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Recruitment Disruption and the Role of Unaffected Populations for Potential Recovery After the *Pinna nobilis* Mass Mortality Event

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A devastating mass mortality event (MME) very likely caused by the protozoan *Haplosporidium pinnae* first detected in 2016 in the Western Mediterranean Sea, is pushing the endemic bivalve *Pinna nobilis* to near extinction. Populations recovery, if possible, will rely on larval dispersal from unaffected sites and potential recolonization through recruitment of resistant juveniles. To assess the impact of the MME on the species' larval recruitment, an unprecedented network of larval collector stations was implemented over several thousands of kilometers along the Western Mediterranean coasts during the 3 years after the onset of the MME. The findings of this network showed a generalized disruption in recruitment with dramatic consequences for the recovery of the species. However, there were exceptions to this pattern and recruits

were recorded in a few sites where the resident population had been decimated. This hints to the importance of unaffected populations as larval exporting sources and the role of oceanographic currents in larval transport in the area, representing a beacon of hope in the current extremely worrying scenario for this emblematic species.

Keywords: critically endangered, mass mortality, recruitment, larval connectivity, Mediterranean Sea, hydrodynamic model, Lagrangian trajectories, recovery

INTRODUCTION

The Mediterranean endemic bivalve *Pinna nobilis* has been pushed to an extremely worrying, near-extinction status by an unprecedented mass mortality event (MME) starting in early autumn 2016 in the western Mediterranean Sea (Vázquez-Luis et al., 2017) and rapidly spreading eastward (Cabanellas-Reboredo et al., 2019; Katsanevakis et al., 2019; Kersting et al., 2019; Panarese et al., 2019). The first histological examinations already revealed the presence of a haplosporidan-like parasite within the digestive gland of affected pen shells (Darriba, 2017; Vázquez-Luis et al., 2017) and a subsequent study described the haplosporidan parasite as *Haplosporidium pinnae* (Catanese et al., 2018). This parasite, but also mycobacteria and other potential pathogens have been described in several sites affected by the MME (Carella et al., 2019, 2020; Čižmek et al., 2020; Lattos et al., 2020). The implications of the presence of different pathogens in the development of the disease has still to be clarified. Most known and studied *P. nobilis* populations in the Western Mediterranean Sea have almost completely disappeared, with mortality rates exceeding 90% (Vázquez-Luis et al., 2017; Panarese et al., 2019; García-March et al., 2020) and populations in the Eastern Mediterranean and Adriatic Sea are suffering the same fate (Katsanevakis et al., 2019; Kersting et al., 2019; Čižmek et al., 2020; Öndes et al., 2020; Özalp and Kersting, 2020). There is the exception, however, of several sites with very specific environmental settings where *P. nobilis* populations remain unaffected to date: Fangar Bay (Delta del Ebro, Spain), Mar Menor (Spain), Rhône Delta (France), Etang de Thau (France), Diana and Urbino pools (Corsica, France), Venice lagoon (Italy), inner Kalloni Gulf (Greece) (Catanese et al., 2018; Cabanellas-Reboredo et al., 2019; Kersting et al., 2019; Simide et al., 2019; Prado et al., 2019; Foulquie et al., 2020; Zotou et al., 2020). This worrying scenario has led to the recent inclusion of the species as Critically Endangered on the IUCN Red List (Kersting et al., 2019). While *P. nobilis* populations are disappearing at an accelerating rate, it is remarkable that the congeneric species *P. rudis*, which shares habitat with *P. nobilis* in many locations (Giacobbe and Leonardi, 1987; Kersting and García-March, 2017) remains unaffected by the MME (Catanese et al., 2018).

Potential natural recovery from this dramatic situation relies on recruitment, which will depend mainly on, (1) larval supply and transport from unaffected sites, and (2) the existence and potential reproduction of resistant individuals in the affected sites. Therefore, assessing the recruitment potential of *P. nobilis* after the mortality outbreak is mandatory to evaluate the role of this first step toward the recovery of the species. Once settled, post-recruitment survival will of course depend on the potential existence of pathogen-resistant individuals.

Artificial recruitment (i.e., by means of larval collectors) has proved to be a useful tool for assessing recruitment potential in *P. nobilis* (Cabanellas-Reboredo et al., 2009; Alomar et al., 2015; Kersting and García-March, 2017; Wesselmann et al., 2018), providing insights into larval supply and recruitment previous to the exposure to pressures like predation or dislodgement (Kersting and García-March, 2017). *Pinna nobilis* larval collectors were specifically designed and used for the first time by De Gaulejac et al. (2003). Later on, several studies have used larval collectors to study different aspects of *P. nobilis* recruitment, adapting this design to the specific conditions of study sites and experimental settings (Cabanellas-Reboredo et al., 2009; Kersting and García-March, 2017; Wesselmann et al., 2018). In Cabanellas-Reboredo et al. (2009) and in Kersting and García-March (2017) larval collectors were used to assess the larval settlement period of *P. nobilis* in the Balearic and Columbretes islands, respectively. Both studies established the peak of the settlement period between August and September. In Kersting and García-March (2017) larval collectors were used as well to assess recruitment of the species in the long-term, showing the high interannual variability in recruitment rates of this species over a 9-year period and suggesting a positive correlation between water temperature and recruitment rates. This study also evidenced the feasibility of using larval collectors to obtain *P. nobilis* spat to be placed afterward in protected cages submerged *in situ*, where recruits can be grown to be used later for restocking or restoring actions in impacted populations. Larval collectors have been used as well to assess genetic connectivity in *P. nobilis*, showing the existence of source and sink populations and the connectivity potential of the species (Wesselmann et al., 2018).

Because of the current status of the species and the general importance of recruitment in the recovery of impacted populations, an extensive effort (both spatial and human) has been undertaken to tackle *P. nobilis* recruitment in larval collectors over several thousands of kilometers along the Western Mediterranean coasts, the region first impacted by the MME (Vázquez-Luis et al., 2017), and in the Adriatic Sea, where the MME was first recorded in the final year of this study (2019) but most populations still remained unaffected (Kersting et al., 2019; Čižmek et al., 2020; Kipson unpublished data). As a result, the present study aims to provide an overall interannual picture of *P. nobilis* recruitment during 3 years after the 2016 MME, as well as to compare that information with the health status of different populations, in order to assess potential larval

connectivity and the role of recruitment in the future recovery of the species in the area.

MATERIALS AND METHODS

Study Sites

Larval collectors were installed in 37 sites distributed along the coast of the Western Mediterranean Sea including north Africa, and in the northern Adriatic Sea (**Figure 1**) during the reproductive seasons of 2017–2019. The sites were selected according to the occurrence of *P. nobilis* populations previous to the mortality outbreak, with many of them subjected to periodical monitoring. However, most of the populations (with the exception of Scandola, Embiez Islands, Alfacs Bay, Mar Menor, Arzew and Kristel bays, and Brijuni MPA) were affected by the MME by the time the first collectors were installed at the beginning of the summer of 2017. The impact of the MME on each location has been assessed in previous studies (Vázquez-Luis et al., 2017; Vicente et al., 2018; Cabanellas-Reboredo et al., 2019) or during the installation of collectors in the present study.

Time series of *P. nobilis* recruitment in larval collectors previous to this study were available for some of the selected sites: the Columbretes Islands (Kersting and García-March, 2017), Embiez Islands (Vicente et al., 2017, 2018; Vicente, 2020), Calpe (García-March, unpublished data), Cabrera (Vázquez-Luis, unpublished data), and for Pollença and Magaluf (Hendriks, unpublished data).

Larval Collectors

Larval collectors consisted of a series of plastic mesh bags containing entangled nylon filament or onion bags (see De Gaulejac et al., 2003; Cabanellas-Reboredo et al., 2009; Kersting and García-March, 2017; Vicente, 2020, for more details). The bags were attached to a main rope that was fixed to a concrete mooring and kept vertical by a submerged buoy, covering a 0.5–20 m depth range (**Figure 2**).

Larval collectors were moored annually in early summer (June) and removed in mid-autumn (November) from 2017 to 2019 (see **Table 1** for details), thus covering the main reproduction and settlement period of the species (Cabanellas-Reboredo et al., 2009; Deudero et al., 2017; Kersting and García-March, 2017). Once removed, the bags were immediately opened, and all *P. nobilis* recruits were carefully collected from the nylon mesh following the procedure in Kersting and García-March (2017). Observation of *P. nobilis* recruits was undertaken with the naked eye, allowing the detection of recruits of sizes down to 0.3 cm antero-posterior length. Recruits extracted from the collectors were either installed in aquaria (García-March et al., 2020; Vicente, 2020) or in growth cages in the field following Kersting and García-March (2017). It must be noted that at small sizes distinguishing *P. nobilis* from *P. rudis* juveniles can be difficult. In bigger juveniles, *P. rudis* can be easily distinguished by the lower number of radiating ribs (4–5 ribs) and scales, which are also bigger and sturdier than in *P. nobilis* (**Figure 3**). This issue is easily solved by keeping the juveniles in growth cages or in aquaria, where they grow to a size that allows identification. In addition, genetic analyses were used to contrast with morphological identification in 5 juveniles. Nevertheless, even if small, a certain identification error must be assumed, especially if juveniles die before growing to the needed size.

Lagrangian Trajectory Modeling

The high-resolution regional hydrodynamic model WMOP (Juza et al., 2016; Mourre et al., 2018) was used to simulate backward trajectories from the observation sites where recruitment was recorded, with the objective to identify the potential origin of larvae transported by ocean currents over the basin during the recruitment period. The WMOP model, developed at the Balearic Islands Coastal Observing and Forecasting System (SOCIB)[1], provides daily predictions of the Western Mediterranean circulation from the Strait of Gibraltar to Corsica and Sardinia with a 2 km spatial resolution. The WMOP surface currents result from the effects of 3-dimensional basin-to-coastal-scale ocean processes driven by atmospheric forcing (winds, evaporation-precipitation and heat fluxes), river inflows and open boundary inputs over a realistic bathymetry. The model, based on the ROMS modeling system (Shchepetkin and McWilliams, 2005), is nested in the larger scale Mediterranean model from the Copernicus Marine Service (Clementi et al., 2017). The model air-sea fluxes are computed through bulk formulae applied to the high-resolution atmospheric fields provided by the Spanish Meteorological Agency (AEMET) Hirlam (for years 2017 and 2018) and Harmonie (for year 2019) models. The climatological runoffs of the six major rivers of the modeling domain are implemented as point sources of low saline waters. Further details of the forecasting system and model evaluations can be found in Juza et al. (2016), Mourre et al. (2018), and Aguiar et al. (2020). Operational data assimilation of sea level, sea surface temperature, Argo profiles and Ibiza Channel High-Frequency radar was implemented in November 2018, using the method described in Hernandez-Lasheras and Mourre (2018).

Moreover, the daily average wave-induced drift provided by the Copernicus Marine Service Mediterranean Sea waves model (Korres et al., 2019a,b) was added to the WMOP currents to represent the contribution of surface ocean waves.

The TRACMASS algorithm (Jönsson et al., 2015) was used to generate Lagrangian trajectories over a 1-month period to approximate larval period duration (Deudero et al., 2017; Kersting and García-March, 2017; Trigos et al., 2018). Virtual particles were released once a week during the recruitment period from July 1st to September 15th (Cabanellas-Reboredo et al., 2009; Kersting and García-March, 2017) from all sites and for all years where recruitment was recorded, with the exception of Mar Menor because of its low exchange with open waters (i.e., semi enclosed coastal lagoon). In the case of Arzew and Kristel bays in Algeria, a single location (Arzew) was used given the proximity of the two sites. Cluster of 1,000 particles were released at each location, and modeled trajectories were the result of advection by the WMOP surface currents and wave-induced drifts plus a diffusive term accounting for the effect of model uncertainties and unresolved processes.

[1] www.socib.es

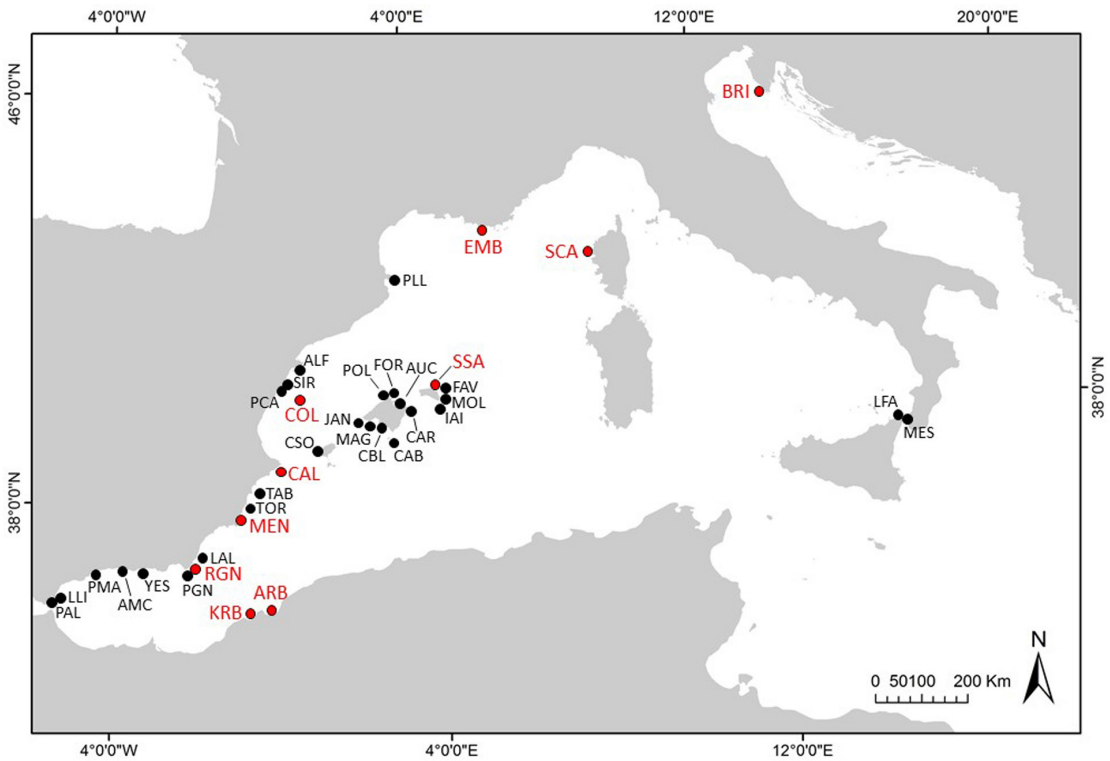


FIGURE 1 | Larval collector sites in the Western Mediterranean and Adriatic seas. In red, sites where recruitment was recorded in, at least, one season. Full name of sites in **Table 1**.

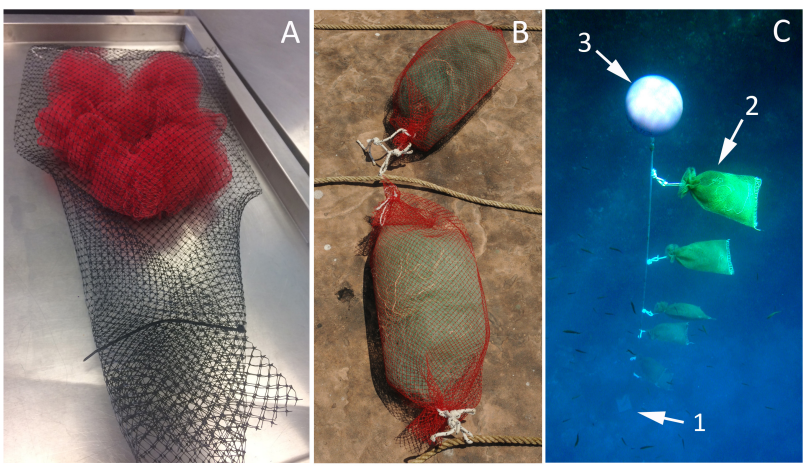


FIGURE 2 | Larval collectors. Plastic mesh bags containing onion bags **(A)** and entangled nylon filament **(B)**. **(C)** Components of a larval collector: concrete mooring (1), bags (2) and submerged buoy (3).

RESULTS

Larval Recruitment

Pinna nobilis recruits were found in the collectors installed at 10 sites (Scandola, Embiez Islands, Son Saura, Columbretes Islands, Calpe, Mar Menor, Cabo de Gata, Arzew and Kristel bays, and Brijuni); while no recruits were retrieved from the collectors in the remaining sites (**Table 1**). All sites had been impacted by *H. pinnae*, either before or during the study, apart from the sites in Algeria, Croatia and Mar Menor (Spain) (**Table 1**). Only one of the MME-affected sites, Columbretes Islands, recorded recruitment in the larval collectors during the three reproductive

TABLE 1 | Larval collector sites, 2017–2019 recruitment data and year of affection by the MME.

Site		Country	Recruits 2017	Recruits 2018	Recruits 2019	MME	Collectors (n)	Bags (n)	Depth (m)
Brijuni MPA	BRI	Croatia	n. i.	n. i.	**72**	no	3	3	6–10
Strait of Messina	MES	Italy	Disappeared	Disappeared	Disappeared	2017	4	3	6–7
Lake Faro	LFA	Italy	0	Disappeared	Disappeared	2017	4	2	3–4
Reserve Naturelle de Scandola	SCA	France	**18**	n. i.	**3**	2018	3	10	4–18
Embiez Islands	EMB	France	n. i.	**12**	0	2019	3	10	4–18
Port Lligat	PLL	Spain	n. i.	Disappeared	n. i.	2018	1	3	3
Son Saura	SSA	Spain	0	**1**	Disappeared	2017	1	3	5
Favàritx	FAV	Spain	0	n. i.	n. i.	2017	1	3	5
La Mola	MOL	Spain	0	0	Disappeared	2017	1	3	5
Illa de l'Aire	IAI	Spain	0	0	Disappeared	2017	1	3	5
Reserva Marina de Llevant-Cala Ratjada	CAR	Spain	0	0	n. i.	2016	3	2	10–12
Parque Nacional del Archipiélago de Cabrera	CAB	Spain	0	0	0 (1)	2016	1	3	5
Cala Blava	CBL	Spain	0	n. i.	n. i.	2016	1	3	5
Magaluf	MAG	Spain	0	0	0	2016	3	2	6
Jaulas Andratx	JAN	Spain	0	0	0	2016	3	5	0.5–3
Pollença	POL	Spain	0	0	0	2016	3	2	5
Cap Formentor	FOR	Spain	0	n. i.	n. i.	2016	1	3	3–5
Aucanada	AUC	Spain	0	n. i.	n. i.	2016	1	3	5
Badia dels Alfacs (Delta del Ebro)	ALF	Spain	0	0	0	2018	10–15	1	0.5–2
Serra d'Irta	SIR	Spain	n. i.	n. i.	Disappeared	2017	1	3	5
Prat de Cabanes	PCA	Spain	n. i.	n. i.	Disappeared	2017	1	3	5
Reserva Marina de las Islas Columbretes	COL	Spain	**187**	**5**	**2**	2017	1	6	5–13
Caló de s'Oli	CSO	Spain	0	n. i.	n. i.	2016	1	3	5
Calpe	CAL	Spain	**9**	0 (30)	0 (2)	2016	3	12	5–18
Reserva Marina de la Isla de Tabarca	TAB	Spain	0	0	0	2016	2	4	2–11
Torrevieja	TOR	Spain	0	n. i.	n. i.	2016	2	2	5
Mar Menor	MEN	Spain	**1**	0	n. i.	no	2–5	2	1–3
SAC, SPAMI Fondos Marinos Levante Almeriense	LAL	Spain	0 (2)	0	n. i.	2016	1–3	1–3	13–20
Reserva Marina Cabo de Gata–Níjar	RGN	Spain	**3** (6)	0	n. i.	2016	3	2	10–20
Parque Natural Cabo de Gata-Níjar	PGN	Spain	0 (1)	0	n. i.	2016	1	1–3	15–18
Los Yesos	YES	Spain	n. i.	0	n. i.	2016	1	3	6.5
Paraje Natural Acantilados de Maro-Cerro Gordo	AMC	Spain	n. i.	0	n. i.	2016	1	3	9
Puerto pesquero de Málaga	PMA	Spain	n. i.	0	n. i.	2016	1	3	9.5
La Línea	LLI	Spain	n. i.	0	n. i.	2017	2	3	5
Puerto de Algeciras	PAL	Spain	n. i.	0	n. i.	2017	1	3	20
Arzew bay	ARB	Algeria	n. i.	**60** (13)	**102** (15)	no	1	10	5–10
Kristel bay	KRB	Algeria	n. i.	**37** (8)	**30** (12)	no	1	10	5–10

In bold, sites where recruitment has been recorded.
n.i.: not installed.
In brackets, P. rudis recruits when occurred.

seasons (2017–2019). Besides this site, all other sites where a large number of recruits was recorded, were located in unaffected or partially unaffected regions. The congeneric species *P. rudis*, unaffected by the mortality, recruited in several sites during the study (**Table 1**).

Time series of *P. nobilis* recruitment in larval collectors previous to this study (i.e., Columbretes Islands, Embiez Islands, Calpe, Cabrera, Pollença, and Magaluf) showed that, although with the inherent interannual variability, recruitment in larval collectors at these sites was recorded annually before the MME.



FIGURE 3 | *Pinna nobilis* (left) and *P. rudis* (right) juveniles at a size of 5–6 cm (antero-posterior length). Notice how the number of radiating ribs and the morphology of the scales clearly differs in both species.

Because larval collectors are installed in shallow waters, they are highly exposed to storms and intentional or accidental removal; collectors at 8 sites were lost due to these causes during at least 1 recruitment season (**Table 1**). All extracted recruits from MME affected sites that were kept in growth cages died presumably because of *H. pinnae* during the first months, as did the ones taken to aquaria according to García-March et al. (2020).

Larval Transport

The Lagrangian trajectory model from the sites where recruitment was recorded shows the potential geographical origin of larvae during the main reproduction and recruitment period of the species (**Figure 4**). After disregarding the sites where *P. nobilis* had disappeared because of the MME (i.e., most of the coast of Spanish mainland coast and the Balearic Islands), three main regions harboring unaffected populations remain as potential larval sources in the Western Mediterranean: French Mediterranean coast, Delta del Ebro region and the north African coasts (mainly Algeria). The northern sites showing recruitment (i.e., Son Saura, Embiez Islands, and Scandola) received larvae potentially from the French coasts, while southern locations (i.e., Calpe, Cabo de Gata, Arzew, and Kristel bays) were nourished by the north African coasts. Columbretes Islands represented an in-between situation, receiving larvae both from the south (north Africa) and the north (Delta del Ebro region) (**Figure 4**). According to the model, Mar Menor, which hosts unaffected populations, could be also considered as an exporting site. However, its limited water exchange with the open sea will probably hinder its potential role as a significant larval donor.

DISCUSSION

The occurrence of successful recruitment events is crucial for the potential recovery of *P. nobilis* populations in the Mediterranean regions impacted by the MME. However, the general picture drawn by the results of the larval collectors' network set up for this study reflects the negative consequences of the mortality on larval recruitment, while opening a little window of hope at a few sites.

Larval Recruitment After the MME

Collapse of regional larval recruitment in many marine invertebrate species has been associated to the loss of adults after catastrophic events, seriously hindering recoveries (Miner et al., 2006; Miller et al., 2009; Lessios, 2016; Hughes et al., 2019). As expected, the high mortality rates recorded during the MME have impacted *P. nobilis* reproduction and are therefore impairing recruitment. In general, the results of this study show a disruption of *P. nobilis* larval recruitment over a vast geographical area in the Western Mediterranean Sea during 3 years after the start of the MME.

There were, however, some exceptions to this generalized absence of *P. nobilis* recruitment. Among the sites already affected by the MME, recruitment was recorded every year (2017–2019) in the Columbretes Islands, despite the fact that pen shell populations deceased in this area during the summer of 2017 (Cabanellas-Reboredo et al., 2019; Kersting et al., 2019). Moreover, although to a lesser extent, recruits were also recorded as well during at least one season in Scandola (Corsica, France), Son Saura (Spain), Calpe (Spain), Mar Menor (Spain), and Cabo de Gata (Spain) (**Table 1**). Larval recruitment was abundant in 2018 and 2019 in other Mediterranean regions like the northern Adriatic Sea (Croatia) or some sites in the southern Mediterranean like Algeria, where the mortality is still arriving (Kersting et al., 2019; Čižmek et al., 2020) and many *P. nobilis* populations remained unaffected. Recruitment recorded in these sites was similar to that recorded in the Columbretes Islands before the MME (Kersting and García-March, 2017). The same applies to Scandola and Embiez Islands (France), where larval recruitment was recorded during the years preceding the mortality that impacted these sites in 2018 and 2019, respectively (Vicente et al., 2020).

Larval Export and the Importance of Non-impacted Populations

Even though earlier studies proposed a larval period of 10 days for *P. nobilis* (Butler et al., 1993; De Gaulejac and Vicente, 1990), recent research has suggested that larval stages could last at least 1 month (Deudero et al., 2017; Kersting and García-March, 2017; Trigos et al., 2018). Populations of *P. nobilis* in the Western Mediterranean Sea show high genetic connectivity, functioning as a meta-population with source-sink dynamics (Wesselmann et al., 2018), which would agree with longer pelagic stages and larval transport in the area.

All known pen shell populations along the Spanish Mediterranean coast disappeared between 2016 and 2017 due to the MME, with little or no evidence of resistant individuals. There was the exception, however, of two sites with particular environmental conditions (i.e., Delta del Ebro bays -Alfacs and Fangar-, and the hypersaline coastal lagoon Mar Menor) which seem to remain at least partially

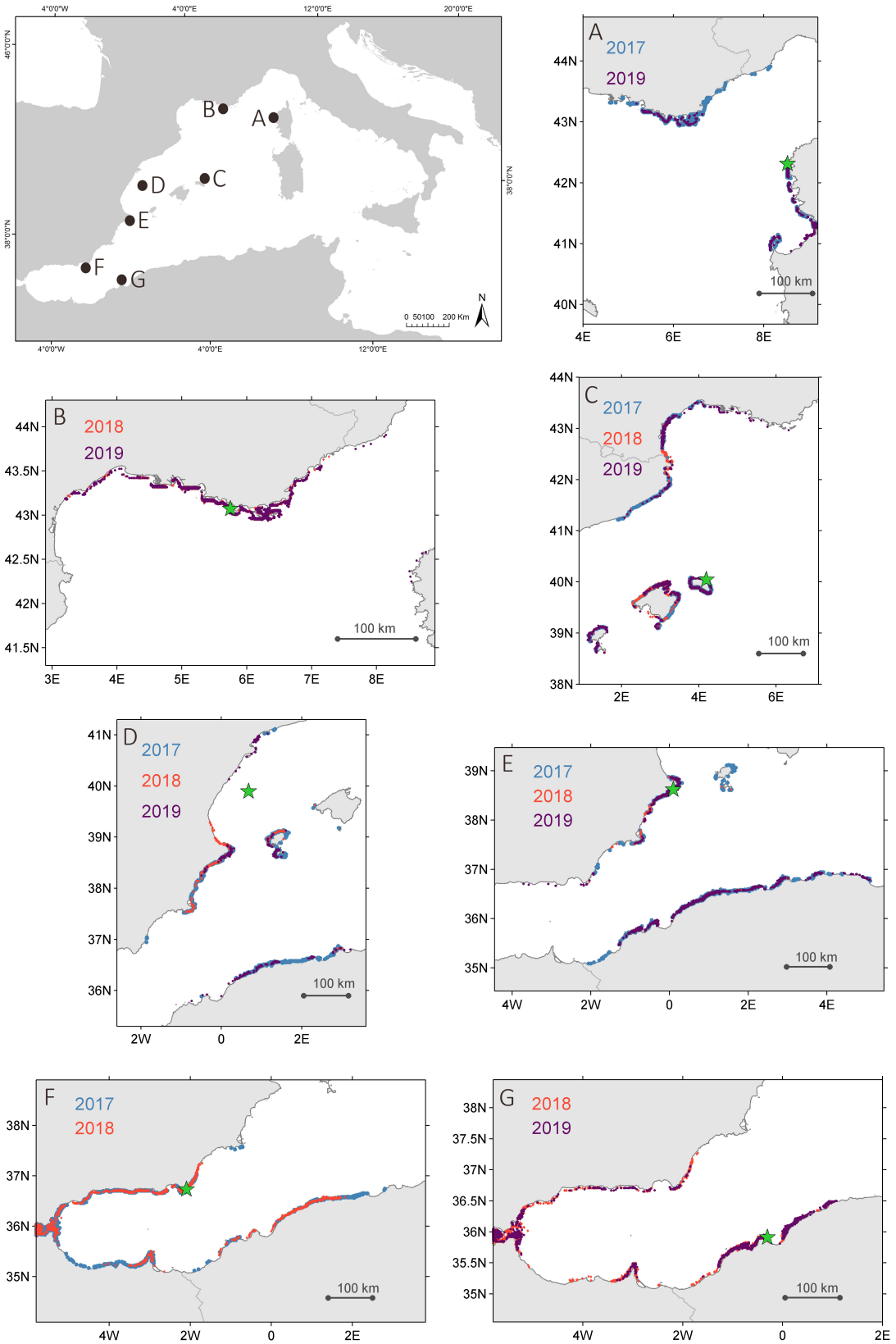


FIGURE 4 | Results of the Lagrangian trajectory model showing the potential origin of *P. nobilis* larvae for each site and year, **(A)** Scandola, **(B)** Embiez, **(C)** Son Saura, **(D)** Columbretes, **(E)** Calpe, **(F)** Cabo de Gata, **(G)** Arzew. Sites are represented on the maps by the green star.

pathogen-free (Vázquez-Luis et al., 2017; Catanese et al., 2018; Cabanellas-Reboredo et al., 2019; Prado et al., 2019; Giménez-Casalduero et al., in press).

The Columbretes Islands was the only location in the Western Mediterranean where recruits were found in the collectors every year (2017–2019). The pen shell mortality reached the Columbretes Islands (located between Spanish mainland and the Balearic Islands, **Figure 1**) in the summer of 2017 (Cabanellas-Reboredo et al., 2019). Surprisingly, during that summer, while most of the pen shells in the Columbretes Islands were sick and dying, the larval collectors registered a decadal maximum in recruitment according to the long-term recruitment data available for this site (Kersting and García-March, 2017). In 2018 and 2019 recruitment in Columbretes was much lower, however, still existent and in the range of the considerable interannual variability recorded at this site (Kersting and García-March, 2017).

The mortality context during those years forced an exclusion experiment in Columbretes, where practically all pen shells deceased during the summer of 2017. Therefore, local recruitment stopped, and most recruits recorded in the collectors must have been transported to the Columbretes area from somewhere else. Pre-mortality results on larval settlement obtained by Kersting and García-March (2017) already suggested the importance of external larval sources and the dispersion capacities of the species, as no differences were found in recruitment in the collectors among sites with and without the presence of pen shells in the Columbretes Islands. The results of the Lagrangian trajectory model for this area showed four major areas that could be acting as larval donors to the Columbretes Islands, i.e., Delta del Ebro region, Ibiza and Formentera Islands, southern Spanish mainland, and north Africa. In these regions, the only sites still holding living *P. nobilis* populations in 2017–2019 were Delta del Ebro, Mar Menor, and both studied sites in Algeria.

The closest unaffected site, Delta del Ebro (∼100 km north of the Columbretes Islands), hosts one of the largest *P. nobilis* populations in the Mediterranean Sea (Prado et al., 2014). *Pinna nobilis* populations in this site have survived the MME apparently due to the low salinity conditions in the area, greatly influenced by agricultural discharges from rice cultivation (Prado et al., 2019; García-March et al., 2020) and this area has been already considered as a main source of *P. nobilis* larvae (Wesselmann et al., 2018). Surprisingly, even though *P. nobilis* populations in the Delta del Ebro remain mostly unaffected, collectors installed in this location have never recorded larval settlement, and according to Prado et al. (2019) the local availability of planktonic larvae is very low. These populations seem to rely mainly on sporadic recruitment events and the absence of recruitment inside the bay has been hypothesized to be associated to processes causing larval mortality such as freshwater discharges or even pollution (Prado et al., 2019). Nevertheless, as showed by Wesselmann et al. (2018), these populations seem to be exporting larvae, which hints to the fact that even though larval mortality inside the bay might be high, larvae could be transported into the open sea. Larval transport out of the Alfacs Bay could be favored by surface currents, which are intense and flowing out of the bay in the summer (Cerralbo et al., 2018).

However, the results of the oceanographic model show a complex scenario that goes far beyond the Delta del Ebro, showing at least two other regions holding unaffected populations potentially acting as larval donors to the Columbretes Islands: north African coasts (mainly Algeria) and Mar Menor in southern Spain. As reported in this study, *P. nobilis* populations in the monitored sites in Algeria were unaffected by the MME and located in coastal areas well connected to the open sea, thus fully capable of exporting larvae. According to the model, this region could be the most important larval donor to the Columbretes Islands in the current MME context. The case of Mar Menor is not as clear, mainly because of the nature of the site, being a semi enclosed coastal lagoon with very little exchange with the open sea, which would impede a significant larval export. Nevertheless, hypothetically larvae of at least these three areas, could be reaching the Columbretes Islands transported by the complex and variable pattern of currents in this transition region, where the southward flowing Northern Current changes direction toward northeast to form the Balearic Current, also intermittently influenced by northward inflows flowing through the Ibiza Channel. This diversity in larval origins could be crucial in fostering potential recoveries in this area.

In 2017, larval collectors recorded recruitment as well in a few sites south of the Columbretes Islands (i.e., Calpe and Cabo de Gata-Níjar). Altogether, according to the long-term recruitment data series in the Columbretes Islands (Kersting and García-March, 2017) and the results presented here, 2017 seems to have been a year of successful *P. nobilis* larval recruitment. The Lagrangian trajectory model points out to the north African coast as the main area holding unaffected populations that could be acting as a source of larvae for these sites during those years. Mar Menor is also shown here as a potential source by the model, but as already mentioned, there is a major concern about its connectivity potential due to limited seawater exchanges. Regarding the Balearic Islands, sporadic recruitment was detected in 2018 in Son Saura (Menorca). In this case, according to the model, larvae could origin from the north, i.e., the coast of France, where in fact several *P. nobilis* populations were still unaffected in 2018 (Kersting et al., 2019). It is remarkable that none of the other sites in the Balearic Islands holding historical larval settlement data (i.e., Cabrera, Pollença, and Magaluf) registered recruitment after the MME.

This pattern moved eastwards along the coast as other western Mediterranean sites were sequentially impacted by the mortality. Recruitment was recorded in 2018 in the Embiez Islands (France) before the mortality affected this site but ceased afterward. In Scandola (Corsica), first affected by mortality in 2018, recruitment fell from 18 in 2017 to 3 recruits in 2019. In this last case, larval origin seems more diverse, enclosing both northern sites (Occitania, France) and southern ones (southern Corsica and northern Sardinia), while in Embiez Islands recruitment seems to be more dependent on local

and near-by populations and thus ceased when those were impacted by the MME.

It must be considered that *P. nobilis* larval recruitment has shown to have an important interannual variability (Kersting and García-March, 2017) and in pre-mortality circumstances low recruitment values were also recorded during some years. Nevertheless, the scenario presented here is different, showing an interannual absence of recruitment over great extensions of coast, including sites were recruitment was recorded annually prior to the MME. This is also showing that recruitment originating from local populations was also playing an important role before the MME, thus in many populations recruitment resulted probably from a mixed pool of local and imported larvae.

As previously reported in other studies (Catanese et al., 2018), the congeneric species *P. rudis* remains unaffected by the mortality and its recruits are still being recorded in many larval collectors and in the field (this study, García-March et al., 2020).

Future Consequences

Long-term follow-ups of recoveries after disease-triggered die offs of marine invertebrates have shown that recovery can be slow and geographically heterogeneous (Miner et al., 2006; Miller et al., 2009). Of course, in the case presented here it is understood that populations' recoveries through recruitment will only occur if at least some of the settled individuals show resistance to the disease, which represents an important additional obstacle. All juveniles settled in the collectors and installed in growth cages within the MME-affected sites died before the first year of age, presumably because of *H. pinnae* infection. However, if resistant juveniles could establish, recovered sites could eventually export larvae to other locations and trigger a stepping stone recovery process through larval export and connectivity. Nevertheless, potential recoveries of mortality-impacted populations will presumably differ among sites and will be highly dependent on their geographical location relative to unaffected populations and the oceanographic current patterns in the area. According to Sanna et al. (2013), *P. nobilis* populations seem to share a common origin and a recent eastward expansion across the Mediterranean, likely facilitated by marine currents. Therefore, a similar mechanism could mediate in the recovery and, therefore, new expansion of the species after the MME if resistant recruits should occur.

In the best scenario, i.e., with resistant juveniles, successful recoveries through recruitment could take a long time and it must be regarded that natural recruitment is also limited by other factors such as predation, especially in protected sites, where predators are abundant (Kersting and García-March, 2017). In fact, in predator-rich environments, a refuge size of 45 cm has been estimated for the species, which would represent an age of about 8 years (Kersting and García-March, 2017). Therefore, it is of great importance to start assessing recruitment in the field and recruit's survival, especially in those sites where recruits have been observed in the collectors.

Altogether, our results show a worrying scenario for the species and highlight the importance of unaffected *P. nobilis* populations as larval exporting sites, which could play a main role in a potential, although probably slow, recovery. This applies as well to the Adriatic and Eastern Mediterranean Seas, where unaffected populations are being described as the MME spreads eastwards (Kersting et al., 2019; Čižmek et al., 2020; Zotou et al., 2020). In addition, (1) the status "unaffected" is not static and these sites could be affected by the mortality in the near future (e.g., Alfacs Bay, Prado et al., 2019); and (2) some of these unaffected sites are highly anthropized and subjected to multiple stressors that may cause mortalities on their own (e.g., Mar Menor, García-Ayllon, 2018). As suggested by the IUCN (Kersting et al., 2019), these unaffected sites need to be protected, while *P. nobilis* populations along the north African coasts need to be urgently assessed, especially regarding their important role as larval donors in the region. Through this internationally joint effort, we also want to stress the importance of coordinated pan-Mediterranean research and monitoring to continue tackling the mid and long-term effects of the *P. nobilis* MME.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

DK wrote the manuscript with contributions of MV-L, IH, and BM. All authors participated in the field work and contributed to the final version of the manuscript.

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