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Growth rates of the Critically Endangered fan mussel *Pinna nobilis* in the Slovenian Sea (northern Adriatic)

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ABSTRACT: The fan mussel *Pinna nobilis* is a bivalve endemic to the Mediterranean Sea that is listed as Critically Endangered on the IUCN Red List. Its decline is due to a disease that has led to mass mortalities throughout the Mediterranean. The Gulf of Trieste (northern Adriatic) used to harbour one of the densest populations of *P. nobilis*, but since 2019, it has also been affected by this disease. The aim of this work was to analyse the growth of *P. nobilis* in the Slovenian part of the Gulf, with 3 case studies: (1) *in situ* measurement of adults before the mass mortality event (MME), (2) *in situ* measurement of juveniles after the MME and (3) *ex situ* measurement of juveniles kept in the laboratory. The pre-MME growth rate was comparable to that in other areas of the Gulf. In the first years of life, the growth rate of *P. nobilis* is higher than the growth rate reported in the southern Adriatic, and comparable to the growth rate in the Spanish lagoons. This is probably related to the physico-chemical conditions and confirms the potential of the area for restoration actions. Captive growth of juveniles could be an effective conservation measure, although juveniles kept in the laboratory grow more slowly than those in the sea, probably because of their lower immune response. Temperature plays an ambivalent role, as it increases the growth rate but also triggers the parasites responsible for the MME, which is of concern, given the recent rise of seawater temperatures and heatwaves.

KEY WORDS: Fan mussel · Model growth · Temperature · Conservation · Northern Adriatic

1. INTRODUCTION

The fan mussel *Pinna nobilis* Linnaeus, 1758, endemic to the Mediterranean, is the largest bivalve in the Mediterranean and one of the largest in the world (Zavodnik et al. 1991). All pinnids are exceptionally fast-growing bivalves, with the fastest growth rate recorded in the related species *P. rudis* (Richardson et al. 1999, Hernandis et al. 2021). The growth patterns of *P. nobilis* populations can change under different environmental conditions (García-March et al. 2020) and over time; for example, Kersting & García-March (2017) found a lower growth rate of juvenile of *P. nobilis* that coincided with the spread of the invasive alga *Lophocladia lallemandii*. The fan mussel provides numerous ecosystem services. It filters large quantities of detritus and retains a high proportion of organic matter (Trigos et al. 2014). The high mass-specific clearance rate of *P. nobilis* (0.55 to 14.55 l g^{-1} in individuals of 30 cm) measured in the laboratory by Hernandis et al. (2023), in combination with their large size, confirms the assumption that fan mussels are outstanding filter feeders. Such a role is particularly important in confined environments where large populations that survive the disease are still present. This is the case in the Mar Menor lagoon, Spain, where the water filtration service provided by this species has been estimated to be up to 10% of the lagoon volume (Hernandis et al. 2023). The size of the animals influences not only the quantity, but also the

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quality of food intake, with small specimens ingesting detritus with higher organic content than larger ones, which feed mainly on phyto- and zooplankton (Haberle et al. 2020). *P. nobilis* also provides a hard substrate in soft-bottom areas, increasing spatial heterogeneity and creating a surface that can be colonised by other benthic species (Rabaoui et al. 2015, Iannucci et al. 2023, Burić et al. 2025). It also plays a key role in the trophic web by serving as prey for other species such as *Octopus vulgaris* (Fiorito & Gherardi 1999) and hosting commensals such as the crustaceans *Pontonia pinnophylax* and *Nepinnotheres pinnotheres* (Rabaoui et al. 2008, Acarli et al. 2019).

In autumn 2016, the first mass mortality event (hereafter MME) in *P. nobilis* was observed on the southeastern coast of the Iberian Peninsula, where mortality rates exceeded 90% within a few weeks, and by June 2017, the MME had spread northwards, with mortality reaching up to 100% in some locations (Vázquez-Luis et al. 2017). These events spread rapidly eastwards and soon most populations across the whole Mediterranean were in sharp decline (Kersting et al. 2019, Katsanevakis et al. 2022). In 2019, the mass mortality extended to the Aegean Sea (Zotou et al. 2020) and the Adriatic Sea, with reports along the coast of Albania and Croatia (Čižmek et al. 2020), and reached the northern part of the Gulf of Trieste in 2019 (Manfrin et al. 2023) and the Slovenian part in 2020 (B. Mavrič pers. obs.). In 2020, MMEs were also reported from the Dardanelles (Özalp & Kersting 2020).

A haplosporidian parasite, first described in 2018 as *Haplosporidium pinnae* (Catanese et al. 2018) and found in the digestive glands of the affected fan mussel (Darriba 2017, Vázquez-Luis et al. 2017), was held responsible as the main cause of the MME. This parasite was detected at all sites affected by the MME (Katsanevakis et al. 2019, Panarese et al. 2019, Scarpa et al. 2020), but other pathogens such as mycobacteria and viruses were also observed in affected *P. nobilis* individuals (Carella et al. 2020, Scarpa et al. 2020, Carella et al. 2023). In particular, a previously undescribed picornavirus (*P. nobilis picornavirus*, PnPV) that infects the immune cells of *P. nobilis* was discovered and linked to the MME (Carella et al. 2023), as it leads to immunosuppression in both natural and captive specimens (Carella et al. 2024).

P. nobilis was already protected by the EU Habitats Directive (92/43/EEC, Annex IV), the Protocol for Specially Protected Areas and Biological Diversity in the Mediterranean of the Barcelona Convention (Annex II), and the national legislation of most Mediterranean countries, but due to the sharp decline of its global population and its high risk of extinction, it was classified as Critically Endangered in the IUCN Red List of Threatened Species in 2019 (Kersting et al. 2019). The main research priorities recommended by the IUCN are: increase the frequency of monitoring, prepare a rescue programme to strengthen the resilience of the species and identify *P. nobilis* hotspots (IUCN 2018). A recent review emphasised the importance of studying the age and growth of *P. nobilis* in different environments (Basso et al. 2015c) in order to obtain more information on the resilience of populations and define the best conditions for their survival.

The Gulf of Trieste used to host one of the densest populations of *P. nobilis* in the Mediterranean (Lipej et al. 2012, Tempesta et al. 2013, Lipej et al. 2016), and a study conducted in 2013 in the northern part of the Gulf (Miramare Marine Protected Area [MPA], Italy) showed a higher growth rate of *P. nobilis* in the first years compared to other areas (Tempesta et al. 2013), such as the southern Adriatic (Šiletić & Peharda 2003) and the Columbretes Islands (Kersting & García-March 2017). A comparable growth rate was reported for Spanish lagoons (García-March et al. 2020). The Gulf of Trieste was selected as a pilot site for restoration activities in the frame of 2 projects: LIFE Pinna (LIFE20NAT/IT/001122 LIFE PINNA) and Interreg Ita-Slo TRECap.

The aim of the present work was to analyse the growth rate of *P. nobilis* in the Slovenian Sea (southern part of the Gulf of Trieste), based on the available field and laboratory data.

2. MATERIALS AND METHODS

2.1. Study area

The Slovenian coast stretches for ca. 40 km in the southern part of the Gulf of Trieste, a shallow, semienclosed embayment in the northernmost part of the Adriatic Sea (Mediterranean Sea). The greatest depth (approx. 40 m) can be found in the waters off Piran. The area is characterised by the lowest winter temperatures in the Mediterranean Sea, which can fall below 10°C (Boicourt et al. 1999). The average salinity is 37, but it is influenced near the coast by freshwater inflow, mainly from the Isonzo River (Mozetič et al. 1998). Looking at the long-term series, the lowest monthly average salinity (32.8) occurs in June, the month with the highest interannual variability, and a second local minimum of salinity (34.6) is reached at the surface (0.3 m) in October. Salinity at depth (10 m) fluctuates much less, and ranges between 36.5 and 38.5 (Malačič et al. 2006). The input of freshwater, which also provides nutrients, has a significant impact on the phytoplankton community and thus on the entire marine food web in the Gulf (Malej et al. 1995).

2.2. Field and laboratory work

The growth rates of *Pinna nobilis* were measured in 3 different case studies: (1) *in situ* measurements of adults before the MME (years 2011 to 2012), (2) *in situ* measurements of juveniles after the MME (year 2023) and (3) *ex situ* measurements of juveniles kept under controlled conditions in open system aquaria after the MME (years 2022 to 2023). The measurements were carried out in such a way as to minimise stress to the animals. The biometric features analysed were the height of the unburied shell (h), the maximum width at the point of maximum dorso-ventral length of the shell (L_{max}), the minimum width at the point where the shell was buried in the sediment (L_{min}) and the total antero-posterior shell height (H_{tot}). For *in situ* experiments (Case Studies 1 and 2), the height of the unburied shell (h), the maximum length (L_{max}) and the minimum length (L_{min}) were measured; for *ex situ* experiments (Case Study 3), the total antero-posterior shell height (H_{tot}) and the maximum width (L_{max}) were measured.

In Case Study 1, the annual growth of *P. nobilis* was measured at a site in the Strunjan Landscape Park at a depth of 3 to 4 m (Fig. 1), as part of the inventory of biological elements in the Strunjan Landscape Park (sensu Lipej et al. 2012). At this site, 17 fan mussels were labelled, and 3 biometric features (h, L_{min} and L_{max}) were initially measured to the nearest 0.1 cm on 2 August 2011 (t_0). After 1 yr (t_1), on 27 July 2012, only 11 of them could be measured again, as the labels of the others had been lost. H_{tot} was then calculated using the following formula:

$$H_{tot} = (1.79\, L_{min} + 0.5 \pm 0.2) + h \qquad (1)$$

as described by García-March & Ferrer (1995) and Šiletić & Peharda (2003). The average monthly sea surface temperature in the period of the measurements (from August 2011 to July 2012) was obtained from the oceanographic buoy 'Vida' located in the waters off Piran (https://www.nib.si/mbp/en/; accessed on 23 April 2024).

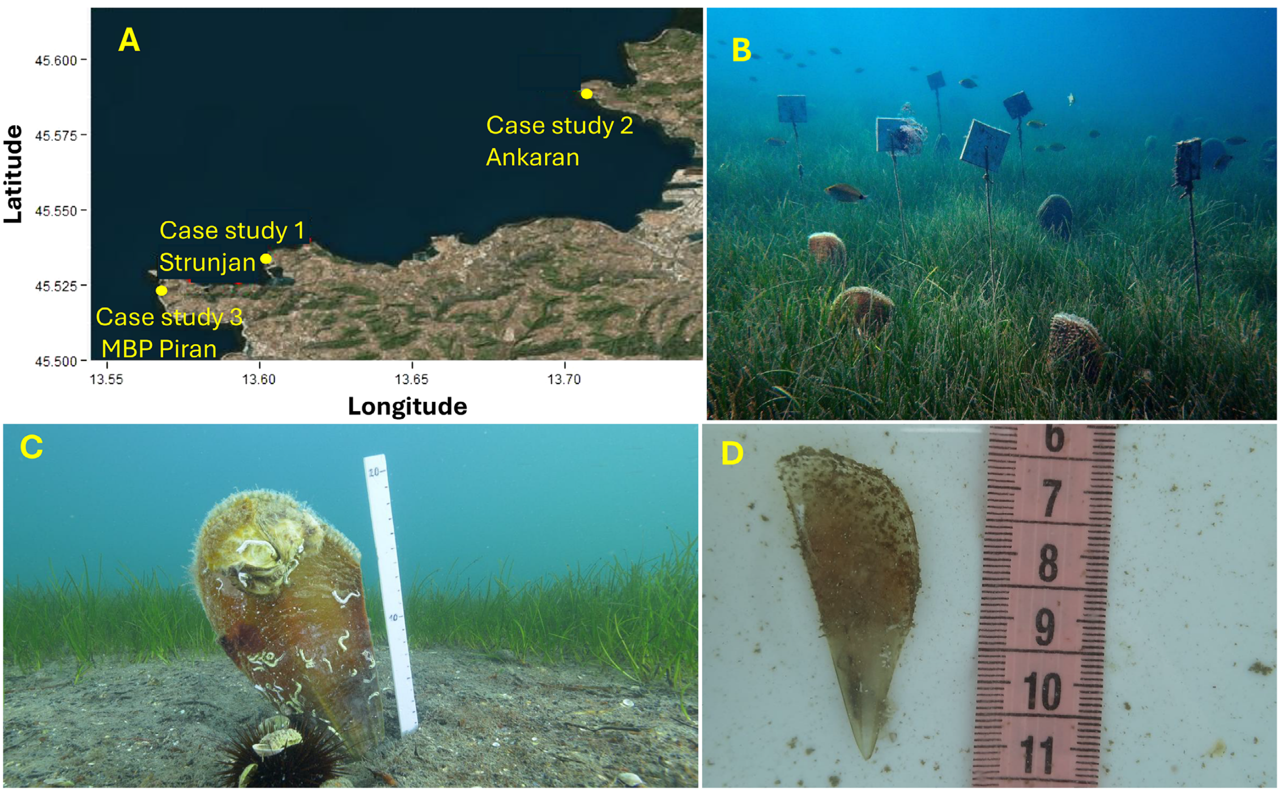

Fig. 1. (A) Location of the 3 case studies. (B) Case Study 1: *Pinna nobilis* tagged in Strunjan in 2011, photo by Tihomir Makovec. (C) Case Study 2: *P. nobilis* juveniles measured in Ankaran in 2023, photo by Ciril Mlinar. (D) Case Study 3: *P. nobilis* juveniles measured at the facilities of the Marine Biology Station in Piran, Slovenia; photo by Valentina Pitacco

In Case Study 2, the monthly growth rates of 6 juveniles of *P. nobilis* were measured *in situ*. During 2 yr of monitoring after the MME, a total of 29 juveniles were found and tagged at 6 sites in Slovenian coastal waters. Only 1 site, Ankaran, was suitable for monthly monitoring, as the poor visibility at other sites made it impossible to find the specimens most of the time. At this site, 9 juveniles were found at depths between 2 and 5 m, but only 6 were found during the second monitoring, so they were tagged and monitored monthly. The h and L_{max} were measured monthly from January to July 2023 (Mlinar 2023), and ranged from 10 to 16.5 cm at t_0. After death, the H_{tot} and L_{max} of the empty shells were measured, to test the formula for calculating H_{tot} from L_{max} (Tempesta et al. 2013), which led to an underestimation of the actual H_{tot}. Since only a small number of individuals were available to determine a better formula for H_{tot}, we kept the height of unburied shell (h) as a parameter in this case study. Four of them died after 7 mo, 1 after 8 mo and 1 after 9 mo. It was not possible to determine the cause of death.

In Case Study 3, the average monthly growth of small *P. nobilis* juveniles kept in the facilities of the Marine Biology Station (MBP) in Piran was measured in 2 periods: first from November 2022 to February 2023, and then from November 2023 to February 2024. In the first period, the animals were measured once per month. In the second period, the frequency was reduced to once every 3 months, to limit the stress on the animals. The fan mussels came from endangered sites, such as mussel farms, where they were at risk of being injured or killed, and from larval collectors installed in the summers of 2022 and 2023 as part of the Life Pinna and TRE-Cap projects according to the guidelines of Kersting & Hendriks (2019) and Kersting et al. (2020). In 2022, a total of 13 animals were collected (H_{tot}: 0.5 to 2.4 cm) and 39 were collected in 2023 (H_{tot}: 0.6 to 8 cm). Some of them died shortly after collection, and they tested positive for *Haplosporidium pinnae* (Pitacco et al. 2025). Only specimens that survived more than 3 mo in the laboratory were considered, leaving only 31 animals for the analyses (10 from 2022 and 21 from 2023). The juveniles were kept in an open system with UV sterilisation and fed with commercial food 3 times a week. The temperature corresponded to the ambient temperature of the seawater and was measured with a hand-held thermometer twice per week. It fluctuated between 9.2 and 14.5°C in 2022, and between 11.9 and 19.3°C in 2023. In this case study, the H_{tot} and L_{max} were measured directly.

2.3. Data analyses

For Case Study 1, a Gulland-Holt plot was created using the data from the measurements of *P. nobilis* shells. The H_{tot} calculated for each individual at time t_0 and the annual growth rate, expressed in cm yr^{-1} (i.e. the difference between the values measured in the 2 years), were used. The H_{tot} was calculated from the measurements of the h and L_{min}. In Case Study 2, the h at time t_0, obtained from *in situ* measurements of each individual, and the average monthly growth rate, expressed in cm mo^{-1}, were used. In Case Study 3, the H_{tot}, obtained from direct measurements of each individual, and the average growth rate, expressed in cm mo^{-1}, were used. Non-parametric Spearman's correlation (Spearman 1907) was used to test the relationship between the growth rate and the height (H_{tot} in Case Studies 1 and 3, h in Case Study 2) of the shells at time t_0.

From the adult specimens measured in 2011 to 2012 (Case Study 1), a growth curve was constructed according to the method of Šiletić & Peharda (2003), which was first used for the study of *P. nobilis* in the Mljet National Park (Croatia), and was also applied by Tempesta et al. (2013) for the study of *P. nobilis* in Miramare MPA (Italy). Šiletić & Peharda (2003) estimated the growth parameters of *P. nobilis* using the von Bertalanffy equation:

$$L_t = L_\infty \left(1 - e^{-k(t-t0)}\right) \quad (2)$$

where L_t is H_{tot} at a given time t, L_∞ is the asymptotic shell length, or 'maximum' shell length of the population, and t_0 is an 'error factor' that takes into account the size of the individuals at time 0 (Gulland & Holt 1959). The constants of the von Bertalanffy growth curve were estimated using the linear regression line relating the H_{tot} of tagged individuals and their growth rate expressed in cm yr^{-1} (Šiletić & Peharda 2003). In this method, the point at which the line crosses the x-axis corresponds to the L_∞ value and the slope of line corresponds to the k value. To validate the growth curve calculated in this way, empty shells of *P. nobilis* kept in the Slovenian Museum of Natural History were measured and their age was estimated based on the number of rings created by posterior adductor muscle scars (PAMS). Following Richardson et al. (1999), they grow annually, with the exception of the first year, so age is calculated as the number of rings plus 1. The use of rings to study age and growth has some limitations, but this method was the only one available that guaranteed the integrity of the specimens kept in the museum. The most recent method by García-March et al. (2020) does not conserve the integrity of the shells. The method used is not accurate for the oldest specimens, but for young specimens such as those in the present work (up to 4–5 yr old), it can serve as an approximation of age (Garcia-March & Márquez-Aliaga 2007).

The expected H_{tot} calculated with the curve was then compared with the measured H_{tot}. The growth curve was then compared with the curves provided in the literature for different locations in the Mediterranean: Miramare MPA, northern Adriatic (Tempesta et al. 2013), Mljet National Park, southern Mediterranean (Šiletić & Peharda 2003), and sheltered areas and lagoons in Spain, western Mediterranean (García-March et al. 2020).

In Case Study 2, the correlation between the average growth of juvenile pinnids measured *in situ* and the monthly average temperature recorded by the Slovenian Environment Agency in 2023 at the mareographic station in Koper (ARSO 2023) was tested. A chi-square test applied to Kruskal-Wallis (KW) ranks (Kruskal & Wallis 1952) was used to check for differences in H_{tot} and the average growth rate of the juveniles kept in *ex situ* facilities (Case Study 3) between the 2 years (2022–2023 and 2023–2024). The same test was performed for the temperatures measured in the aquaria during the period of maintenance of the pinnids.

Results were considered significant at $p < 0.05$. The analyses were performed with R version 4.0.2 (R Development Core Team 2023), using the packages lattice (Sarkar 2008) and ggplot2 (Wickham et al. 2016).

3. RESULTS

3.1. Case Study 1: *in situ* pre-MME adult growth rates

The average monthly sea surface temperature during the study period was 17.8°C, with a maximum of 26.1°C in July and a minimum of 7.5°C in February.

The annual growth of *Pinna nobilis*, determined by the tagging experiment from 2011 to 2012, was between 0.88 and 12.9 cm yr^{-1}. The annual growth rate decreased significantly with increasing shell height (Spearman's correlation, $r_S = -0.760$, $p = 0.009$), as shown in the Gulland-Holt plot in Fig. 2A.

The constants of the von Bertalanffy growth curve were estimated using the linear regression line (adjusted $R^2 = 0.705$, df = 9, $p = 0.0007$), which relates the H_{tot} of the tagged individuals to the annual growth rate in cm yr^{-1} (Fig. 2A). According to this method, the point where the regression line crosses the *x*-axis corresponds to 47.5 cm (L_∞), and the slope of the line corresponds to 0.41 (*k* value), so that the following growth curve was created for *P. nobilis* in the Strunjan Landscape Park (Fig. 2B):

$$L_t = 47.5\ (1-e^{-0.41(t-t0)}) \quad (3)$$

The counting of annual rings in the individuals kept in the Slovenian Museum of Natural History and at the MBP in Piran (Table 1) gave consistent results for specimens collected in Izola and Ankaran (Specimens 19, 4, 3, 44). In contrast, the H_{tot} values estimated for

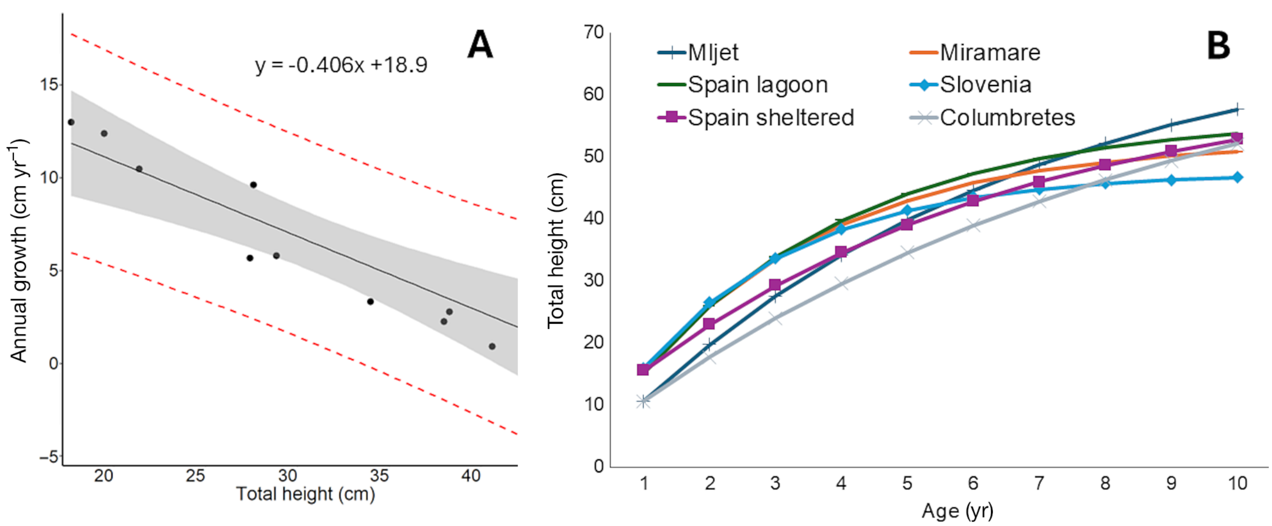

Fig. 2. (A) Total height and annual growth of *Pinna nobilis* in Case Study 1. Grey band: 95% confidence interval; dashed red line: prediction interval. (B) Von Bertalanffy growth curves relating total height with age for the Slovenian population and for different locations in the Mediterranean Sea: Miramare, northern Adriatic (Tempesta et al. 2013), Mljet, southern Mediterranean (Šiletić & Peharda 2003), sheltered areas and lagoons in Spain, western Mediterranean (García-March et al. 2020), and the Columbretes Islands (Kersting & García-March 2017)

Table 1. Total height (H_{tot}), maximum length (L_{max}), number of visible rings, expected age (Exp. age) based on the number of rings, and expected H_{tot} (Exp. H_{tot}) calculated with the von Bertalanffy equation for the expected age of *Pinna nobilis*. Dates are given as d/mo/yr

Code	Location	Date	H_{tot} (cm)	L_{max} (cm)	No. of rings	Exp. age (yr)	Exp. H_{tot} (cm)
76	Sečovlje Salina, Seča	22/02/2023	54.0	17.7	8	9	46.3
69	Sečovlje Salina, Seča	15/02/2023	51.1	17.0	6	7	46.0
19	Belveder, Izola	13/10/2021	25.0	9.3	none	<2	<27
4	Belveder, Izola	13/10/2021	53.0	16.0	4 or more	>5	>41.4
3	Belveder, Izola	13/10/2021	54.2	15.3	8 or more	>9	>46.3
44	Ankaran	15/07/2014	45.2	15.0	7	8	45.7
67	Sečovlje Salina, Seča	13/02/2023	41.8	13.2	7 or more	>8	>45.7

specimens collected in Seča and Piran based on the von Bertalanffy equation were underestimated, with the exception of Specimen 67, which had an overestimated H_{tot} (Table 1).

3.2. Case Study 2: *in situ* post-MME juvenile growth rates

The results of the tagging experiment on *P. nobilis* juveniles after the MME (2023) are shown in the Gulland-Holt plot in Fig. 3A. The average growth rate ranged from 0.3 to 1 cm mo^{-1}. No significant correlations were found between the height of the shell at time t_0 and the average monthly growth rate (Fig. 3A, Spearman's correlation, p = 0.419). A correlation was found between the average monthly growth of the 6 specimens and the monthly temperature (Fig. 3B, Spearman's correlation, r_S = 0.821, p = 0.034). The increase in temperature from May (15.8°C) to June (21.9°C) corresponded to an overall increase in the growth rate of the young specimens from an average of 0.5 to 1.7 cm mo^{-1} (Fig. 3B), but unfortunately, most of the specimens had died by the end of July, and the 2 surviving specimens did not grow at all during the summer. One of these 2 specimens died in August and the other in September.

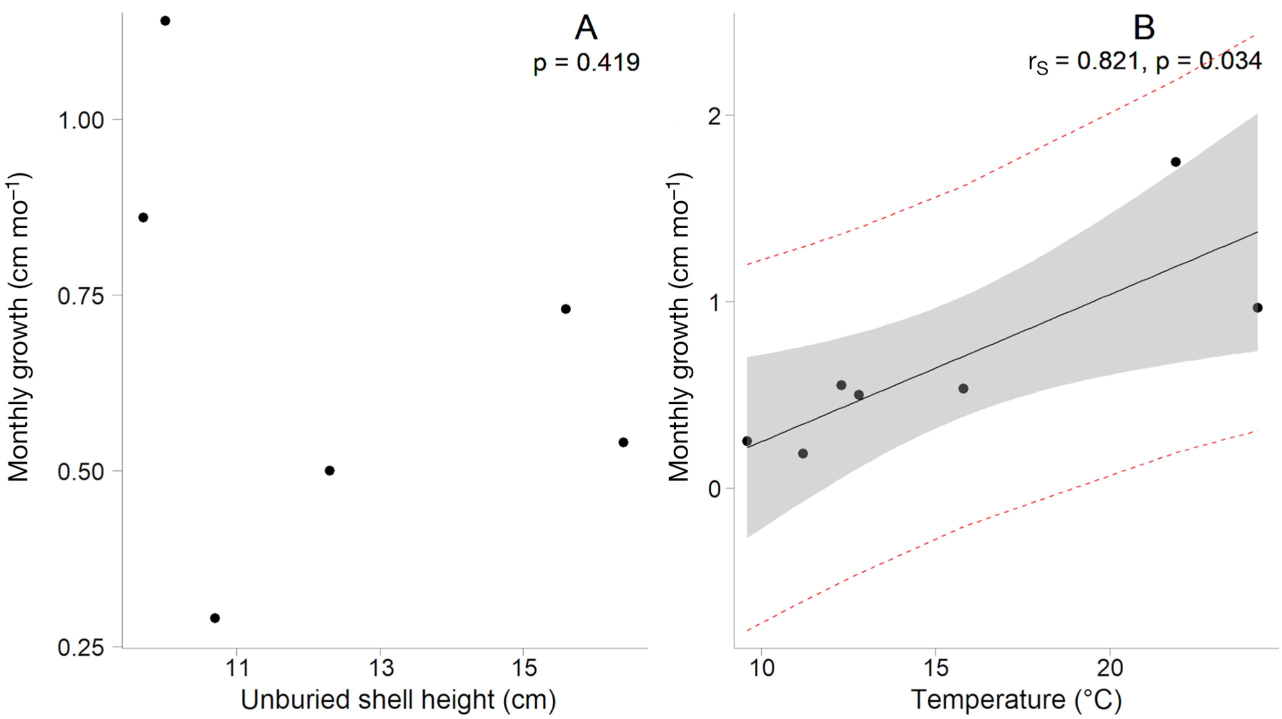

Fig. 3. (A) Unburied shell height (*h*) and average monthly growth of juveniles *in situ* in Case Study 2. (B) Relationship between average monthly growth rate of pinnids and average monthly sea temperature. Grey band: 95% confidence interval; dashed red line: prediction interval

3.3. Case Study 3: *ex situ* post-MME juvenile growth rates

The results of the measurements of *P. nobilis* juveniles kept in *ex situ* facilities at MBP Piran after the MME (2022–2024) are shown in the Gulland-Holt plot in Fig. 4. No significant correlation was found between the initial total shell height and average monthly growth (Fig. 4A, Spearman's correlation, p = 0.619). The growth rate was highly variable, ranging from 0.1 to 1 cm mo^{-1}. The initial shell size was not significantly different between the 2 years (KW chi-squared = 1.69, df = 1, p = 0.193), but the growth rates in 2023–2024 (0.1 to 1 cm mo^{-1}) were significantly higher than those in 2022–2023, which ranged from 0.1 to 0.4 cm mo^{-1} (Fig. 4B, KW chi-squared = 9.49, df = 1, p = 0.002). In the measurement period from November to February, water temperatures were significantly higher in 2023–2024 (Fig. 4C, KW chi-squared = 19.25, df = 1, p < 0.0001), with average (±SE) values of 13.8 ± 0.07°C, compared to 2022–2023, when the average temperature was 11.7 ± 0.07°C.

4. DISCUSSION

The general growth strategy of *Pinna nobilis*, with rapid growth in the first years and subsequent slowing down, is a characteristic of the species that has been observed in various areas of the Mediterranean (Šiletić & Peharda 2003, Katsanevakis 2006, Kersting & García-March 2017). The growth rates calculated for the Slovenian populations studied before the MME showed that the growth of *P. nobilis* in the Strunjan Landscape Park (2011 to 2012) was comparable to that measured in the Miramare MPA from 2008 to 2011 (Tempesta et al. 2013). The growth curves of the 2 populations in the Gulf of Trieste show faster growth rates in the first few years than that of the Croatian population studied in Mljet (Šiletić & Peharda 2003). The 2 curves calculated for the Gulf of Trieste intersect with the curve calculated for the Croatian population around the sixth year and then slowly approach their peak, while the Croatian curve continues to rise. In contrast, the growth curves for the populations studied in other areas of the Mediterranean are different. In particular, the growth rate of

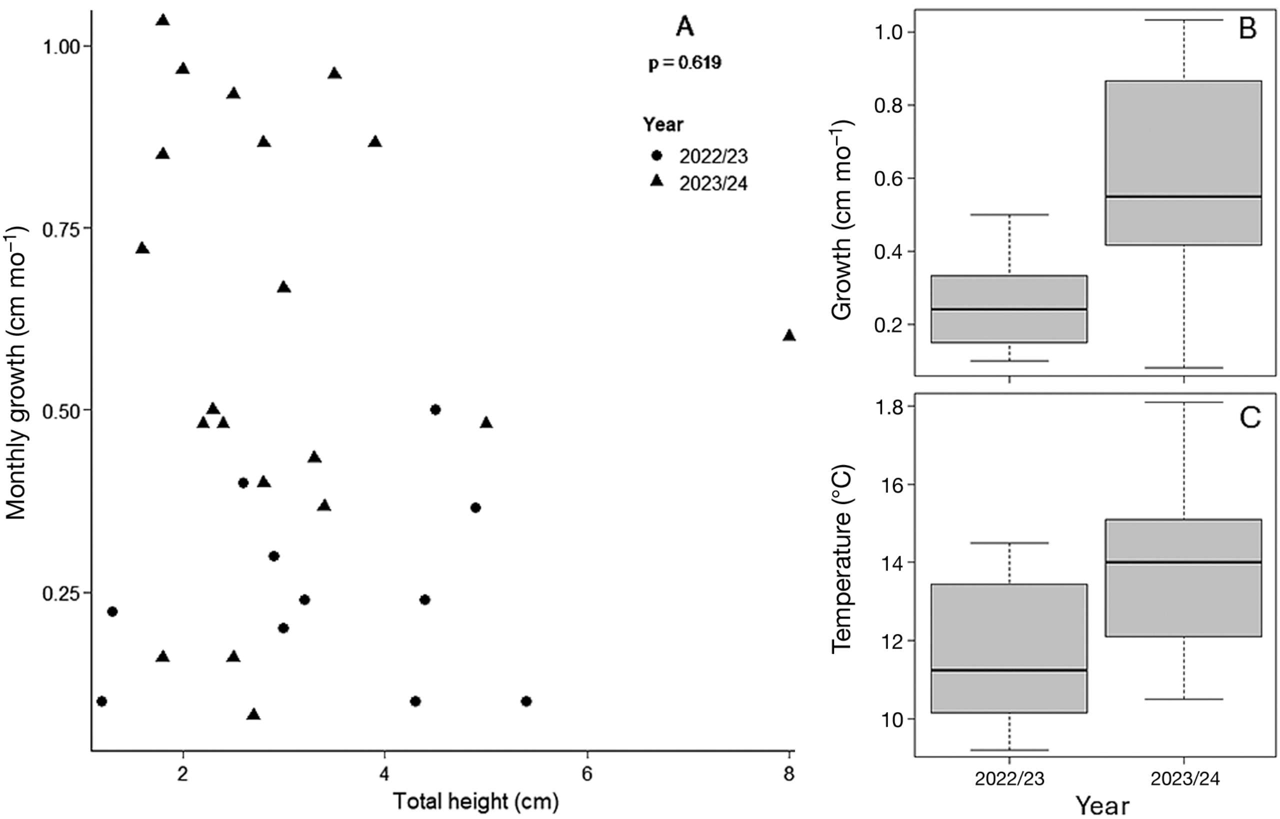

Fig. 4. (A) Total height and average monthly growth of juveniles kept in the laboratory in 2022 to 2023 and 2023 to 2024 in Case Study 3. (B) Average growth rate of pinnids and (C) average monthly temperature measured in aquaria. Lower edge of the box: first quartile; upper edge of the box: third quartile; horizontal line inside the box: median. Whiskers extend from the box to the most extreme data points within 1.5× interquartile range of the box edge

P. nobilis in the first 6 yr of life in the Gulf of Trieste was higher than that of the populations studied in the Spanish sheltered marine areas (García-March et al. 2020) and in the Columbretes Islands (Kersting & García-March 2017). The growth curve fitted for the Slovenian populations is comparable to that of *P. nobilis* in Spanish lagoons. The population living in Spanish lagoons grew faster in the first 7 yr of life than the Spanish population living in marine areas (Kersting & García-March 2017, García-March et al. 2020). A similar trend with higher growth rates in the first 6 to 7 yr was calculated for the *P. nobilis* population in lagoons in Spain, while the Spanish population in open waters showed lower growth rates in the first 6 to 7 yr, but higher growth rates in the following years (Fig. 2B). These results are supported by the fact that a shell of 25 cm from the museum showed no visible rings, suggesting that the animal was younger than 2 yr. It is known that the growth rates of pinnid populations can be influenced by oceanographic conditions (Hendriks et al. 2012). One reason could be the higher food availability in paralic environments compared to the open sea: individuals from eutrophic environments showed higher growth rates than those from oligotrophic conditions (Alomar et al. 2015). This is probably also the reason for the faster growth in the Gulf of Trieste than in the southern Adriatic (Šiletić & Peharda 2003), as the northern Adriatic has a much higher trophic index (Fiori et al. 2016). The rapid growth in the first years of life could give *P. nobilis* in the Gulf of Trieste an advantage in recovery over other populations in the Adriatic, as they reach the size at which they are safe from most predators more quickly. They could also reach sexual maturation faster, as the temporal pattern of gonadal development in *P. nobilis* depends on the size of the bivalve, and begins when individuals are larger than 16.5 cm (Deudero et al. 2017).

Conversely, according to the calculated model, *P. nobilis* in Slovenia grows more slowly in the following years than in the other areas, reaching an expected height of 46.7 cm after 10 yr. Populations of *P. nobilis* in eutrophic environments showed a lower maximum age (García-March & Ferrer 1995) and a lower survival rate, especially during the first life stages (Alomar et al. 2015), which may be related to the more stressful extreme conditions of lagoon/estuarine ecosystems. In contrast, populations in open waters in well-preserved environments, as reported by Kersting & García-March (2017) for the Columbretes Islands, showed slow population dynamics with maximum sizes of 72 cm, and few recruits, with most individuals large than 45 and 55 cm. The low number of individuals smaller than 45 cm suggests that this may be the refugee size for this site. The expected maximum size for the Slovenian population studied is the lowest among the sites compared. Other areas such as the Ionian Sea showed higher values as well (Katsanevakis 2006). Only the maximum total heights reported from the Grado Marano lagoon (Curiel et al. 2020) and the Sea of Marmara (Karadurmuş & Sari 2022) were smaller. The measurements on empty shells preserved at the Slovenian Museum of Natural History and the MBP in Piran essentially support these results, but at the same time show some individual variability in specimens older than 6 yr, with some individuals growing faster and others slower than expected. These differences could be related to the intrinsic limitation of the method, as a variable number of PAMS are hidden under nacreous deposits in the oldest specimens (>6 yr old), with a consequent underestimation of age (Garcia-March & Márquez-Aliaga 2007). They could also depend on the interannual variability of environmental parameters, such as temperature, and anthropogenic pressure. Stochastic fluctuations in the growth of fan mussels were probably caused by local natural stressors and anthropogenic impacts in populations living in Spanish estuaries and lagoons (García-March et al. 2020), as well as by the invasive alga *Lophocladia lallemandii* in the Columbretes Islands (Kersting & García-March 2017). The small numbers of specimens available for the analyses and the short period of the experiment, mainly related to the Critically Endangered status of the species and its biology (low recruitment, high mortality rates of juveniles), leave uncertainties in the assessment of the maximum age, and the intra- and interannual variability of the growth rates. Consequently, further long-term studies are needed to fill the knowledge gaps.

The monthly average growth of young specimens (<15 cm) examined after the MME was not related to the initial shell size. This could be due to the limited size range of the examined specimens, especially in Case Study 3, and the high variability between individual juveniles. Conversely, both the animals measured *in situ* and those kept in the aquaria at the MBP in Piran showed a higher growth rate with increasing water temperature. This result is consistent with results reported for the south-east coast of Spain, where *P. nobilis* grew 0.3 to 0.6 mm d^{-1} at water temperatures between 12 and 19°C, and more than 0.8 mm d^{-1} at temperatures above 19 to 22°C (Richardson et al. 1999). Of concern is the fact that the animals began to die at a water temperature of 24 to 25°C, both in the aquaria and in the field. These results are consistent with laboratory experiments: high mortality has been observed at temperatures above 26°C (Basso et al. 2015b) and 25°C (Prado et al. 2020b), and Hernandis et al. (2023) found that temperatures of 23 to 28°C are close to the tolerance range of *P. nobilis*. The growth rate measured in the present work did not increase as expected with increasing temperatures above 20°C, which could be a sign of stress in the animals. It is known that pinnid shells have a high organic matter content (Richardson et al. 1999), so rapid growth is associated with a high cost to the carbon and energy budget of the organism. This may explain why growth rates decrease during the period of gonadal maturation (Richardson et al. 1999). However, temperature is also crucial for the disease causing MMEs in *P. nobilis*: according to modelling work, expression of the disease appears to be related to temperatures above 13.5°C (Cabanellas-Reboredo et al. 2019). *P. nobilis* juveniles are likely tolerant to warming for short periods (Basso et al. 2015a), but a prolonged period of high temperatures is stressful for them (Basso et al. 2015b). Pathogen infection also increases the sensitivity of *P. nobilis* to water temperature, which subsequently leads to mass mortality (Lattos et al. 2023). In fact, mass mortality has been observed in late summer/autumn, when cumulative thermal stress is higher. The same period is critical for other marine benthic species, such as the Mediterranean stony coral *Cladocora caespitosa* (Kružić et al. 2012, 2014, 2016). In the summer and autumn of 2023, the Gulf of Trieste experienced several marine heatwaves. In October 2023, the lowest temperature in the area was 25°C, above the normal temperatures for this time of year, which are between 16 and 22°C (data from the oceanographic buoy 'Vida'; accessed on 8 December 2023).

The oceanographic buoy is the closest site to our experiment where abiotic parameters are regularly measured, and represents a good proxy for the abiotic temporal trend of the Slovenian part of the Gulf in general. Captive growth of juveniles during the first life stage could be an effective conservation measure to protect them from predation and physical damage, but further monitoring is needed to assess the actual survival of new generations of *P. nobilis* after the MME in the Gulf of Trieste. The juveniles kept in the laboratory grew more slowly than those measured in the sea. These results are consistent with similar experiments conducted in Spain, where *P. nobilis* juveniles kept in the laboratory showed lower growth and survival rates than their field counterparts of the same age (Prado et al. 2020a). This higher mortality could be related to the fact that captive conditions for *P. nobilis* are not optimal. Mortality in captivity has been linked to the presence of opportunistic pathogens such as *Vibrio mediterranei* (Prado et al. 2020b), and recent studies have revealed that animals show a more effective immune response in the wild, compared to animals in aquaria, even when infected with PnPV (Carella et al. 2024). The growth rates of juveniles in protective cages at sea can vary as well. For instance, growth rates in the first years under protective cages in the Columbretes Islands (Kersting & García-March 2017) were similar or slightly lower than those reported by Kožul et al. (2012) for juveniles kept in cages in the Adriatic, but slightly higher than those observed by Hendriks et al. (2012) in cages in Mallorca (western Mediterranean).

As temperature plays such a critical, ambivalent role, the recent increases in seawater temperatures and heatwaves, which also affect the northern Adriatic (Ličer & Malej 2021), makes the survival of juveniles even more difficult.

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