA2, 10.9%), or much higher, as in the spring scenario of the Bonifacio Strait (DBO, 29.3%). Similar observations can be made for the autumn scenario. Therefore, it could be of interest to further investigate this question of demographic interdependence in the edible sea urchin.

For a species like *P. lividus*, which has a relatively long PLD, the conducted Lagrangian simulations showed both a high rate of local retention regardless of the season and a non-significant potential for exchange between more distant areas. This supports the hypothesis of connectivity among *P. lividus* populations across different sub-regions of the NW Mediterranean, aligning with the findings of Paterno et al. (2017). However, the present study also demonstrates that these connectivity relationships between more distant areas are not consistent over a nine-year period. The results presented in this study align with the high temporal and interannual variability observed as a general feature in sea urchin settlement and recruitment (McEdward and Miner, 2001). Furthermore, this study also supports hypotheses historically put forth

Table 3

Fate of particles released in each zone parameterized in simulations conducted in the Northwestern Mediterranean using the MARS3DMed model, averaged over the studied temporal period (2010–2018), for each seasonal scenario.

Spring			Fall						
n°	station	mean NRP*	mean DS*	mean LR*	n°	station	mean NRP*	mean DS*	mean LR*
1	BA2	80.389%	10.989%	8.622%	1	BA2	84.878%	10.067%	5.033%
2	BA1	82.511%	8.444%	9.089%	2	BA1	71.600%	10.400%	17.989%
3	SP1	87.633%	10.000%	2.356%	3	SP1	82.733%	16.844%	0.422%
4	SP2	77.722%	9.122%	13.189%	4	SP2	70.344%	20.089%	9.567%
5	SP3	64.967%	8.289%	26.733%	5	SP3	55.178%	4.378%	40.422%
6	FR2	76.000%	13.088%	11.522%	6	FR2	67.344%	14.367%	18.300%
7	FR1	73.622%	14.700%	11.667%	7	FR1	67.422%	26.844%	5.744%
8	IT10	71.533%	17.911%	10.567%	8	IT10	73.878%	18.844%	7.267%
9	IT9	75.511%	19.844%	4.644%	9	IT9	70.633%	24.233%	5.178%
10	IT8	67.356%	14.000%	18.644%	10	IT8	76.456%	13.311%	10.233%
11	IT7	73.600%	24.767%	1.656%	11	IT7	68.700%	28.578%	2.722%
12	IT6	56.989%	15.611%	27.400%	12	IT6	53.044%	13.011%	33.967%
13	CAP	61.989%	27.411%	10.578%	13	CAP	67.322%	24.233%	8.444%
14	WC2	84.356%	2.667%	12.978%	14	WC2	81.689%	3.422%	14.900%
15	WC1	67.422%	20.978%	11.600%	15	WC1	72.700%	15.578%	11.711%
16	ECO	59.778%	18.778%	21.489%	16	ECO	63.489%	26.667%	9.856%
17	DBO	50.944%	29.233%	19.811%	17	DBO	62.533%	28.011%	9.467%
18	NSA	71.267%	17.478%	11.256%	18	NSA	67.989%	23.667%	8.311%
19	WSA	73.622%	10.833%	15.589%	19	WSA	81.567%	9.078%	9.344%
20	ESA	86.989%	1.900%	11.122%	20	ESA	86.989%	2.844%	10.167%
21	IT5	88.367%	1.533%	10.067%	21	IT5	92.467%	1.456%	6.078%
22	IT4	82.067%	3.356%	14.578%	22	IT4	66.011%	2.744%	31.278%
23	IT3	76.589%	1.600%	21.811%	23	IT3	57.378%	2.033%	40.589%
24	IT2	86.922%	1.800%	11.278%	24	IT2	88.989%	0.733%	10.267%
25	IT1	54.189%	16.489%	29.311%	25	IT1	48.133%	11.744%	40.133%

*NRP = non-retained particles, DS = distant settlement (when a particle reaches a favourable zone for its installation), *LR (local retention).





Fig. 4. Density maps of particles along their trajectories for particles eventually reaching a settlement zone, aggregated over each year of the 2010–2018 period for (A) spring release and (B) fall release.

by scientists in the literature, attempting to explain observations of heterogeneity in the distribution of sea urchin larvae in the water column, particularly physical factors such as circulation and coastal topography, especially orientation and exposure to waves (Hereu et al., 2004), which would be interesting to explore with higher-resolution coastal models. Population genetics studies conducted in the Mediterranean have revealed that there is no genetic structuring at the scale of Corsica in the edible sea urchin (Duchaud et al., 2021). When comparing these findings with our results, we observe regular and recurrent exchanges between Corsica and Sardinia, as well as between Corsica and the coasts of the Ligurian and Tyrrhenian Seas. These patterns suggest a significant



Average temperature patterns of change (MARS3DMed) - 2010 to 2018 Trend line slope = 0.18

Fig. 5. (A) Patterns of change in surface temperatures extracted from the MARS3DMed model for the period 2010 to 2018. The black line represents the average temperature, while the red and blue lines represent the minimum and maximum quantiles, respectively. Focus on the sub-period 2010 to 2014 (B) and 2015 to 2018 (C). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

level of genetic mixing in this particular sub-basin.

Population genetics studies conducted on edible sea urchins have revealed population genetic structure at a scale encompassing the entire island of Corsica (Duchaud et al., 2021). The results of this study support the hypothesis that Corsican sites may be regularly supplied with allochthonous larvae over time, and that these larvae spawned on Corsican coasts can disperse far enough to settle in other areas, as their larval lifespan is long enough to allow for such dispersal (Cowen et al., 2006).

Studies conducted on a broader scale, such as Duran et al. (2004) on populations of edible sea urchins in twelve localities across southwest Europe, have revealed high levels of genetic diversity but low levels of genetic structure. This suggests a strong degree of gene flow between populations and panmixis within the Mediterranean and Atlantic basins (the principle that individuals are distributed homogeneously within a population and contribute, in reproductive terms, to the formation of the next generation). The study suggests that gene flow is occurring over large distances, and our results highlight that for a relatively long larval lifespan, the passive larvae of *P. lividus* are capable of establishing connectivity relationships in distant areas from their spawning site, using regularly traveled trajectory channels over the years, involving regular larval exchanges and gene flow over time.

Other larger-scale studies, such as Penant et al. (2013), discuss the

genetic differentiation of *P. lividus* between the Atlantic Ocean and the Mediterranean Sea, as well as among different Mediterranean basins. According to their findings, it is unlikely that chaotic genetic patchiness is the sole factor responsible for such differentiation. Chaotic genetic patchiness refers to an unexpected and complex pattern of genetic distribution observed within a population, characterized by genetic variations that are clustered in patches of varying sizes and shapes.

Penant et al. (2013) thus propose that other factors may explain the divergence among basins and mention stable hydrological exchanges over several years, which aligns with our results indicating consistent channels and connectivity patterns over time, as indicated by the Gini index and low variation coefficients. If exchanges between basins are regular over time, it is possible that coastal populations of edible sea urchins are genetically homogeneous within these regular exchange zones but highly differentiated from basins that have no communication. In this case, the barriers are not physical obstacles but rather limitations in dispersal beyond the larval lifespan due to marine currents. Consequently, it would be interesting to combine larval dispersal modelling approaches with population genomics to enhance the robustness of the results. However, comparing these two approaches is challenging because genetics incorporates information across multiple generations and proximity, whereas larval dispersal approaches do not have the same scope.



Fig. 6. Coefficient of Variation (CV%) of particle density along their trajectories for particles that eventually reach a settlement zone, for the period 2010 to 2014 (A) and the period 2015 to 2018 (B), based on the springtime spawning scenario conducted using the MARS3DMed model in the Northwestern Mediterranean.



Fig. 7. Map showing connectivity relationships (excluding local retention) for different release and recruitment measurement zones in *P. lividus* in the Northwestern Mediterranean. Green lines represent connectivity relationships with Gini indices ranging from 0.5 to 0 (indicating consistent connectivity relationships over the study period), while red lines illustrate rare or exceptional relationships over time. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Regarding the two spawning scenarios, spring and autumn, our study provides additional information compared to other approaches used by specialists in the development of *P. lividus* (Duchaud et al., 2021).

Although the patterns, main channels followed, and trends in connectivity relationships are indeed comparable, it appears that the average percentages of distant settlement and local retention are higher in autumn than in spring. This could be explained by the higher average speed of currents in autumn-winter compared to spring-summer in the NW Mediterranean, with the main currents strengthening (MARS3D data). Thus, larvae are potentially carried further during this period. The current patterns for these two periods and the use of a species with a relatively long PLD suggest that the differences in both the densities of the trajectories taken and the connectivity relationships are not significant. Therefore, these results can be qualitatively interpreted in a comparable manner, but they must be interpreted quantitatively with caution. In terms of larval quantity produced, several studies, including those in other basins, assert that autumn spawning is significantly lower in quantity than spring spawning, leading to lower connectivity and colonization probabilities due to high larval mortality regardless of the season (Antoniadou and Vafidis, 2009; Ouréns et al., 2011; Murillo-Navarro and Jiménez-Guirado, 2012).

In fact, there is probably variability in spawning periods within the NW basin itself. De la Uz et al. (2018) suggested that gonadal indices (GIs) exhibit irregular trends, making it challenging to identify the reproductive pattern of the edible sea urchin across the entire Mediterranean basin. Ghirardini et al. (2005) measured GIs to assess the quality of male and female sea urchin spawners, but acknowledged that the quantity of gonads cannot be equated with reproductive quality. They also demonstrated that the origin of sea urchins can influence the quality of spawners, as coastal waters quality affects larval growth rate.

Recent studies (El Idrissi et al., 2023; Marengo et al., 2023) focusing on the presence of pollutants in seawater from mining residues have highlighted the existence of a coastal current that transports the pollution along the west coast of Cap Corse, flowing in a north-south direction. These currents do not seem to be captured by the MARS3DMed model due to its high resolution (1.2 km), whereas they are located closer to the coastline, about a hundred meters offshore. Specifically, El Idrissi et al. (2023) studied the contamination of *P. lividus* larvae by these trace elements and also demonstrated the north-south coastal movement of contamination along the west coast of Cap Corse. These observations strongly suggest that dispersion processes and potentially population exchanges at micro-scales may occur. The use of models at different scales could help clarify these questions issues.

Finally, considering the variations in surface temperatures and their confirmed upward trend as indicated by the study of this variable in the MARS3DMed model, the observed marked differences in trajectory density variations between two temporal periods, namely 2010 to 2014 and 2015 to 2018, align with studies demonstrating that global change is likely to influence the trajectories and dispersion distances of planktonic organisms (Herrmann et al., 2014). These factors are of utmost importance, especially given research supporting an escalating global warming trend in the Mediterranean over recent decades, particularly impacting surface waters (Pastor et al., 2020). Recent studies have emphasized the warming of marine waters at global scale (Yin et al., 2018) and locally within Mediterranean basins and sub-basins, with an acceleration of this phenomenon between 2014 and 2015 (Margirier et al., 2020). A perspective in the study of P. lividus dispersion routes would be, over a temporal period of at least ten years, to attempt to observe the influence of environmental changes such as temperature increases on the distances traveled, and possibly expand the study beyond the scope of MARS3DMed in the Northwestern Mediterranean, using broader-scale models such as the Med MFC physical multiyear product (Escudier et al., 2020) to further elucidate connectivity relationships involving the Balearic Islands or the Southern coast of Sardinia.

The results obtained in this study regarding global change and illustrating variations in the dispersal routes of *Paracentrotus lividus* larvae in response to increasing surface temperatures in the Mediterranean should be considered alongside studies focusing on the impact of global change on larval development and recruitment. This includes assessing the consequences of such stress on their physiology. Studies conducted in the Canary Islands on two aspects of global change,

warming waters and acidification, have shown that sea urchin larvae can develop despite natural variations in pH in their environment, demonstrating a certain level of plasticity (García et al., 2018). However, experiments conducted under conditions predicted by future scenarios indicate that rising temperatures could potentially impact the survival of P. lividus larvae by altering the energy budget allocated to development under stressful conditions (García et al., 2015a). Furthermore, these studies also demonstrate that the adverse effects of pH reduction, beyond natural variations, on sea urchin larvae and their settlement could be mitigated by increased water temperatures, indicating that larval development and the performance of P. lividus are improved by slight temperature increases despite a pH decrease (García et al., 2015b). Therefore, studies focusing on tolerance measurements under stressful conditions could significantly enhance future larval dispersal models, providing more precise information on spawning dates and potentially lethal temperature and pH conditions for larvae, thereby making future models more realistic.

This study offers valuable insights into larval dispersion routes and connectivity relationships among habitats for the edible sea urchin on a Northwestern Mediterranean scale. However, it is clear that the next logical step and the continuation of this research would involve validating these hypotheses and refining these models using various approaches. These could include population genetics studies at different scales within the basin and physiological research to precisely determine spawning periods in relation to Mediterranean sub-regions. This would also entail taking into account the differing quality of spawning areas and the quantity of released particles.

5. Conclusion

This study has unveiled the primary patterns and main dispersion routes taken by P. lividus larvae during their larval lifespan in the NW Mediterranean. The study's findings reveal basin-scale connectivity, with consistent connections observed over time between Sardinia, Corsica, and the coastlines of the Ligurian and Tyrrhenian Seas. Minimal seasonal variation was observed between the two spawning seasons identified in the literature. These results align with those generated by other scientific approaches, such as population genetics, which indicate a lack of genetic structuring within the edible sea urchin population in Corsica. Furthermore, local retention appears to play a significant role in specific areas, although finer-scale current data may be necessary to confirm this. Exploring the application of the Gini index and other indicators to assess the regularity or irregularity of observed connectivity phenomena over an extended temporal period could provide valuable insights for integrating modelling studies with the development of tools and indicators for managing exploited species. In addition, in light of climate observations regarding the warming of surface waters in the NW Mediterranean, it appears that dispersion trajectories, and thus the routes taken by larvae and potentially the connectivity relationships between subpopulations, may be influenced by future warming scenarios.

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. Appendix

The table below and the associated description provide details about the release dates of the particles used for conducting these simulations. These dates have been extracted from the NOAA database (https://www.noaa.gov/) and correspond to the days within the period from 2010 to 2018, during which sea surface temperatures in the Northwestern Mediterranean were between 17 °C and 18 °C. This temperature range corresponds to a spawning signal for the sea urchin *Paracentrotus lividus* in this geographical area. Starting from each of these dates, the particles underwent larval transport for a duration of 37 days, as mentioned in the bibliography (Duchaud et al., 2018).



dates (where 17°C < T°C sea surface < 18°C)

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C. Barrier et al.

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