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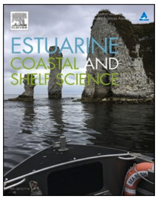

From loss to life: how empty *Pinna nobilis* shells enhance motile macroinvertebrate habitats in soft-bottom environments

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ABSTRACT

The noble pen shell (*Pinna nobilis*) is experiencing mass mortality events across the Mediterranean Sea. In the northern Adriatic, as in many other regions, soft-bottom habitats are now covered with numerous empty shells. To assess their ecological role, we conducted underwater SCUBA surveys using quadrats in 2023 and 2024. We examined the function of empty shells as refuges for motile epibenthic macroinvertebrates across vegetated and unvegetated habitats. Specifically, we compared invertebrate diversity among habitats with and without shells, assessed the influence of shell orientation on community composition, and identified taxa characteristic of each habitat type using non-invasive methods that did not displace shells. Most shells remained upright, though their density and orientation varied among the six study locations. We recorded fauna from seven classes, with malacostracans and gastropods being the most species-rich groups. Biodiversity metrics differed markedly among the four microhabitat types (sediment, sediment with shells, meadow, meadow with shells), reaching the highest values in meadows with shells and the lowest in bare sediment. Malacostracans and polyplacophorans were significantly more abundant in samples containing shells, while other taxa showed no consistent trends. Shell orientation did not affect the composition of motile fauna, but distinct assemblages were associated with specific habitat types. These findings highlight the ecological importance of *P. nobilis* shells as microhabitats that enhance coastal biodiversity even after the death of the organism and underline the potential negative consequences of their degradation or removal.

1. Introduction

The Mediterranean endemic species, *Pinna nobilis* Linnaeus, 1758 is one of the largest bivalves in this region. It is now critically endangered, due to a mass mortality event (MME), that started in 2016 in the Spanish Mediterranean Sea (Vázquez-Luis et al., 2017). The mortality was initially linked to the parasite *Haplosporidium pinnae*, detected in the digestive gland of affected animals (Catanese et al., 2018; Vázquez-Luis et al., 2017). Subsequent research, however, revealed the presence of additional bacteria and viruses in sick specimens, suggesting a multifactorial disease. In combination with thermal stress, these pathogens have caused dramatic population declines (Carella et al., 2023; Grau et al., 2022; Lattos et al., 2023; Scarpa et al., 2020). The disease, which in some area killed 80-100% of the population, has spread throughout Mediterranean Sea, affecting all regions (Kersting et al., 2019) The onset of the disease is associated with temperatures above 13.5 °C and salinity between 36.5 and 39.7 (Cabanellas-Reboredo et al., 2019). Only some isolated populations in the whole Mediterranean Sea remained mostly unaffected, mainly the ones in lagoons and estuaries and last research shows that even those are now suffering from disease-induced decline (Labidi et al., 2023; Nikolaou et al., 2024). The Adriatic Sea, which used to host one of the biggest densities of *P. nobilis* in the Mediterranean Sea (Basso et al., 2015), was one of the last regions to be affected with the disease (Čižmek et al., 2020). In the Gulf of Trieste, MME was first recorded in 2019 in the northern part (Manfrin et al., 2023) and in 2020 along the Slovenian coast (Pitacco et al., 2026).

The noble pen shell typically inhabits soft to mixed bottoms (with reefs, rocks and sandy patches) (Tsatiris et al., 2018), mainly between 0 and 32 m depth and is most commonly found in seagrass meadows (Basso et al., 2015). Hydrodynamics strongly influence its ecology, affecting both food availability and mortality rates due to wave action and the orientation of the shells (Basso et al., 2015). In the northern Adriatic, it most often inhabits muddy to sandy bottoms, dominated by *Cymodocea nodosa* (Ucria) Ascherson (Curiel et al., 2020; De Luca and Candotto, 2016; Hanžek-Turnšek, 2018). Seagrasses shelter pen shells from waves (Hendriks et al., 2011) and predation, while pen shells in

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turn enhance community diversity and possibly seagrass growth, by enriching sediments with biodeposits (feces and pseudofeces) that fertilize seagrass roots (Stacy Zhang & Silliman, 2019). Seagrass meadows themselves provide a wide range of ecosystem services, including carbon sequestration, pollutant retention, protection against coastal erosion and the support of diverse communities (Barbier, 2017; Cullen-Unsworth and Unsworth, 2013). They are also breeding and nursery areas for numerous species, including invertebrates. Yet, these habitats are decreasing globally, with 14% of all seagrass species considered at elevated risk of extinction, due to pollution and habitat degradation (Short et al., 2011).

Like seagrass, *P. nobilis* delivers many ecosystem services, most notably improving water clarity by filtration and habitat provision. These bivalve filters large amounts of detritus and retains high proportion of organic matter (Trigos et al., 2014). Its diet is largely derived from nearby organic sources, including material from seagrass leaves, algae, and epiphytes (Cabanellas-Reboredo et al., 2010). Importantly, *P. nobilis* also acts as a habitat builder. Its large, rigid shell provides three-dimensional structure on otherwise soft bottoms, offering substrate for sessile species and shelter for motile fauna. Even before the onset of MME, however, information on epibionts and associated organisms was relatively scarce (Basso et al., 2015). Nevertheless, studies documented hundreds of invertebrate taxa inhabiting the shell surface of living individuals (Zavodnik, 1967; Addis et al., 2009; Corriero and Pronzato, 1987; Cosentino et al., 2007; Giacobbe, 2002; Plećaš, 2017; Rabaoui et al., 2009; Šiletić and Peharda, 2003), with 331 taxa recorded up to 2017 (Plećaš, 2017). In Slovenian coastal waters, surveys from 2007 to 2017 showed that 13% of observed *P. nobilis* shells were dead (Hanžek-Turnšek, 2018), indicating a substantial proportion of empty shells even before the mass die-off. Since MME, only two studies in the northern Adriatic have focused on fauna associated with empty shells: one focused on molluscan assemblages (Iannucci et al., 2023) and the other one focused on seasonal variability of macrofauna colonizing the shells (Burić et al., 2025).

To our knowledge, no study has yet compared macroinvertebrate assemblages between habitats with and without empty *P. nobilis* shells across vegetated and unvegetated bottoms. This study addresses that gap. Specifically, we aimed to assess the role of empty shells in the Slovenian coastal sea, with a focus on large motile invertebrates. Our objectives were to: (1) compare invertebrate diversity across microhabitats with or without shells in seagrass and unvegetated areas, (2) evaluate whether shell orientation (upright vs. lying) influences community composition, and (3) identify taxa characteristic of different habitat types. To minimize further disturbance of these vulnerable ecosystems, we emphasized the use of non-invasive methods, without displacing shells.

2. Materials and methods

2.1. Study area

The Slovenian coastal sea lies within the Gulf of Trieste; a shallow semi enclosed basin located at the northernmost part of the Adriatic Sea. This area experiences significant tidal fluctuations (Boicourt et al., 1999) for the Mediterranean Sea and low winter temperatures, with an average around 10 °C (Grilli et al., 2020). The basin is characterized by varying temperatures and salinity due to freshwater inflows (Olivotti et al., 1986). In winter and autumn, the water column is weakly stratified, and the opposite is true for spring and summer, and the circulation is dependent on tides, winds and seasonal differences in river discharge (Malačič and Petelin, 2009). The whole area is heavily urbanized and influenced by aquaculture, fishing and tourism. Noble pen shells in Slovenia were observed in the depths between 1 and 13 m depth before MME (Hanžek-Turnšek, 2018).

In this area we chose 6 locations, with different habitats (bare sediment vs. seagrass meadow) and different coastal exposures (Fig. 1, Table 1). The seagrass species was mainly *C. nodosa*, which was mixed with *Nanozostera noltei* (Hornemann) Tomlinson & Posluszny in one location (Table 1). In each location, we selected two depths where empty pen shells were most abundant, ranging between 2 and 7 m depth (Table 1), to perform underwater surveys.

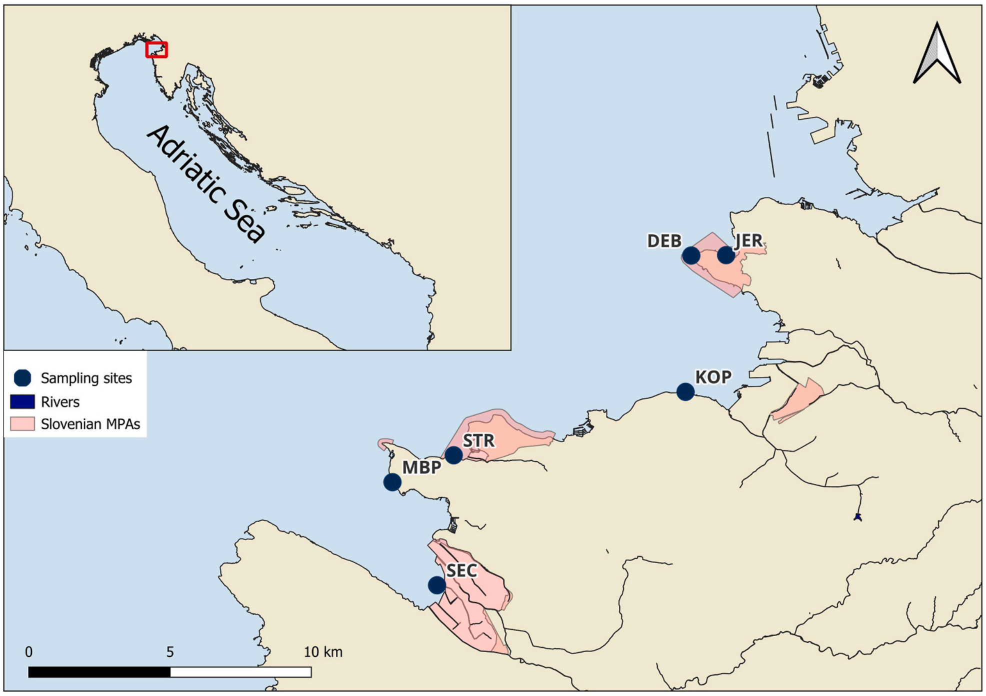

Fig. 1. The map of the study area displays protected areas in pink and the sampling stations as blue dots, with their characteristics detailed in Table 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1
Overview of the six sampling stations included in this study. For each site, geographic coordinates, quadrat sampling date, depth, habitat type, and coastal exposure are provided.

Location	coordinates	date	depth (m)	habitat	coastal exposure
Marine Biology Station (MBP)	45°31′4.78" 13°34′4.84"	June 21, 2023	• 3 • 5	sediment sediment	open
Sečovlje (SEC)	45°29′7.50" 13°35′20.47"	July 19, 2023	• 3 • 5	*C. nodosa* meadow sediment	bay, river mouth
Koper (KOP)	45°32′54.00" 13°42′0.38"	October 3, 2023	• 3.5 • 6	*C. nodosa* + *N. noltei* meadow *C. nodosa* meadow	open
Sv. Jernej (JER)	45°35′31.40" 13°43′3.09"	July 24, 2024	• 3 • 5	*C. nodosa* meadow *C. nodosa* meadow	bay
Strunjan (STR)	45°31′36.81″ 13°35′43.99"	August 7, 2024	• 4 • 7	sediment sediment	bay
Debeli rtič (DEB)	45°35′30.33" 13°42′6.14"	August 29, 2024	• 5 • 6	*Cymodocea* meadow *Cymodocea* meadow	open, cape

2.2. Underwater surveys and laboratory analysis

Underwater surveys were performed in the warm part of the year 2023 and 2024 (Table 1). In each location two dives were performed. In the first one, two depths were decided based on the density of empty pen shells and habitat. Then 50 m transects were laid at this depth, following the coastline. Shells positioned in 1 m belt of both sides of the transect were counted and their orientation was noted as either "lying" or "upright", including only shells with more than half remaining. Shells with oblique orientation were counted as "upright", so all shells still protruding from the sediment were "upright". If seagrass meadow was present the average height of shoots was measured, by measuring the height of three shoots in three parts of each transect (Supplement 1 (Table S1)).

During the second dive, 10 quadrats, each with an area of 0.25 m^2, were placed on the bottom in the same area next to each transect. Where possible, half of the quadrats contained shell and the other half did not (Fig. 2). In some cases, due to bad underwater conditions, less than 10 quadrats were analyzed (for further details see Table S1). In one case (location MBP) data on the density and orientation of the shells was gathered from the survey in 2022 (18.07.). First, all fish were caught within the quadrat using hand net and a narcotic and measured and determined. The data on fish fauna are included in a separate paper (Trkov et al., in prep.). Later, all motile epibenthic invertebrates larger than 1 cm, including bivalves and polyplacophorans, were caught from within the quadrat by two people. Shells were examined using forceps and a torch to extract internal fauna. Common and easily identifiable species were counted and determined *in situ*, while others were photographed and/or brought back to the laboratory. There they were either determined using suitable taxonomic keys and then returned to the sea or preserved in ethanol for further analysis and identification. All measures were taken not to disturb the habitat and if moved, the shell was returned to its original position.

2.3. Data analysis

Data analysis was conducted using RStudio 2025.05.1 (packages: tidyverse, MASS, dplyr, ggplot2, ggpubr, rstatix, VennDiagram, grid, car, and vegan), Microsoft® Excel®, and PRIMER v7. We first tested whether shell characteristics, specifically, shell orientation and the proportion of lying shells, varied between sampling periods, which could reflect progressive decay. After not meeting the assumptions of normality (Shapiro–Wilk test) and equal variance (Levene's test) , we used the Wilcoxon rank-sum test.

Biodiversity indices (abundance, species richness, Shannon diversity index, and Pielou's evenness index) were calculated for each quadrat. Normality and homogeneity of variance were assessed prior to further analysis (Shapiro–Wilk test, Levene's test). To compare biodiversity metrics across habitat types (Sediment, Sediment Pinna, Meadow, Meadow Pinna), referred also as microhabitats, we used the Kruskal–Wallis test, followed, when appropriate, by Dunn's multiple comparison test with adjusted p-values. These results were visualized using boxplots.

To evaluate whether shell orientation within quadrats containing shells influenced biodiversity indices, we applied the Wilcoxon rank-sum test. Differences in the abundance of animal classes between sites with and without shells were analyzed using a negative binomial generalized linear model (NB GLM) to account for over dispersed count data. The three most abundant animal classes were visualized using boxplots, while full model outputs are reported in the text.

Community-level differences among habitat types were visualized in metric mMDS plots of bootstrapped group averages. Data were first transformed with square root and resemblance matrix calculated with Bray-Curtis similarity. Differences were statistically tested using PERMANOVA with one fixed factor (habitat, with four levels), followed by pairwise comparisons. SIMPER analysis was performed to identify species contributing most to within-group similarities. A Venn diagram was used to illustrate the number of species shared among different habitat

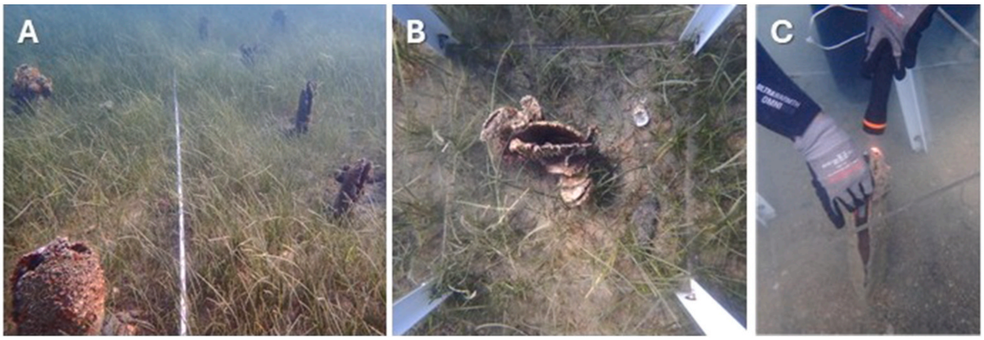

Fig. 2. Habitat overview and sampling methods. (A) Transect line deployed in a seagrass meadow. (B) Example of a quadrat containing an empty *P. nobilis* shell. (C) Examination of fauna inside an empty shell.

types. Based on SIMPER results, univariate analyses were repeated for the five most influential species using the Kruskal–Wallis test and Dunn's test for post hoc comparisons.

3. Results

3.1. Shell characteristics in the study area

The density of *P. nobilis* shells varied across study sites and depths, ranging from 0 to 95 shells per 100 m^2 (Fig. 3A). In unvegetated sites (MBP and STR), shell density tended to increase with depth, whereas in vegetated sites (KOPE, JER, and DEB), it showed the opposite pattern. The highest densities were recorded at MBP and DEB, both hydrodynamically exposed sites. The average seagrass shoot height ranged from 24.3 to 29.8 cm at locations SEC, JER, and DEB, and was both the lowest and highest at KOP—19.4 cm at the 3.5 m transect and 30.5 cm at the 6 m transect, respectively. Shell orientation also differed among sites, with MBP and DEB showing the highest proportions of upright shells—83% and 91%, respectively (Fig. 3B). Across most locations, a greater proportion of shells lay flat at deeper depths, although DEB exhibited the opposite pattern. This difference in depths was most significant in locations JER and STR, where more than 90% of all shells in deeper transects were lying flat. Overall, most shells remained upright at the time of sampling, with only 30% lying flat (Fig. 3C). No significant differences in shell density or orientation were observed between the two sampling periods (Wilcoxon rank sum test; $p > 0.05$).

3.2. Biodiversity across habitat types

In total we found 70 species belonging to 7 animal classes – Bivalvia, Echinoidea, Gastropoda, Holothuroidea, Malacostraca, Ophiuroidea and Polyplacophora. Most species were malacostracans (25) and gastropods (20). The list of animals found in this study can be found in (Supplement 1 (Table S2)). Four samples were empty, i.e. they did not contain macroinvertebrates.

Biodiversity metrics varied across habitat types, reflecting differences associated with the presence or absence of *P. nobilis* shells and surrounding vegetation. Fig. 4 shows different biodiversity indices for motile invertebrates in four habitat types. Abundance, species richness, and the Shannon diversity index (H′) showed similar patterns, with the seagrass meadow containing shells showing the highest values, bare sediment the lowest, and intermediate values observed in sediment with shells and meadow without shells. These differences were supported by Kruskal–Wallis and Dunn's tests ($p < 0.05$). On the other hand, Pielou's evenness index (J′) showed no statistical differences among habitat types (Kruskal–Wallis; $p > 0.05$), but J′ values were heavily dispersed among samples in the sediment group, often due to low specimen counts within quadrats.

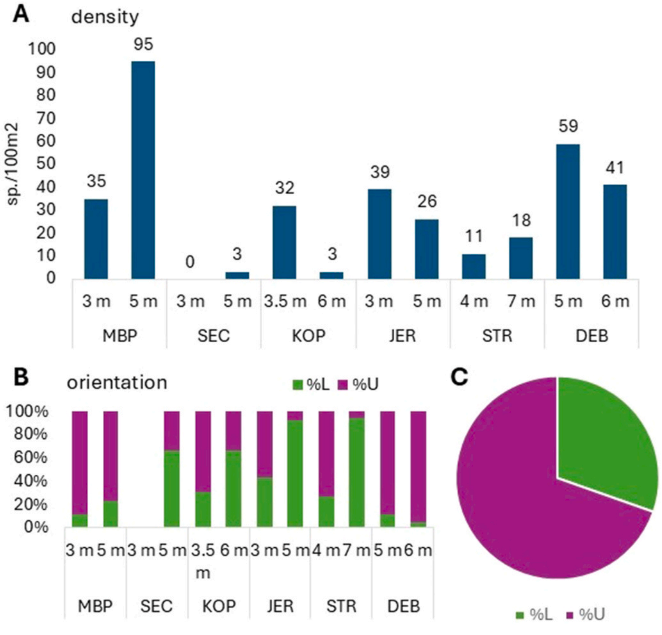

Fig. 3. Density (A) and orientation of empty *Pinna nobilis* shells at individual locations (B) and across all sites combined (C) within the study area. Abbreviations: L – lying, U – upright. For explanation of the abbreviations of the locations, see Table 1.

When comparing the abundance of different animal classes in relation to the presence or absence of shells, clear differences emerged among groups. Malacostracans and polyplacophorans were significantly more abundant in samples with shells, while no consistent changes were detected in the remaining classes. The outcomes of the negative binomial GLM are summarized in Table 2, and boxplots of the three most representative classes are shown in Fig. 5. Because some classes were represented by low counts, resulting in very wide incidence rate ratio intervals, these results should be interpreted with caution—particularly for Echinoidea, where estimates were unstable (see Table 2).

We further investigated differences in biodiversity indices (abundance, species richness, Shannon H′, and Pielou's J′) between samples containing lying shells and those with upright-positioned shells. In none of the cases the results were statistically significant, indicating that the position of *P. nobilis* shells did not lead to detectable changes in community structure of the studied motile invertebrates.

3.3. Community composition and indicator species

To further examine differences in community structure among habitat types, multivariate analyses were conducted. The mMDS ordination (Fig. 6) showed clear separation of samples by habitat, with a high correlation between ordination distances and the resemblance matrix ($\rho = 0.98$ at $m = 8$). This was confirmed by PERMANOVA, where both the overall test (Pseudo-F = 9.48, p(perm) = 0.001, 998 permutations) and the pairwise comparisons (t = 2.01–3.73, p(perm) = 0.001, 999 permutations) indicated significant differences among habitats. The highest similarity was observed between the meadow and meadow pinna groups (average similarity 36%), while the greatest dissimilarity occurred between sediment and sediment pinna (average similarity 12%).

In line with the broader patterns of community differentiation, species composition analyses revealed clear contrasts among habitat types. The meadow habitat with shells supported the highest number of exclusive species (14), followed by the bare sediment with shells (11 species). In contrast, only a single species occurred exclusively in the bare sediment without shells (Fig. 7). Notably, no species were shared between the bare sediment without shells and the meadow habitat with shells. Across all four habitat types, only three species were consistently present, namely the gastropods *Thericium vulgatum* (Bruguière, 1792) and *Hexaplex trunculus* (Linnaeus, 1758), as well as the hermit crab *Paguristes streaensis* Pastore, 1984. Along with hermit crabs *Pagurus anachoretus* Risso, 1827 and *Diogenes pugilator* (Roux, 1829), these species contributed most to the similarities within habitats according to SIMPER analysis (Table 3). Consistent with these patterns, both meadow habitat types exhibited much higher within-habitat similarity (44% and 47%) compared to the sediment habitats (20% and 28%), as also reflected in the tighter bootstrap regions shown in Fig. 6.

The five most abundant species were also those contributing most to differences between habitats. Their distribution patterns varied markedly (Fig. 8) and were supported by Kruskal–Wallis and Dunn's tests ($p < 0.05$). *T. vulgatum*, the most abundant species, peaked in both seagrass meadow habitats, regardless of shell presence, and was least abundant on bare sediment (Fig. 8A). *P. straensis* and *H. trunculus*, the second and third most abundant species, showed similar trends,

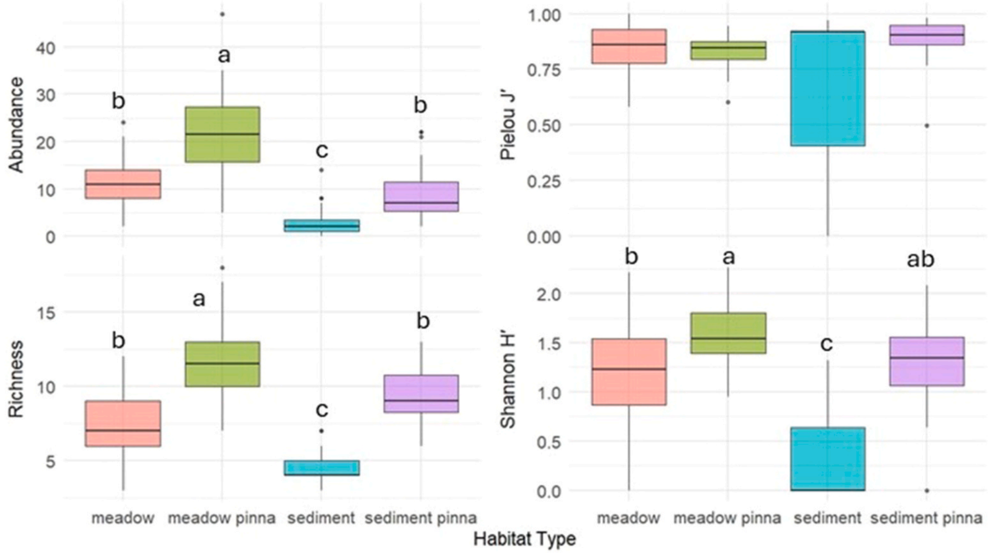

Fig. 4. Differences in motile invertebrate community metrics across habitat types. Different letters show statistical differences between habitat types (Dunn's test).

Table 2
Results of the negative binomial GLM analysis of the abundance between shell presence and absence across taxonomic classes. Abbreviations: IRR – incidence rate ratios; adj. p – adjusted p-values (FDR-corrected).

Class	IRR (95% CI)	adj. p
Bivalvia	1.34 (0.68–2.66)	0.6312
Gastropoda	1.54 (1.06–2.22)	0.0581
Malacostraca	2.51 (1.84–3.41)	**3.99E-08**
Holothuroidea	2.65 (0.99–7.05)	0.1027
Polyplacophora	6.95 (1.77–27.30)	**0.0219**
Ophiuroidea	1.49 (0.09–23.81)	0.8894
Polychaeta	1.49 (0.09–23.81)	0.8894
Echinoidea	0.00 (0.00–Inf)	0.9985

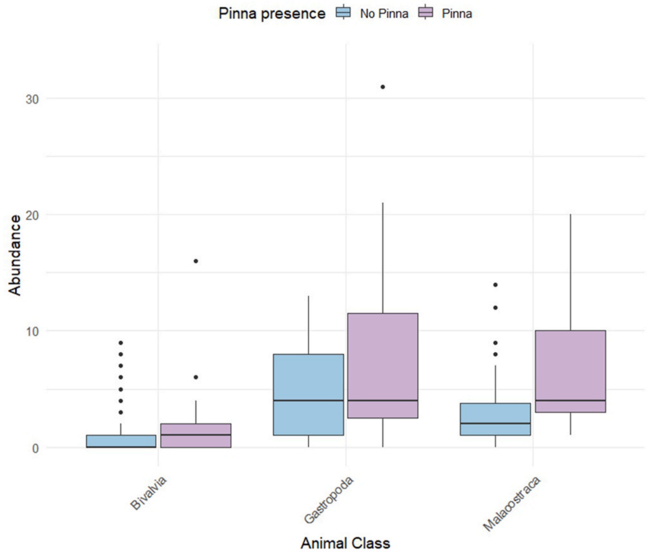

Fig. 5. Abundance of three most representative classes in habitats where *P. nobilis* shells were present (purple) or absent (blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

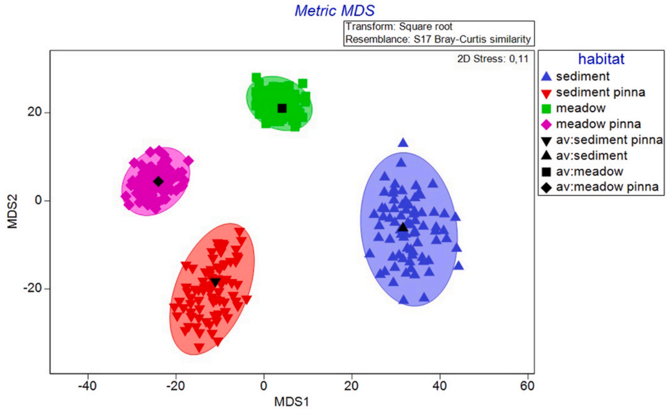

Fig. 6. Community composition across habitats shown in multivariate space (mMDS), based on 75 bootstrapped averages. Polygons indicate 95% bootstrap regions.

although *H. trunculus* was particularly abundant in meadows containing empty shells (Fig. 8B and C). By contrast, *P. anachoretus* was strongly associated with habitats containing empty shells, irrespective of the surrounding vegetation (Fig. 8D). The opposite pattern was observed for *D. pugilator*, which was most abundant in habitats without shells, especially bare sediment.

4. Discussion

4.1. Shell characteristics in the study area

The density of empty *P. nobilis* shells observed in our study was comparable to densities reported in the area before the MME. This is noteworthy given that in our survey, the animals were already dead and the shells were already decaying. However, we specifically surveyed depths where shells are most abundant, which may have influenced the results. Prior to MME, average densities in the Gulf of Trieste ranged from 0.3 to 27 ind./100 m^2 near the Isonzo river mouth – Isle of Cona (De Luca and Candotto, 2016) to 0.3–15.3 ind./100 m^2 in the Marano and Grado lagoon (Curiel et al., 2020). In Slovenian coastal waters, densities were 1–39 ind./100 m^2, with maximum values of up to 200 ind./100 m^2 recorded between 2 and 6 m depth (Hanžek-Turnšek, 2018). Although the highest densities of *P. nobilis* are often reported in seagrass meadows or on the edge between seagrass meadows and sandy

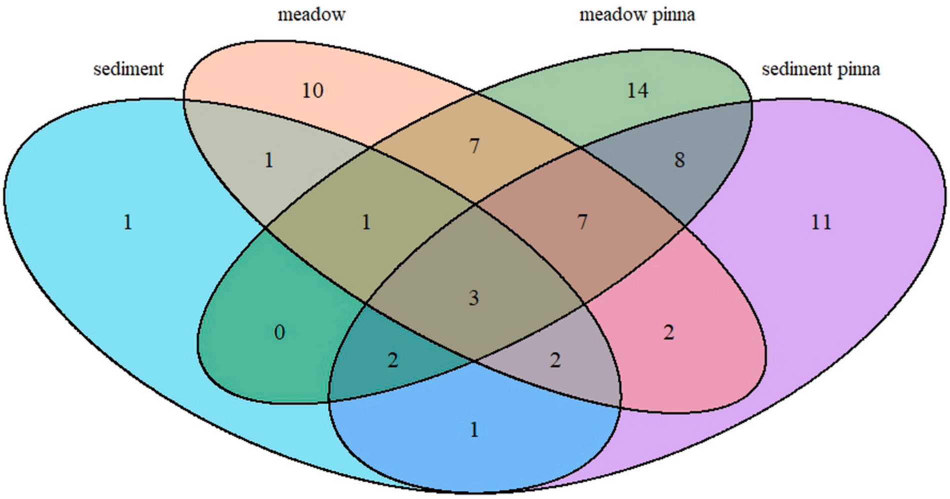

Fig. 7. Shared and unique species across habitats. Numbers in the Venn plot indicate the species present in one or more habitat types.

Table 3

Species contributing most to within-habitat similarity (SIMPER analysis). Abbreviations: Avg. similarity – average similarity; Avg. abun. – average abundance; Av. sim – average similarity; Sim/SD – similarity-to-standard deviation ratio; Cont. (%) – contribution to overall similarity.

Habitat	Avg. similarity	Species	Av. abun.	Av. sim	Sim/ SD	Cont. (%)
Sediment Pinna	27.88	*Pagurus anachoretus*	1.33	11.94	0.92	42.8
		Thericium vulgatum	0.89	7.67	0.68	27.5
Sediment	20.22	*Diogenes pugilator*	0.71	8.24	0.44	40.8
		Thericium vulgatum	0.44	6.29	0.33	31.1
Meadow	44.13	*Thericium vulgatum*	2.00	23.71	1.57	53.7
		Paguristes streaensis	1.03	10.04	1.01	22.8
Meadow Pinna	46.56	*Thericium vulgatum*	2.16	13.30	1.47	28.6
		Hexaplex trunculus	1.79	10,97	1.55	23.56
		Pagurus anachoretus	1.64	9.81	1.39	21.08

patches (Coppa et al., 2010), we recorded the highest densities in some unvegetated locations (e.g. MBP). This may be linked to favorable hydrodynamic conditions. Furthermore, in this and some other unvegetated locations (MBP and STR), seagrass meadow was present until recently (Ivajnšič et al., 2022), which may be a factor influencing the distribution of the shells.

Shell orientation patterns revealed further insights. Most shells were still standing upright, although orientation varied across locations. Standing shells gradually accumulate sediment particles originating from detached epibionts and suspended material in the water column within their cavities, which increases their weight and acts as ballast, helping them remain upright and more firmly anchored in the seabed. Nevertheless, in almost all sites, lying shells were more frequent in deeper transects than in shallower ones. This was unexpected, as stronger wave action in shallow areas would typically cause displacement of the shells. Once detached from the sediment, shells lying on the seabed become more susceptible to hydrodynamic transport and may be redistributed to different depths depending on local geomorphology. However, two sites with the highest proportion of lying shells, STR and JER (over 90% lying), are both subject to heavy anchoring, particularly in deeper zones where anchoring is allowed. The opposite trend observed at DEB, located in the strictly protected zone of the Debeli rtič Landscape Park where anchoring is forbidden, further highlights the role of anchoring in determining shell orientation. Additionally, recent research from the same area showed that seabed damage and marine litter correlate positively with the proportion of lying shells (Trkov et al., in revision), supporting the interpretation that human activities contribute to shell displacement.

We detected no significant differences in shell density or orientation between the two sampling years, suggesting that most empty shells remained present on the seabed and that the majority still stands upright. These structures, despite deterioration, continue to provide important microhabitats in the Slovenian coastal sea, at least in the short to medium term. Nevertheless, shell decay is inevitable and will affect the function of empty shells in the long term.

4.2. Biodiversity enhancement by empty *P. nobilis* shells

Our results showed higher abundance and diversity indices in microhabitats containing *P. nobilis* shells. Similar findings have been reported in the southern Central Mediterranean Sea, where empty shells hosted species absent from adjacent bare sediment and supported higher abundances than surrounding soft bottoms (Rabaoui et al., 2015). In those cases, the effect was largely attributed to sessile species, which have limited options for attachment on unconsolidated sediments, apart from scattered stones. In our study, however, motile macrofauna alone showed the same trend: regardless of seagrass presence, biodiversity was consistently higher when shells were present. Empty shells create crevices and refuges for motile species and enhance habitat heterogeneity (Iannucci et al., 2023), which is further amplified once sessile fauna colonize the shell surface.

Within seagrass meadows, samples that included empty shells exhibited the highest abundance, species richness, and Shannon diversity values, confirming that this microhabitat was the most diverse among those examined. The mutual relationship between *P. nobilis* and seagrasses is well established: meadows stabilize sediments and provide food resources for the bivalves, while *P. nobilis* enhances water clarity and nutrient cycling (Addis et al., 2009). Seagrass meadows themselves increase macrofaunal diversity regardless of shoot density (Gintowt et al., 2025). Our findings therefore support the idea that both seagrasses and shells act as habitat builders, and that their cumulative effects persist even after the death of the bivalves. Indeed, biodiversity metrics were similar between seagrass meadows without shells and unvegetated sediments containing shells, indicating that both structures function as

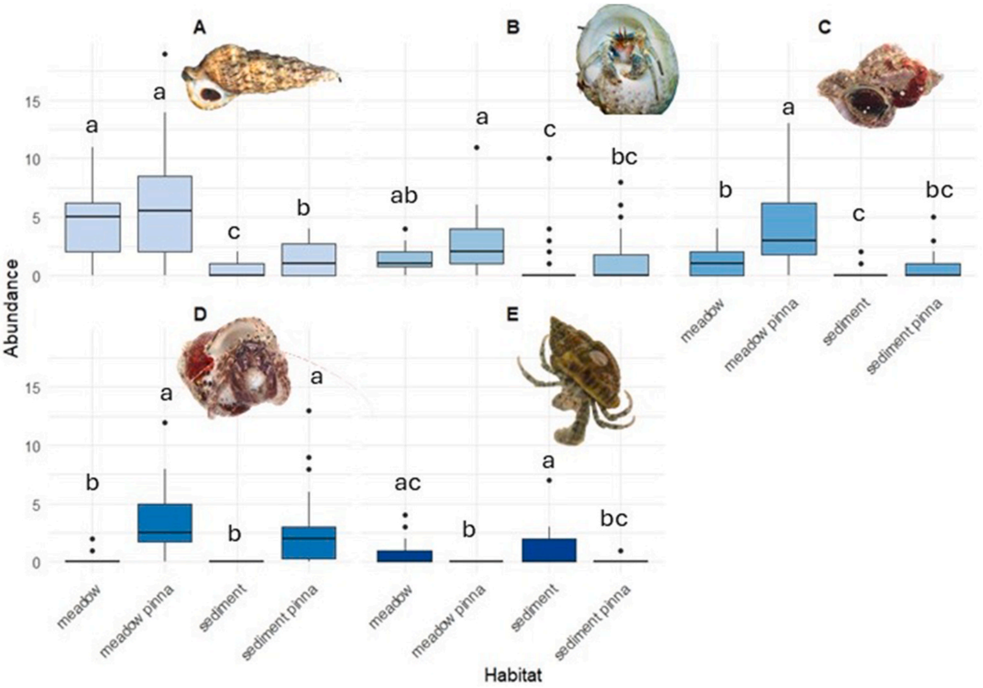

Fig. 8. The distribution of abundance of species, which contributed most to similarities among different habitat types; *Thericium vulgatum* (A), *Paguristes streaensis* (B), *Hexaplex trunculum* (C), *Pagurus anachoretus* (D) and *Diogenes pugilator* (E). The different small letters indicate statistical differences between habitat types (Dunn's test).

bioengineers of comparable importance. Previous work has highlighted the unique contribution of dead shells to biodiversity. Munguia (2007) reported that 66% of the 70 epibenthic taxa recorded on dead pen shells were absent from adjacent seagrass habitats. Comparatively, in our study 42% of the 57 species recorded in seagrass meadows were found exclusively in shell-containing microhabitats, while in unvegetated sites 76% of 37 species occurred only where shells were present. These results suggest that the role of pen shells on bare sediments is even more pronounced than within seagrass meadows, as they provide critical shelter and feeding opportunities for motile fauna that would otherwise be exposed on open bottoms. Interestingly, a Sardinian study found lower colonization of pen shells within seagrass meadows compared to bare sediment sites, possibly reflecting high productivity in estuarine habitats (Addis et al., 2009). In nutrient-rich lagoons or near river inputs, plankton biomass and organic matter are often elevated, promoting dense epibiont growth on shells. The absence of seagrass also allows greater water flow around shells, facilitating the delivery of larvae and spores, while increased light availability may promote algal colonization in shallow areas.

It is likely that the inclusion of sessile fauna in our study would have revealed additional patterns, as these organisms are immotile and highly sensitive to local conditions, unlike motile macrofauna which can relocate under unfavorable circumstances (Rabaoui et al., 2009). This may also explain why we observed no differences in biodiversity indices between upright and lying shells. In contrast, Burić (Burić et al., 2025). reported higher abundance and richness on upright shells compared to lying ones, although their Shannon diversity values did not differ. This discrepancy may be due to the different groups studied: sessile organisms depend on stable, exposed surfaces for attachment and feeding, while lying shells often have one valve in direct contact with sediment, smothering potential colonizers. Motile species, by contrast, exploit the habitat and resources around the shell equally, regardless of orientation. This was mostly observed in two groups (Malacostraca and Polyplacophora), which were more abundant in quadrats with shells, illustrating the importance of hard substrates for these groups as places of feeding and hiding.

Finally, the consistent evenness across habitats in our study indicates that, although richness and diversity varied, no single species dominated the assemblages. The exception was bare sediment, where high variability in evenness reflected low abundances and, in some samples, the absence of fauna altogether. Previous research demonstrated a correlation between the density of empty pen shells within seagrass meadows and the abundance of animals utilizing them as shelters (Kuhlmann, 1994). It however, remains unclear whether shells primarily act as sites of attraction, by concentrating species already present in the area, or as sites of production, by facilitating population growth. Further research is needed to disentangle these processes.

4.3. *Drivers of community composition across habitats*

The composition of benthic communities is strongly shaped by habitat features that provide surfaces for colonization, shelter, or feeding opportunities. Cosentino (Cosentino et al., 2008) reported that the pen shell supports a diverse assemblage of small snails that graze on epiphytes growing on the shell, thereby sustaining a substantial grazing community. In contrast, the most abundant epibionts recorded on *P. nobilis* are suspension feeders, which share the same feeding niche as the host and may even compete with it for suspended particles (Rabaoui et al., 2009). Following the death of the mollusk, sessile coverage increases greatly, often reaching 80–95% of the shell surface (Iannucci et al., 2023). Without the hosts activity, fouling organisms can proliferate, suggesting that epibionts may actually thrive more successfully on empty shells, after the death of the mollusk. In our study, bivalves were the most abundant class of suspension feeders and tended to be more common on shells, compared to the sediment bottom, although this pattern was not statistically significant. This may be due to the naturally high abundance of bivalves in dense seagrass meadows, particularly at Sečovlje, where a thick matte of *C. nodosa* provides additional habitat. Oysters and pectinids, which were already present on *P. nobilis* shells before the MME, however, appeared to be even more abundant on empty shells and were frequently observed growing on the inner surfaces of the valves (pers. obs.), where they are likely better protected from predators.

Munguia (2007) observed, that the species, which were found on the pen shells, were not unique to this habitat, but they are generally found in lower densities in microhabitats without shells. Our results are consistent with this finding, as most abundant species were also present in microhabitats outside pen shells, while species restricted to particular microhabitats tended to be rare. For example, large decapods were often hiding in empty shells, but no more than two individuals were found per shell. These findings show the importance of empty pen shells as refuges for decapods, such as *Pilumnus* spp., *Galathea squamifera* Leach, 1814, *Polybius navigator* (Herbst, 1794) and *Xantho poressa* (Olivi, 1792). Furthermore, in the future they might prove important also as a hiding place from the large predator, which is invading this region, the blue crab (*Callinectes sapidus* Rathbun, 1896). Rabaoui et al. (2009) found that motile species had much higher turnover between shells than sessile organisms, with each pen shell supporting a unique assemblage. When communities across shells were pooled, they contribute substantially to overall gamma-diversity. Notably, beta-diversity at small spatial scales was about ten times higher for motile species than for attached fauna.

Characteristic species analysis across microhabitats highlighted distinct distribution patterns among gastropods and hermit crabs. The hermit crab, *D. pugilator*, found almost exclusively in microhabitats without a pen shell, is characteristic of sedimentary bottoms, and its abundance is affected by anthropogenic activities, such as dredging and coastal development works (García Raso and Manjón-Cabeza, 2002). In contrast, *H. trunculus*, a predatory rock-dwelling murex snail, typical for rocky bottoms, was very abundant in our study, especially in the seagrass meadows and in association with empty shells. This supports the role of *P. nobilis* shells and seagrass meadows in hosting a rich community, inhabited also by highest trophic guilds, which in this place find an abundance of food. Similarly, *P. anachoretus*, was a species highly associated with shells. Historically reported from infralittoral rocky bottoms in the region (Stalio, 1877), its presence further emphasizes the role of pen shells as “hard-bottom oases” within predominantly sedimentary habitats of the northern Adriatic.

Beyond invertebrates, empty *P. nobilis* shells provide nesting, feeding, and shelter for higher taxa such as cephalopods and fishes. The importance of these structures for fish communities is discussed in detail elsewhere (Trkov et al., in prep.).

5. Conclusions

A question arises, what is the importance of these results, if the shells are slowly degrading over time due to natural causes? The MME has led to near-total collapse of *P. nobilis* populations across the Mediterranean Sea. Many empty *P. nobilis* shells remain anchored in place and continue to serve its habitat-building role. Understanding the biodiversity associated with both live and dead pen shells, across different habitat types, is therefore important for assessing the ecological consequences of the decline of *P. nobilis* and the potential for its partial functional replacement by empty shells. Analogously, Munguia (2007) reports that dead pen shells of a related species constitute the predominant hard substrate available for colonization in St. Joe Bay, Gulf of Mexico, which is of great importance for local biodiversity. Therefore, the results of our study are not only relevant to the period after the MME but also offer insight of significance of the empty shells if the species recovers in the future or is replaced by another species.

To conclude, empty *P. nobilis* shells provide refuge for motile macroinvertebrates, thus increasing local biodiversity. The shells enhance biodiversity regardless of shell orientation and seagrass meadows enhance community structure even further. By influencing the rate of new shell availability, *P. nobilis* pathogens may indirectly shape the distribution and reproductive success of species dependent on these microhabitats. This study was spatially and temporally limited, and our findings should therefore be interpreted within the context of the studied area and sampling period, although they align with observations reported in previous studies.

The findings of this study highlight the ecological legacy of *P. nobilis* and call for preservation of the remaining shells structures, as well as including post-mortality habitat roles in conservation planning. Measures should be taken to protect those vulnerable habitats from harmful human activities, such as anchoring, dredging, construction and collection. The spatial distribution of the shells, which remains very dense throughout the area, extends beyond the protected zones designated primarily for seagrass meadows.

Declaration of generative AI and AI-assisted technologies in the manuscript preparation process

During the preparation of this work the authors used ChatGPT 5.0 in order to improve the language and gather literature. After using this tool, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

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CRediT authorship contribution statement

Ana Fortič: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Validation, Visualization, Writing – original draft. **Valentina Pitacco:** Conceptualization, Funding acquisition, Investigation, Validation, Writing – review & editing. **Domen Trkov:** Conceptualization, Investigation, Methodology, Validation, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2026.109789.

Data availability

Data will be made available on request.

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