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# Population status of the Critically Endangered fan mussel *Pinna nobilis* in Thau Lagoon (France)

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ABSTRACT: Since 2016, the noble pen shell *Pinna nobilis*, a unique and emblematic giant bivalve endemic to the Mediterranean Sea, has been affected by mass mortality events (MMEs), primarily due to the pathogen *Haplosporidium pinnae*. To date, all known populations located in the open sea have been decimated by epizootics, and *P. nobilis* is currently classified as a Critically Endangered species. The last refuge areas with *P. nobilis* populations are now in coastal lagoons. This study assesses the status, size, density, and spatial distributions of *P. nobilis* populations in Thau Lagoon (Occitany, France). At the end of January 2024, 1931 live individuals were recorded at 30 different surveyed sites. Our surveys indicate various size-class distributions ranging from young recruits to adults. Examining the spatial distribution of *P. nobilis* revealed high-density populations in specific areas (up to 25 ind. 100 $m^{-2}$). *P. nobilis* is present from the edges of the lagoon to the central and deeper zones (up to 9 m deep). Although Thau Lagoon experienced a localized MME at the end of 2020, driven by the presence of *H. pinnae*, this study reveals the occurrence of new individuals in previously infected areas, indicating signs of population recovery and potential resilience. All these observations suggest that Thau Lagoon represents one of the very last sanctuaries for *P. nobilis* in the Mediterranean Sea.

KEY WORDS: Fan mussel · *Pinna nobilis* · Endangered species · IUCN Red List · Coastal lagoon · Conservation · Mediterranean Sea · Bivalvia · Sanctuary

## 1. INTRODUCTION

*Pinna nobilis* Linnaeus, 1758, commonly known as the noble pen shell or fan mussel, is an endemic Mediterranean species. With its shell reaching lengths up to 120 cm (Vicente & Moreteau 1991, Zavodnik et al. 1991), the fan mussel is considered the second-largest bivalve in the world after the tropical giant clam *Tridacna gigas* and is also known for its longevity, with the age of some individuals exceeding 45 yr (Rouanet et al. 2015). Its large size provides a hard substrate for a diverse range of epibionts, such as ascidians, hydroids, sponges, and mollusks (Corriero & Pronzato 1987, Cosentino & Giacobbe 2007, Rabaoui et al. 2009, Vicente 2020), hence producing complex assemblages and rich networks of epibiont species in soft environments (Cosentino & Giacobbe 2008). When *P. nobilis* was still abundant in the open sea, seagrass meadows, especially those dominated by *Posidonia oceanica*, were the preferred habitat for the species (Combelles et al. 1986, Butler et al. 1993, Hendriks et al. 2011, Vázquez-Luis et al. 2014, Coppa et al. 2019). As a filter feeder, *P. nobilis* can filter up to 2500 l of water per day (Hernandis-Caballero 2021), removing inorganic and organic particles from the water column (Trigos et al. 2014), thereby improving water quality and clarity while contributing to the overall health and productivity of the ecosystem (Pensa et al. 2022).

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The species exhibits sexual dimorphism, with males and females displaying distinct reproductive characteristics. *P. nobilis* reproduction is characterized by successive hermaphroditism with protandric asynchronous maturation of gametes (de Gaulejac 1995). Hence, fertilization only occurs in populations that consist of individuals of various ages with both mature males and females. The period of sexual activity usually extends from March to October, with a peak of active gametogenesis and alternating gamete emission between June and August (de Gaulejac et al. 1995a,b, Deudero et al. 2017). The post-embryonic development cycle goes through a planktonic 'trochophore larva' stage (during which the first shell is formed), followed by a swimming veliger larva stage, and finally, settlement as a pediveliger. The pediveliger larva eventually settles onto suitable substrates and undergoes metamorphosis to become a juvenile bivalve. This settlement process is critical for the establishment of new populations and the overall distribution of the species (Trigos et al. 2018). The recruitment phase usually takes place at the end of summer, between late August and early September, when water temperatures are at their highest (Cabanellas-Reboredo et al. 2009).

The precarious status of the remaining populations underscores the importance of implementing additional actions to prevent the species from becoming extinct, such as completing its reproductive cycle in controlled environments. Although spawning and reproduction has been closely studied *in vivo* and *in vitro*, attempts to breed in vitro have been unsuccessful. To date, only the pediveliger stage has been reached (Trigos et al. 2018). Success in producing larvae in captivity has been limited, with laboratory-grown oocytes being smaller than those from field samples, suggesting nutritional deficiencies in captive diets (Hernandis et al. 2023). Furthermore, experimental efforts should prioritize addressing bacterial infections as a major bottleneck in the *P. nobilis* larval rearing process, particularly at the pediveliger stage (Trigos et al. 2018).

Once abundant across the Mediterranean Sea, the species has experienced a drastic decline over the past decades in both population numbers and abundance, mostly attributed to habitat loss and anthropogenic disturbances (Basso et al. 2015), and since autumn 2016, to recurring episodes of mass mortality events (MMEs) (Vázquez-Luis et al. 2017, Cabanellas-Reboredo et al. 2019), most of which were caused by the parasite *Haplosporidium pinnae* (Catanese et al. 2018, Katsanevakis et al. 2019, Panarese et al. 2019, Grau et al. 2022). The species has now been classified as Critically Endangered on the IUCN global Red List of Threatened Species (Kersting et al. 2019). The remaining populations were predominantly found in coastal lagoons and estuaries across France, Italy, and Spain (Foulquié et al. 2020, Nebot-Colomer et al. 2022, Peyran et al. 2022). Consequently, these ecosystems were considered as sanctuaries for the species, and studies on lagoon populations have become essential for conservation purposes.

In 2020, along the Occitan coast, all known populations, including those from a few lagoons, seemed to be exposed to the parasite (Grau et al. 2022, Peyran et al. 2022, Donato et al. 2023). At that time, Thau Lagoon appeared to be one of the last lagoons spared by the epizootic (Foulquié et al. 2020). The persistence of populations that have been spared by the parasite in some coastal lagoons has drawn attention to these particular environments (Foulquié et al. 2023, Labidi et al. 2023, Papadakis et al. 2023, Nebot-Colomer et al. 2024). Given the risk of species extinction, we conducted comprehensive censuses and extensive surveys have been conducted in Thau Lagoon between June 2020 and January 2024. This study brings updated data regarding the size distributions, individual spatial distribution, densities, and status of *P. nobilis* populations within this lagoon in a critical context of conservation.

## 2. MATERIALS AND METHODS

### 2.1. Study area

Located in the south of France on the Occitan coast, between Sète and Marseillan (Hérault) (Fig. 1), the Thau lagoon is the largest and deepest lagoon on the French Mediterranean coast. Covering an area of 7500 ha, its average depth is 4.5 m. In its central part, the depth occasionally reaches 10 m, and at Balaruc-les-Bains, the Vise underwater exsurgence creates a conical depression reaching a depth of 29 m.

Drained by a dozen rivers, the Thau Lagoon watershed covers an area of 285 km$^2$. The Vène is the only permanent river, due to its karstic origin. In addition to these surface freshwater inputs, there is the permanent contribution of the submarine spring of the Vise, whose flow varies according to climatic conditions. Most of the exchanges between the sea and the lagoon take place through canals of the city of Sète (up to 278.3 m$^3$ s$^{-1}$ of exchanged volume), while the exchanges through the Pisse-Saumes canal do not exceed 12.33 m$^3$ s$^{-1}$ (Burtchaell 2000). The lagoon also exchanges with the Rhône à Sète canal in the

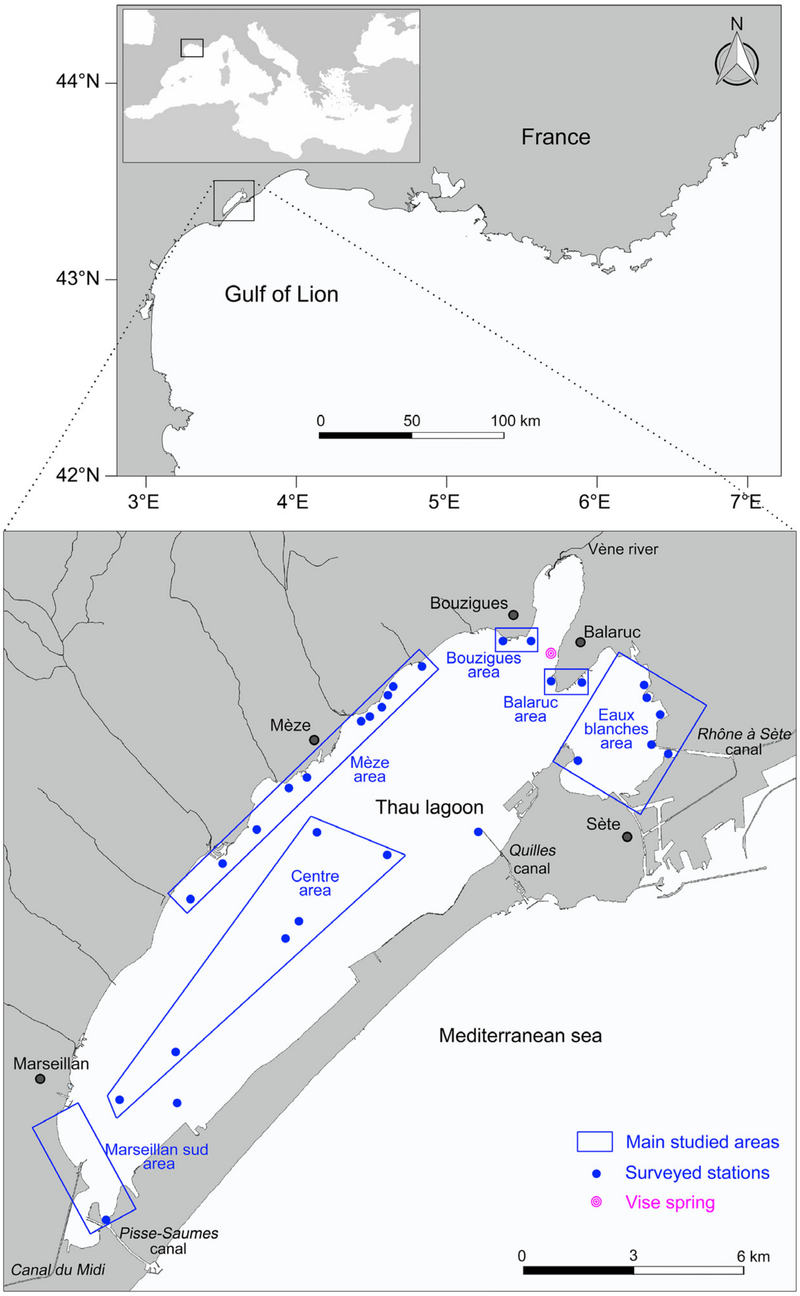


Fig. 1. (a) Location of the Thau Lagoon (north-western Mediterranean Sea). (b) Main studied areas and surveyed stations in the lagoon. Maps were created using QGIS 3.30.1 software (https://qgis.org/en/site/) (coastline data obtained from https://diffusion.shom.fr and https://www.marineregions.org; rivers data obtained from https://www.data.gouv.fr)

north-east and the Canal du Midi in the south-west. The confined nature of the Thau Lagoon has been demonstrated by water circulation studies (Fiandrino et al. 2012, 2017). These studies have also shown that the residence time of the waters in the lagoon is, on average, 110 d.

The average water temperature varies between 14 and 18°C. In winter, the temperature ranges between 4° and 10°C (Fleury et al. 2023) and may exceed 30°C during summer. Salinity is variable, conditioned by weather conditions, and oscillates between 34 and 40 PSU, with values relatively close to those measured in the open sea. In winter, salinity can occasionally drop to 28 PSU at some points in the lagoon (Fleury et al. 2023). Regarding oxygenation, excluding occasional anoxic crises, the northern wind regimes, coupled with exchanges with the sea, allow for good oxygenation of the lagoon. During summer 2023, the dissolved oxygen concentration ranged from 2.51 to 10.61 mg $l^{-1}$ depending on the sites and depth (Syndicat Mixte du Bassin de Thau unpubl. data). The large macrophytobenthos biomass, estimated at (mean ± SD) 10073 ± 2006 t dry weight (Gerbal & Verlaque 1995), also contributes significantly to the oxygenation of the lagoon via photosynthetic activity.

The lagoon hosts large mixed seagrass beds (*Zostera marina*, *Z. noltei*, *Cymodocea nodosa*, and *Ruppia cirrhosa*), covering nearly 15% of the overall area and mainly distributed along the edges. Commercial and recreational activities are practiced throughout the lagoon, including shellfish farming, fishing, boating, and kitesurfing. Some of these activities can have a negative impact on *Pinna nobilis* populations (trampling, mooring, etc.), especially those located in shallow waters (Hendriks et al. 2013, Vázquez-Luis et al. 2015).

### 2.2. *P. nobilis* surveys

The surveys were conducted between June 2020 and January 2024 at 30 stations located in 6 main areas (Fig. 1b). Three main prospecting methods were implemented during the surveys, all carried out either by SCUBA diving or snorkeling and freediving, being towed by a boat, or using a diver propulsion vehicle (DPV), depending on the characteristics of each site (depth, visibility, distance from the shore, ease of access, etc.).

Random surveys were used to conduct comprehensive inventories of fan mussels in order to obtain a quick overview of their spatial distribution. During this type of survey, the diver towed a surface buoy equipped with a GPS device to geolocate each observed *P. nobilis*.

Random standardized 50 m transects were performed along a penta-decameter, and *P. nobilis* individuals were counted 1 m on either side of the transect to obtain the density of individuals per 100 $m^2$, which is the commonly adopted unit of measurement.

A third prospecting method was implemented for the central (and deeper) areas of the lagoon. It involved towing the diver from a surface boat along straight paths, allowing for the coverage of long distances while recording and geolocating each observation made by the diver. By mapping the diver's routes and observations onto a GIS, we obtained additional density and abundance measurements for large areas.

For each geolocated fan mussel, the dominant habitat was recorded, namely: *Zostera marina* and *Z. noltei* meadows, seaweed carpet on soft bottom, sandy-muddy and shell debris bottoms, pebbles, soft rock, and riprap blocks. The geographical positioning data acquired during the surveys were processed using QGIS software.

### 2.3. Biometrics

Morphometric parameters of individuals, including height above sediment ($H_s$), greatest shell width ($W$), and shell width above sediment ($w_s$), were measured using a divider compass and tape measure or with a caliper for very small individuals.

The total height ($H_t$) of living *P. nobilis* can be estimated from $H_s$, $W$, and $w_s$ using different models (Moreteau & Vicente 1982, de Gaulejac & Vicente 1990, de Gaulejac 1993, García-March & Ferrer 1995, Tempesta et al. 2013). For our study, and after validation through measurements of actual $H_t$ on 50 dead individual valves, we established that the García-March & Ferrer (1995) formula ($H_t = (1.79\ w_s + 0.5) + H_s$) was the most reliable for estimating the total height of *P. nobilis* in Thau Lagoon.

### 2.4. Developmental stages

To gain a deeper insight into the species' population dynamics within the lagoon, including its structure, growth, survival and reproductive patterns, as well as to evaluate the overall health of the population and its regenerative potential, we considered 3 size classes: 0–20 cm (juveniles), 20–30 cm (sub-adults), and >30 cm (adults), according to Butler et al. (1993) and Richardson et al. (1999).

### 2.5. Statistical analysis

A factor analysis of mixed data (FAMD) (Pagès 2004) was conducted to assess the relationship between habitats, mean depth, mean density and abundance variables among 20 surveyed stations. To compare means of $H_t$ among different habitats and different areas, a Kruskal-Wallis test was performed because the samples were independent of each other and the distribution of $H_t$ did not follow a normal distribution. The FAMD and Kruskal-Wallis tests were performed using the 'FactoMineR' package (Lê et al. 2008) implemented in R 4.4.0 (R Core Team 2021).

## 3. RESULTS

We recorded a total of 2317 individuals distributed across 6 main areas and 30 stations in the Thau Lagoon. Among those, 386 (16.6%) individuals were found dead. Individuals were observed between depths of 0.8 and 9.1 m in various habitats and different sedimentary facies (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/n055p021_supp.pdf). The spatial distribution extended from the edges to the center of the lagoon. The estimated total height ranged between 10.37 and 68.93 cm, with a mean of 31.94 ± 0.48 cm.

### 3.1. Evolution of mortality between 2020 and 2024 encompassing MMEs

Surveys carried out since June 2020 indicated a wide-ranging evolution of mortality rates across different locations and times, with some sites showing almost no mortality and others experiencing devastating MMEs while later showing some signs of recovery and resilience (Fig. 2).

In June 2020, only the Pisse-Saumes site exhibited a significant mortality rate of 48%, mainly affecting older individuals, while other stations showed good vitality. However, from July to December 2020, mortality rates increased notably at several sites located in the Eaux blanches area: the mortality increased from 7 to 55% and from 6.7 to 46% at the Barrou and Lafarge stations, respectively. Yet the Sète station reported full survival rates by the end of 2020.

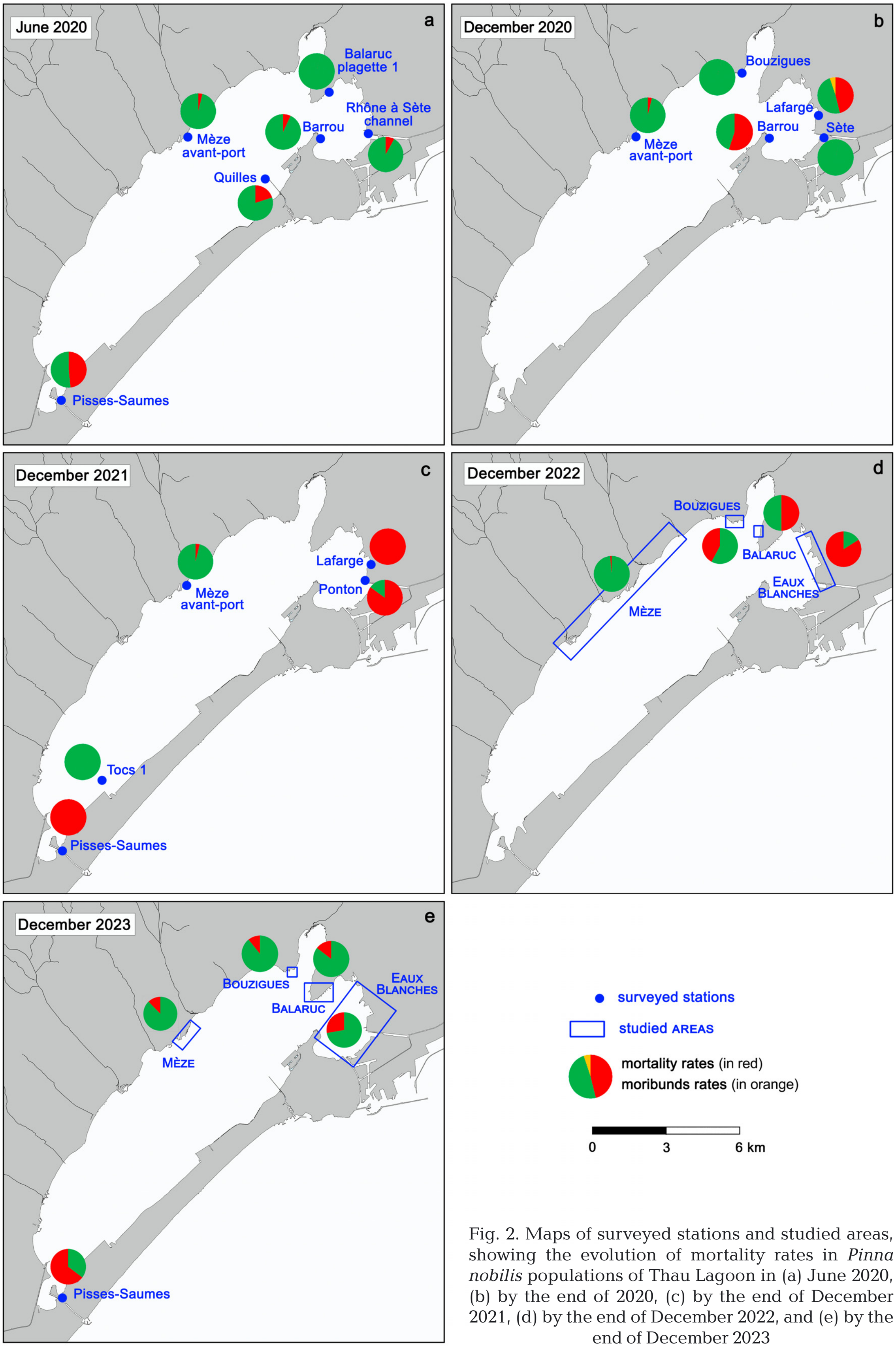


Fig. 2. Maps of surveyed stations and studied areas, showing the evolution of mortality rates in *Pinna nobilis* populations of Thau Lagoon in (a) June 2020, (b) by the end of 2020, (c) by the end of December 2021, (d) by the end of December 2022, and (e) by the end of December 2023

In 2021, The Pisse-Saumes, Ponton and Lafarge stations experienced mortality rates between 85 and 100%, indicating MMEs. Meanwhile, the Tocs and Mèze areas maintained healthy populations including recruitment events, suggesting resistant or locally unaffected populations.

Between July and December 2022, the surveys revealed a stark contrast in mortality rates among different areas. The Mèze area had a thriving population with a mortality rate of less than 1.6%, whereas the Eaux blanches area experienced a high mortality rate of 84%.

In 2023, the surveys showed no signs of abnormal mortality (i.e. no sudden observation of numerous recently dead or dying individuals in a localized area) and recruitment was observed even in sites previously affected by MMEs, such as in Lafarge and Pisse-Saumes stations, marking a notable recovery from the massive die-offs experienced in previous years.

### 3.2. *Pinna nobilis* distribution across Thau Lagoon

The reported densities were from monitoring performed between January 2023 and January 2024, considering 14 coastal stations and 6 central stations (Fig. 3). The observed densities across sites ranged from 0 to 25 ind. per 100 m$^2$ (Table 1), with a mean (±SE) density of 1.97 ± 0.18 ind. per 100 m$^2$.

The FAMD showed that the deepest stations (Center A, C1, C2, B, Prés du Baugé and Ponton) exhibited the lowest densities and abundances (the Ponton station stands out from the other 5 due to its habitat). In

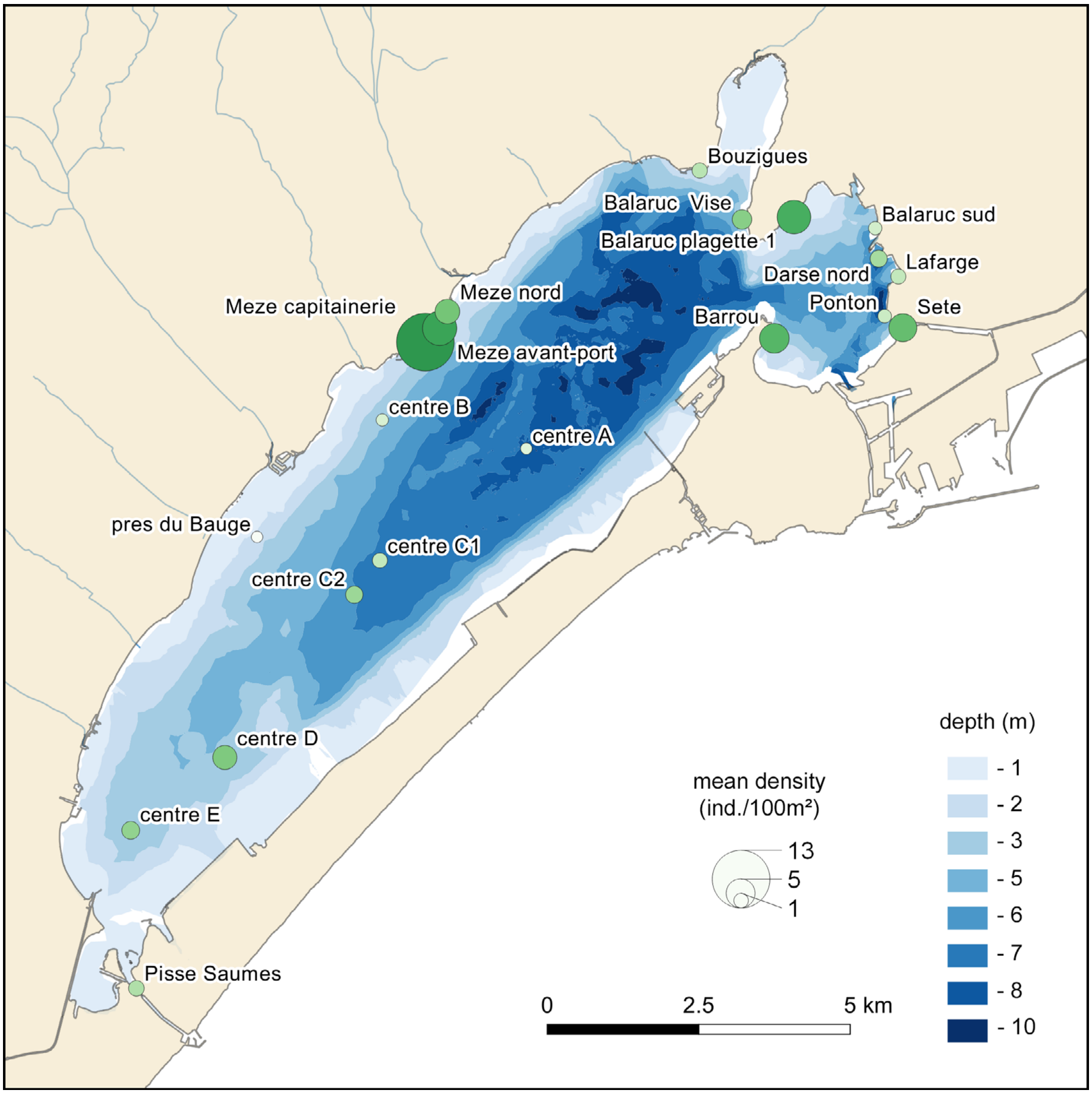


Fig. 3. Locations of the surveyed stations and mean density measurements of *Pinna nobilis*

Table 1. Mean densities of live *Pinna nobilis* in Thau Lagoon. Str: number of standardized 50 m transects; TdTr: covered distance by towed diving transect; NA: not applicable

| Area | Station | Dominant habitat | Str | TdTr (km) | Mean depth (m) | Density (ind. per 100 m$^2$) Min. | Max. | Mean ± SE |
|---|---|---|---|---|---|---|---|---|
| Eaux blanches | Ponton | Sand and mud | 4 | NA | 3.6 | 0 | 2 | 0.75 ± 0.48 |
| | Sète | Sand and *Zostera* | 12 | NA | 1.9 | 0 | 15 | 4.75 ± 1.29 |
| | Lafarge | Riprap blocks | 15 | NA | 1.5 | 0 | 7 | 1.13 ± 0.53 |
| | Darse nord | Riprap blocks | 17 | NA | 2.4 | 0 | 8 | 1.71 ± 0.59 |
| | Balaruc sud | Riprap blocks | 22 | NA | 2 | 0 | 4 | 0.68 ± 0.22 |
| | Barrou | Sand and mud | 15 | NA | 1.5 | 0 | 19 | 5.20 ± 1.35 |
| Balaruc | Balaruc Vise | *Zostera* and seaweed carpet | 33 | NA | 2.3 | 0 | 7 | 2.39 ± 0.30 |
| | Balaruc plagette 1 | *Zostera* | 3 | NA | 1.4 | 5 | 9 | 6.33 ± 1.33 |
| Bouzigues | Bouzigues | *Zostera* and seaweed carpet | 23 | NA | 2 | 0 | 6 | 1.22 ± 0.29 |
| Mèze | Mèze capitainerie | *Zostera* | 7 | NA | 1.4 | 7 | 19 | 13.00 ± 1.65 |
| | Mèze avant-port | *Zostera* | 6 | NA | 1.2 | 2 | 9 | 6.5 ± 0.62 |
| | Mèze nord 1 | *Zostera* | 6 | NA | 1.3 | 1 | 8 | 3.83 ± 0.95 |
| | Prés du Baugé | *Zostera* and seaweed carpet | 16 | NA | 1.5 | 0 | 2 | 0.15 ± 0.09 |
| Marseillan sud | Pisse-Saumes | Riprap blocks and *Zostera* | 13 | NA | 3.4 | 0 | 5 | 1.31 ± 0.41 |
| Centre | Centre A | Seaweed carpet | NA | 0.6 | 8.7 | 0 | 1 | 0.19 ± 0.12 |
| | Centre B | Seaweed carpet | NA | 5.1 | 4.6 | 0 | 7 | 0.39 ± 0.13 |
| | Centre C1 | Seaweed carpet | NA | 0.9 | 6.5 | 0 | 2 | 1.13 ± 0.24 |
| | Centre C2 | Seaweed carpet | NA | 0.7 | 6.3 | 0 | 5 | 1.78 ± 0.39 |
| | Centre D | *Zostera* and seaweed carpet | NA | 1.5 | 3.7 | 0 | 25 | 3.67 ± 1.6 |
| | Centre E | *Zostera* and seaweed carpet | NA | 4.2 | 3.4 | 0 | 11 | 1.92 ± 0.3 |

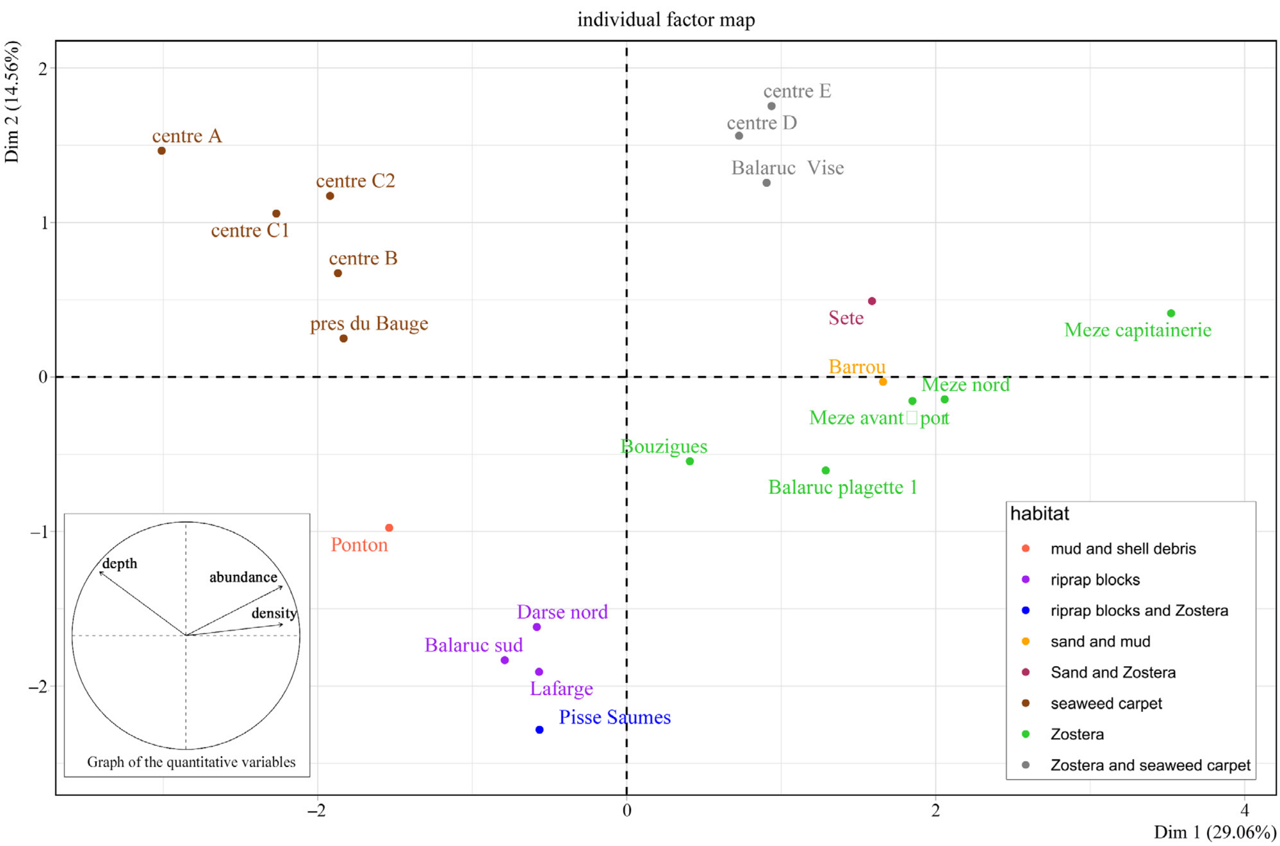


Fig. 4. Station clustering for *Pinna nobilis* surveys, considering depth, abundance, and density parameters using a factor analysis of mixed data

contrast, the shallower stations (Mèze capitainerie, Mèze nord, Mèze avant-port, Balaruc plagette 1, Sète, and Barrou) harbored the highest densities and abundances. In comparison, the shallow sites Pisse-Saumes, Lafarge, Balaruc sud, and Darse nord exhibited low densities and abundances. Within areas, densities were heterogeneous, which is likely explained by depth and habitats (Fig. 4) as well as previous MMEs observed in stations close to connections with the open sea (see Fig. 2).

Some areas harbored dense populations, such as in waters off the city of Mèze, where 580 live individuals could be geolocated between Mèze capitainerie and Mèze avant-port stations during the 2022 surveys (Fig. 5). Here, some fan mussels settled very close to the shore in depths of less than 1 m; areas highly susceptible to human activities.

Moreover, regarding habitats, individuals were primarily observed in *Zostera* and seaweed carpet habitats, accounting for 51.81 and 36.71% of the total abundance, respectively, underscoring the eventual preferential substrate for the species. The other habitats had much lower abundances, comprising the remaining 11.48% of the population (Fig. S2).

### 3.3. Demographic structure

$H_t$ was found to be significantly different between the habitats (overall $p < 0.0001$) (Fig. 6a). Average $H_t$ was roughly similar in *Zostera*, seaweed carpet, sand, sand and mud, and sand and shell debris. However, the highest variations in $H_t$ were observed in *Zostera* and seaweed carpet habitats. All other substrates were mainly colonized by smaller individuals (Fig. 6a).

When considering Mèze, Eaux blanches and Balaruc areas, individuals of all sizes were observed, from 10 cm (in Mèze and Eaux blanches areas) to 70 cm (in Balaruc), suggesting that recruitment regularly occurred in these areas (Fig. 6b) and that recruits may develop to latter adult stages. The p-value ($p < 0.0001$) of the Kruskal-Wallis test indicated that there were statistically significant differences in $H_t$ between the different areas (Fig. 6b).

The Balaruc area was characterized by a dominant adult population, comprising 58.75% of its total, with sub-adults making up 33.13% and juveniles the smallest group at 8.13% (Fig. 6c). In contrast, the Eaux blanches area presented a remarkably balanced distribution among life stages, with each size class representing about one-third of the whole population. The Mèze area showed a higher proportion of adults and sub-adults, which together accounted for over 92% of its population. Analysis of the distribution of different life stages (juveniles, sub-adults, and adults) across the 3 studied areas revealed distinct patterns in population structure that may reflect underlying ecological dynamics or habitat preferences.

## 4. DISCUSSION

This study took place in the context of intense monitoring of residual populations of *Pinna nobilis*


Fig. 5. Zoom in the Mèze area, along 4 surveyed stations: (1) Mèze capitainerie; (2) Mèze plagette 2; (3) Mèze plagette 1; and (4) Mèze avant-port. White lines: random routes; green dots: live *Pinna nobilis* observed on either side of the routes (meaning that individuals are potentially present between the 2 white lines, given the low visibility and the presence of filamentous algae preventing exhaustive detection of all *P. nobilis*, especially the youngest individuals settled in dense *Zostera* seagrass meadow)

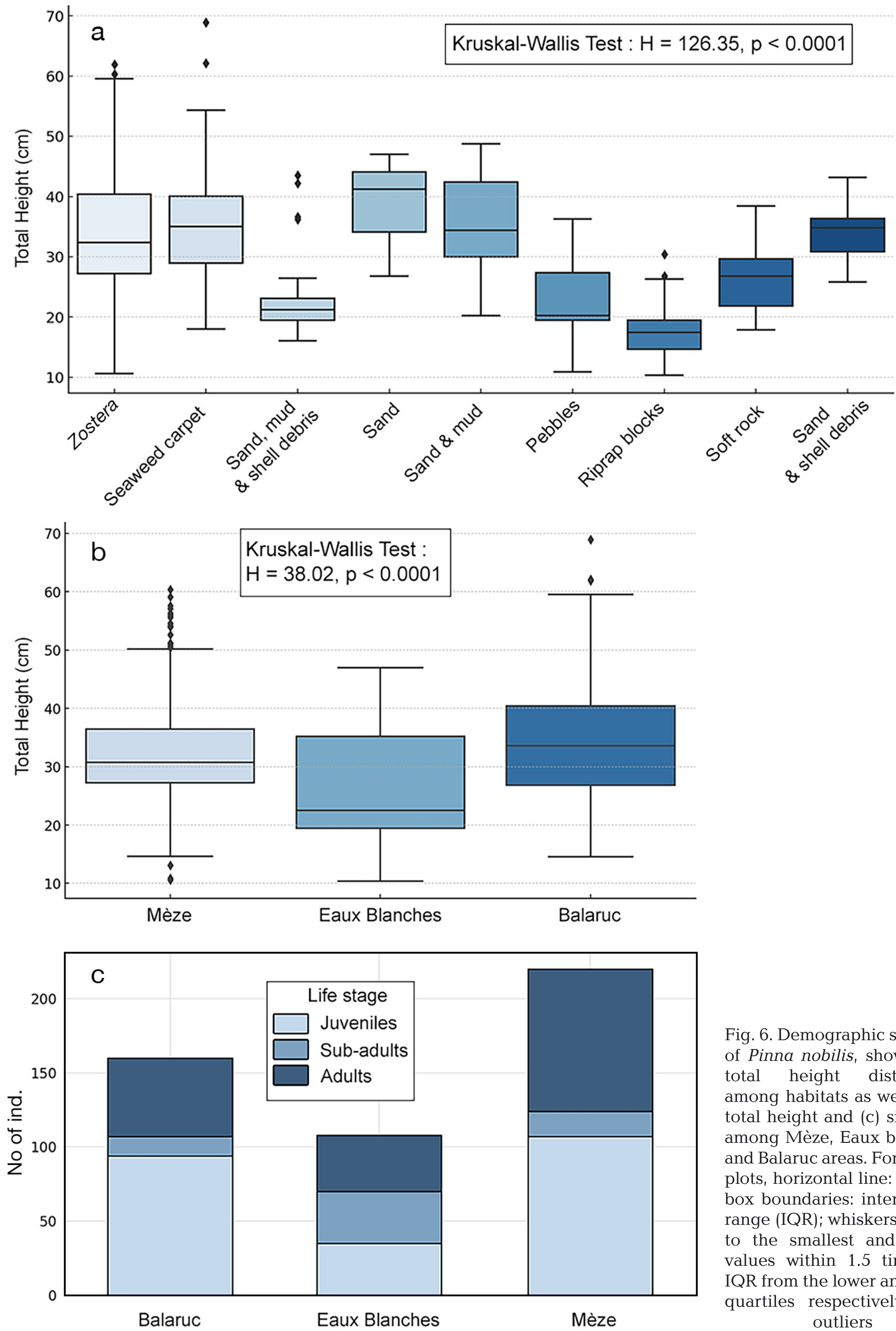


Fig. 6. Demographic structure of *Pinna nobilis*, showing (a) total height distribution among habitats as well as (b) total height and (c) size-class among Mèze, Eaux blanches, and Balaruc areas. For the box plots, horizontal line: median; box boundaries: interquartile range (IQR); whiskers: extend to the smallest and largest values within 1.5 times the IQR from the lower and upper quartiles respectively; dots: outliers

across the Mediterranean Sea at the international level. Since the number of individuals alive in the open sea is now close to zero due to successive MMEs, the surveillance of a few sanctuary areas where a high number of healthy *P. nobilis* can still be observed is important for conservation aspects. The sanctuaries are mostly lagoons, of which Thau probably harbors the densest populations. Although lagoons were first thought to be spared from the highly pathogenic parasite *Haplosporidium pinnae*, recent studies have shown that lagoon populations of *P. nobilis* may be exposed to pathogens, resulting in localized high mortality rates (Donato et al. 2023, Foulquié et al. 2023, Labidi et al. 2023, Papadakis et al. 2023). Through this study, we have provided an updated situation on the population status of *P. nobilis* in Thau Lagoon, one of the very last sanctuaries in the Mediterranean Sea.

### 4.1. Mortality in the refuge area of the Thau Lagoon

Interestingly, highly contrasting patterns of mortality rates were observed during the study period. The areas connected to the open sea (i.e. Eaux blanches area and Pisse-Saumes station) displayed higher mortality rates than the areas further from the open sea (i.e. Mèze area), probably due to the local emergence of *H. pinnae* detected in moribund individuals (Foulquié et al. 2023). Observed abnormal mortalities have been detected since June 2020, suggesting that the parasite could occasionally emerge within the lagoon and successfully cope with its specific environmental parameters, including the annual variations in temperature and salinity, perhaps taking advantage of a favorable time window during which the physico-chemical parameters approach those of the open sea. For instance, the Eaux blanches area is directly influenced by the open sea through the channels of the city of Sète. This means that variations in temperature and salinity there are less pronounced in that area than in the rest of the lagoon. The water is notably warmer in winter and cooler in summer (Audouin 1962).

Even if the parasite still contaminates the lagoon from the sea, most contamination in this confined space probably results from successive temporal infection of *P. nobilis* or from an intermediate host that occasionally releases the parasite. The route of contamination should be better characterized in future studies.

It is noteworthy that areas located further than 2.5 km from the connection to the sea displayed low mortality rates. Whether the parasite is present but unable to survive and infect individuals will be addressed in the continuation of our monitoring. The potential presence of resistant individuals should also be addressed (Vásquez-Luis et al. 2021, Salis et al. 2022, Coupé et al. 2023). If so, such a reservoir of resistant individuals could be an avenue for considering population reinforcement or repopulation. To this end, the search for prominent resistance determinants is crucial, and promising studies on this subject have recently emerged (Salis et al. 2022, Coupé et al. 2023).

### 4.2. Densities and abundance

Compared to the recent demographic studies performed in 2019 and 2020 (Foulquié et al. 2020, Peyran et al. 2022), the Mèze and Balaruc areas showed significant increases in population density in 2023 (Table 2). This suggests a notable increase in the population, consistent with the high recruitment rates observed at most of the surveyed sites since 2022. Despite the ongoing epidemic at sea, the increase in densities in these 2 areas tends to confirm the refuge effect of the lagoon.

In the Eaux blanches area, the density slightly decreased in 2023 compared to the density observed by Peyran et al. (2022), which was before the *H. pinnae* parasite detection. The relative stability in this area despite the MME at the end of 2020 indicates a capacity for resilience, allowing for a partial recovery of previous densities. Regarding the Marseillan area and considering that the mortality rate was 100%

Table 2. Evolution of mean densities between 2019 and 2023 among 4 areas of the Thau Lagoon

| Survey date | Area | No. of transects | Mean (±SE) density (ind. 100 $m^{-2}$) | Reference |
|---|---|---|---|---|
| 2019 | Mèze | 16 | 1.6 ± 0.7 | Peyran et al. (2022) |
| | Eaux blanches | 6 | 2.6 ± 0.7 | |
| | Marseillan | 2 | 7.3 ± 2.7 | |
| 2020 | Balaruc | 4 | 2.75 ± 1.18 | Foulquié et al. (2020) |
| | Marseillan | 3 | 5.33 ± 0.33 | |
| 2023 | Mèze | 11 | 10.45 ± 1.59 | Present study |
| | Eaux blanches | 48 | 1.72 ± 0.34 | |
| | Balaruc | 3 | 6.33 ± 1.33 | |
| | Marseillan | 13 | 1.31 ± 0.41 | |

in 2021, the mean density recorded at the end of December 2023 is a sign of recovery within the previously decimated population.

The overall *P. nobilis* population of Thau Lagoon was estimated after censuses by Peyran et al. (2022) to be (mean ± SE) 61 976 ± 44 066 individuals. Surveys conducted since May 2020 (especially those carried out since July 2022) have shown that *P. nobilis* has settled in various areas, including those where the species was previously referenced as absent. In addition, whereas the species was supposed to be confined to the edges of the lagoon in previous surveys at superficial depths (between 0.5 and 3 m deep), we established that *P. nobilis* is present at deeper sites, between depths of 3 and 9 m, which represents more than 4000 ha (approximately 53% of the total surface area of the lagoon) that still need to be censused. Therefore, the estimated population could be much larger than previously reported.

According to surveys carried out during this study, differences in densities within different sectors of the lagoon are presumably linked to the presence of potentially suitable habitats for the establishment of abundant fan mussel populations. For instance, *Zostera* seagrass bed areas, which are favorable habitats, are primarily distributed along the edges of the pond in shallow waters. Other series of density measurements will need to be carried out, especially in the central and deeper zones of the lagoon, predominantly inhabited by the seaweed carpet habitat, in order to obtain more density measurements in these areas and to be able to compare them with the shallower sectors.

### 4.3. Demographic structure

Recruitment and development of *P. nobilis* are influenced by a complex combination of biological and environmental factors. Prado et al. (2020a) investigated the main factors controlling recruitment patterns in Alfacs Bay (Ebro Delta), including gonadal development, abundance of critical life stages, and the effect of environmental factors. Their study suggests that environmental stress (potentially including freshwater discharges) may affect larval availability and reduce fertility, influencing recruitment patterns. Regarding the influence of habitats on recruitment, Prado et al. (2014) studied habitat use and size structure of *P. nobilis* populations in Alfacs Bay and highlighted the critical role of specific habitat conditions in supporting dense populations in shallow waters. Concerning food availability, a dynamic energy budget (DEB) model developed for *P. nobilis* has revealed that abundant food slightly affects size at maturation but significantly increases fecundity at ultimate age (Haberle et al. 2020). This indicates that food availability plays a crucial role in the reproductive success and population dynamics of the species.

*P. nobilis* growth rate is highly variable, and lagoons have been identified as optimal environments for fast growth but low longevity (García-March et al. 2020a). Alomar et al. (2015) aimed to evaluate the growth and survival rates of *P. nobilis* in different environments exposed to distinct human activities. They found that individuals in eutrophic environments (like lagoons), presumably with higher food availability, showed higher growth rates but lower survival rates, especially during the first life stages. This underscores the complex relationship between nutrition, environmental stress, and the survival of the species. However, many coastal lagoons and harbors experience greater anthropogenic pressures, which implies increased stress for fan mussels living in these areas (García-March et al. 2020b, Giménez-Casalduero et al. 2020, Prado et al. 2021).

In our study, the distributions of different life stages across the 3 studied areas suggest varied ecological and environmental factors at play, influencing the demographic structure and possibly reflecting various stages of population dynamics. While the Mèze and Balaruc areas show higher proportions of adults and sub-adults, the Eaux blanches area stands out for its balanced distribution of life stages.

The Eaux blanches sector presents a peculiar case within the context of our study. Despite being a historically polluted area of the lagoon (Fauvel 1966, Monna et al. 2000, Léauté 2008, Rousselet et al. 2014) and having experienced mass mortality events by the end of 2020 (due to *H. pinnae* in at least one site), it shows a remarkably even distribution among all life stages. Considering the significant environmental stressors (including pollution and the impact of MMEs), this balanced distribution suggests a complex interplay of factors. It may indicate that *P. nobilis* has developed specific adaptations to cope with polluted conditions, or the observed population structure could be a direct outcome of the selective pressures imposed by pollution and epizootic, differentially impacting survival rates or developmental transitions across life stages. The even spread across life stages in an environment subjected to such adverse conditions raises intriguing questions about the resilience and adaptability of the species. Despite the challenges posed by pollution and disease, the maintenance of the population structure suggests possible compensatory mechanisms that enable its persistence, offering valuable insights into the dynamics of resilience in the face of environmental stressors and disease outbreaks (Natalotto et al. 2015, Box et al. 2020, Carella et al. 2023, Lattos et al. 2023).

### 4.4. Conservation aspects

In recent years, researchers expected that areas free from the parasite could become natural sanctuaries for *P. nobilis* because populations there were apparently spared from MMEs. Unfortunately, this assumption is currently in question, as these expected sanctuaries are being lost one by one (Labidi et al. 2023, Papadakis et al. 2023, Donato et al. 2023, Nebot-Colomer et al. 2024).

To provide a comprehensive understanding of the status of Thau Lagoon as one of the last sanctuaries for *P. nobilis*, it is essential to compare its values of abundance and densities with those of some other coastal lagoons or related environments, such as deltas, semi-enclosed gulfs, and marine lakes, where the species was abundant until recently.

In Spain, before 2016, the Mar Menor lagoon harbored a large population of *P. nobilis* estimated at (mean ± SE) 1 609 943 ± 3309 individuals (Giménez-Casalduero et al. 2020). Between 2016 and 2019, the lagoon faced successive severe environmental crises (in addition to the action of *H. pinnae*), which drastically impacted the *P. nobilis* population (Giménez-Casalduero et al. 2020, Cortés-Melendreras et al. 2022, Nebot-Colomer et al. 2022). A recent study showed a lack of recruitment and worrying signs of probable extinction of the species in this lagoon (Nebot-Colomer et al. 2024). In Alfacs Bay (Ebro Delta, Spain), a population assessment conducted in 2011–2012 estimated around 90 000 individuals with a mean density of 1.61 ind. per 100 $m^2$ (Prado et al. 2014). The first disease outbreaks occurred in July 2018, potentially caused by the combined action of a bacterial pathogen and *H. pinnae*, leading to an MME in this area (Prado et al. 2021). The latest surveys carried out in 2022 and 2023 as part of the European Life Pinnarca program showed that the remaining population could consist of only a few thousand living individuals, with 73 to 78% of the observed individuals found dead (J. R. García-March et al. unpubl. data).

In Italy, the population of fan mussels of the Venice lagoon initially showed resistance to MMEs, with a population exhibiting very high density values of up to 12–16 ind. $m^{-2}$ (Russo 2012). In 2021, abnormal mortalities were reported (ISMAR 2021), and recent surveys carried out as part of the European Life Pinnarca program have shown mortality rates ranging from 70 to 90% (J. R. García-March et al. unpubl. data, R. Gonzalez et al. unpubl. data). The Lake Faro area (northeast Sicily) was historically home to a significant population of *P. nobilis*, with over 400 living individuals recorded (Bottari et al. 2017, Donato et al. 2021). However, the condition of the population deteriorated further in 2018 with the onset of an MME (Donato et al. 2021). The most recent study has only identified around 20 living individuals, all settled in brackish-water areas (Donato et al. 2023), with a poor observed recruitment rate and likely several MMEs caused by different pathogens (Lunetta et al. 2024).

In Greece, Lake Vouliagmeni historically hosted a large population of fan mussels, with an estimated total abundance of 8500 individuals in 2006 (Katsanevakis 2009). In the last surveys, conducted between May 2022 and May 2023, no living individuals were found (Papadakis et al. 2023). In 2019, the inner part of the Kalloni Gulf was home to the largest remaining population of *P. nobilis* in the eastern Mediterranean, with an estimated total abundance of 684 000 individuals (Zotou et al. 2020). In the latest surveys, only 252 living individuals were found (Papadakis et al. 2023).

In Tunisia, the Bizerte lagoon was known to host populations of fan mussels with high densities reaching up to 17 ind. per 100 $m^2$ (Rabaoui et al. 2008). In 2016, new surveys revealed the highest density values of 30 ind. per 100 $m^2$ (Labidi et al. 2023). In March 2018, a significant MME was detected, and mortality reached 100% in the surveyed sites except in the eastern part of the Lagoon, where some living specimens were found in 2022 and successful recruitment was also observed (Labidi et al. 2023).

Our study suggests that the estimated overall population of the Thau Lagoon could still exceed 100 000 individuals despite the high mortality rates observed during the MME in 2020. Such a high population is remarkable among French lagoons. While harboring populations of fan mussels that show good vitality, signs of reproduction, and recruitment, other surveyed sanctuaries, such as Diana Pond in Corsica and the Grazel lagoon in Occitania, have a much more limited overall population in terms of abundance (Foulquié et al. unpubl. data). Therefore, special attention should be paid to the protection of the Thau population, minimizing human impacts (trampling, mooring, wild harvesting), especially in the shallow locations as well as in the *Zostera* seagrass meadows and seaweed carpets that seem to be the most suitable habitats for the species.

The population of Thau Lagoon is likely isolated due to the loss of open sea populations, and population renewal probably relies on local mature individuals. In this context, the current size of the Thau population could be sufficient to maintain genetic diversity. This trait was assessed by Peyran et al. (2021) using microsatellite markers, revealing that the genetic diversity of *P. nobilis* is well preserved in the Thau Lagoon populations. Such monitoring should be continued and completed by using non-neutral markers involved in the acclimation or adaptation to both abiotic and biotic factors. This study is ongoing and should provide new insights to assess whether the observed resilience is due to genetic factors or environmental conditions that are unfavorable for the development of the pathogen.

Furthermore, juvenile specimens of *P. nobilis* can be successfully raised in long-term captive conditions (García-March et al. 2020b, Prado et al. 2020b, Cortés-Melendreras et al. 2022, Hernandis et al. 2022, 2023). These captive-bred juveniles could be used for reintroduction where natural populations have been lost, helping to restore and conserve the species in their natural habitats.

### 4.5. Concluding remarks

The resistant populations of *P. nobilis* in the Thau Lagoon are critical for the potential repopulation of the species into the adjacent open seawaters, where the species was present before the epidemic, and potentially into the entire Gulf of Lion through the dispersal of larvae. Thau Lagoon acts as a natural sanctuary for healthy populations, either because of the specific environmental conditions of the lagoon that seem to limit the spread of pathogens or due to a potential natural resistance of these fan mussels that has developed over the long term (specifically to adapt to the particular conditions of lagoons), which would make them more resistant to *H. pinnae* and other pathogens. These resistant individuals are crucial for both natural (via larval dispersal) and assisted (through translocations) efforts to repopulate areas where *P. nobilis* populations were once dense but have been decimated and where the presence of the parasite may be considered low or even absent.

The status of Thau Lagoon as a critical sanctuary for *P. nobilis*, potentially the last of its kind in the Mediterranean, accentuates the importance of our study and the urgent need for targeted conservation efforts. As we continue to unravel the complex dynamics governing these populations, it is clear that a multifaceted conservation approach including habitat protection, monitoring, and directed interventions aimed at safeguarding the species will be essential. The global conservation community should prioritize the protection of the Thau Lagoon and its *P. nobilis* populations as a matter of urgency, ensuring that this ecosystem continues to serve as a beacon of hope for the survival of the species in the Mediterranean. In this respect, citizen science has shown its importance in the early reporting of MMEs caused by *H. pinnae* and monitoring the epidemic (Cabanellas-Reboredo et al. 2019). Therefore, this type of initiative, together with awareness-raising programs and educational activities, should be continued and encouraged.

Future research is required to better understand the ecological and environmental factors contributing to the survival of *P. nobilis* in Thau Lagoon, which can assist in the restoration of populations elsewhere. Exploring the potential for assisted repopulation efforts could be a pivotal step in a successful conservation strategy for this species.

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