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Tracking a mass mortality outbreak of pen shell *Pinna nobilis* populations: A collaborative effort of scientists and citizens

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A mass mortality event is devastating the populations of the endemic bivalve *Pinna nobilis* in the Mediterranean Sea from early autumn 2016. A newly described Haplosporidian endoparasite (*Haplosporidium pinnae*) is the most probable cause of this ecological catastrophe placing one of the largest bivalves of the world on the brink of extinction. As a pivotal step towards *Pinna nobilis* conservation, this contribution combines scientists and citizens' data to address the fast- and vast-dispersion and prevalence outbreaks of the pathogen. Therefore, the potential role of currents on parasite expansion was addressed by means of drift simulations of virtual particles in a high-resolution regional currents model. A generalized additive model was implemented to test if environmental factors could modulate the infection of *Pinna nobilis* populations. The results strongly suggest that the parasite has probably dispersed regionally by surface currents, and that the disease expression seems to be closely related to temperatures above 13.5 °C and to a salinity range between 36.5–39.7 psu. The most likely spread of the disease along the Mediterranean basin associated with scattered survival spots and very few survivors (potentially resistant individuals), point to a challenging scenario for conservation of the emblematic *Pinna nobilis*, which will require fast and strategic management measures and should make use of the essential role citizen science projects can play.

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The pen shell *Pinna nobilis* (Linnaeus, 1758), is the largest bivalve of the Mediterranean Sea where it is endemic; and with its size of up to 1.2 m height ranks as one of the largest worldwide^{1–3}. This species grows on soft-bottom coastal areas and mainly inhabits seagrass meadows (dominated by *Posidonia oceanica* and *Cymodocea nodosa*), but also occasionally thrives on unvegetated bottoms, maërl beds, or among boulders^{2,4–6}. In favourable conditions the lifespan of *P. nobilis* is up to 50 years⁷ and the species develops a key ecological role. Pen shells filter water and retain large amounts of organic matter from suspended detritus⁸, contributing to water clarity. In addition, its shell provides a hard-surface within a soft-bottom ecosystem, which is colonized by many different benthic species^{9–11}, and at high densities can create high-diversity biogenic reefs¹². It also plays a key role in the trophic web, serving as prey of other species (e.g., *Octopus vulgaris*^{13,14}) and host of symbionts like the crustaceans *Pontonia pinnophyllax* and *Nepinnotheres pinnotheres*¹⁵.

Several anthropogenic pressures such as pollution^{16,17}, anchoring^{18,19}, harvesting²⁰, habitat degradation^{21,22} and environmental threats like for example global warming, which induces a decrease in juveniles' survival rate²³ have contributed to accelerate the decline of pen shell populations in the last century, making this emblematic species one of the most important bio-indicators of ecosystem status in the Mediterranean basin. This decline has in turn led to list the pen shell as an endangered and protected species under Annex IV of the Habitats Directive (European Council Directive 92/43/EEC), Annex II of the Barcelona Convention, and national legislation in most Mediterranean countries.

Recently, pen shell's population health in Spain has plummeted, causing concern and a status change from "Vulnerable" category to "Critically Endangered" with a serious extinction risk (Orden TEC/1078/2018). This is due to a Mass Mortality Event (MME^{24,25}) that affected *P. nobilis* populations of the south-western Mediterranean Sea starting in early autumn 2016 with extremely high mortality levels (reaching up to 100% at monitored populations²⁶). Thereafter, severe mortality was also observed in pen shell populations from the north-western Mediterranean (Italian and French coasts²⁷) and as far as the Aegean sea²⁸. As in two regions of Italy (Campania and Sicily) a mycobacterial disease has recently been associated with the mortality episodes of *P. nobilis*²⁹, the role of a *Mycobacterium* sp. in a complex disease pathogenesis cannot be discarded. However, also in Italy³⁰ there is compelling evidence that the main cause of this mortality wave is the protozoan *Haplosporidium pinnae*, a new species genetically related to the group of Haplosporidian parasites²⁷. Different life stages of this parasite have been detected in diagnosed sick pen shells. The sporulation stage of the protozoa has been detected in the digestive gland, while the uninucleate and the less frequent plasmodial stages have been found in the connective tissue and the gut epithelium. This type of infection triggers a heavy inflammatory response with harmful physiological responses for the host (e.g., precluding the digestion process), finally causing the death of the animal^{27,31}.

Haplosporidian endoparasites have been the cause of mortality events in other bivalve populations. They have been specifically well-studied in cases of molluscs of commercial interest, most likely due to the socio-economic repercussions. The best studied members of the group are *Haplosporidium nelsoni* and *Bonamia ostreae* which cause die-backs in the oysters *Crassostrea virginica* (Atlantic coasts of USA^{32,33}) and *Ostrea edulis* (European coasts^{34,35}), respectively. Several studies suggest a key role of the environment affecting the life-cycle of these parasites^{32,36,37}. The disease prevalence and intensity shows seasonal patterns; for example, a peak of prevalence at higher summer temperatures and salinity was observed for *H. nelsoni*^{38,39} and *Bonamia exitiosa*^{40,41}. While *B. ostreae* shows the same pattern for salinity (prevalence decreases at lower salinities), in contrast, the parasite outside its host showed higher survival and esterase activities at 4 °C and 15 °C than at 25 °C^{42,43}. Little is known about the environmental dispersal of Haplosporidians although oceanic currents have been suggested as a potential factor driving the expansion of these parasites^{42,44}. The quick northward expansion of the disease along the Iberian peninsula during the present outbreak²⁶, with early outbreaks in the Central Mediterranean²⁸, agrees with the hypothesis of a pivotal role of currents in disease dispersal at regional but also basin-wide scales. The occurrence of healthy *P. nobilis* populations in specific areas (e.g., Alfacs Bay in the Ebro Delta, with low salinity caused by freshwater discharges) points towards a relation between environmental factors such as salinity and/or temperature on disease prevalence or survival of *H. pinnae*.

However, the study of rapid and vast pathogen dispersal (e.g., invasive diseases) as well as the relationship with environmental parameters is often constrained by the scale⁴⁵ and time-period needed for observations. The problem of intense sampling effort can be resolved with networks of citizen and scientists, which can multiply the spatio-temporal sampling effort without the economic and logistic constraints of scientific sampling⁴⁶. Here, we have combined observations of scientists and citizens to track the mass mortality outbreak caused by the new species-specific parasite *H. pinnae*²⁷ in order to test if dispersal speed is coherent with local current patterns and to investigate if there are environmental factors aiding the infection of pen shell populations by the pathogen. This could provide an indication of further future dispersal of the pathogen beyond the western Mediterranean basin and current infection areas and pin-point populations at risk in the near future.

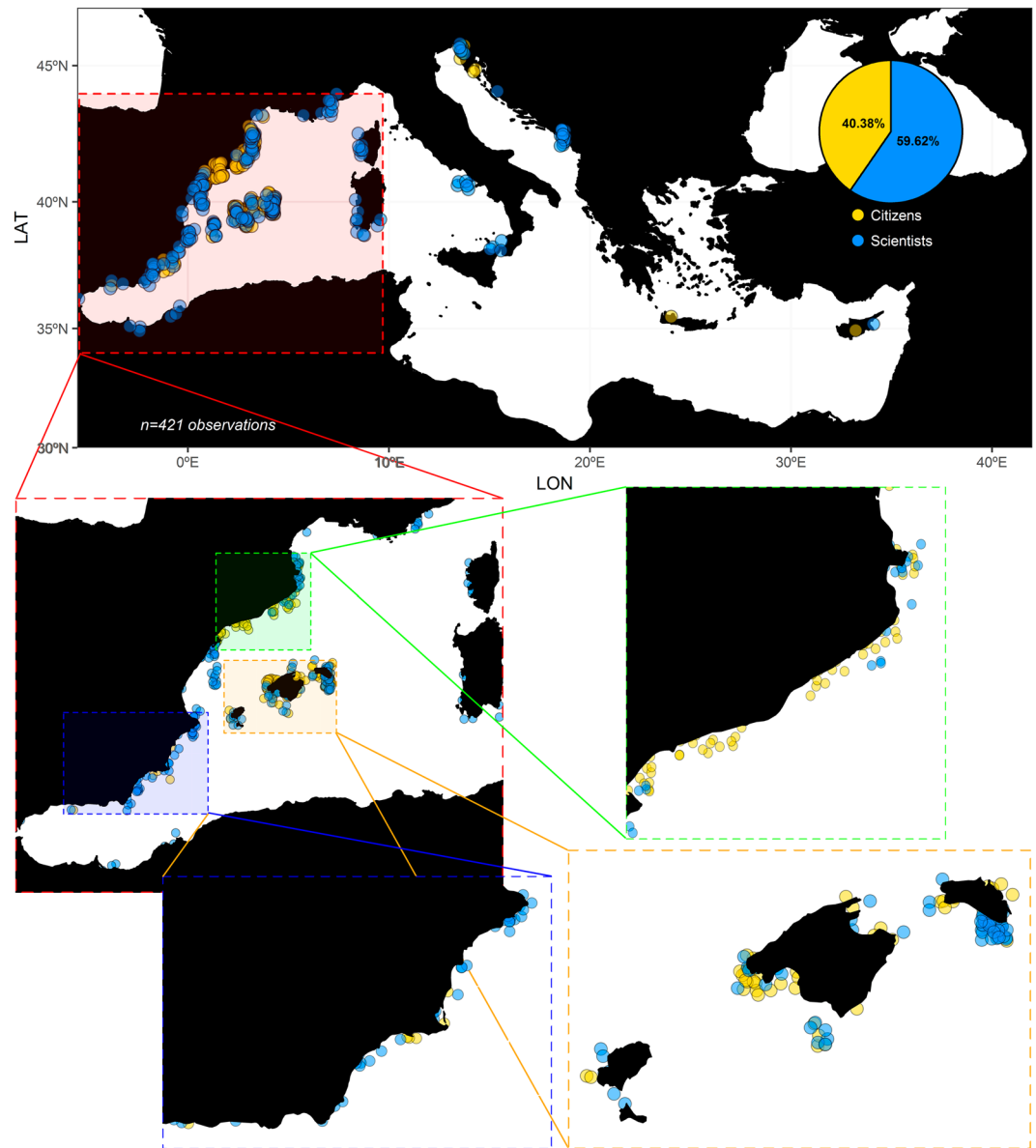


Figure 1. Observations of *P. nobilis* health conducted by citizens (yellow circles) vs. scientists (blue circles), with zoomed in areas where most observations were done.

Results

A total of 251 observations from September 2016 to April 2018 reported by the Mediterranean scientific network were combined with the 170 observations by citizens (June 2017–April 2018; ~26 monthly observations) to yield a total of 421 observations (40.38 and 59.62% reported by citizens vs. scientists respectively; Fig. 1 and Table A in Supplementary Material). Initially 289 observations were reported from the sea-watchers' platform, which were scrutinized by expert scientists to filter out possible confusions between congeneric species *P. nobilis* and *P. rudis* as well as other kind of errors in the reports by sea-watchers. The spatio-temporal representation of this combined data set (Fig. 2) points to the southern part of the Iberian Peninsula as the first region where the MME was detected (Fig. 2A), while the Balearic Islands were the second area affected by this severe mortality in a relatively short time (Fig. 2B). Later, and after a relatively long period of time (8 months), the signs of the disease were sequentially detected on a northward trajectory along the Valencian coast (Fig. 2C,D). At the end of 2017, the MME was observed on the Catalan coast and beyond Spanish waters in some sites around Corsica (Fig. 2E). During the first months of 2018, mortality was observed at specific sites along the Italian coast (Fig. 2F). However, specific localities in the Mediterranean Sea still harboured *P. nobilis* populations in good condition for the duration of this mortality wave (from September 2016 to April 2018). For example, no signs of the disease have been detected at the Mar Menor coastal lagoon and Ebro Delta areas (highlighted with blue circles in Fig. 2C,F), despite the fact that there was 100% mortality in the surrounding areas. Similarly, in the entire Central and Eastern Mediterranean *P. nobilis* populations remained unaffected until April 2018 (Figs 1A,B and 2A in Supplementary Material).

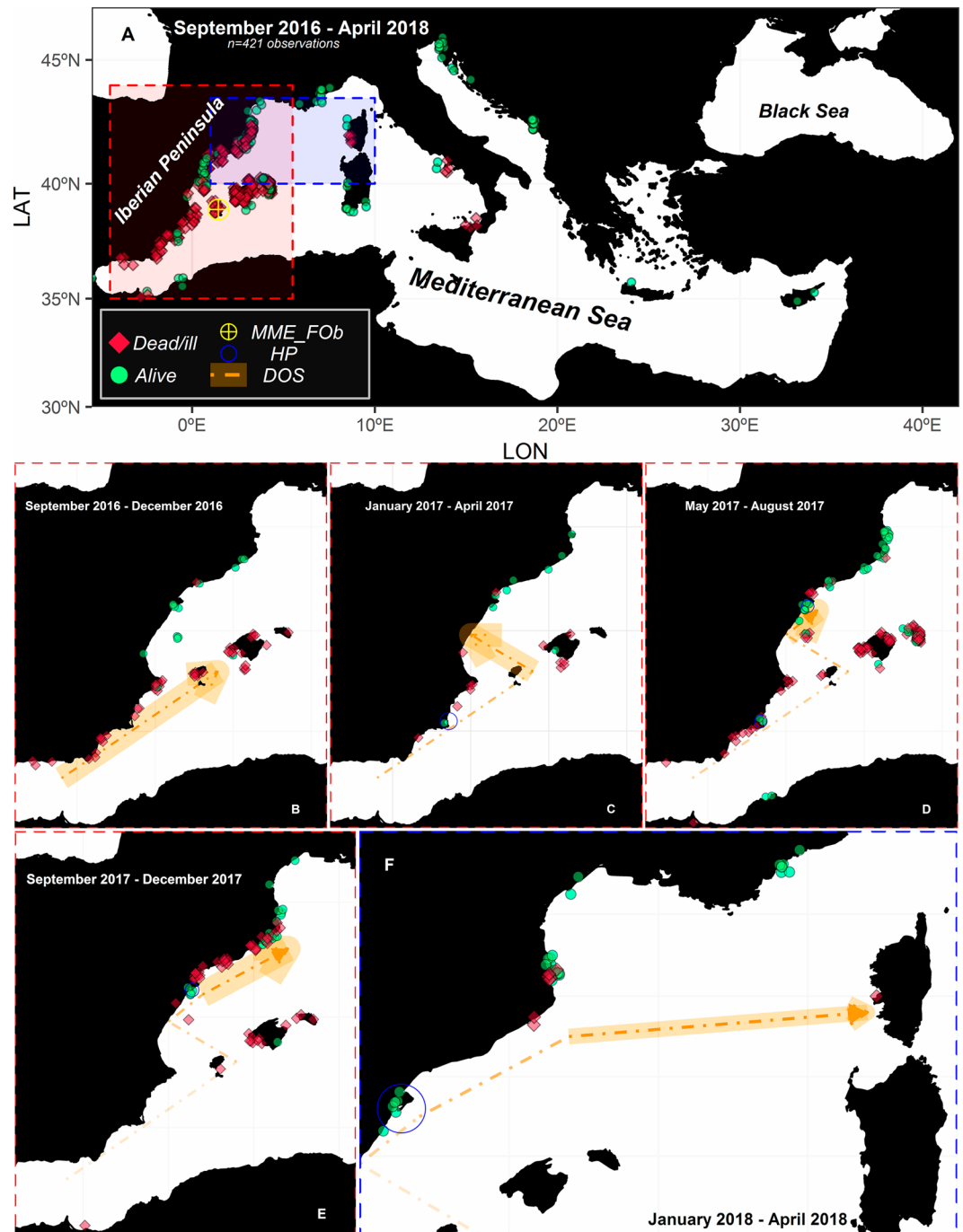


Figure 2. Disease observations based on the health status of *P. nobilis* (Dead/ill vs. alive, represented by red diamonds and green circles respectively) for the whole period from September 2016 to April 2018 (A). Spatio-temporal zooms of such observations are represented in panels B–F. Note that the crossed yellow point indicates the zone where the mortality was observed for the first time (Mass Mortality Event First Observation; MME_FOb), blue empty circles surround Healthy Populations (HP) and orange arrows denote Disease Observations Sequence (DOS).

The model current simulations suggest that the parasite *Haplosporidium pinnæ* has probably dispersed regionally by currents (mp4 animation in Supplementary Material and Fig. 3). The backward trajectories ending on the southern coast of Mallorca (p_2 at Fig. 3) in October 2016 indicate a possible origin along the coast of Alicante and Murcia, which is in agreement with the observations of the disease (orange trajectories at Fig. 3). Moreover, the transit time is consistent with the observations, showing only a 1-day difference between the average arrival time at p_2 and the observed date (average time; Table 1). A similar agreement is found in the second simulation using forward trajectories from the Ebro River area in June 2017 (blue trajectories in Fig. 3). A slow northward propagation is described in the model, with an average time of arrival of the particles in the final point (p_2) 3 days before the observed infection (Table 1). This

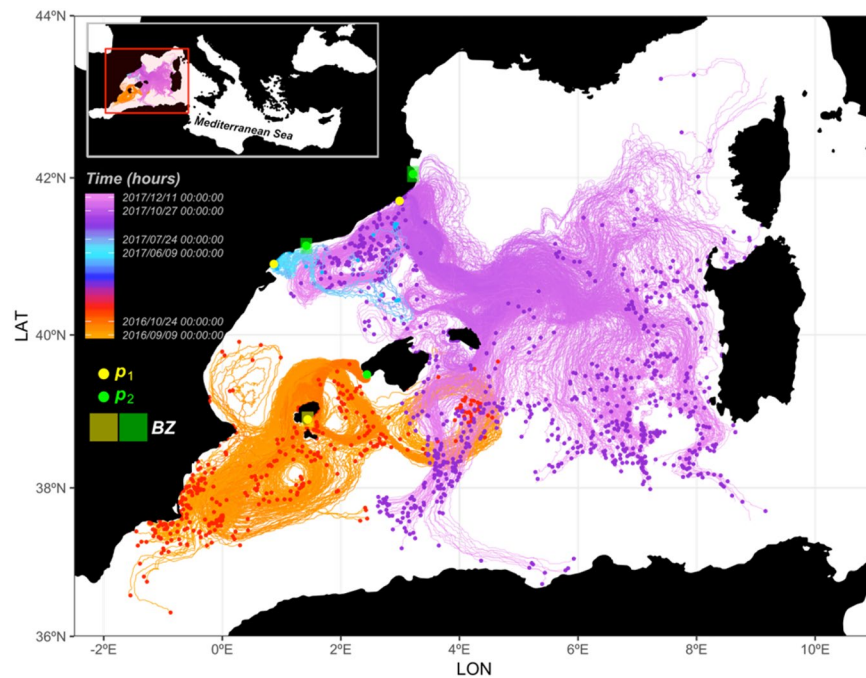


Figure 3. Drift simulations: backward simulations in the Balearic Islands area (orange path), forward simulations at L'Ametlla de Mar area (blue path) and, forward simulations at the north Catalonia area (purple path). Note that points at the end of the paths indicate the particle final position. Simulations were inferred between point 1 (p_1 ; infected point) and point 2 (p_2 ; no signs of infection at the beginning of the simulation and infection at a known time interval of the simulation). The rectangle indicates 650 km² buffer zone around a given point.

Simulation	Area	LonLat p_1	LonLat p_2	$Omme_f$	AET_f	FET_f	LET_f
Backward	Balearic Islands	2.45°E 39.50°N	1.44°E 38.91°N	2016/09/28	2016/09/29	2016/09/09	2016/10/16
Forward	L'Ametlla de Mar	1.42°E 41.14°N	0.87°E 40.91°N	2017/07/14	2017/07/11	2017/06/25	2017/07/24
Forward	North Catalonia	2.99°E 41.71°N	3.22°E 42.05°N	2017/12/07	2017/11/11	2017/11/07	2017/12/04

Table 1. Observed vs. estimated dates for the arrival of particles subset at buffer areas in the three drift simulations conducted. Nomenclature: Longitude and latitude (LonLat) at point 1 (p_1) and point 2 (p_2); Observed date of MME ($Omme_f$); Estimated average date (of particles subset) for the arrival of the particles at p_2 (AET_f); First date for the arrival of the particles at p_2 (FET_f); Last date for the arrival of the particles at p_2 (LET_f).

agreement in both simulations is quite remarkable given the uncertainties inherently present in the model predictions. As mentioned in Section 4.2, the cluster approach provides a way to take into account these uncertainties. The backward simulation shows a wide range of possible departure times, with an average approximately at the observed date as the first particle left p_1 19 days before and last particle left p_1 18 days after the observed date (Table 1), providing insights into the range of possible scenarios for particle drifts given specific surface current conditions over a period of several weeks. The simulated departure dates for L'Ametlla de Mar are more skewed, as the first particle arrives at p_2 19 days before and last particle left p_2 10 days after the observed infection date (Table 1). The third simulation providing forward trajectories from a location along the Catalan coast in December 2017 (purple trajectories at Fig. 3) indicates an overall south-eastward dispersion towards Mallorca, Menorca, Corsica and Sardinia islands, and the Algero-Provençal basin. Some of the particles still reached the area of observed infection, with an average arrival 26 days before the observed infection date. The last particle reaching p_2 arrived only 3 days before the observed infection (Table 1). Even if the agreement is not as good as in the two previous cases, these results still support the hypothesis of disease dispersion by surface currents given the uncertainties present in the model and observations.

After arrival to local sites, temperature and salinity appear to be decisive in the development of the disease ($p < 0.01$ and $p < 0.001$, respectively; 69.5% deviance explained) according to the GAM model. In fact, the disease expression (pen shell dead or ill) seems to be closely related to temperatures above 13.5 °C and with a salinity range between 36.5 and 39.7 psu (Fig. 4).

Discussion

Assuming that the mass mortality events described in this study have been caused by the newly described parasite *H. pinnae*²⁷, model simulations of particle drift dictated by regional surface currents suggest that parasite dispersion by surface currents could play an important role at a regional scale, as has been suggested before for other Haplosporidian species⁴⁴. Despite the lack of resistant forms in *Bonamia* species (sporal stage or sporulation

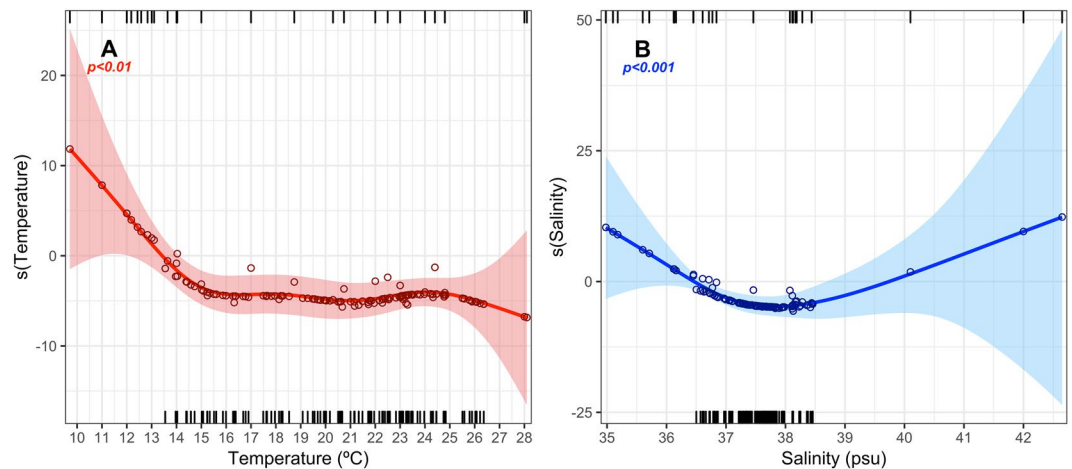


Figure 4. Partial smoothed effect of Temperature (A) and Salinity (B) on the disease expression (note that zero marks the shift on the response; >0 corresponds to higher probability of disease absence, while <0 to higher probability of disease expression). Fitted lines (solid line), 95% confidence intervals (shaded area) and partial residuals (hollow points) are shown for univariate effects. Top and bottom tick marks on x -axis represent values of the observed covariable for the absence and presence of signs of infection respectively.

process have never been detected²⁷), some studies support that *B. ostreae* and *B. exitiosa* spread via water currents and strong tide currents^{42,47} contributing to a rapid expansion but with a reduced spatial range (within a bay or in sites sharing commune water bodies but with reduced survival of the cells outside the host⁴⁷). Such constricted dispersion does not seem likely for the pattern of parasite dispersion in this study, where the spores of *H. pinnae* would be dispersed over long distances for an extended time period (at least for a few weeks; Fig. 3 and mp4 animation in Supplementary Material). However, this hypothesis is compatible with Haplosporidians with a sporal stage, since though dispersal in most such parasite species (e.g., *H. nelsoni*) is poorly understood and remains purely speculative, several studies suggest that dispersion by currents is the most plausible dispersion mode^{33,48}. Spores or at least sporulation of the pen shell parasite *H. pinnae* have been detected in the epithelium of digestive tubules^{27,31}, and spore ornamentations, which may aid in flotation⁴⁹, have been detected in other molluscan protozoan parasites⁴⁹. Therefore, the presence of such resistant spores with attachments (e.g., long tape-like filaments attached to the spore wall) possibly providing buoyancy²⁷ in the life-cycle of *H. pinnae*, suggests that this parasite could be readily dispersed by currents - the remarkable agreement obtained in this study between the arrival of virtual particles and observed infection at sites strongly supports this hypothesis. Alternatively, there could be a hypothetical involvement of planktonic species⁵⁰ as an intermediate host, as suggested for *H. nelsoni* and *H. costale*^{33,51}. The intrinsic uncertainty of the model linked to the turbulent nature of ocean flows and the existence of fine-scale littoral processes that remain unresolved in the model inevitably generate uncertainties in the computation of ocean trajectories. A major outcome of the modelling study was that some areas were successively infected with a time delay in reasonable agreement with the observations, which indicates that surface currents could act as a main driver for the transport of the parasite across the Mediterranean basin. Moreover, not only model simulations, but also the very limited knowledge of certain key stages of the parasite life cycle could be a potential uncertainty source. At the moment, the time-frame from parasite colonization of a given area and infection and virulence in the host is unknown; therefore pen shells might be infected for some time before showing signs of disease. This means that both scientists and sea-watchers only detect the infection when *P. nobilis* shows signs of disease (e.g., pale and withdrawn mantle, valves that do not close or do it very slowly), but the parasite could have the ability of infecting the pen shell some days, weeks or even months before. Moreover, an unknown time could elapse between the infection and the death of *P. nobilis*. These un-estimated and unknown time-steps could induce a potential bias causing the uncertainty and discrepancy between observations and predictions. Similarly, the origin of this parasite is speculative because of the limited information available for some areas such as the North-African coast. For instance, a die-off has been detected in certain counties along that coastline, but the timing of this event is completely unknown, which constricts our capacity to identify the exact source of the infection. Further uncertainty is also associated to the role and origin of the Mycobacteria species recently found in two regions of Italy and associated to mass mortality events of *P. nobilis*²⁹. In otherwise healthy individuals, significant mortality (up to 82%) appears to be associated to the presence of *Vibrio mediterranei* and its degree of pathogenicity is currently under investigation (P. Prado, pers. communication).

The dynamics of Haplosporidian parasites is modulated by environmental conditions⁴⁴ and therefore also the prevalence of *H. pinnae* after its arrival by currents at a given area is subject to the environmental conditions in such area. Based on our modelling results, the expression of disease seems to be related to temperatures above 13.5 °C and a salinity range between 36.5–39.7 psu, although the upper limit of the salinity should not be considered accurate due to the lack of such data (salinities above 38.5 psu) - monitoring further dispersal of the parasite in the eastern Mediterranean, where prevailing salinities are higher than in the western Mediterranean, will allow the accurate estimation of the upper salinity limit. A similar pattern has been also observed for other

Haplosporidians parasites. For example, the congeneric species *H. nelsoni* is highly sensitive to temperature and salinity, which influence both its geographic distribution and seasonal infection patterns^{32,36,37}. Specifically, field and *in vitro* experiments demonstrated that the ability of *H. nelsoni* to proliferate or survive decreases at lower salinities³⁸ and its prevalence and virulence is affected seasonally by temperature oscillations; its prevalence decreases in the late winter, due to the exposure to low temperatures³⁹. *B. exitiosa* shows a similar pattern of tolerance of environmental conditions^{40,41}. However, *B. ostreae* showed higher survival outside its host and viability at lower temperatures (4–15 °C than at 25 °C), although the same positive relationship was observed regarding disease prevalence and salinity (higher prevalence at salinities >35 psu than <20 psu)⁴². These patterns suggest a species-specific tolerance to environmental conditions⁴⁴, and could explain why, despite infection of the surrounding areas (with extinct populations), there are areas that shelter *P. nobilis* populations that are still in good condition. This is quite probably due to the salinity range outside the common Mediterranean salinity range of 36.7–39.5 psu⁵²; this is the case, for example, of Alfacs Bay, strongly affected by discharges of the Ebro River^{53,54}, and the Mar Menor coastal lagoon, a confined area with high salinity up to 40 psu⁵⁵. However, it is important to remark that pen shells living in the Mar Menor lagoon or Alfacs Bay are vulnerable populations since changes in water conditions (currents, salinity and temperature) can still lead to the disappearance of those populations by a sudden exposure to the parasite or by increased virulence. Similarly, the observation of healthy *P. nobilis* populations at the northernmost Catalan Coasts and French Coasts in April 2018 (Fig. 2F) were probably related to the fact that the arrival of the parasite coincided with unfavourable low-winter temperatures (<13.5 °C⁵⁶). In fact, by May 2018, when temperatures increased above 13.5 °C, mass mortalities were detected in these populations (pers. com. García-March).

In the last decades, the participation of citizens in science has experienced an exponential growth, probably due to the ecological awareness and the wide range of possibilities offered by the latest technologies (e.g. web portals, mobiles, apps to report live observations⁵⁷). In this study, citizen science has played an essential role in the follow-up of a mass mortality event with a rapid expansion across an extensive area (western Mediterranean basin). Citizen science can overcome the logistics barriers of scientific monitoring, contributing with several observations at high spatial-temporal scales, as for example to track disease-carrying tiger mosquitoes⁴⁶. However, citizen observations require a strict quality control for the reliability of data reported^{58,59}. In our case, a scientific team was involved in the careful validation of each citizen observation based on: (i) the experience of sea-watcher (e.g., scuba diving instructor vs. kayak fan, the first with a supposed better experience observing pen shells), (ii) complementary information (e.g., habitat type, with rocky bottoms the essential habitat for the congeneric species *P. rudis*) and, essentially, with (iii) photographic evidence (the most important and essential additional information for validation). In fact, more than half of the reported observations of healthy *P. nobilis* were removed (58.82%) after being carefully scrutinized by the scientific team. Most of such errant observations made reference to a very similar species; *P. rudis*. This congeneric species remains in good health conditions and seems to be resistant to the disease, with recent mortality rates according to its natural rates, and not higher than before the outbreak^{6,60}. However it is difficult to discern between species due to anatomical similitudes³. When the technological problems of sharing observations are overcome, future efforts should be focused on minimizing the hard work of manually filtering citizens' observations⁵⁸. Notwithstanding the applicability of citizen observations, the best solution would appear to be the combination of citizen science with traditional scientific methods that combine tracking of mortality events in sentinel populations with detection of *H. pinnae*, allowing the two approaches to complement each other⁴⁶. Therefore not only validation of layman observations, but also a coordinated, scientific monitoring program for the Mediterranean would be beneficial to follow the spread of mortality events.

Overall, our results point to a challenging scenario for the conservation of the emblematic *P. nobilis*. Most likely, currents will carry the parasite along the whole Mediterranean basin, and are already reaching the healthy populations of the central (e.g., Sardinia - June 2018; pers. com. Coppa) and eastern Mediterranean (e.g., Lesvos Island, Greece - August 2018²⁸). In addition, the dispersal of the disease to distant localities could be assisted by vessels through their ballast waters, which constitutes one of the major vectors of primary and secondary introduction of alien species in the Mediterranean⁶¹. The extreme virulence of *H. pinnae*^{26–28} will probably devastate *P. nobilis* populations, except for populations confined in areas with environmental conditions beyond the tolerance limits of the parasite (constant low-temperatures and abnormally high or low salinity values) or the potential resistant individuals. The high genetic homogeneity of Mediterranean pen shell populations, with little differentiation between recently disappeared populations in more "open" waters and these scattered survival spots⁶², seriously compromises the recovery of the species as they likely share the same susceptibility for the parasite. Also, the inbreeding coefficient (F_{IS}) was positive and significant at the western Mediterranean locations⁶². Inbreeding can greatly reduce the average individual fitness, and loss of genetic variability from random genetic drift can diminish future adaptability to a changing environment⁶³. Despite the theoretical possibility that spots with surviving populations could act as a larval source for the spread of the species in larger areas⁶², this is only possible if they act as source populations, there is a favourable connection between these sites by local currents⁶⁴, and recruits meet with parasite-free conditions in the localities of settlement. Another possible source for the recovery of populations might be the presence of surviving resistant individuals. However, this possibility seems to be compromised by several bottle-necks. Even if now and then there are sightings of healthy and maybe resistant individuals, they are extremely scattered, reducing the probability of reproduction among them (as male and female gametes are released to the water column and fertilization is external²¹), so relatively dense populations might be needed to assure successful fertilization. In the case of overcoming this reproductive handicap, if the scattered resistant individuals were able to produce some recruits, their natural mortality would be very high, because the species is extremely vulnerable to predators when young^{6,14}. Furthermore, the pen shell's slow growth-rate and dynamics (e.g., only individuals larger than 37 cm of shell length - at least 4 years old - released gametes in experimental conditions⁶⁵) turn this species highly vulnerable to catastrophic events and predict a

very slow recovery of the species even if recruits manage to establish in infected areas. Therefore, it is crucial to act while there are still specimens in healthy conditions, and to protect and monitor surviving individuals. As illegal harvesting of *P. nobilis* still occurs in many Mediterranean countries (e.g.⁶⁶), better enforcement of the legislation for the protection of the species and actions for public awareness are needed to protect unaffected populations. The participation of citizens in protection campaigns and the monitoring of the status of populations all over the Mediterranean basin can play a key role.

Material and Methods

Data collection. We compiled data on mortality of pen shell populations starting from the first MME warning (28th September of 2016 at Ibiza, Balearic Islands, Spain; crossed yellow point at Fig. 2A) to April 2018. Scientific data was compiled from: (i) data published in different scientific documents^{26,67,68} and (ii) scuba diving monitoring of pen shell populations conducted by most of the scientific groups involved in the study of the *P. nobilis* (expert network). In order to complement the scientific data with multiple and simultaneous observations at many sites, a module open to citizens was added to (project NACRAS; launched on 2th of June of 2017) the website: <http://www.observadoresdelmar.es> (translated in English as “sea-watchers”). This platform allows citizens to report their observations about pen shell sightings and health state (alive, dead, or ill; the latter defined as a slow closing response of the valves or a pale and withdrawn mantle) with some complementary information (a spatio-temporal reference; date and GPS coordinates, temperature, salinity, depth, and habitat). After uploading an observation, the scientific team of the module curated each record based on sea-watcher experience, availability of complementary information and/or an uploaded photo, and frequently, through a dialogue with the sea-watcher.

From these sources, essential information like recent abnormal mortality, date, GPS coordinates, temperature, salinity, and depth were extracted for each observation to fit predictive models (see section Data analyses below). A trustworthy curated observation of one individual of a population reported as dead or ill under suspicious (not by predators, anchoring etc.) conditions was included in the model. Temperature and salinity data were extracted from the nearest available point of the database ‘EN4.2.1: quality controlled subsurface ocean temperature and salinity profiles and objective analyses’ (downloaded from <https://www.metoffice.gov.uk/hadobs/en4/> on April 30th 2018⁶⁹) except for sites where hydrographic values were carefully measured *in situ* by scientists (e.g., the Mar Menor coastal lagoon, the Alfacs Bay affected by River Ebro discharges). The EN4.2.1 dataset contains monthly objective analysis of temperature and salinity with the corrections⁶⁹ in a 1-degree grid and 42 different depths (from 5 m to 5000 m), spanning a period from 1900 to present.

Data analyses. The potential role of the surface currents on the expansion of the disease was investigated simulating the drift of 1000 virtual particles (*Par*) in a high-resolution regional model of the western Mediterranean Sea, the WMOP model^{70,71}. This model is developed and operated by SOCIB, the Balearic Islands Coastal Observing and Forecasting System. The WMOP model provides daily predictions of hydrodynamic conditions with a 2-km resolution from the Strait of Gibraltar to Corsica and Sardinia. It is a regional implementation of the Regional Ocean Modelling System (ROMS⁷²), downscaling simulations from the Copernicus Marine Service Mediterranean model, and forced by the high resolution HIRLAM model from the Spanish Meteorological Agency. Details of the operational system can be found in^{70,71}. An important aspect of this system is the multi-platform evaluation of the model predictions using available *in situ* and satellite observations, both in real-time and delayed modes^{70,71}, including daily validation updates provided on SOCIB website. The surface currents predicted by the operational model in 2016 and 2017 were used to simulate the drift of virtual particles from locations and times associated with observations of infected *P. nobilis* during the following 45 days. The TRACMASS algorithm⁷³ was used to generate the Lagrangian trajectories. A cluster of 1000 particles was seeded at each starting location, and advected by model surface currents plus a diffusive term adding a random displacement at each time step to account for model uncertainties and unresolved processes. Simulations were performed both in forward and backward modes to track the potential destination and provenance of the particles as described by the model surface current conditions. More concretely, simulations of currents were conducted in areas and within time-intervals ($t_0, \dots, t_n$; time in days) where the arrival of the disease (final time; t_f) at a given point (p_i) was detected by observations of first absence of mortality (pen shell alive at p_i, t_0) and then indications of mortality by probable infection (pen shell dead or ill at p_i, t_f). Given the available dataset, one backward simulation (from 2016/10/24 to 2016/09/09 in the Balearic Islands) and two forward simulations (from 2017/06/09 to 2017/07/24 in the L’Ametlla de Mar area and from 2017/10/27 to 2017/12/11 in North Catalonia) were produced in order to analyse the time for a particle to drift: (i) from p_1 (visible mortality at p_1, t_0) to p_2 (no infection observed at p_2, t_0 and mortality at p_2, t_f) in the case of forward simulations (tracking particles destination), and inversely, (ii) from p_2, t_f to p_1 in the case of backward simulation (tracking particles provenance). To predict the beginning of a local mortality event at a given point (p_1 or p_2 in the case of backward or forward simulation, respectively), the subset of simulated particles drifting within a buffer zone of 650 km² around selected point (as center of such buffer zone) were selected before extracting the final time (arrival time; t_f) of each of these particles. These predicted times were compared checking the time delay between empirical dates of *P. nobilis* infected in the starting (p_1) and ending locations (p_2).

The relationship with establishment success of the disease after arrival and environmental variables was addressed using a generalized additive model (GAM) with the *gam* function of the *mgcv* library within R software⁷⁴. GAMs extend general linear models allowing for complex correlations between response and explanatory variables⁷⁵. In this sense, the potential effect of temperature (*Temp*) and salinity (*Sal*) on the presence/absence of the disease (*Disease*) was tested fitting a binomial GAM [*Disease* ~ *s(Temp)* + *s(Sal)*]. It is important to highlight that a subset of data was selected to fit the GAM ($n = 271$ observations; 232 presence and 39 absence of disease). Only data with a probable spatio-temporal prevalence of the disease were selected, avoiding the bias caused by the spatio-temporal absence of the disease (e.g., data from Eastern Mediterranean where the disease has not yet been detected and the *P. nobilis* populations are still healthy).

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Author Contributions

Original idea and planning I.E.H. and M.C.-R. Implementation of the hydrodynamic model and computation of the particle trajectories by B.M. M.C.-R. analysed the data and prepared the figures. M.C.-R. and I.E.H. interpreted the data and wrote the first draft. I.E.H., M.V.-L., and M.C.-R. prepared the revised manuscript. Á.A. helped design the animation provided in Supplementary Material section. M.C.-R., M.V.-L., E.Á., S.D., P.A., E.B., A.B., S.C., J.R.G.-M., S.G., F.G.C., L.H., S.V.J.-G., S.K., D.K.K., V.M., B.M., F.P.P., S.J.P., P.P., J.T.-M., J.deV., N.V., F.Z.B., and I.Z. participated in the fieldwork. All authors contributed to the writing of and reviewed the manuscript.

Additional Information

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