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Unexpected residual habitats raise hope for the survival of the fan mussel *Pinna nobilis* along the Occitan coast (Northwest Mediterranean Sea)

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ABSTRACT: In 2019, the status of the Mediterranean fan mussel *Pinna nobilis* was elevated to 'Critically Endangered' on the IUCN Red List, in response to the pandemic caused by the parasite *Haplosporidium pinnae*. Identifying refuge habitats, free from parasites, is critical to the survival of the mussel. The distribution of *P. nobilis* was investigated along the Occitan coast (Northwest Mediterranean Sea) because of the presence of a unique lagoonal system that may provide potential refuges. Interviews with users and managers were conducted to identify target zones where the species was sighted. *In situ* surveys were carried out to define the main aggregations of fan mussels and characterize the habitat. Line transects were deployed to count and measure individuals to estimate density, abundance, and size distribution. Population densities were variable, ranging from 0.6 ± 0.2 (SE) to 70.8 ± 7.6 ind. 100 m^{-2} , representing one of the highest densities reported in the Mediterranean Sea. The total abundance of individuals across the coast was extrapolated to 163 000, with 87 % located in Thau and Salses-Leucate, highlighting these lagoons as essential for the survival of the species. This study also revealed the diversity of habitats colonized by *P. nobilis*. In the context of the pandemic, only the lagoon populations remain unaffected and provide natural refuges that have disappeared from all open-water coastal areas. However, the conditions in these lagoons could become unfavorable, leading to the collapse of the last *P. nobilis* populations. We therefore propose that Thau and Salses-Leucate lagoons, which harbor the largest remaining populations of *P. nobilis*, should be declared as conservation priorities.

KEY WORDS: Habitat use · Size distribution · Abundance estimation · Population density · Conservation

1. INTRODUCTION

The fan mussel *Pinna nobilis* Linnaeus, 1758 is an endemic bivalve of the Mediterranean Sea which lives half-buried in soft-bottom substratum, generally associated with seagrass meadows (*Posidonia oceanica*, *Zostera marina*, *Z. noltei*, or *Cymodocea nodosa*). The species usually colonizes the subtidal area, up to 60 m deep (Basso et al. 2015b); beyond

this depth, meadow development is limited by light and water transparency (Butler et al. 1993). Because of this association, the distribution of *P. nobilis* populations is usually aggregative and patchy. However, while this association is widely accepted, dense populations can also be found in muddy bottoms such as in lagoons (Katsanevakis 2006) or even in degraded habitats like harbors (Alomar et al. 2015) or maerl beds (Basso et al. 2015b).

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As a filter feeder, *P. nobilis* plays an important ecological role by removing large amounts of detritus and organic matter (Basso et al. 2015b), and thus helps to maintain the clarity of the water column and increases the rate at which organic matter is recycled (Trigos et al. 2014). Although these are still preliminary results, their filtration rate was calculated to be around 6 l h^{-1} (Riva 2003). Strayer et al. (1999) estimated that some bivalve populations can filter 100% of the entire water column per day. *P. nobilis* are large bivalves, some with a total shell length of $>1 \text{ m}$, so a dense population could have an important role in maintaining the quality of the environment. The large shells of *P. nobilis* are also colonized by a widely diverse community of epibionts, as they provide a hard substratum in soft-bottom areas which contribute to an increase in habitat complexity and local biodiversity (Giacobbe 2002, Rabaoui et al. 2009).

From antiquity until the 19th century, *P. nobilis* was regularly exploited for several uses. The byssus was used as sea silk for the fabrication of luxury clothing, and the nacre of the shell was used to make buttons and jewelry. Today, while no longer directly exploited, *P. nobilis* populations are still under high pressure, mainly due to human activities (anchoring, pollution, habitat reduction, and fragmentation) which have led to the decline of the species (Öndes et al. 2020). As a consequence, since 1992, the fan mussel has been under strict protection according to the European Council Directive 92/43/EEC (Annex IV), and several countries around the Mediterranean Sea have implemented national conservation plans.

The species is currently facing a major ongoing crisis that threatens its survival. Since October 2016, mass mortalities have been observed for fan mussel populations, caused by the protozoan parasite newly described as *Haplosporidium pinnae* (Catanese et al. 2018). The first signs of the epidemic were observed in southeast Spain (Vázquez-Luis et al. 2017), and it has now spread throughout the entire Mediterranean Sea (García-March et al. 2020b). To date, most of the infected populations have been devastated (Katsanavakis et al. 2022). This is an unprecedented disappearance of a marine species for which neither the mortality rates (around 100%) nor the speed of propagation has ever been recorded (Cabanelas-Reboredo et al. 2019). This epidemic could therefore lead to the extinction of the species, given that its distribution is restricted to the Mediterranean Sea. In response to this critical situation, the status of the species was reevaluated and was updated to 'Critically Endangered' on the IUCN Red List (Kersting et al. 2019). However, a few populations in the infected area are

still in good condition and remain less affected by the parasite, for example in Alfacs Bay and Mar Menor in Spain (García-March et al. 2020b, Prado et al. 2020).

Despite being a highly emblematic species and the urgent need for its conservation, the ecology and biology of *P. nobilis* remain poorly documented (Basso et al. 2015b). It is thus necessary to amass baseline knowledge about the stock and natural distribution of the species, including the location of main populations, to implement effective protection strategies.

The Occitan coast, located in the northwestern part of the Mediterranean Sea, in the Gulf of Lion, is formed by a mosaic of different landscapes including rocky and sandy coasts and about 40 000 ha of wetland, allowing the development of high biodiversity. Further, while on average, lagoons make up 13% of coastlines around the world, they represent almost 50% of the coast of the Gulf of Lion (Mouillot et al. 2005), and they may be considered as priority areas for *P. nobilis* conservation as lagoons are the only habitat where live populations of *P. nobilis* remain along the Spanish coastline. Although fan mussels have been observed in Occitan lagoons, the distribution of populations of *P. nobilis* has never been fully investigated along the Occitan coast and within the many different types of habitat found in the area. The main objectives of the present study were to (1) investigate the spatial distribution of the species, (2) characterize the aggregations of fan mussels in terms of density, size structure, and type of habitat, and (3) provide an estimate for the total number of fan mussels across the Occitan coast. This work was carried out before fan mussel populations in this region were decimated by *H. pinnae* and could thus be used as a pre-pandemic historical reference to implement efficient conservation strategies.

2. MATERIALS AND METHODS

2.1. Study area

The study was conducted in the Gulf of Lion, from the Spanish border to the Rhône delta, within the area defined as the Occitan coastline, including ports and lagoons (Fig. 1). Based on a preliminary literature review and interviews of local users and managers, we focused on the localities described in Table 1 that were identified as places that *Pinna nobilis* was most likely to colonize. Three lagoons, with different morphological and physicochemical characteristics, were selected. Salses-Leucate and Thau lagoons are among the largest lagoons in the Gulf of Lion and are on av-

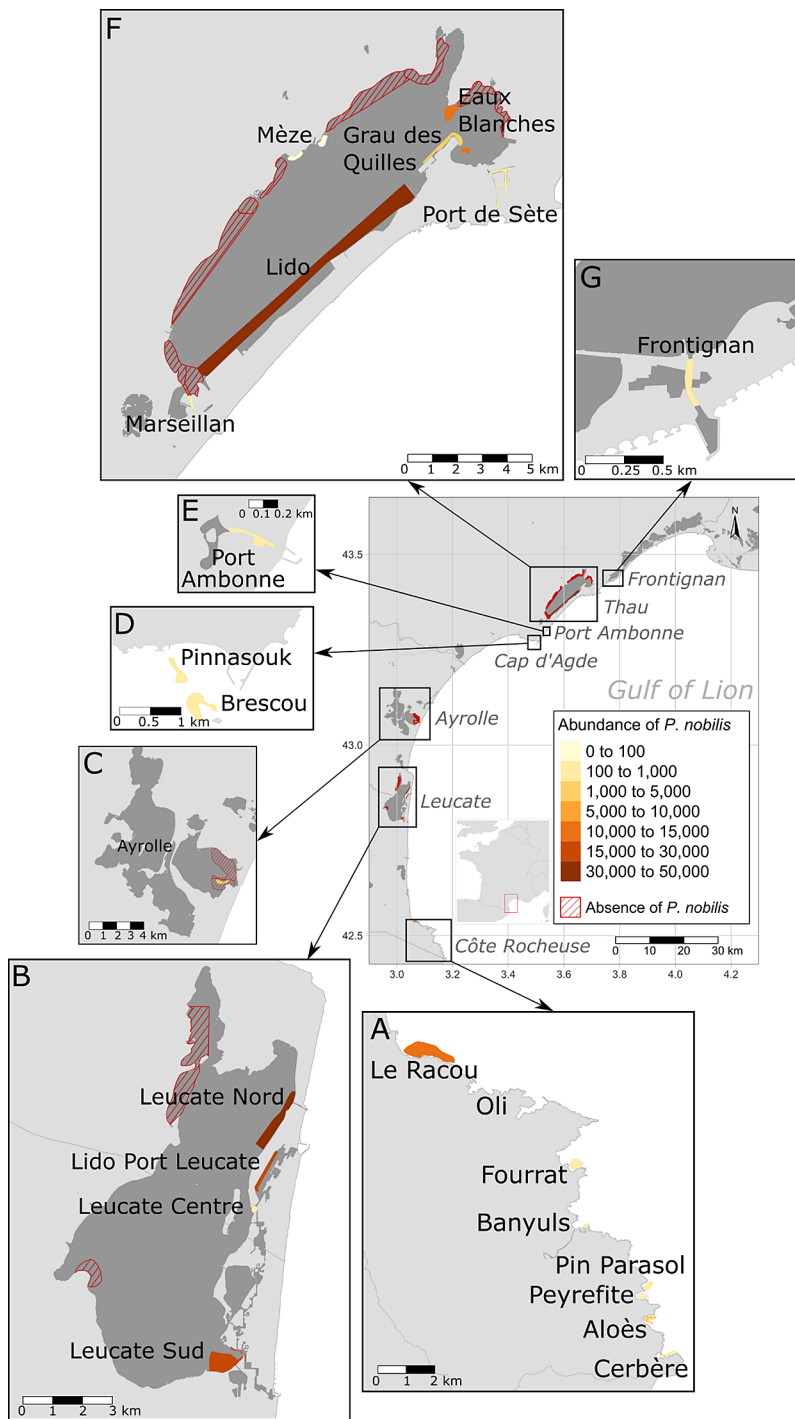


Fig. 1. Study area, showing all surveyed sites, the respective estimated abundances of fan mussels, and the areas where the species was absent. (A) Côte Rocheuse, (B) Salses-Leucate, (C) Ayrolle, (D) Cap d'Agde, (E) Port Ambonne, (F) Thau, (G) Frontignan. Light grey: land; dark grey: lagoons

erage almost 2 and 4 m deep, respectively. Their water conditions are similar to seawater, as they are highly connected to the sea through 2 channels (Grau des Pisses-Saumes in the south, Grau des Quilles in

the center) and a port (Port de Sète in the North) in Thau, and through 2 channels that both cross a port in Salses-Leucate (Grau de Leucate with Port Leucate in the north and Grau de Saint-Ange with Port Barcarès in the south, but the latter was not included in the study as no fan mussel was present). Ayrolle is a much smaller lagoon with a very restricted influx of fresh water and an average depth of 0.75 m, but with a strong connection to the sea through a deeper channel. Almost the entire surface of the lagoon is covered by *Zostera noltei*. Two localities, open to the sea, were included (Côte Rocheuse and Cap d'Agde). Côte Rocheuse is characterized by small beaches and bays that alternate along a rocky coast. The type of substrate varies depending on the site but was mostly composed of sand, rocks, or matte, and all selected areas were covered by *Posidonia oceanica*. All data from Côte Rocheuse were extracted from a previous study detailed by Iwankow (2015). In Cap d'Agde, the area was not homogeneous, as one site (Brescou) was mainly covered by dead matte of *P. oceanica* and meadow, and the other (Pinnasouk) was overrun by an invasive alga, *Caulerpa cylindracea*. *P. nobilis* aggregations were also observed in 2 other smaller harbors (Frontignan, Port Ambonne), and thus these localities were also added to the study. The number of surveyed sites was different from one locality to another, depending on the surveyed area and its homogeneity, and varied from one site in Ayrolle, Port Ambonne, and Frontignan to 8 sites within Côte Rocheuse.

2.2. Field surveys

The main goal of the study was to characterize the spatial distribution of *P. nobilis* aggregations along the Occitan coastline, within the context of the

ongoing mass mortality, so as to define priority conservation zones. Since the study region was very large (about 220 km of coastline), it was necessary to reduce the size of the search area. Interviews with

Table 1. Characteristics of sites sampled for the presence of *Pinna nobilis*: type of habitat, surface area of suitable habitat, percentage of suitable habitat within the locality, number of transects surveyed (N_T), surface surveyed at each site (S_T), percentage of suitable habitat covered, mean depth of individuals within a site, type of substrate at each site, vegetation if present, minimum, maximum, and mean densities of living individuals (\pm SE), and estimated abundance calculated for each site with a 95% confidence interval (presented as \pm values). **Bold** values represent total values for localities with >1 site; Dash (-): not applicable

Locality	Site	Type of habitat	Surface of suitable habitat (m ²)	Percentage of suitable habitat	Transects		
					N_T	S_T (m ²)	Suitable habitat covered (%)
Côte Rocheuse	Cerbère	Open sea	19000	0.2	6	600	3.2
	Aloès	Open sea	25000	0.2	7	700	2.8
	Peyrefite	Open sea	16000	0.14	6	600	3.8
	Pin Parasol	Open sea	12000	0.1	6	600	5
	Banyuls	Open sea	5000	0.05	6	600	12
	Fourrat	Open sea	22000	0.2	6	600	2.7
	Oli	Open sea	2000	0.02	6	600	30
	Le Racou	Open sea	124000	1.1	6	600	0.5
	Total	-	225000	1.9	49	4900	2.2
Salses-Leucate	Lido Port Leucate	Port	35000	0.06	6	720	2.1
	Leucate Centre	Lagoon	6000	0.01	8	1200	20
	Leucate Nord	Lagoon	400000	0.7	17	4080	1
	Leucate Sud	Lagoon	170000	0.3	14	3000	1.8
	Total	-	611000	1.1	45	9000	1.5
Ayrolle	Ayrolle	Lagoon	448209	3.4	12	2880	0.6
Cap d'Agde	Brescou	Open Sea	6500	0.01	3	720	11.1
	Pinnasouk	Open Sea	2000	0.003	2	480	24
	Total	-	8500	0.01	5	1200	14.1
Port Ambonne	Port Ambonne	Port	8500	13.1	13	3120	36.7
Thau	Port de Sète	Port	20000	0.03	3	720	3.6
	Eaux Blanches	Lagoon	500000	0.7	6	720	0.1
	Grau des Quilles	Lagoon	25000	0.03	5	1200	4.8
	Lido	Lagoon	3174605	4.2	25	6000	0.2
	Mèze	Lagoon	6000	0.008	16	2400	40
	Marseillan	Lagoon	5000	0.007	2	480	9.6
	Total	-	3730605	4.9	57	11520	0.3
Frontignan	Frontignan	Port	9836	16.4	3	720	7.3

Table 1 continued on next page

local users, both professional (fishermen, managers of ports or marine protected areas) and recreational (divers, kite surfers, etc.) along the coastline were conducted and added to the information from several unpublished documents such as management documents, impact studies, or environmental surveys to identify target locations where the species had previously been reported. *In situ* visual searches were then performed by random dives at these sites to verify outcomes of the interviews, and finally, to find the areas colonized by *P. nobilis* and those where the species is absent. This step also allowed identifying the habitats colonized by *P. nobilis* to pinpoint new areas with similar characteristics that were not initially mentioned in the interviews.

In each area where fan mussels were observed, a zonation was defined according to the homogeneity of the habitat, based on aerial photos. These areas, colonized by *P. nobilis*, were considered suitable habitats for the species, regardless of environmental conditions, and targeted for a detailed screening by SCUBA diving. Each zone was considered constant and homogeneous and was described by recording the following parameters: depth, type of substrate (coarse sand, fine sand, or mud), and the presence/absence of seagrass or/and algae with the identification of the species in case of presence. All areas where no fan mussels were found were not considered suitable habitats for the species and were removed from this analysis.

Table 1 (continued)

Mean depth (m)	Type of substrate	Vegetation	Density (ind. 100 m ⁻²)			Estimated abundance
			Min	Max	Mean	
8.5	Rock + meadow	<i>Posidonia oceanica</i>	0	5	2.5 ± 0.9	482 ± 320
6.2	Sand + meadow	<i>Posidonia oceanica</i>	7	24	15 ± 3	3706 ± 1337
4.7	Sand + meadow + matte	<i>Posidonia oceanica</i>	2	7	3.8 ± 0.9	632 ± 256
14.5	Sand + meadow	<i>Posidonia oceanica</i>	0	6	1.7 ± 1.1	197 ± 229
5.0	Sand + meadow + matte	<i>Posidonia oceanica</i>	2	6	4.3 ± 0.9	233 ± 85
8.3	Rock + meadow + matte	<i>Posidonia oceanica</i>	0	3	1.8 ± 0.5	401 ± 205
5.7	Rock + sand + meadow	<i>Posidonia oceanica</i>	0	2	1 ± 0.3	23 ± 11
7.5	Sand + meadow	<i>Posidonia oceanica</i>	4	21	9.3 ± 2.7	11605 ± 5958
7.5	–	–	–	–	–	17279 ± 8401
0.7	Mud + meadow	<i>Zostera noltei</i>	55.8	100	70.8 ± 7.6	24792 ± 4778
1.1	Mud + meadow	<i>Zostera marina</i>	0	10.8	2 ± 1.4	119 ± 154
0.9	Fine sand + meadow	<i>Zostera noltei</i> + <i>Ruppia cirrhosa</i>	0	27.1	7.7 ± 2.1	30882 ± 16133
1.7	Fine sand + meadow	<i>Zostera marina</i>	0	58.3	14.5 ± 5.1	24690 ± 16258
1.1	–	–	–	–	–	80483 ± 37323
0.9	Shell mud + meadow	<i>Zostera noltei</i>	0	1.7	0.6 ± 0.2	2801 ± 1460
4.2	Sand + matte	–	1.3	3.3	1.9 ± 0.8	126 ± 88
3.9	Sand + algae	<i>Caulerpa cylindracea</i>	8.8	9.6	9.2 ± 0.6	183 ± 16
4.1	–	–	–	–	–	309 ± 104
2.1	Shell mud	–	0	6.7	1.2 ± 0.6	104 ± 90
5.9	Shell sand	–	0	12.1	4.0 ± 4.9	806 ± 1579
1.9	Mud + meadow	<i>Zostera marina</i>	0	5	2.6 ± 0.7	13194 ± 6471
2.2	Sand + meadow	<i>Zostera noltei</i>	0	33.3	10.2 ± 7.2	2542 ± 3169
1.9	Coarse sand + meadow	<i>Zostera noltei</i>	0	13.3	1.4 ± 0.5	44974 ± 32588
1.3	Shell sand + meadow	<i>Zostera noltei</i>	0	7.9	1.6 ± 0.7	95 ± 75
2.9	Mud	–	5.4	9.2	7.3 ± 2.7	365 ± 184
2.7	–	–	–	–	–	61976 ± 44066
3.4	Shell mud	–	4.6	7.1	5.97 ± 0.90	587 ± 142

2.3. Estimation of density of individuals and population size in each locality

The density measurements were performed over 1 year, between spring 2018 and spring 2019, when all previously described areas were surveyed in detail. Within each targeted area of suitable habitat, 60 m long transect lines were randomly deployed, and all individuals within 1 or 2 m from each side of the line were counted and measured (see Section 2.4), thus covering 120 or 240 m² per transect, depending on the water transparency. The number of transect lines varied depending on the size of the surveyed zone, as the objective was to cover a minimum of 1% of the surface of the suitable habitat in

each locality. The mean density was expressed as the number of specimens per 100 m² for each site, and the population size (total abundance) was estimated by relating the mean density to the total surface of suitable habitat at a given site.

2.4. Size estimation

As fan mussels live half-buried in the sediment, it is not possible to directly measure the total length of the shell and as such, shell length was estimated following the same method as described by Peyran et al. (2021). The maximum width, minimum width, and unburied length were all meas-

ured as per García-March et al. (2002). The equation developed by de Gaulejac (1993) and detailed by Peyran et al. (2021) was then used to estimate the total length.

The size of individuals was used to estimate their stage related to sexual maturity (i.e. separating juveniles from adults) following the methods described by Iwankow (2015), where growth models from different study sites and derived from Martínez et al. (2014) were averaged and the different life stages of *P. nobilis* were deducted from this mean model. Sexual maturity coincides with a slowdown in growth, which happens when individuals reach about 24.5 cm in length. We used this value as a threshold; individuals below this threshold were considered juveniles and those above, as adults. Kersting & García-March (2017) showed that average (\pm SD) recruit size ranged from 0.95 ± 0.49 to 4.15 ± 1.73 cm of total shell length; thus individuals smaller than 6 cm (rarely observed, as they are difficult to find in seagrass and algal beds) were considered as recruits of the year.

2.5. Statistical analysis

To look for similarities between sampled sites, a factor analysis of mixed data (FAMD) was carried out by using the 'FactoMineR' package (Lê et al. 2008) implemented in R software v 4.0.3 (R Core Team 2018), which allowed us to consider both quantitative and qualitative variables simultaneously. All parameters measured within sampled sites were used as active data, including the type of habitat (lagoon, open sea, port), mean depth, type of substrate (mud, sand, rock, shell sand, etc.), presence or absence of vegetation, its cover (no cover, scattered, dense) and the species of vegetation present, the density of fan mussels, and their mean size. All of the data used are listed in Table A1 in the Appendix. Mean densities of fan mussels were also compared depending on the type of habitat (lagoon, open sea, or port) and the presence or absence of vegetation. To do so, homogeneities of variances were first tested with Levene's test using the 'car' package (Fox & Weisberg 2019) implemented in R software and, as variances were not homogeneous (Levene's tests, $p < 0.001$), 2 non-parametric Kruskal-Wallis tests were performed, followed by a Wilcoxon-Mann-Whitney post hoc test for pairwise comparisons, using the 'rstatix' package (Kassambara 2021). We used a significance level of $\alpha = 0.05$.

3. RESULTS

3.1. Surface of suitable habitat and spatial distribution

The surface of suitable habitat which hosts fan mussels within a given locality varied among sites, and the proportion ranged from 0.01% in Cap d'Agde to 16.4% in Frontignan (Table 1). In Salses-Leucate and Thau lagoons, which are the 2 areas with the largest abundances of *Pinna nobilis* individuals, the percentage of suitable habitat was 1.1 and 4.9%, respectively, of the total lagoon area. In Salses-Leucate, almost all of the periphery was explored, except for some areas where diving was not possible because of the presence of oyster farms (Fig. 1). However, the species was absent from all of the western surveyed zones, and the main aggregations were found near the channels connecting the lagoon to the sea (Grau de Leucate in the north and Grau de Saint Ange in the south). In Thau, the situation was similar to Salses-Leucate where the entire periphery of the lagoon was explored, and where the distribution of fan mussels was very heterogeneous, as most of the individuals were found close to a connection with the sea (Grau des Quilles in the north, Grau des Pisses-Saumes in the south, and the harbor at Port de Sète). *P. nobilis* was absent from most of the western part, except at Mèze, where few individuals were observed. In the Ayrolle lagoon, most of the individuals were found in the channel connecting the lagoon to the sea, as all other areas of the lagoon were too shallow and likely dry during certain periods of the year. In Cap d'Agde, fan mussels were found in 2 main areas: Brescou, located next to a small island, and Pinnasouk, a small isolated area in front of the entrance to the port. In Port Ambonne, individuals were observed in all un-dredged parts of the harbor. In Frontignan, individuals were mostly located in the channel connecting the port to the sea.

3.2. Population density

A total of 2074 living and 184 dead specimens (empty shells) were observed over 184 transect lines covering a total surface of 33340 m² over 1 year (between spring 2018 and spring 2019). The percentage of suitable habitat covered within a site ranged from 0.1% in Thau at Eaux Blanches to 36.7% in Port Ambonne (Table 1). The population density (mean \pm SE) was highly variable depending on the sampled site, ranging from 0.6 ± 0.2 ind. 100 m⁻² in Ayrolle to

70.8 ± 7.6 ind. 100 m⁻² in Salses-Leucate at Lido port Leucate (Table 1). These 2 sites presented similar characteristics: both were very shallow (0.9 and 0.7 m deep, respectively), with similar types of substrate, and covered by *Zostera noltei*.

3.3. Population size estimation

Estimated abundance, within a given sampled site, was calculated as the product of the surface of suitable habitat, based on aerial images, and the estimated population density. Local estimations were aggregated and yielded a total stock estimate of 163 539 ± 91 586 *P. nobilis* individuals for the Occitan coast (Table 1). The highest abundances were found in the 2 largest lagoons, Salses-Leucate and Thau, with 80 483 ± 37 323 and 61 976 ± 44 066 individuals, respectively, which thus represents 87 % of the total stock of fan mussels at the scale of the Occitan coast

(Table 1, Fig. 1). In Thau, the highest total abundance was related to a large homogeneous area, the Lido, whereas in Salses-Leucate, individuals were more evenly distributed throughout the surveyed sites. The lowest abundances were found in open-sea sites, such as at Côte Rocheuse, where 6 of 8 sites had abundances between 23 and 632 individuals, and in small ports such as in Port Ambonne and Frontignan, with 104 and 587 specimens, respectively. These last sites provide small areas of suitable habitat which limit the total abundance possible.

3.4. Size distribution and maturity

Total shell length of living individuals ranged from 5.07 cm in Thau at the Lido to 68.50 cm in Leucate Sud (Fig. 2), and the mean size per site ranged from 11.95 cm in Côte Rocheuse, at Le Racou, to 45.8 cm in Port Ambonne. In total, across all sites surveyed *in*

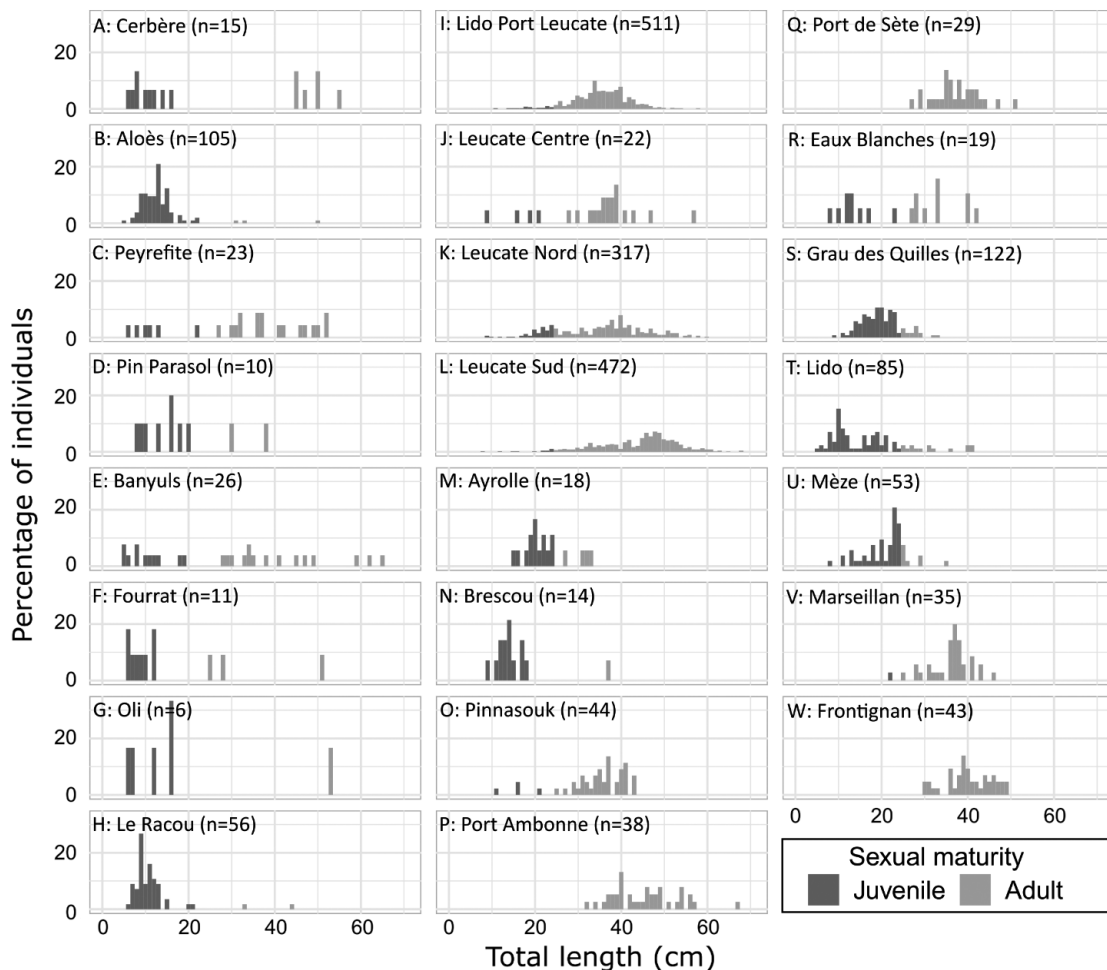


Fig. 2. Total shell length distribution of living fan mussels within each sampled site

situ, 2 recruits, 567 juveniles, and 1642 adults were measured. As expected, because recruits are almost impossible to see in seagrass beds, only very few were counted. Size distribution was unimodal at most sites, and they were dominated only by adults or only by juveniles (Fig. 2). However, several sites, Eaux Blanches in Thau, Leucate Nord in Salses-Leucate, and Banyuls, Peyrefite, and Cerbère in Côte Rocheuse, showed a bimodal distribution. In Salses-Leucate, all sampled sites were dominated by adults and only a few juveniles were present at Leucate Nord and Leucate Centre, whereas in Thau, juveniles were dominant in almost all areas, except at Port de Sète and Marseillan. Juveniles were also more abundant than adults for all sites in Côte Rocheuse.

3.5. Characteristics of the habitats colonized by *P. nobilis*

All observed individuals were located in shallow areas with a mean depth ranging from 0.7 m in Salses-Leucate at Lido Port Leucate to 14.5 m in Côte

Rocheuse at Pin Parasol (Table 1). Several types of substrate were encountered during the *in situ* surveys, from mud to rock (see Table 1), sometimes exposed, sometimes covered by meadows or algae. Among sampled sites, 18 were covered by vegetation, mostly phanerogams, as only Pinnasouk at Cap d'Agde was covered by an invasive alga (*Caulerpa cylindracea*), and 5 were bare sediment.

The 2 first dimensions resulting from the FAMD represented 36.9% of the total variance among sites (Fig. 3). The analysis showed that, when considering the parameters measured in the present study, sampled sites were structured into 3 groups that were linked to a type of habitat (Fig. 3). One group was almost entirely composed of sites located in the open sea, the second included the ports and Brescou (Cap d'Agde) and Marseillan (Thau), and the third grouped lagoon sites with Pinnasouk (Cap d'Agde) and Lido Port Leucate (Salses-Leucate). Mean depth and parameters associated with underwater vegetation cover (including presence/absence, species, and coverage) were the main variables which contributed significantly to the clustering of sites (see Table A1).

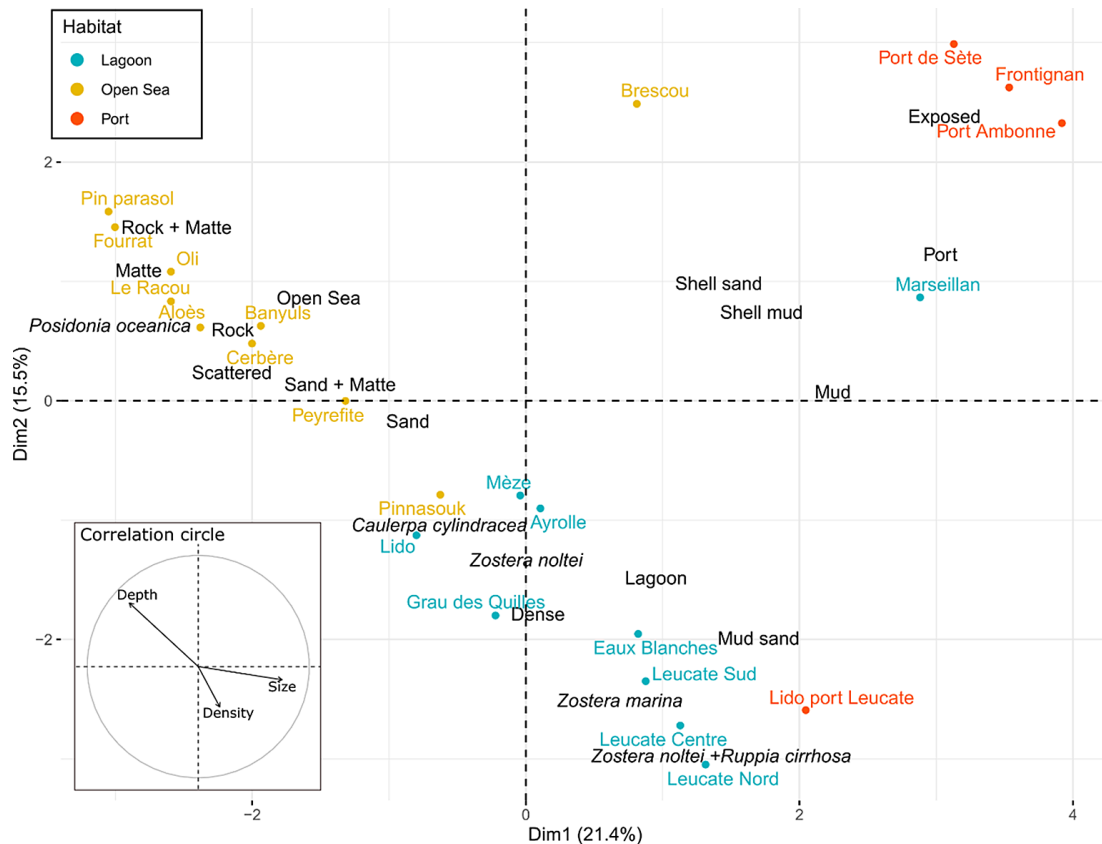


Fig. 3. Factor analysis of mixed data showing sampled sites and variables involved in the analysis. Modalities of qualitative variables are represented in black, quantitative variables are represented in the correlation circle, and colors correspond to the 3 different types of habitat

In contrast, the type of substrate was weakly and non-significantly involved in clustering sites. Sites among the group of open-sea sites and the group of lagoon sites were distributed along a depth gradient and were separated by the species of vegetation. The group with ports, plus Brescou and Marseillan, was excluded from the depth gradient and was characterized by bare sediments.

When comparing the type of habitat, mean population density was highest in ports and lowest in lagoons (Table 2). However, a non-parametric Kruskal-Wallis test was performed showing that the mean densities of *P. nobilis* were significantly different depending on the type of habitat (Kruskal-Wallis test, $p = 0.0233$) but, after pairwise comparisons, it appeared that it was significantly different only when comparing lagoon and open-sea sites (Wilcoxon-Mann-Whitney post hoc test, $p = 0.014$). Moreover, although mean density seemed to be higher at sites where vegetation was present than at those with bare sediment, the difference was not significantly different (Kruskal-Wallis test, $p = 0.2052$).

4. DISCUSSION

In the context of the ongoing fast and dramatic mortality due to a recent parasite expansion, the goals of the present work were to identify the main *Pinna nobilis* aggregations in the Gulf of Lion and highlight their characteristics before the parasite invasion. Identification of the remaining local populations of *P. nobilis* will be essential to ensure the rapid implementation of conservation plans. The present work highlights the importance of lagoons, as the largest aggregations were found in Thau along the Lido site with about 45 000 fan mussels and more than 30 000 in Salses-Leucate at the Leucate Nord site. However, the densities of fan mussels within

Table 2. Mean \pm SE density of living fan mussels (ind. 100 m^{-2}) depending on the type of habitat and depending on the presence or absence of vegetation. Pairwise tests indicated that the only significant comparison was between lagoon and open-sea sites (asterisk; Wilcoxon-Mann-Whitney test, $p = 0.014$)

	Number of transects	Density
Lagoon	105	4.8 ± 0.9
Open sea	54	5.1 ± 0.8
Port	25	18.8 ± 6.3
Presence of vegetation	160	7.4 ± 1.2
Absence of vegetation	24	2.8 ± 0.7

these 2 lagoons varied among the surveyed sites, even when the environmental conditions appeared to be similar, leading to a very patchy global distribution. Individuals were found in shallow areas ($<14.5\text{ m}$) and on different types of soft substratum (from coarse sand to mud), with or without vegetation (algae or seagrass meadow), although the presence of phanerogams appeared to be favorable to the presence of fan mussels.

A total of only 2 recruits were observed for all surveys, raising questions about their absence. In the present study, fieldwork was mainly conducted in the spring and early summer of 2018 and 2019, which is outside the settlement period that occurs at the end of August through the beginning of September (Cabanellas-Reboredo et al. 2009). The smallest individuals observed were thus recruits from the previous year, meaning that the observed individuals were around 1 yr old. Another reason for the low numbers of recruits observed may be the difficulty associated with finding them. When associated with seagrass meadows, shell size affects the detectability of specimens, as small and medium-sized individuals are covered by leaves (Katsanevakis 2006, Rabaoui et al. 2010, Basso et al. 2015b). Furthermore, Hendriks et al. (2012) demonstrated that the probability of finding individuals of *P. nobilis* in meadows is positively associated with shell size and that this association is consistent between sites. In our study, small individuals (i.e. recruits of the year) were absent at sites where the substrate is covered by meadows, but if present, it would have been very difficult to see them because of the leaves. From our work, we cannot consider the absence or the abundance of recruits as a reliable variable.

4.1. Characterization of the habitats colonized by *P. nobilis*

The association of fan mussels and *Posidonia oceanica* meadows is well described (Richardson et al. 1999, Basso et al. 2015b) and is further illustrated at the Côte Rocheuse sites in the present work. Fan mussels were also observed in association with other species of phanerogams, mostly *Zostera marina* and *Z. noltei* in lagoons, and with *Caulerpa cylindracea*, an invasive alga that covered almost all sediments in Pinna-souk at Cap d'Agde. Relatively dense populations were also found on substrates without meadows, such as in Thau at Port de Sète or Marseillan. Similar results were found by Addis et al. (2009) in the Gulf of Oristano, Sardinia, where the density of individuals

was higher at an estuary site (12 ind. 100 m⁻²) than within the meadows (3–4 ind. 100 m⁻²). In another study based in Lake Vouliagmeni (Korinthiakos Gulf, Greece), a substantial population of *P. nobilis* was reported, although marine seagrass was absent (Katsanevakis 2006). Overall, fan mussels can live in bare sediment, and the presence of meadow is a favorable factor rather than a limiting one. In our work, the main aggregations were generally found in seagrass, which demonstrates the advantages offered by meadows that have been widely described in the literature (Duarte et al. 1999, Hendriks et al. 2008, 2011, 2012).

During the study, fan mussels were observed buried in several types of substrate, from mud to coarse sand, demonstrating that, even if the nature of the substratum may impact the development of the population, it is not a limiting factor, as long as it is soft. Only hard bottom appeared unsuitable for settlement. Muddy environments present both advantages and disadvantages. The predominance of muddy detritus in the diet of fan mussels was previously reported (Davenport et al. 2011, Najdek et al. 2013, Trigos et al. 2014), and the high concentration of organic matter available in muddy environments provides an abundant source of food. However, resuspension of fine sediments during turbulent weather in shallow areas could interfere with filtration and may have negative impacts on respiration. Muddy substrates, rich in organic matter, are generally more subject to anoxia when hydrodynamics are low, which can enhance the production of hydrogen sulfide, leading to the death of individuals (Prado et al. 2014, Basso et al. 2015a).

Considering the difficulty and the time required to collect relevant data on marine currents, the hydrodynamics were not measured during our survey. However, hydrodynamics may be one of the key parameters responsible for the structuring of fan mussel distribution. Several studies (García-March et al. 2007b, 2016, 2020a, Hendriks et al. 2011, Prado et al. 2021) pointed out that high hydrodynamics may be a limiting factor for the settlement and the development of fan mussels. For example, García-March et al. (2007a) demonstrated that drag forces, generated by waves, increase mortality in shallow open-sea populations by breaking or dislodging shells. García-March et al. (2016) showed that bimodal currents generated by waves also affect gaping activity by reducing the gape angle and increasing the number of movements, which are both associated with defensive reactions, likely to limit the ingestion of undesirable particles. The hydrodynamics in the open sea are usually higher than in lagoons, particularly on the Occitan coast, which is subjected to strong winds and sea-

states that can impact coastal habitats (Petrenko et al. 2005, Renault et al. 2012); this could explain the lower abundances found at our open-sea sites. However, within the lagoons, the highest densities of fan mussels were mostly found in sites close to a connection to the sea, where there are water exchanges, for example in Salses-Leucate at Leucate Nord, Leucate Sud, and in Thau at Grau des Quilles. Similar situations have been reported in Aquatina Lagoon, Italy (Marrocco et al. 2018), in the Ghar el Melh, Tunisia (Zakhama-Sraieb et al. 2011), in Alfacs Bay, Spain (Prado et al. 2014), and in Mar Menor, Spain (Giménez-Casalduero et al. 2020), where *P. nobilis* individuals were found in aggregations near the mouth of the lagoon. However, this was not the case in Lake Vouliagmeni, as individuals were distributed all around the saltwater lake (Katsanevakis 2007). The aggregation of *P. nobilis* around connections to the sea could be explained by a constant water flow from the sea, delivering food and larval supply. Several authors hypothesized that fan mussel distribution might instead be determined by the oxygen conditions in the habitat (Zakhama-Sraieb et al. 2011, García-March et al. 2016), as the presence of at least a minimum of water motion ensures the renewal of water and helps to maintain good water quality, particularly in lagoons where eutrophication is not rare (Carpenter et al. 1998, Lloret et al. 2008, Padedda et al. 2019).

At most of the sampled sites, adults and juveniles did not seem to cohabitate. Several studies have reported depth-related size segregation of fan mussels, with smaller individuals in shallow habitats and larger individuals in deeper habitats (Katsanevakis 2006, García-March et al. 2007a). Here, except for Côte Rocheuse, all individuals were restricted to shallow waters (<6 m). This is especially true for lagoons, as the maximum depth was 2.9 m at Marseillan in Thau. The restriction to shallow habitat may be due to the correlation of depth with other parameters such as hydrodynamics, type of substrate, reduction in the food supply, oxygen availability etc., that may impact growth (García-March et al. 2007a,b), rather than directly linked to depth, as *P. nobilis* has been observed in deeper habitats (14 m along the Côte Rocheuse in the present work; 12–13 m in Lake Vouliagmen, Katsanevakis 2006; up to 46 m in Cabrera National Park, Balearic Islands, Vázquez-luis et al. 2014; and 50 m in Korinthiakos Gulf, Katsanevakis 2007).

During the survey, we did not have any information about initial recruitment and, thus, mortality rates could differ depending on the habitat. The growth rate can be highly variable depending on the type of

habitat where fan mussels live, and thus size is not always a good proxy for age and survival (García-March et al. 2020a). However, large individuals were found in all types of habitat, showing good survival over a span of years. This study thus highlights the large diversity of habitat colonized by *P. nobilis*. While the species is generally considered highly sensitive to perturbations, it seems that fan mussels are highly capable of adapting to various environmental conditions (Alomar et al. 2015). In our study, the highest densities and abundances were found in lagoons, which was quite surprising considering that these habitats usually concentrate high levels of anthropic activities and erratic climatic variations that lead to disturbed and unstable environmental conditions (Viaroli et al. 2008, Snoeijs-Leijonmalm et al. 2017, Padedda et al. 2019). Open-sea habitats of the Occitan coast thus appear to be even more restrictive, likely because of the hard hydrodynamic conditions, as described above, or because predation pressure might be higher.

4.2. Importance of lagoons

Although several open-sea sites hosted high fan mussel mean densities, lagoons represent the main reservoirs for the species along the Occitan coast, with 87 % of the total estimated stock found in the lagoons of Thau and Salses-Leucate. The highest mean density of individuals was found in Salses-Leucate at the Lido of Port Leucate site with 70 ind. 100 m⁻², which is one of the highest densities of *P. nobilis* ever recorded in the literature. A similar value was found in the Gulf of Gabes, Tunisia, where density reached 56 ind. 100 m⁻² (Rabaoui et al. 2010). In Thau lagoon, high densities, around 30 ind. 100 m⁻² were also reported in the Tocs site (M. Foulquié pers. comm.). Although some high values around 10–15 ind. 100 m⁻² have been recorded (Venice lagoon, Italy, Russo 2012; Mar Menor, Spain, Giménez-Casalduero et al. 2020; around the Balearic Islands, Spain, Vázquez-Luis et al. 2014), the most common values in most areas range around 1–2 ind. 100 m⁻² (Rabaoui et al. 2010, Basso et al. 2015b, Trigos & Vicente 2018, Tsatiris et al. 2018). Fan mussel populations have also been found in other marine lagoons of the Mediterranean Sea, for example, in the Diana saltwater pond in Corsica (de Gaulejac et al. 2005, Simide et al. 2019), Lake Vouliagmeni, Greece (Katsanevakis 2009), Aquatina lagoon, Italy (Marrocco et al. 2018), Ghar el Melh lagoon, Tunisia (Zakhama-Sraieb et al. 2011), and Mar Menor and Alfacs Bay, Spain (Prado et al. 2014, Giménez-Casalduero et al. 2020), and were previously

reported in Thau lagoon (Foulquié et al. 2020). However, comparisons of aggregation densities among different studies are complicated, because of large variations in the the sampling design and analyses. As reported by Rabaoui et al. (2010), some of the densities are not representative of wide regions, as they are based on a small number of plots that were not randomly placed, but instead high-density patches were targeted for sampling. Regardless of the imprecision of the different measurements, previous studies available in the literature (Katsanevakis 2009, Prado et al. 2014, Simide et al. 2019, Foulquié et al. 2020, Giménez-Casalduero et al. 2020), together with our work confirm that lagoons throughout the Mediterranean Sea are essential habitats for the fan mussel.

Even in lagoons that hosted high densities and abundances, the distribution was very patchy, and densities varied between 2 and 70.8 ind. 100 m⁻² in Salses-Leucate and between 1.4 and 10.1 ind. 100 m⁻² in Thau. In the 3 lagoons sampled in our study, fan mussels were mainly located along the eastern banks, close to the connections to the sea, and there were very few individuals in the western parts away from the channel connections with the sea. In the lagoons surveyed, western areas are the most affected by freshwater dilutions occurring during rainy events. Both Salses-Leucate and Thau receive freshwater inflows from sources which decrease the surrounding salinity: 2 western karstic springs (Font Estramar and Font Dame in Salses-Leucate) and the Vène and Pallas rivers, as well as the submarine spring of the Vise which emerges under water, near Balaruc, in Thau (Fleury et al. 2007), which could explain the absence or low density of fan mussels in these areas. Similar results were found in the Gera Gulf (Lesvos Island, Greece), where higher densities of fan mussels were found near the connection to the sea (Tsatiris et al. 2018), and in Alfacs Bay, where individuals settled in the southern part of the bay and were absent from the northern part which receives irrigation channels from rice fields (Prado et al. 2014). The proximity to freshwater inflows can lead to high salinity fluctuations, which is a structuring factor that may limit the survival of fan mussels. Overall, the optimal trade-off between sheltered habitats and salinity drives the distribution of *P. nobilis* populations in coastal lagoons.

4.3. Perspectives for conservation

Lagoons on the Occitan coast, mainly Thau and Salses-Leucate, are currently the major reservoirs for fan mussels. Given the ongoing mass mortality, these

lagoonal habitats raise hope for the survival of the species, given that, for now, lagoons remain less affected or unaffected by the parasite while almost all populations in the open sea have been devastated (Kersting et al. 2019). Similar situations have been reported throughout the Mediterranean Sea, for example in Alfacs Bay, a semi-confined estuary, where *P. nobilis* populations remain less affected by the outbreak (Prado et al. 2021). The main hypothesis for the survival of individuals in lagoons is that the parasite *Haplosporidium pinnae*, the cause of the mass mortalities, could be less tolerant to low-salinity waters (García-March et al. 2020b). Lagoons thus provide potential habitats where a healthy fan mussel population could be naturally protected by environmental conditions that are unsuitable for the parasite. Previous studies have shown the high connectivity potential of the species along the Spanish coast (Wesselmann et al. 2018) and the Occitan coast (Peyran et al. 2021). Kersting et al. (2020) placed larval collectors along the coast to assess recruitment after the beginning of the pandemic. They found recruits in areas where *P. nobilis* has been decimated, indicating that larvae came from another source population. Using the Lagrangian trajectory model, they estimated that larvae found in collectors in Son Saura (Spain) or on Embiez Island could be native to Occitanie. They thus have evidence of recruitment of larvae in 2018 which could come from the Occitan coast. In July 2018, mass mortalities started to occur along the southern Occitan coast, but some marine populations were still healthy. However, as lagoon populations represented 87% of the total abundance on the coastline, it is also likely that larvae caught in larval collectors came from Occitan lagoons. Populations in lagoons may thus play a key role in the replenishment and recovery of the species along the coast through larval export, even up to distant areas.

As lagoons are transition areas between land and sea, they are usually characterized by a high rate of dynamic change during the year. They act as receptacles for input from watersheds that may have a high level of pollution and, because of their location, they also concentrate anthropic activities such as fisheries, aquaculture, or recreational activities. As a result, the ecological conditions of a lagoon can quickly degenerate, leading to conditions such as eutrophication, which can have dramatic consequences on benthic fauna (Lloret et al. 2008, Rodríguez-Gallego et al. 2017). This type of scenario already occurred in Mar Menor, in 2015, when the lagoon suffered an intense phenomenon of eutrophication, leading to the death of benthic organisms (García-Ayllon 2018) or in the lagoon of Ayrolle, where the entire *P. nobilis* popula-

tion disappeared between 2018 and 2019, with no evidence of *H. pinnae*. The situation is thus very worrying, as the species is on the brink of extinction and its survival is likely to depend on populations located in unstable habitats. These areas should thus be treated as conservation priorities.

In the years following this study, most of the main marine populations were decimated by the parasite and, although it is difficult to survey the entire coastline in detail, no observation of living fan mussels was reported. To date, most of the lagoon populations are still healthy. However, the parasite was detected in several areas in Salses-Leucate, causing moderate to high mortality rates, depending on the site. The pandemic is thus still ongoing, and there is an urgent need to continue to survey healthy populations as it may simply be a question of time before mass mortality events begin to spread throughout lagoons.

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Appendix.

Table A1. Results of the factor analysis of mixed data for qualitative and quantitative data. Cos²: quality of the representation; Ctr: contribution to the construction of each dimension; v-test: significance of variables. If a modality is $-2 < v\text{-test} < 2$, its coordinate is not significantly different from 0 on this axis. Significant values are indicated in **bold**

		Dimension 1			Dimension 2		
		Ctr to Dim.1	Cos ²	v-test	Ctr to Dim.2	Cos ²	v-test
Qualitative variables							
Type of habitat	Lagoon	0.9	0.1	1.2	8.6	0.6	-3.2
	Open sea	7.5	0.8	-3.6	2.9	0.2	1.9
	Port	8.6	0.7	3.2	2.9	0.1	1.6
	Total	17.0			14.5		
Type of substrate	Matte	1.5	0.2	-1.2	0.5	0.0	0.6
	Mud	2.4	0.3	1.6	0.0	0.0	0.1
	Mud sand	2.9	0.3	1.9	5.8	0.3	-2.2
	Rock	0.9	0.1	-0.9	0.1	0.0	0.3
	Rock + matte	1.9	0.3	-1.4	0.9	0.1	0.8
	Sand	1.7	0.3	-1.6	0.0	0.0	-0.1
	Sand + matte	1.1	0.2	-1.1	0.1	0.0	0.3
	Shell mud	1.4	0.2	1.2	0.6	0.1	0.7
	Shell sand	1.0	0.2	1.1	1.0	0.1	0.9
	Total	14.9			8.9		
Presence/absence of vegetation	Absence	8.8	0.6	3.3	10.5	0.4	3.1
	Presence	2.4	0.6	-3.3	2.9	0.4	-3.1
	Total	11.2			13.4		
Cover of vegetation	No cover	8.8	0.6	3.3	10.5	0.4	3.1
	Scattered	6.4	0.7	-3.2	0.6	0.0	0.8
	Dense	0.1	0.0	0.4	9.9	0.7	-3.4
	Total	15.2			21.0		
Species of vegetation	<i>Caulerpa cylindracea</i>	0.1	0.0	-0.3	0.3	0.0	-0.4
	No vegetation	8.8	0.6	3.3	10.5	0.4	3.1
	<i>Posidonia oceanica</i>	9.6	0.8	-3.8	2.3	0.1	1.6
	<i>Zostera marina</i>	0.6	0.1	0.8	6.7	0.4	-2.4
	<i>Zostera noltei</i>	0.1	0.0	0.3	4.2	0.3	-2.0
	<i>Zostera noltei + Ruppia cirrhosa</i>	0.4	0.1	0.6	3.8	0.3	-1.7
	Total	19.5			27.8		
Quantitative variables							
	Depth	8.6	0.4		0.3	10.0	
	Density	0.8	0.0		0.1	4.0	
	Size	12.7	0.6		0.0	0.4	

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