

Universidade de Évora - Escola de Ciências e Tecnologia Universidade de Lisboa - Instituto Superior de Agronomia

Mestrado em Gestão e Conservação de Recursos Naturais

Dissertação

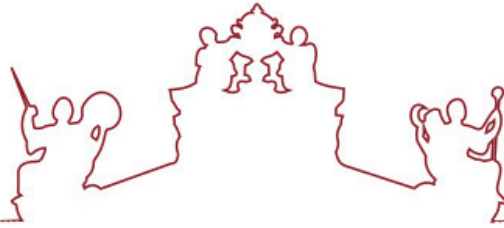
Life within *Mytilus galloprovincialis* beds along the Portuguese coast

Rita Faria Calado dos Santos

Orientador(es) | Teresa Paula Cruz
Cristina Espírito Santo

Évora 2025





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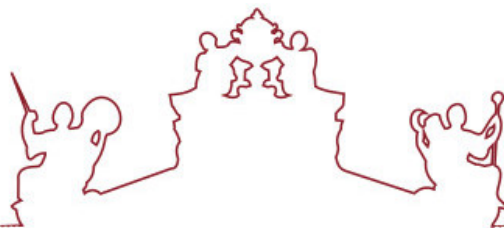
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"In the end, we will conserve only what we love, we will love only what we understand, and we will understand only what we are taught."

("No final, conservaremos apenas o que amamos, amaremos apenas o que entendemos, e entenderemos apenas o que nos é ensinado.")

- Baba Dioum, 1968

Resumo

A vida nos recifes de *Mytilus galloprovincialis* ao longo da costa portuguesa

Os recifes de mexilhão são habitats biogénicos e hotspots de biodiversidade devido à sua complexidade estrutural. Contudo, apesar do elevado interesse biogeográfico da costa portuguesa, os estudos sobre a biodiversidade de macroinvertebrados em recifes de mexilhão intertidais continuam limitados, concentrando-se, sobretudo, na região norte. Este estudo investigou a variabilidade espacial das comunidades de macroinvertebrados associadas à espécie *Mytilus galloprovincialis* ao longo da costa rochosa intertidal portuguesa, considerando padrões em larga escala (entre locais) e em pequena escala (entre transectos de um mesmo local). Foi também analisada a variação entre micro-habitats (plataformas horizontais, poças de maré e paredes verticais) e o papel de características físicas dos recifes de mexilhão. Foram identificados 72 táxones, dominados pelas classes Bivalvia, Malacostraca, Gastropoda, Polyplacophora e Polychaeta. As análises multivariadas gráficas e estatísticas mostraram que a principal fonte de variação da estrutura das comunidades de macroinvertebrados associadas à espécie *M. galloprovincialis* foi a diferença entre os locais amostrados ao longo da costa portuguesa, nomeadamente entre: o grupo do norte (Montedor e Valadares); grupo de Peniche (Ponta do Trovão e Consolação) e Queimado; e os restantes locais que não se agruparam entre si (Magoito, Cabo Raso, Foz, Almogrove e Alteirinhos). Embora a variação entre micro-habitats e transectos tenha sido significativa, não foi considerada tão importante como a variação entre locais. As restantes variáveis selecionadas como responsáveis pela variação biológica encontrada estão relacionadas com características físicas dos recifes de mexilhão, como o tamanho dos mexilhões e respetivo grau de heterogeneidade, bem como a capacidade de retenção de sedimentos. Este estudo destaca a importância ecológica dos recifes de mexilhão e a necessidade da sua conservação e gestão sustentável.

Palavras-chave: Recifes de mexilhão; Comunidades de macroinvertebrados; Características físicas dos recifes de mexilhão; Micro-habitats; Variabilidade espacial.

Abstract

Life within *Mytilus galloprovincialis* beds along the Portuguese coast

Mussel beds are biogenic habitats and biodiversity hotspots due to their structural complexity. Yet, despite the high biogeographic interest of the Portuguese coast, studies on macroinvertebrate biodiversity in intertidal mussel beds remain limited, mainly focused on the northern region. This study investigated the spatial variability of macroinvertebrate assemblages associated with *Mytilus galloprovincialis* along the Portuguese rocky intertidal coast, considering large-scale (shores) and small-scale (transects within shores) patterns. Variation among microhabitats (horizontal platforms, rock-pools and vertical walls) and the role of mussel bed physical characteristics were also assessed. A total of 72 taxa were identified, dominated by the classes Bivalvia, Malacostraca, Gastropoda, Polyplacophora and Polychaeta. The graphical and statistical multivariate analyses revealed that the main source of variation in the structure of macroinvertebrate communities associated with *M. galloprovincialis* was the difference between the sampled shores along the Portuguese coast, particularly between: the northern group (Montedor and Valadares); Peniche (Ponta do Trovão and Consolação) and Queimado group; and the remaining shores which did not group together (Magoito, Cabo Raso, Foz, Almogrove and Alteirinhos). Although the variation between microhabitats and transects was significant, it was not considered as important as the variation between shores. The remaining variables selected as responsible for the biological variation observed were related to the physical characteristics of the mussel beds, such as mussel size and associated degree of heterogeneity, as well as sediment retention capacity. This study highlights the ecological importance of mussel beds and the need for their conservation and sustainable management.

Keywords: Mussel beds; Macroinvertebrate assemblages; Mussel bed physical characteristics; Microhabitats; Spatial variability.

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Abbreviations

AIC – Akaike Information Criterion

ALM – Almogrove

ALT – Alteirinhos

CIEMAR – Marine Sciences Laboratory

CO – Consolação

CR – Cabo Raso

dbRDA – Distance-based Redundancy Analysis

DistLM – Distance-based Linear Model

HAC – Hierarchical Agglomerative Clustering

IUCN – International Union for Conservation of Nature

MA – Magoito

MAFs – Marine Animal Forests

MO – Montedor

nMDS - nonmetric Multidimensional Scaling

PERMANOVA - Permutational Multivariate Analysis of Variance

PT – Ponta do Trovão

QUE – Queimado

SIMPER - Similarity Percentages Analysis

SIMPROF – Similarity Profile Routine

VA – Valadares

WoRMS – World Register of Marine Species

1. Introduction

Mussel beds are prime examples of rocky intertidal Marine Animal Forests (MAFs) (Arribas et al., 2014; Flores-Garza et al., 2014; Rossi et al., 2017; Craeymeersch & Jansen, 2019). Serving as ecosystem engineers, they create three-dimensional structures that enhance biodiversity by providing protection from physical (e.g. desiccation during low tide, hydrodynamic pressures during high tide), and biological (e.g. predation) stresses, thereby offering refuge to a variety of marine species that would otherwise be unable to withstand the harsh and fluctuating conditions of both marine and terrestrial environments, which characterize the intertidal ecosystem (Crain & Bertness, 2006). Additionally, mussel beds contribute to nutrient cycling (Prins & Smaal, 1994; Smaal et al., 2019), carbon sequestration (Sea et al., 2022) and substrate stabilization (Widdows & Brinsley, 2002), while also serving as a fundamental food source for predators (Ysebaert et al., 2009) and acting as nursery grounds for juveniles of various marine invertebrate species (Gosselin & Chia, 1995; Silva et al., 2003; Mercegue et al., 2021; Seabra et al., 2019; Seabra et al., 2020).

As a coastal nation, Portugal maintains a strong connection to the sea, with fishing and shellfish harvesting deeply entrenched in Portuguese cultural identity. These customs date back centuries, playing a vital role in the country's gastronomic, economic and recreational sectors (Rius & Cabral, 2004; Oliveira et al., 2013). Along the Portuguese coast, humans harvest the species *Mytilus galloprovincialis*, also known as the Mediterranean mussel, as a food resource, for commercial purposes, or as bait (Rius & Cabral, 2004; Ferreira et al., 2013). This species dominates the intertidal mussel beds (Boaventura et al., 2002; Veiga et al., 2020), attaching itself to various physical microhabitats, such as rocky platforms, rock-pools, crevices, and vertical walls (Ramos, 2017).

In Portugal, current knowledge on mussel beds remains largely confined to studies on the mussels themselves. Research has focused on the relationship between site accessibility and human harvesting intensity on mussels (Rius & Cabral, 2004), the direct effects of human trampling on mussel beds (Veiga et al., 2023) and the use of mussels as bioindicators in environmental contamination studies (Moreira et al., 2004; Lima et al., 2007; Sousa et al., 2009; Figueiredo et al., 2022). Additionally, comparative analysis of mussel bed variables between urban and non-urban shores (Veiga et al., 2020), assessments of the effectiveness of mussel cultivation practices (Araújo et al., 2020), investigations into patterns of distribution, abundance (Boaventura et al., 2002; Espírito-Santo, 2007; Ramos-Oliveira et al., 2021) and dimensional structure of mussels (Espírito-Santo, 2007), as well as morphological analysis (Espírito-Santo,

2007) have been conducted in the last decades. However, there is currently limited existing literature on the biodiversity and taxonomy of marine benthic macroinvertebrates associated with mussel beds in Portugal, with recent studies predominantly concentrated in the northern region (Oliveira et al., 2014; Torres et al., 2022; Torres, 2023; Veiga et al., 2023).

The main objective of this study is to describe spatial patterns of variation at both large and small scales in the macroinvertebrate assemblages associated with rocky intertidal *M. galloprovincialis* beds along the Portuguese coast. Furthermore, this study is important for promoting awareness regarding the potential indirect impacts of mussel harvesting and trampling. This is imperative for the conservation not only of mussel populations, but also for the entire biodiversity reliant upon the presence of this particular MAF. The next section presents a literature review on MAFs, particularly focusing on rocky intertidal mussel beds, followed by a section describing the specific objectives and hypotheses of this study.

2. Literature Review

2.1. Perspectives on Marine Animal Forests (MAFs)

2.1.1. Connecting Ecological Concepts

The perception of linking forests to terrestrial ecosystems dominated by plant communities is ingrained in our consciousness. Nonetheless, an analogous concept to that of terrestrial forests can be observed in marine environments, popularly known as Marine Animal Forests (MAFs) (Rossi et al., 2017). First described by Alfred Russel Wallace in his book “The Malay Archipelago” in 1869, these animal-dominated ecosystems are mainly composed of sessile megabenthic (larger than 1 cm) suspension-feeding organisms (e.g., sponge aggregations, coral reefs, bryozoans, bivalve or polychaete beds, amongst others) (Rossi, 2013). Due to their unique functional and structural attributes, these communities are considered biodiversity hotspots, adding a third dimension to otherwise planar environments like sand, mud or rock, creating habitats that may not exist in adjacent areas (Rossi, 2013). MAFs are composed of biological entities deemed as “ecosystem engineers”, a concept first introduced to the scientific community in 1994 by Jones and his research colleagues. These authors have defined "ecosystem engineers" as species with the ability to impact the availability of resources for other organisms either directly or indirectly, through considerable physical alterations in biotic and abiotic factors. Consequently, these biodiversity hotspots play a crucial ecological role by undertaking an important nursery function (Cau et al., 2020), absorbing carbon (Sea et al., 2022), providing habitat for underwater and intertidal wildlife (Rossi et al., 2017), stabilizing benthic

sediments (Widdows & Brinsley, 2002) and increasing nutrient exchange (Prins & Smaal, 1994; Smaal et al., 2019).

2.1.2. Diversity and Distribution of MAFs: An Insight into the World of Intertidal MAFs

MAFs are ubiquitous in all oceanic regions, from shallow waters to greater depths within the marine ecosystem (Soares et al., 2017). These types of forests exhibit variable distribution across latitudes, ranging from tropical to polar regions (Gutt et al., 2017; Reyes-Bonilla & Jordán-Dahlgren, 2017) and inhabiting both warm, temperate and cold water environments. Tropical coral reefs are possibly the most researched by the scientific community among all MAFs, thriving in shallow, warm and oligotrophic aquatic habitats (Rossi et al., 2017). However, coral reefs can also be found at depths up to 1500 meters (Roberts et al., 2006). Sponges, another versatile type of organism, are frequently found in many marine benthic communities across all latitudes and depths (Rossi et al., 2017), even in polar regions, despite the extremely harsh environmental conditions (McClintock et al., 2005).

When it comes to accessibility, it becomes apparent that certain ecosystems are easier to study than others. The rocky intertidal zone provides a convenient opportunity for marine research given its intermittently air-exposed nature during low tide, allowing the observation of aquatic organisms without the need for any specialized equipment. Within this given ecosystem, bivalve beds (Arribas et al., 2014; Flores-Garza et al., 2014; Craeymeersch & Jansen, 2019), as well as polychaete reefs (Gravina et al., 2018; Wilson & Hayek, 2019), are another important example of MAFs that support highly structured and diverse assemblages.

2.2. Living in the Rocky Intertidal Ecosystem

2.2.1. Characterization

The rocky intertidal zone, which encompasses the transitional boundary between marine and terrestrial environments, has emerged as an ecosystem of considerable ecological significance due to the diverse array of organisms that inhabit it (e.g. Underwood, 2000; Helmuth & Hofmann, 2001). Intertidal species face the challenge of adapting to the dynamic physical conditions associated with both marine and terrestrial ecosystems, making them of particular interest to biological researchers. During periods of low tide, a variety of terrestrial stressors, such as notable fluctuations in daily temperature, changes in desiccation levels and exposure to solar radiation, are known to have a significant impact on the physiological function, ecology and

biogeographical distribution of intertidal organisms (Gosselin & Chia, 1995; Seabra et al., 2011). In fact, if these stressors reach extreme levels, they may even lead to mortality (Gosselin & Chia, 1995). To ectotherms, such as marine invertebrates, it is noteworthy that solar radiation, evaporative cooling and convective heat exchange exhibit a potent influence on the regulation of body temperature during exposure to atmospheric conditions (Norris & Kunz, 2012). Several intertidal invertebrate species undergo extreme fluctuations in temperature, ranging from increasing their body temperature by 15 °C above the surrounding water temperature during summer to experiencing freezing temperatures during winter (Carefoot, 1977; Seed & Suchanek, 1992). Furthermore, these organisms must have a certain level of adaptability and resilience to withstand other abiotic factors, such as intense freshwater exposure during storms, as well as the potential risk of damage or displacement due to wave impact (Paine & Levin, 1981; Craeymeersch & Jansen, 2019). For instance, the crab species *Grapsus tenuicrustatus* adjusts its posture to avoid being swept away (Martinez, 2001), while barnacles may develop smaller feeding legs, allowing them to withstand more intense hydrodynamic forces (Arsenault et al., 2001). Similarly, mussels, such as *M. galloprovincialis*, may have smaller and narrower shells in exposed sites (Steffani & Branch, 2003).

Despite its challenging nature, physical factors might also positively influence the distribution and abundance of intertidal organisms. For instance, filter-feeding organisms, such as bivalves, may benefit from the hydrodynamic conditions prevalent in these environments, which create favorable feeding conditions. Onshore currents and tides provide the accumulation of nutrient-rich food sources in the water, including phytoplankton and suspended organic particles (Fréchette & Bourget, 1985; Bustamante et al., 1995), while wave action helps maintain adequate oxygen levels (Bozkurt & Kabdasli, 2013). The shallow water depth also ensures sufficient light penetration for primary production (Hill et al., 1998). Additionally, biological factors such as competition (Mangialajo et al., 2012), predation (Underwood & Jernakoff, 1981), herbivory (Underwood & Jernakoff, 1981; Thomas, 1994) and facilitation (Erlandsson et al., 2011) play significant roles in shaping the distribution and abundance of intertidal species through top-down and bottom-up regulatory mechanisms. These physical and biological mechanisms simultaneously prevent the dominance of any single species within the community and create opportunities for new species to colonize, thereby promoting diversity (Menge, 2000).

2.2.2. Intertidal Habitats as Refuges and Food Sources

The rocky intertidal is not a flat, homogeneous environment. In addition to the abiotic conditions mentioned above, the nature of rock substrates also plays an important role in shaping the ecology and evolution of benthic organisms (Guidetti et al., 2004). Different rock types, such as limestone and granite, are known to create distinct environmental conditions and exert significant influence on the diversity and distribution of marine organisms in epibenthic communities (Bavestrello et al. 2000; Guidetti et al., 2004). For instance, rocks with higher quartz content, such as granite, may induce physiological stress on marine organisms due to the oxidant properties of quartz surfaces (Cerrano et al. 1998; Bavestrello et al. 2000). This can result in fewer species and greater algae mat coverage on quartz-rich substrates compared to carbonate-rich substrates, as supported by the findings of Bavestrello et al. (2000) and Guidetti et al. (2004).

Moreover, the topographical characteristics of the surface can vary, creating a diversity of ecological niches that support different biological communities (Sebens, 1991). Notably, the surface roughness of rocks has been shown to influence the settlement and attachment of organisms, as observed with barnacles, where greater settlement has been recorded on rougher surfaces (Herbert & Hawkins, 2006). Furthermore, in the rocky intertidal zone, several natural processes might promote the formation of physically distinct microhabitats. Due to the erosive forces of both the terrestrial and marine environments, rock constituents may break into fragments, forming boulder fields (Satyam & Thiruchitrabalam, 2018). Rock abrasion and weathering can lead to cavity formation, creating crevices and rock-pools. Horizontal platforms and vertical walls are also common physical microhabitats within the rocky intertidal zone (Satyam & Thiruchitrabalam, 2018).

These microhabitats, commonly known as primary substrate (Lohse, 1993), offer great refuge opportunities for intertidal organisms, reducing their vulnerability to the harsh environmental conditions found in this specific ecosystem (Cartwright & Williams, 2012). Furthermore, as described in the section on Marine Animal Forests, certain organisms create biotic surfaces within the primary physical substrate, thereby earning the classification of secondary substrate (Tsuchiya & Nishihira, 1985; Lohse, 1993). These organisms are capable of using a portion of the available material within the system (e.g., tube-building polychaetes) (Bremec et al., 2013; Gravina et al., 2018) or use their own biological material (e.g., bivalves) (Engel et al., 2017) to build reefs or aboveground aggregations, which can serve as habitat for other organisms (Mercegue et al., 2021).

The interplay of physical and biological components promotes the complexity of the habitat and the spatial heterogeneity of intertidal systems, which are crucial for supporting species diversity, coexistence and survival (Sebens, 1991). In the context of juvenile development, protective microhabitats can enhance growth conditions, ensuring their survival during this particularly vulnerable early life stage. According to the research conducted by Gosselin and Chia (1995), newly hatched *Nucella emarginata* faced a mortality rate close to 100% when exposed to desiccation and predators on an open surface for only 5 hours. In contrast, within the same time frame, the mortality rate of hatchlings was found to range between 1.7% and 36% when sheltered in microhabitats such as filamentous algae *Cladophora columbiana*, *Mytilus* spp. beds and dense assemblages of the barnacle *Semibalanus cariosus* (Gosselin and Chia, 1995). It is known that different habitat features might be associated to different taxa (Johnson et al., 2003; Moschella et al., 2005; Firth & Crowe, 2008). The present study will only address the macroinvertebrate assemblages that are specifically associated with rocky intertidal mussel beds.

2.3. Mussel Beds

2.3.1. Habitat Heterogeneity and Biodiversity on Mussel Beds

Intertidal mussel populations not only play a crucial role in maintaining the trophic chain connection between benthic organisms and phytoplankton through their active filter-feeding mechanism (Kautsky & Evans, 1987; Norling & Kautsky, 2007) but also assume a significant function as ecosystem engineers (Arribas et al., 2014).

Patterns of distribution and abundance of mussel species are variable. These patterns can range from dense, nearly homogeneous beds totally covered by mussels to a mosaic of patches of different sizes (Paine & Levin, 1981; Van de Koppel et al., 2008). Mussels form monolayer aggregations by attaching their byssal threads to both the substrate and the byssal threads of adjacent mussels, which may help prevent their displacement (Smeathers & Vincent, 1979; Tsuchiya & Nishihira, 1986). Thus, as the mussel beds grow, the concomitant requirement for additional space arises, with certain individuals being pushed outward from the existing aggregation, while others are forced to shift upward, resulting in the emergence of a more stratified, multi-layered microhabitat (Tsuchiya & Nishihira, 1986; Wilbur et al., 2023). Within this complex matrix of interconnected mussels, not only is there a decrease in hydrodynamic pressure as mentioned above, but light and temperature are also significantly reduced, while relative humidity is increased (Seed & Suchanek, 1992). This can be attributed to the substantial

amount of water retained within the interstitial spaces which reduces the impact of desiccation and thermal stress. For instance, in 2016, Jurgens and Gaylord conducted a study of infrared thermography within mussel beds. Their findings indicated that the inside temperature of the beds fell between 10 to 15 °C lower than the temperature observed in the adjacent rocky substrate. This observation accentuated the significance of these microhabitats in favor of the survival of associated organisms.

Based on the terminologies commonly used in the literature to describe different levels of biodiversity found on mussel beds, they can be categorized into three "faunal groups" according to their spatial distribution within the microhabitat (Seed, 1996; Commito et al., 2008; Benjamin et al., 2022, and references therein). Taking a top-to-bottom perspective, epibiotic life forms inhabit the external surfaces of mussel shells in a stationary or partially stationary manner. On the other hand, mobile organisms navigate freely within the intricate network of interconnected byssus threads, occupying the interstitial spaces. Finally, the infaunal organisms typically arise among fragments of dead mussel shells, sediment and nutrient-rich biodeposits generated from the mussel's biological processes (Kautsky & Evans, 1987; Seed, 1996; Benjamin et al., 2022). Such biodeposits also serve as an additional food source, promoting the presence of associated fauna (Norling & Kautsky, 2007).

Several authors have documented the presence of communities associated with the Mytilidae family in different parts of the world with considerable biological diversity. For instance, Smith (2001) identified a total of 192 different taxa in intertidal *Mytilus edulis* beds across eight rocky shores along the coasts of the British Isles and the Irish Republic, while Lintas & Seed (1994) recorded 59 taxa in rocky intertidal beds of the same species at a single site near Aberffraw, North Wales. Moreover, *Brachidontes rodriguezii* intertidal beds in Argentina supported a total of 23 taxa across two rocky shores (Adami et al., 2004), while *Perumytilus purpuratus* beds in Chile were found to host 92 taxa across three sites of Punta de Tralca Bay (Prado & Castilla, 2006). Furthermore, *Mytilisepta virgata* beds on the rocky intertidal shore of Cape d'Aguilar, Hong Kong, supported up to 52 taxa (Che & Morton, 1992). Lastly, for *Mytilus galloprovincialis* intertidal beds, two separate studies reported different numbers of associated taxa. Chapman et al. (2005) identified 59 taxa on seawalls at a single site in Sydney Harbour, Australia, while Hodgson et al. (2021) recorded 65 taxa across six hard substratum sites in the embayment of Knysna Estuary, South Africa. Additionally, in both Portugal (Torres et al., 2022) and Spain (Veiga et al., 2022), intertidal *Mytilus galloprovincialis* beds were found to support 58 and 115 taxa across four and two rocky shores, respectively. In all studies involving multiple

sampling sites, the reported total number of taxa represents the combined distinct taxa recorded across all sampled locations in each study.

Despite the presence of a well-represented range of macroinvertebrate taxa in these communities (e.g., annelids, gastropods, bivalves, crustaceans, amongst others), it is a common occurrence for mussel beds to be predominantly dominated by a small number of highly abundant species. Additionally, species that are functionally and taxonomically similar (often belonging to the same family or genus) are frequently associated with distinct mytilid communities worldwide (Seed, 1996).

2.3.2. Factors Affecting Mussel-Associated Biodiversity

It is recognized that mussel beds increase biodiversity. However, the factors that influence the formation of these assemblages are not fully comprehended. In theory, it seems logical to assume that there is a correlation between the level of complexity present in a given habitat and the diversity of species it supports. The majority of research on mussel beds validates this theory, with the physical structure of the mussel matrix being considered one of the drivers that most promotes biodiversity (Seed, 1996). For instance, an increase in the number of mussel layers and interstitial spaces can boost structural complexity, creating more area for other organisms to inhabit (Wilbur, 2023). Consequently, this increase in structural complexity might act as a significant factor in promoting species diversity (Wilbur, 2023). O'Connor and Crowe (2007) also noted that mussel size influences the composition of associated macroinvertebrate assemblages. By comparing patches of larger and smaller mussels, they observed that while species richness did not seem to be affected, the abundance and proportion of organisms were generally higher in patches with larger mussels.

The composition of faunal assemblages can also be influenced by other physical properties of mussel beds, including mussel density, patch size, habitat homogenization, sediment retention, matrix depth and the presence of macroalgae attached to shells (Stewart et al. 1998; Prado & Castilla, 2006; Veiga et al., 2022). Environmental factors such as wave exposure and tidal level also have a significant effect on the richness of associated species (Suchanek, 1980; Prado & Castilla, 2006). In a 2016 study conducted in South America on the subtidal beds of the ribbed mussel (*Aulacomya atra*), Sepúlveda et al. observed a significant influence of latitude on the shaping of macroinvertebrate associated with these mussel beds. This observation further highlights the sensitivity of these ecosystems to diverse hydrographic and topographic conditions.

However, results may be inconsistent and occasionally contradict the findings from previous research. In both Hammond's (2001) and Hodgson's et al. (2021) research, findings indicated no correlation between the size of mussels and the level of species richness and diversity. In 2004, Chintiroglou and his research colleagues also found no apparent relationship between mussel density and diversity of the assemblage. The reason for these distinct results is unknown.

There is currently no agreement among experts about the most effective approach to measure structural complexity within mussel beds. Some authors, such as Aronson and Precht (1995), adopted the application of chain-length approaches in their studies. Fractal analysis (Commito & Rusignuolo, 2000), calculation of a stratum index (Prado & Castilla, 2006) and measurement of shell length (Wilbur et al., 2023) are among the techniques employed by other researchers.

2.3.3. *Mytilus galloprovincialis* on the Portuguese Coast: Ecology, Distribution and Potential Implications of Anthropogenic Pressure on Faunal Assemblages

Along the Portuguese coast, mussel beds are mainly dominated by the species *Mytilus galloprovincialis* (Rius & Cabral, 2004; Espírito-Santo, 2007; Veiga et al., 2020). *Mytilus galloprovincialis* Lamark, 1819 is a bivalve species belonging to the Mytilidae family, commonly referred to as the Mediterranean mussel. The Mediterranean mussel, as its name suggests, is an abundant type of mussel native to the Mediterranean Sea and the southern European Atlantic coast (Braby & Somero, 2006). This species serves as a key ecosystem engineer particularly in the intertidal rocky shores that are either exposed or moderately exposed, possibly due to increased food supplies in this habitat (Boaventura et al., 2002). Morphologically, the adult Mediterranean mussel is characterized by the smooth, elongated triangular shape of its shell, which can reach sizes between 5 cm and 12 cm (Picker & Griffiths, 2011). The shell is usually marked with concentric growth lines and can be bluish black (occasionally brownish) on the outside and white with purple margins on the inside. As a strong filter feeder, *M. galloprovincialis* diet consists of phytoplankton and detritus filtered from the surrounding seawater through the gills (Musella et al., 2020). When it comes to mobility, the life cycle of this species is divided into two distinct phases: a free-swimming larval phase that can disperse over long distances, and a sessile juvenile and adult phase (Picker & Griffiths, 2011; Ramos, 2017). Sexual maturity in individuals of *M. galloprovincialis* is typically reached between the ages of 1 and 2 years (Newell, 1989; Villalba, 1995), with spawning potentially occurring from late autumn to late spring, and

rest from reproductive activity tending to take place in the summer (Da Ros et al., 1985; Okaniwa et al., 2010; Azizi et al., 2020). However, timing and frequency of spawning events may vary geographically among populations worldwide (Okaniwa et al., 2010, and references therein). In Portugal, there is evidence suggesting spawning and recruitment throughout the entire year (Saldanha, 1974 in Espírito-Santo, 2007; Santos, 2000; Ramos-Oliveira et al., 2021). *M. galloprovincialis* displays gonochoristic behavior (Arienzo et al., 2019), where individuals are clearly differentiated as male or female, and utilizes broadcast spawning as its reproductive strategy by releasing gametes into the surrounding water for external fertilization (Fitzpatrick et al., 2012).

Regarding the distribution patterns along the Portuguese rocky coast, Mediterranean mussels are predominantly found in the lower mid-shore zone (Boaventura et al., 2002). This species colonize diverse microhabitats that may possess contrasting ecological conditions such as rocky platforms, rock-pools, crevices and even vertical walls (Ramos, 2017).

Apart from its undeniably ecological significance, *M. galloprovincialis* also holds considerable economic value as a marine resource for human harvesting (Rius & Cabral, 2004) and aquaculture (Oliveira et al., 2013). Portugal, traditionally known for its large seafood consumption by both locals and visitors, features an extensive shoreline. The southern coast is characterized by a pronounced Mediterranean climate, while the northern coast exhibits a maritime-influenced Mediterranean climate (Oliveira et al., 2013). Moreover, the average water temperature in Portugal varies with latitude, ranging from 13 to 20 °C throughout the year (Santos, 1994 in Boaventura et al., 2002), generally presenting lower values in the north and higher values in the south. This coincides with the optimal temperature range for *M. galloprovincialis* population growth demonstrated by Thomas and Bacher (2018), which falls between 13 to 18 °C. Thus, the water temperature variation observed in Portugal seems to provide favorable conditions for the prosperity of *M. galloprovincialis* populations. However, a decrease in the average abundance of *M. galloprovincialis* has been observed from northern to southern shores, based on data from 1997 (Boaventura et al., 2002) and unpublished observations from 2022 by David Mateus. In addition, activities such as mussel cultivation, which involves transferring juveniles from wild beds to cultivation platforms, alongside with adult mussel harvesting for human consumption or use as fishing bait and accidental damage of mussel beds from trampling might disturb the dynamics of these populations (Kaiser et al., 1998; Murray et al., 1999; Airoidi et al., 2005; Smith & Murray, 2005; Veiga et al., 2023).

Intertidal mussel beds, being situated at the interface between land and sea, are especially susceptible to anthropogenic disruptions, particularly during peak periods such as national holidays like Easter or the summer season, when a greater influx of visitors is observed frequenting these areas for recreational purposes or harvesting activities (Rius & Cabral, 2004; Ferreira et al., 2013). Furthermore, the potential influence of human activities on mussel communities extends beyond direct effects, as exemplified by phenomena like climate change (Smith et al., 2006). The removal or disappearance of ecologically significant species, such as mussels, which play a crucial role in maintaining the vitality of intertidal ecosystems, can have a profound impact on the entire associated community (Veiga et al., 2020) and potentially result in significant biodiversity loss.

3. Research Problem: Objectives and Hypotheses

The main objective of this study is to perform a large-scale spatial analysis, providing a description of the macroinvertebrate assemblages associated with *M. galloprovincialis* beds along the Portuguese rocky coast. Given the distinct climatic and hydrodynamic characteristics of the northern and southern coasts of Portugal, this study will test the hypothesis that there is variation in the structure of macroinvertebrate assemblages associated with *M. galloprovincialis* beds according to latitude.

Another hypothesis proposed in this research is that there is variation in the structure of macroinvertebrate assemblages associated with *M. galloprovincialis* beds in different physical microhabitats (rock-pools, rocky platforms and vertical walls). Although mussel beds are also known to occur within crevices, this specific microhabitat was excluded from the study due to its less obvious presence on the northern and central shores.

The similarity of macroinvertebrate assemblages within mussel beds in a specific site of the rocky intertidal zone and those located a short distance away is uncertain. Therefore, it is necessary to investigate a small-scale objective that hypothesizes variation in the structure of macroinvertebrate assemblages associated with *M. galloprovincialis* beds across transects within a shore. This last objective will only be investigated on rocky platforms.

Furthermore, in addition to latitude, physical microhabitats and small-scale spatial variation, this study aims to investigate the relationship between different mussel bed attributes, including variations in size, coverage, density, biomass and capacity for sediment retention, and how these variables may influence the associated macroinvertebrate assemblages. These

features contribute to the structural complexity of the mussel beds, potentially affecting the diversity and composition of the associated fauna, as suggested by Gestoso et al. (2013).

4. Materials and Methods

4.1. Description of the Study Area, Sampling Design and Field Work

This research was conducted along a 590 km stretch of the continental Portuguese Atlantic coast, with data collection occurring between July 2022 and September 2022. Sampling was conducted at 10 rocky shores along the Portuguese coast, ranging from Montedor on the northwestern coast to Alteirinhos on the southwestern Alentejo coast (Figure 1). The criteria for shore selection included the presence of mussel beds and the accessibility of rocky intertidal areas. For safety and workflow optimization purposes, fieldwork days were scheduled according to atmospheric and maritime conditions, with particular emphasis on selecting time periods coinciding with spring tides. The sampling process was carried out during low tide, specifically at the mid-shore, where intertidal *M. galloprovincialis* beds typically occur (Boaventura et al., 2002). To investigate the structure of macroinvertebrate assemblages within *M. galloprovincialis* beds, three distinct microhabitats - rock-pools, horizontal platforms and vertical walls - were considered (Figure 2D, E and F). As mussels did not form considerable beds in certain microhabitats on some shores, it was not possible to sample all microhabitats on each shore. Figure 1 indicates which microhabitats were sampled on each shore. Shore-specific geographical coordinates can be consulted in Table 1.

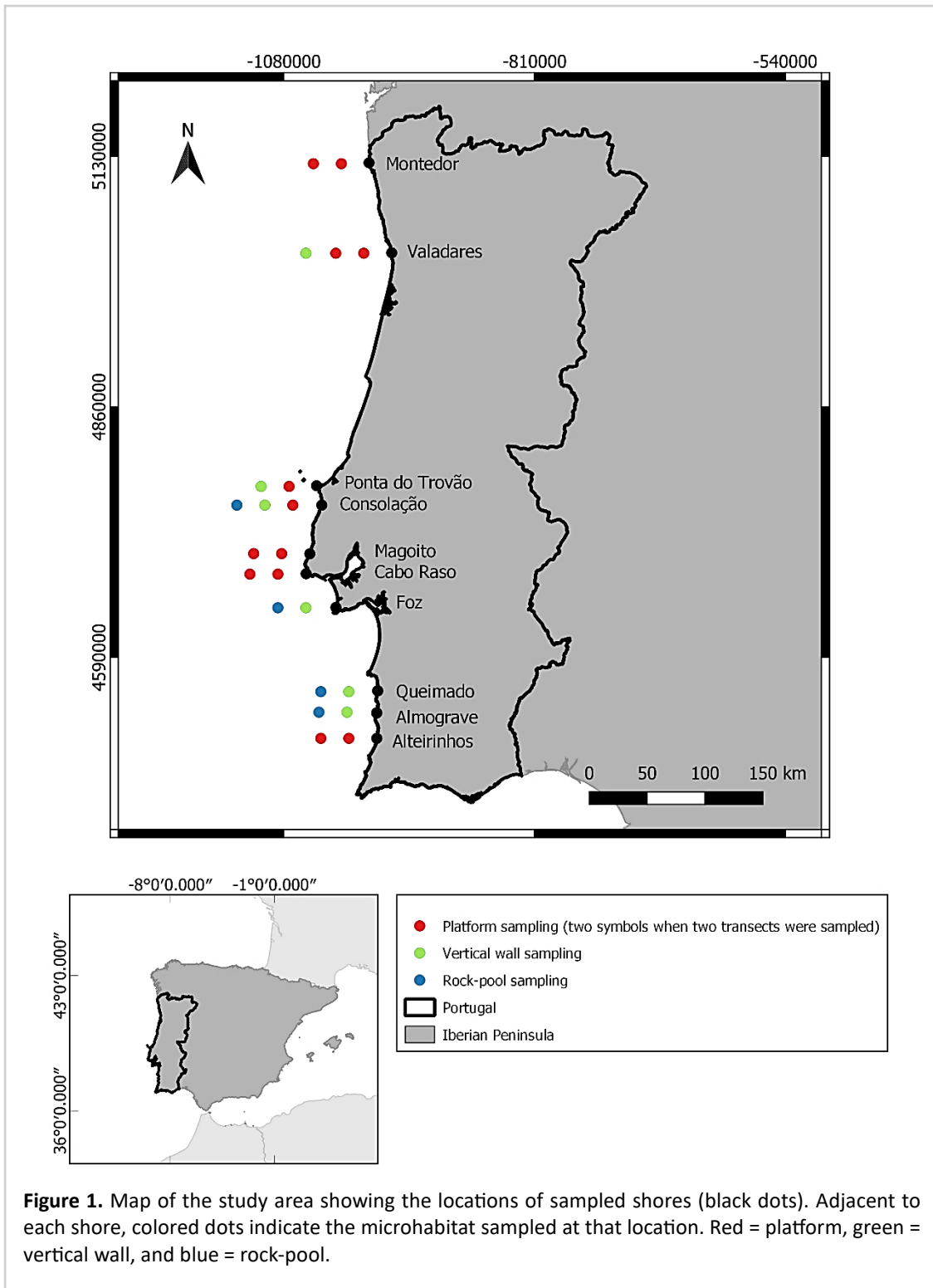


Table 1. Shore name and corresponding geographic coordinates.

Shore	Coordinate 1	Coordinate 2	Latitude	Longitude
Montedor	41°44'53.9"N 8°52'44.1"W	41.748315, -8.878923	41.748315	-8.878923
Valadares	41°05'23.0"N 8°39'26.2"W	41.089721, -8.657289	41.089721	-8.657289
Ponta do Trovão	39°22'14.6"N 9°23'14.1"W	39.370714, -9.387259	39.370714	-9.387259
Consolação	39°19'26.2"N 9°21'41.2"W	39.323955, -9.361436	39.323955	-9.361436
Magoito	38°51'55.7"N 9°27'03.6"W	38.865462, -9.450989	38.865462	-9.450989
Cabo Raso	38°42'30.5"N 9°29'11.5"W	38.708470, -9.486531	38.70847	-9.486531
Praia da Foz	38°27'10.8"N 9°12'00.5"W	38.452988, -9.200151	38.452988	-9.200151
Queimado	37°49'23.3"N 8°47'35.7"W	37.823124, -8.793256	37.823124	-8.793256
Almograve	37°39'13.4"N 8°48'12.9"W	37.653712, -8.803571	37.653712	-8.803571
Alteirinhos	37°31'03.1"N 8°47'29.3"W	37.517530, -8.791462	37.51753	-8.791462

At each studied shore, two random transects, perpendicular to the waterline, were established in the mid-shore, each approximately 10 m wide and of sufficient length to encompass the mid-shore area. These transects were exclusively used to sample the platform microhabitat. Three replicate sampling units of 100 cm² (10 x 10 cm quadrat) were randomly collected within each microhabitat (platforms - two transects, rock-pools and vertical walls) in the mid-shore, with sampling of each replicate involving the removal of all mussels, sediment trapped in the mussel matrix and macroinvertebrate assemblages within that area using a chisel. Additionally, prior to each sampling procedure, a photograph was taken to visually document the initial configuration of the sampled mussel patch with the quadrat in place (Figure 2F). These photographs were captured from angles that ensured a clear and full view of the square area. The collected samples, comprising all contents, were labeled, placed in designated bags and transported to the Marine Sciences Laboratory (CIEMAR) in Sines. Subsequently, they were preserved in a frozen state until further processing.



4.2. Laboratory Analyses

4.2.1. Sample Washing: Separation and Weighing of Mussels, Macroinvertebrate Assemblages and Sediment

In the laboratory, frozen replicates underwent wet sieving (under running water) using two sieves to separate mussels and macroinvertebrate assemblages (retained in a 500 µm mesh) from sediment and other materials (retained in a 200 µm mesh). Mussels larger than 1 cm were extracted from the 500 µm mesh sieve and, after draining excess water, weighed on a digital

scale with a precision of 1 g. For this size category (mussels larger than 1 cm), two types of volumetric measurements were conducted: dry volume and wet volume.

The dry volume was determined by placing the mussels inside a graduated glass cylinder and recording the corresponding volume (Figure 3C). The wet volume was determined by placing the mussels inside the graduated glass cylinder and adding a known volume of water in order to completely submerge them. The combined volume of the mussels plus water was then recorded. This “known volume of water” varied from replicate to replicate, with a larger volume added for replicates with a greater volume of mussels and a smaller volume for those with fewer mussels. The wet volume was subsequently calculated by subtracting the volume of the mussels plus water from the known volume of water added.

The maximum length of each mussel within this size class was measured according to the procedure described in subchapter 4.2.3. After draining excess water, the remaining macroinvertebrate assemblages, mussels smaller than 1 cm in size (hereafter referred to as spat), and residues (such as byssal threads, algae, shell fragments, etc.) retained in the 500 μm mesh were weighed and preserved in 70% ethanol (Figure 3B). The sediment and other materials (hereafter referred to just as sediment) from the 200 μm mesh were also drained, weighed and then discarded. Similar to the procedure for mussels larger than 1 cm, all weight measurements were taken using a digital scale with a precision of 1 g.

4.2.2. Identification and Counting of Macroinvertebrates (Including Mussel Spat)

Following the washing procedure detailed in subchapter 4.2.1, both macroinvertebrate organisms and sieved residual material - retained in the 500 μm mesh – of each replicate were subjected to further examination. Under a dissecting microscope, macroinvertebrate organisms were removed, identified to the species or lowest taxonomic level reachable and counted (Figure 3A).

Due to the substantial amount of mussel spat, a sub-sampling method was used to estimate its abundance. Specifically, replicates with a volume exceeding 30 ml were sub-sampled, whereas mussel spat from replicates with a volume below 30 ml were all counted individually (Figure 3B). Sub-sampling initiated by passing the entire content of the replicate through the 500 μm sieve (at this stage, the macroinvertebrates had already been removed and counted, leaving only residual material and mussel spat preserved in 70% ethanol). The material was then left to dry at room temperature and weighed. Approximately 12 g of the dried replicate

material (equivalent to three full coffee spoons) were then extracted into a petri dish and all mussel spat present in this portion were counted. Finally, using both recorded weights and mussel spat count in the sub-sample, an estimate of the total number of mussel spat within that replicate was made.

Given that barnacles were attached to mussel shells, barnacle abundance was determined through image analysis. By examining photographs taken to measure mussels maximum length (Figure 3D) (see subchapter 4.2.3), the percentage of mussels (larger than 1 cm) with barnacles attached to their shells was calculated and used as an indicator of abundance.

Taxonomic resolution varied according to the conservation status of the organisms and their taxonomic groups. For instance, soft-bodied organisms, such as annelids and cnidarians, showed a higher degradation rate, posing challenges in discerning key features essential for accurate identification. Moreover, organisms such as amphipods and certain isopods were not identified to the species level due to their complex diagnostic characteristics. In these cases, despite efforts to achieve species-level identification, some organisms were identified only to higher taxonomic levels, such as the family level. According to studies on taxonomic sufficiency (Terlizzi et al., 2009; Dauvin et al., 2016; Pitacco et al., 2019), identification of organisms at the genus and family levels is considered adequate for certain research purposes.

Identification was performed using the World Register of Marine Species (WoRMS Editorial Board, 2023) and the following references:

- **Annelids:** Fauvel (1975, 1977), Fauchald (1977), Brinkhurst (1982), Campoy (1982), Tebble & Chambers (1982), George & Hartmann-Schröder (1985), Chambers & Garwood (1992), San Martín (2003), Viéitez et al. (2004), Parapar et al. (2012, 2015);
- **Arthropods:** Bouvier (1923, 1940), Alvarez (1968), Lincoln (1979), Holdich & Jones (1983), Crothers & Crothers (1987), Athersuch et al. (1989), Falciai & Minervini (1995), Hayward & Ryland (1995), Ingle (1996), Naylor & Brandt (2015);
- **Echinoderms:** Tortonese (1965), Hayward & Ryland (1995);
- **Molluscs:** Tebble (1976), Jones & Baxter (1987), Graham (1971, 1988), Hawkins & Jones (1992), Hayward & Ryland (1995), Macedo et al. (1999), Campbell (2006);
- **Cnidarians, Chordates, Nemertean, and Platyhelminthes:** Prudhoe (1982), Hayward & Ryland (1995), Campbell (2006).

4.2.3. Application of Python Programming in Measuring and Counting Mussels (> 1 cm)

Each replicate comprised numerous mussels (> 1 cm), ranging from tens to hundreds, resulting in a labor-intensive and time-consuming process of manually measuring each mussel maximum length using vernier calipers. Therefore, to address this challenge, a more efficient alternative for both counting and sizing the sampled mussels was developed using the Python programming language (David Mateus, unpublished method), as described below.

First, disarticulation of the two valves of each mussel was carried out. Subsequently, a singular valve was positioned on a white tray, with precautionary measures taken to ensure that the valves on the tray remained spatially isolated from one another. Digital images of each tray with a known scale (pen cap) were captured using a Olympus Tough TG-6 camera (Figure 3D). The calibration of each image was conducted using the ImageG software to establish the pixel-to-centimeter ratio. After importing the image into Python, an initial conversion to grayscale was performed. This step aimed to simplify the image data by representing it in shades of gray, thereby accentuating important features, such as the contrast between the black mussel valves and the white background of the tray. Subsequently, a secondary conversion was executed, this time to a binary scale, resulting in an image where pixels were exclusively assigned either black or white values. This binary representation facilitated the distinction of the mussels from the white background. Using the binary scale, the software outlined every valve and added a contour around each one of them. Based on these contours, the software was programmed to insert a circle around each valve and to calculate the diameter of each circle, which in turn represents the maximum length of each mussel in the replicate. The diameter values (maximum length values) were automatically exported to an Excel spreadsheet, facilitating data analysis and enabling efficient data organization. The average and standard deviation of mussels maximum length were calculated for each replicate.

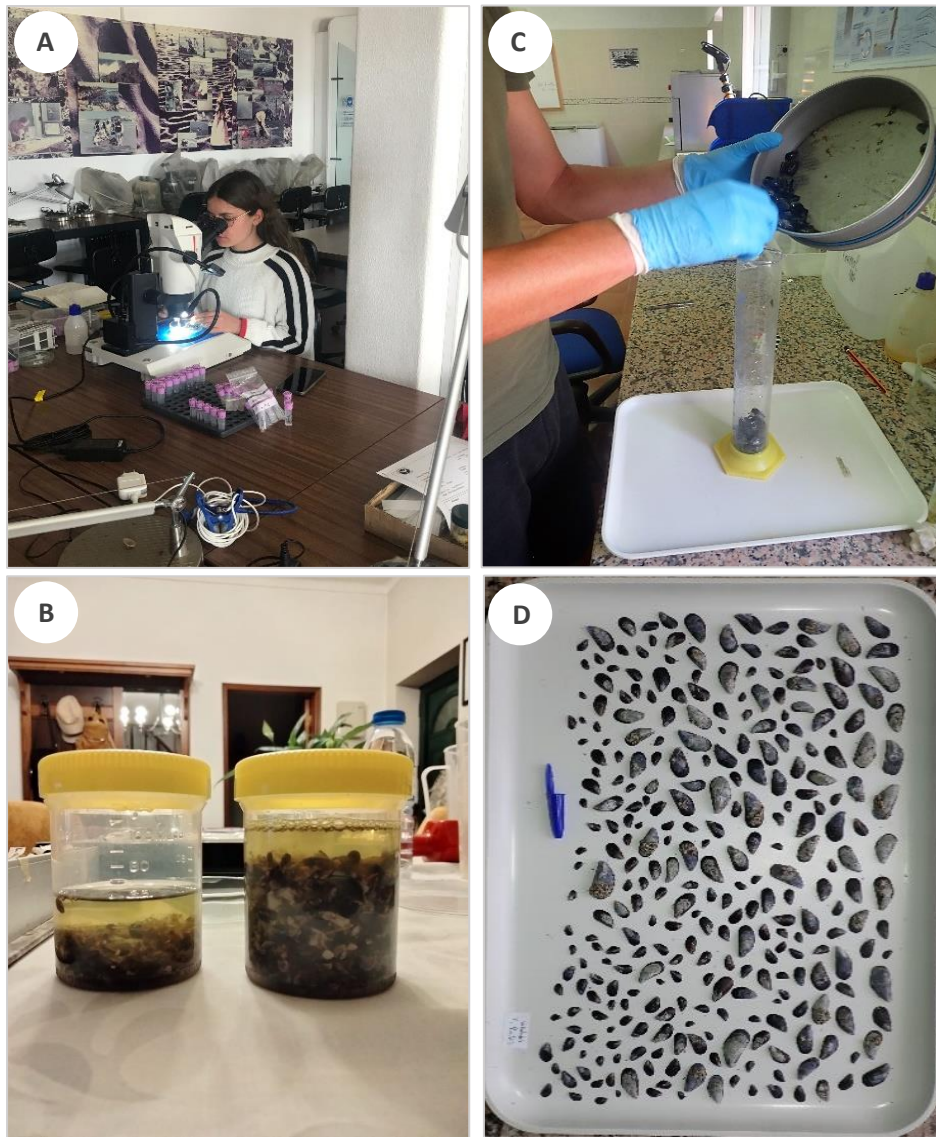


Figure 3. Compilation of photos illustrating some steps from the laboratory procedures: (A) Taxonomic identification at CIEMAR under a dissecting microscope; (B) Replicates with volumes below and exceeding 30 ml, the latter being used for sub-sampling; (C) Measurement of volumes using a 500 ml graduated glass cylinder; (D) Valves arranged on a white tray, prepared for further measurement of maximum length and counting using Python.

4.2.4. Quantifying Mussel Coverage from Image Analysis

Given the observed variability in mussel distribution and coverage across different sampling shores, ranging from dense patches to more isolated occurrences, achieving complete coverage of mussels within the 10 x 10 cm quadrat used in field scrapings was not consistently feasible. Therefore, to estimate the coverage of each replicate area, the SketchAndCalc program, an image-based area calculation tool, was employed. Upon uploading field photographs featuring the quadrat overlaid on mussel patches during sampling (as described in subchapter

4.1 and Figure 4), a known 10 cm reference line (side of the quadrat) was delineated on the image, serving as a scale for subsequent area measurements. After outlining the mussel patch within the quadrat, the program automatically generated area values based on the established scale. These area values were then used to calculate the percentage of mussel coverage.

The list of all quantitative predictor variables mentioned throughout the Materials and Methods chapter, along with their respective descriptions, is provided in Table 2.

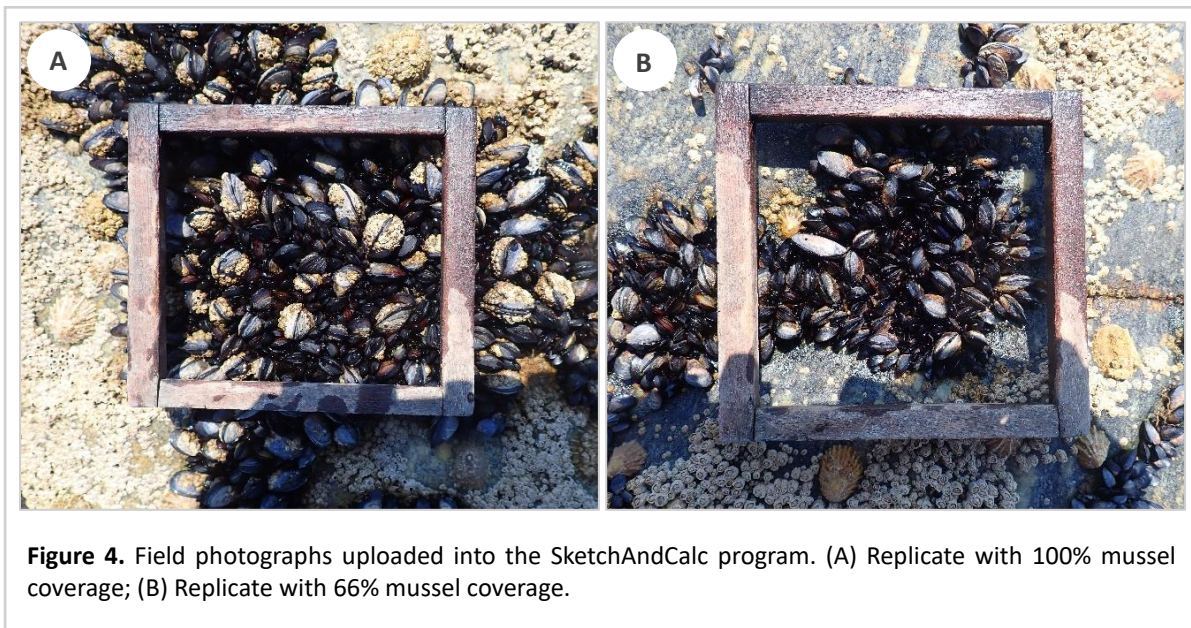


Table 2. List of quantitative predictor variables used in the study and their respective descriptions.

Variable	Description	Unit
Mussel Count (> 1 cm)	Number of mussels larger than 1 cm in size.	None
Mussel Length (> 1 cm)	Average maximum length of mussels larger than 1 cm in size.	cm
SD Mussel Length (> 1 cm)	Standard deviation of maximum length of mussels larger than 1 cm in size.	cm
Wet Mussel Weight (> 1 cm)	Weight of mussels larger than 1 cm in size after excess water has been drained.	g
Wet Material Weight (> 500 μ m)	Weight of all macroinvertebrate assemblages, mussel spat and residues (such as byssal threads, algae and shell fragments) retained on a 500 μ m sieve mesh after excess water has been drained and mussels > 1 cm have been removed.	g

Table 2. (Continuation).

Wet Sediment Weight (> 200 μm)	Weight of sediment and other materials retained on a 200 μm sieve mesh after excess water has been drained.	g
Total Replicate Wet Weight	Weight of the entire replicate, including the sum of the Wet Mussel Weight (> 1 cm), Wet Material Weight (> 500 μm) and Wet Sediment Weight (> 200 μm) variables.	g
Dry Volume (> 1 cm)	Volume occupied by mussels larger than 1 cm in size inside a graduated glass cylinder.	ml
Wet Volume (> 1 cm)	Volume obtained by subtracting the combined volume of mussels and water from the known volume of water using a graduated glass cylinder.	ml
Mussel Coverage	Percentage of the sampling unit area (100 cm^2) occupied by mussels.	%

4.3. Data Analysis

Three types of analyses were carried out: first, a general description of the biological diversity associated with *M. galloprovincialis* beds, including variation in the number of taxa; second, an assessment of the spatial variability in the structure of macroinvertebrate assemblages associated with *M. galloprovincialis* beds, considering differences across shores, transects, and microhabitats; and third, an analysis of how the structure of these macroinvertebrate assemblages relates to predictor variables that may potentially influence them.

All statistical analyses and multivariate plots were conducted using PRIMER software (Clarke & Gorley, 2015) with the PERMANOVA + add-on package (Anderson et al. 2008). All tables and bar charts were generated using Microsoft Excel.

Prior to the graphical and statistical analyses, the biological multivariate matrix underwent the following preliminary procedures to minimize potential overestimation of taxonomic diversity.

Removal of low-abundance, unidentified taxa - Taxa with low abundance that could not be identified to the species level but were known to belong to already identified species within a genus, were removed. Although we knew they belonged to one of the identified species, we could not determine which one. This procedure was implemented instead of aggregating the data of various species within a genus at the genus level.

Consolidation at the family level – When both species-level identifications and a substantial number of individuals identified only at the family level (but belonging to the same family as the identified species) were present, the data were consolidated at the family level. This approach was adopted because individuals identified only at the family level might or might not belong to the same species as those identified at the species level. In the absence of certainty, grouping all individuals at the family level provided a more conservative identification strategy.

4.3.1. General Description of Biological Diversity

First, a general description of the biological diversity sampled was provided, including the total number of individuals sampled across the study and at each shore, as well as the relative abundance of each phylum and class within each shore. Second, the most abundant classes were identified, and the overall abundance of each family and, where applicable, species within these classes was calculated. Bar charts were generated to illustrate these values.

Finally, a stacked column chart was created to illustrate the relative contribution of each taxonomic class and phylum to the overall taxonomic richness, with a continuous red line representing the number of taxa (or taxonomic richness) present at each shore. Since organisms were identified at different taxonomic levels - some to species, others only to genus or higher levels - the overall richness of each class or phylum could be influenced by variations in taxonomic resolution. To address these differences, a second stacked column chart was generated, standardizing all taxa to the family level (except for the phyla Nemertea and Platyhelminthes, and the classes Anthozoa and Demospongiae, which identification did not reach the family level). In this second chart, the relative contribution of each taxonomic class or phylum to the overall family richness at each shore was illustrated, with the number of families (or family richness) per shore, once again, represented by a continuous red line.

A bar chart was generated to illustrate the number of taxa across shores and microhabitats. Additionally, the variation in the total number of taxa (considering all microhabitats) across shores was tested using a univariate PERMANOVA (Anderson, 2001), with shore as the factor. The analysis was based on Euclidean distances and untransformed data. Pairwise comparisons were conducted to further explore the patterns of variation among shores.

4.3.2. Spatial Variation in Macroinvertebrate Assemblages Structure

Multivariate analyses of the macroinvertebrate assemblages structure were performed using the biological matrix (taxa x replicates) and Bray-Curtis dissimilarities on fourth-root transformed data. The fourth-root transformation aimed to mitigate the influence of the dominant presence of *M. galloprovincialis* spat on the calculation of the Bray-Curtis coefficients. Shade plots were generated to facilitate this decision.

Graphical representations of the macroinvertebrate assemblages structure were visualized using ordination by nonmetric Multidimensional Scaling (nMDS). Hierarchical Agglomerative Clustering (HAC) (CLUSTER routine in PRIMER) was also performed on the same biological matrix using group average linking to verify and compare the outcomes obtained from the nMDS (an advisable option for stress values close to 0.2) (Clarke, 1993). For validation purposes, a SIMPROF test (Similarity Profile Routine) was applied to the dendrogram branches (clusters) to determine the statistical significance of the observed clustering patterns (Clarke et al., 2008).

Two Permutational Multivariate Analyses of Variance (PERMANOVA) (Anderson, 2001) were carried out using 9.999 permutations. The first analysis examined the variation between transects (performed exclusively on the platform microhabitat). The second one assessed the variation between shores and microhabitats. For the transect variation analysis, the study employed a design with two factors: (1) Shore (S), a fixed factor with five levels (Montedor, Valadares, Magoito, Cabo Raso and Alteirinhos) and (2) Transect (T), a random factor nested within Shore with two levels (Transect 1 and Transect 2). For the analysis of variation between shores and microhabitats, the experimental design included two orthogonal factors: (1) Shore (S), a fixed factor with 10 levels (Montedor, Valadares, Ponta do Trovão, Consolação, Magoito, Cabo Raso, Foz, Queimado, Almogrove and Alteirinhos) and (2) Microhabitat (M), a fixed factor with three levels (platform, rock-pool and vertical wall). When significant results were indicated by PERMANOVA, appropriate pairwise comparisons were conducted to discriminate patterns among levels of each significant factor or combination of levels if the interaction was significant. When the number of possible permutations was low (< 100) (Anderson et al., 2008), Monte Carlo tests were used to obtain p-values.

A one-way Similarity Percentages (SIMPER) analysis was performed to identify which taxa contributed the most to the patterns detected by the PERMANOVA analysis concerning the factors Shore and Microhabitat, as well as by SIMPROF. A cumulative contribution cut-off of at least 50% was established. Given the large number of SIMPER comparisons across different

shores or groups of shores, segmented bubble plots were generated to facilitate the interpretation of abundance patterns among the most consistent taxa identified in the SIMPER comparisons.

4.3.3. Relationship Between Macroinvertebrate Assemblages Structure and Predictor Variables

The relationship between the structure of macroinvertebrate assemblages (response variable matrix) and the predictor variables measured (those listed in Table 2, along with the factors Shore and Microhabitat) was investigated using a Distance-based Linear Model (DistLM) analysis. Prior to running DistLM, the *Best* selection procedure, based on the Akaike Information Criterion (AIC) (Anderson et al. 2008), was applied to identify the most relevant predictor variables. The analysis was then performed on Bray-Curtis similarities of fourth-root transformed abundance data. Preliminary procedures were carried out prior to running the model, as recommended by Anderson et al. (2008), including checking the collinearity among predictor variables and examining their distributions (using histograms), as these variables should not be highly collinear (e.g., correlation $|r| \geq 0.95$), heavily skewed, or contain extreme outliers. A distance-based redundancy analysis (dbRDA) ordination plot was generated based on the predictor variables selected by DistLM. The fitted variation, along with the percentage of total variation explained by each axis, is provided. If the patterns observed in the dbRDA plot align closely with those in the unconstrained nMDS plot (see section 4.3.2), this would indicate that the model is accurate and effectively captures the overall picture of the multivariate cloud (Anderson et al. 2008).

Note that the Queimado shore was excluded from these analyses due to data loss. nMDS bubble plots were also created to provide an additional visual layer of interpretation, illustrating how the selected predictor variables varied between shores, with bubble size indicating the magnitude of the variable.

5. Results

5.1. General Description of Biological Diversity

A total of 74.406 individuals, belonging to 72 distinct taxa, including 57 different families and 52 species, were observed within the rocky intertidal mussel beds of *M. galloprovincialis* (see Appendix A). Table 3 summarizes the taxonomic composition of macroinvertebrate assemblages at the phylum and class levels, detailing their relative abundance at each shore. Overall, the most consistently abundant classes across the studied shores were Bivalvia, with *M. galloprovincialis* accounting for the majority of it, followed by Malacostraca and Gastropoda.

Table 3. Taxonomic composition (phyla, classes) of macroinvertebrate assemblages associated with rocky intertidal *M. galloprovincialis* beds in Portugal, indicating the relative abundance and total number of individuals sampled per shore. Note that taxa recorded based on presence/absence were not included.

Phylum	Class	MO	VA	PT	CO	MA	CR	FOZ	QUE	ALM	ALT
Cnidaria		0	0	0,2	0,7	1,8	11,7	0,3	0,3	0,1	0,2
Nemertea		0	0	0,2	0,3	0	0,1	0	0,1	0,2	0
Platyhelminthes		0	0	0	0	0	0	0	0	0	0
Mollusca	Bivalvia (<i>M. galloprovincialis</i> < 1 cm)	82,9	91,2	75,4	65,2	86,9	24,1	69,9	47,1	73,9	79,1
	Other Bivalvia	2,2	1	5,2	13,9	1,1	7,1	15,8	43,3	17,9	15
	Gastropoda	1,3	2,2	2,5	5,8	1,9	11,9	6,6	4,8	4,2	0,6
	Polyplacophora	0	0	0,5	1,9	2,8	1	0,3	0,6	0,7	0,3
Annelida	Polychaeta	0,4	0,1	0,4	0,8	0	1,4	0,5	0,9	1,2	0,3
	Clitellata (subclass Oligochaeta)	0,3	0	0	0	0	0	0	0	0	1,5
Equinodermata	Echinoidea	0	0	0	0	0	0	0	0,1	0,1	0
	Ophiuroidea	0	0	0	0	0	0	0	0,3	0,2	0
	Holothuroidea	0	0	0	0	0	0	0	0	0	0
Arthropoda	Pycnogonida	0	0	0,1	0,1	0	1,5	0	0,1	0,1	0
	Ostracoda	0	0	0	0	0	0	0	0	0	0
	Thecostraca	0,4	0,8	0,2	0,7	0,2	0,6	2	0,1	0	0
	Hexapoda	0	0,2	0	0	0	0	0	0	0	0,2
	Malacostraca	12,4	4,4	15,5	10,6	5,2	40,5	4,7	2,4	1,3	2,8
	Total of individuals		6.571	14.144	5.823	5.401	6.009	1.383	1.144	5.441	15.418

Within the class Bivalvia, excluding *Mytilus galloprovincialis*, which constituted the most abundant bivalve species with several hundreds to thousands of individuals per replicate, the collected specimens were numerically dominated by *Lasaea rubra* and *Mytilaster minimus*. Additionally, *Hiatella arctica*, *Musculus costulatus* and *Tellimya ferruginosa* also exhibited relatively high abundances compared to other taxa in this class (Figure 5A). The class Malacostraca was primarily represented by amphipods belonging to the Hyalidae family, complemented to a lesser extent by isopods from the genera *Idotea* and *Jaera*, along with the tanaid *Tanais dulongii* (Figure 5B). Gastropod abundance was predominantly attributed to the Pyramidellidae family, followed by the species *Patella depressa*, *Melarhaphe neritoides*, *Steromphala umbilicalis* and *Patella ulyssiponensis*, which exhibited progressively lower abundances but remained prominent among the taxa (Figure 5C). Although Gastropoda was not the most abundant class, it exhibited the highest diversity, comprising 16 distinct families. The class Polyplacophora, while not as abundant as the previously mentioned taxonomic groups, was well represented by two species: *Acanthochitona crinita* and *Lepidochitona cinerea*, the latter being notably more abundant (Figure 5D). The class Polychaeta, also not as numerically dominant, distinguished itself through considerable diversity, comprising 10 different families (Figure 5E). The Syllidae family emerged as the most prevalent among Polychaeta, followed by Nereididae and Phyllodocidae.

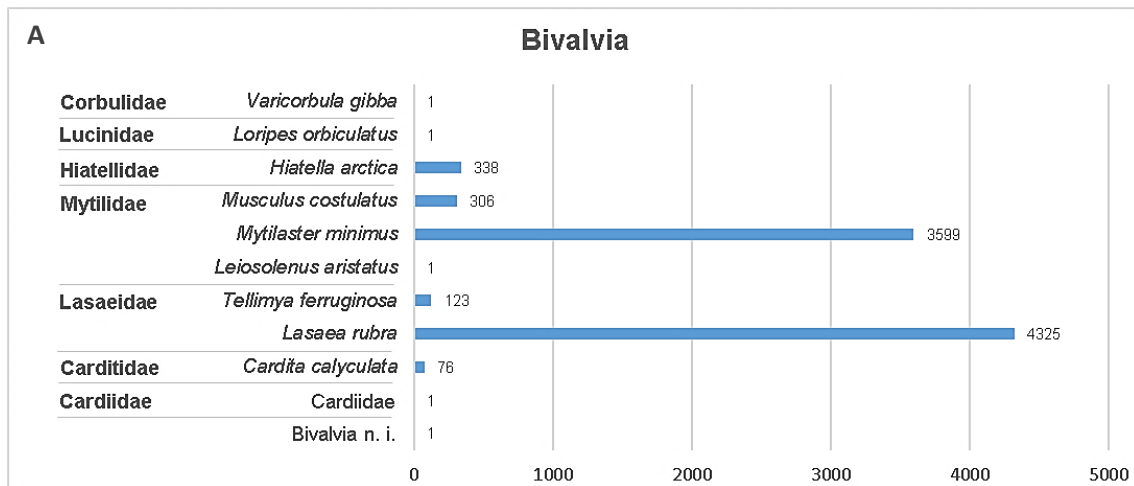


Figure 5 (A). Total abundance of each taxon within the class (A) Bivalvia. The taxa listed in bold on the left side of the graph represent the families sampled within this class. “n.i.” denotes “not identified”.

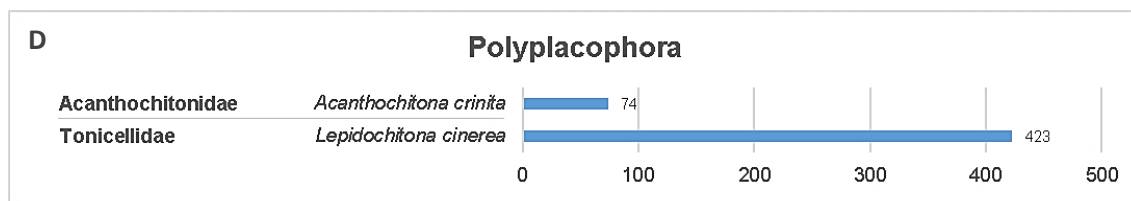
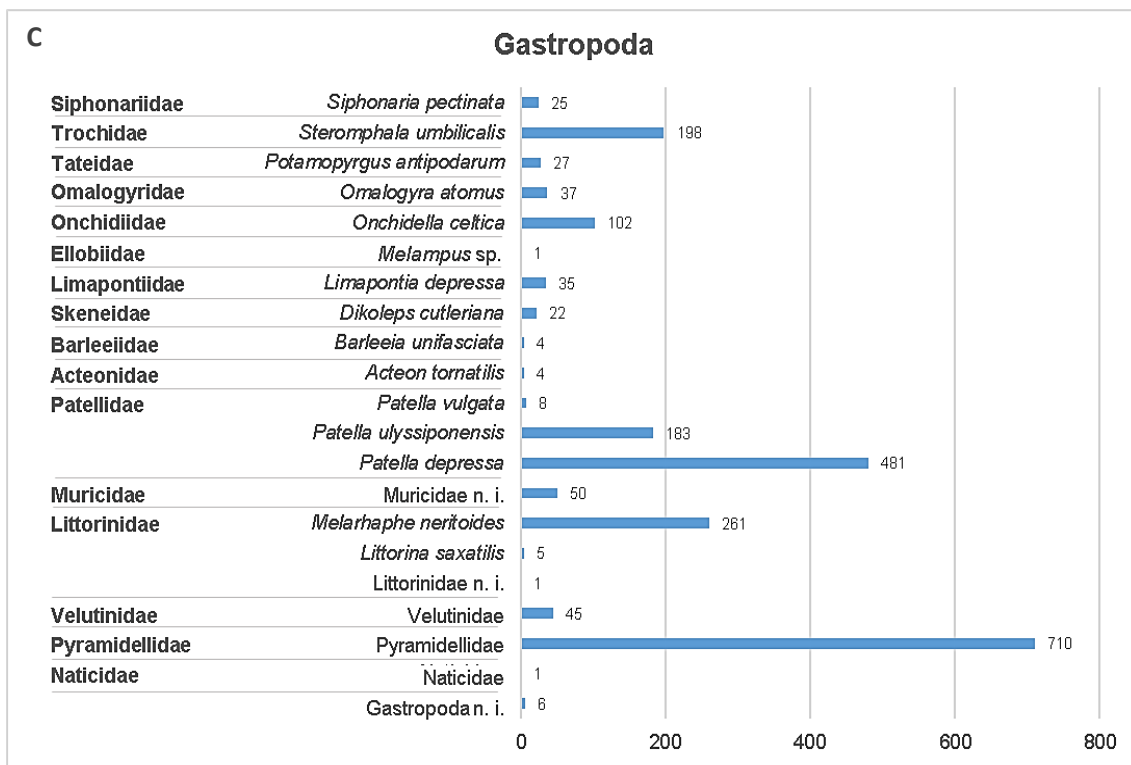
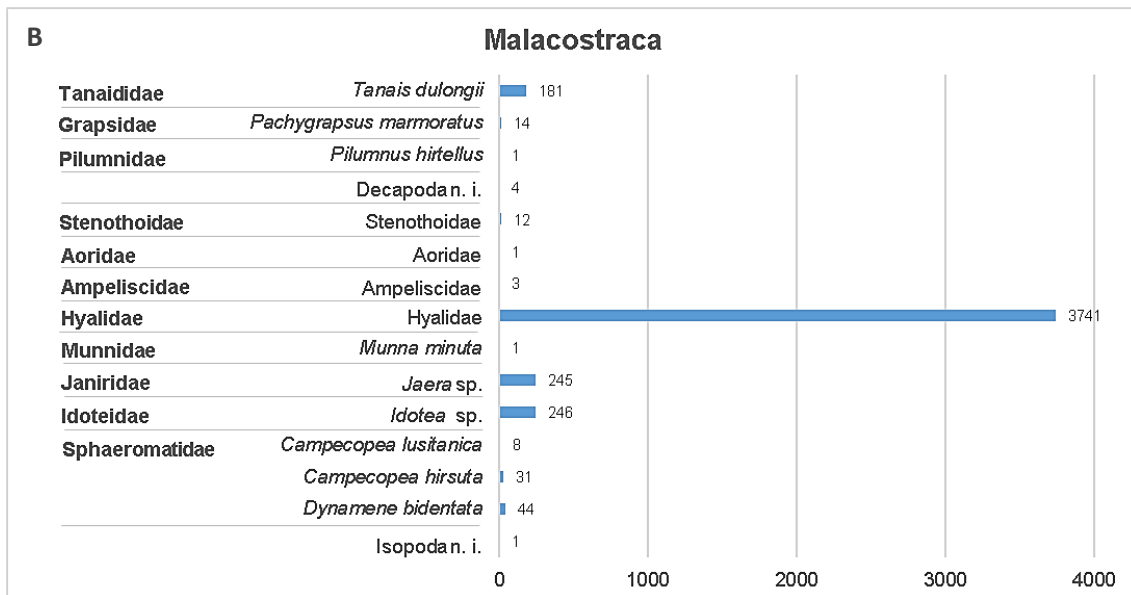


Figure 5 (B-D). Total abundance of each taxon within the classes (B) Malacostraca, (C) Gastropoda and (D) Polyplacophora. The taxa listed in bold on the left side of each graph represent the families sampled within each class. “n.i.” denotes “not identified”.

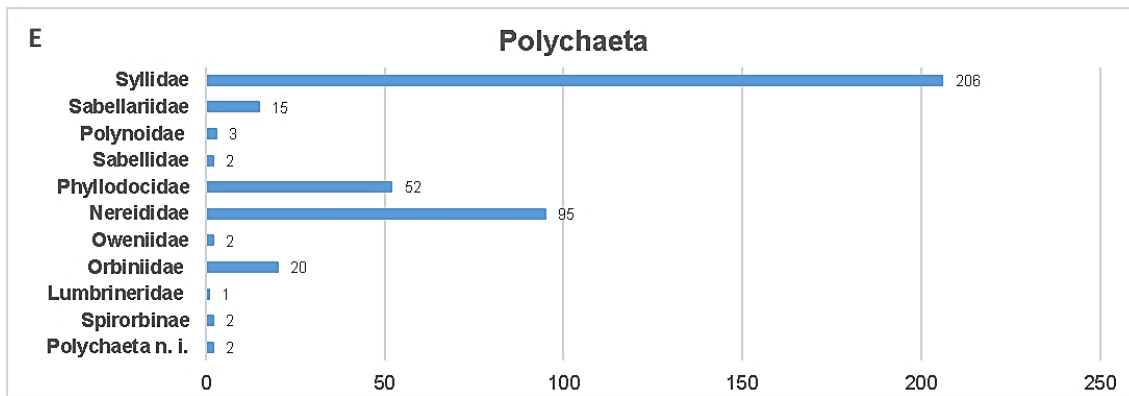


Figure 5 (E). Total abundance of each taxon within the class (E) Polychaeta. The taxa listed in bold on the left side of the graph represent the families sampled within this class. “n.i.” denotes “not identified”.

Regarding taxonomic richness (number of taxa), mussel beds at Consolação on the central coast and Almogrove on the southwestern coast of Portugal exhibited the highest richness, with 46 and 48 taxa, respectively (Figure 6A). Foz, in contrast, had the lowest richness, with only 23 identified taxa (Figure 6A). In terms of the relative contribution of each phylum and taxonomic class to the overall richness at each shore, gastropods consistently represented the richest class at all shores except Cabo Raso, where Malacostraca exhibited the highest richness (Figure 6A). The class Bivalvia also demonstrated high relative richness, particularly at Foz and Queimado. Among the classes where identification reached at least the family level, the least rich classes were Holothuroidea, Clitellata (subclass Oligochaeta), Echinoidea, Ophiuroidea, Ostracoda, and Hexapoda, which were either absent from several shores or represented by only a single taxon. To avoid potential distortion in richness caused by mixing different taxonomic levels in Figure 6A, where some classes may appear less rich simply because they were identified at a higher taxonomic level than others, Figure 6B was generated with normalized taxonomic levels, focusing on the family richness (number of families) and the relative contribution of each phylum and taxonomic class to the overall family richness at each shore. Both graphs provided similar information.



Figure 6. Stacked column charts illustrating the relative contribution of different phyla and taxonomic classes to the total richness at each sampled shore. (A) Taxa identified at various taxonomic levels (relative taxonomic richness); (B) Taxa normalized at the family level (relative family richness). (*) – No identifications to the family level or below were made within the phyla Nemertea and Platyhelminthes, and the classes Anthozoa and Demospongiae. The total taxonomic richness/number of taxa (A) and total family richness/number of families (B) per shore are represented by an overlaid continuous red line (second Y axis).

The variation in taxonomic richness (number of taxa) across shores and microhabitats is shown in Figure 7. There seems to be a greater variation between shores than among microhabitats. The results of the PERMANOVA analysis, testing the variation in taxonomic richness among shores (considering all microhabitats), are summarized in Table 4. The analysis revealed statistically significant variation among shores ($p = 0,0001$). Pairwise comparisons were employed to further explore these differences, revealing that taxonomic richness at Almogrove was significantly higher than on all other shores. No clear pattern of variation was found among the remaining shores (pairwise tests, Table 4). For instance, this lack of a clear pattern can be observed in Foz. The results showed that Foz was statistically similar to Valadares, and Valadares, in turn, was similar to P. Trovão. However, Foz was significantly different from P. Trovão. If there was a clear pattern, which is not the case, Foz would be expected to be similar to P. Trovão, given their shared similarity with Valadares. Similar inconsistencies were observed among the other shores, except for Almogrove.

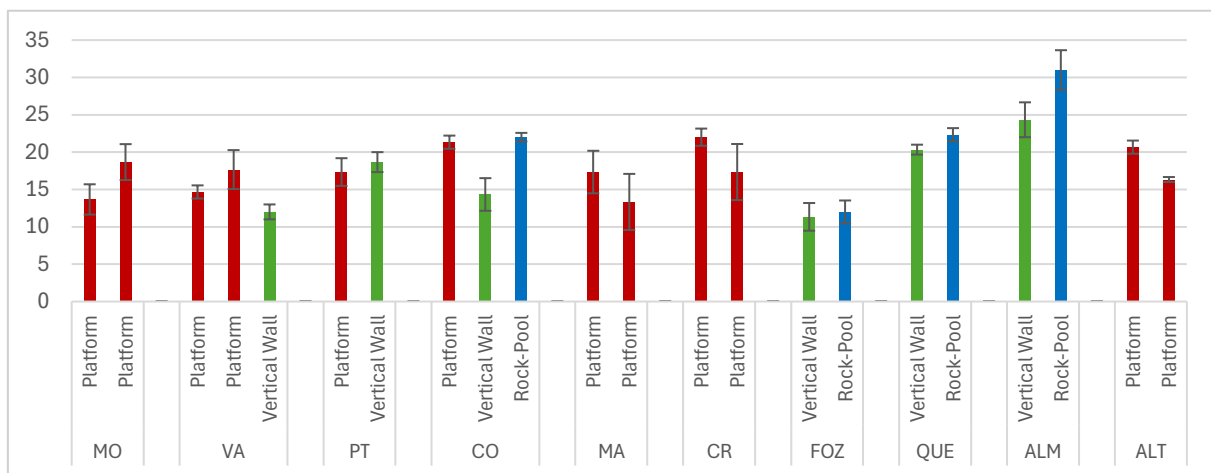


Figure 7. Bar chart illustrating the mean values and corresponding standard errors of macroinvertebrate assemblages richness (number of taxa per 100 cm²) within rocky intertidal beds of *M. galloprovincialis* across different shores and microhabitats. Each microhabitat is represented by a different color: red = platform, green = vertical wall and blue = rock-pool. n = 3.

Table 4. Results of PERMANOVA and pairwise tests to assess differences in macroinvertebrate assemblages richness (number of taxa) within rocky intertidal beds of *M. galloprovincialis* across shores. The analysis utilized Euclidean distances with no data transformation. df – degrees of freedom; MS – Mean Squares; Pairwise “≠” or “=” indicate factor levels with ($p < 0,05$) or without ($p > 0,05$) significant differences, respectively.

PERMANOVA table of results		Macroinvertebrate assemblages			
Source	df	MS	Pseudo-F	P(perm)	Unique Perms
Shore	9	117,8	7,3878	0,0001	5.148
Res	56	15,945			
Pairwise tests to factor Shore	<p>Montedor ≠ Queimado and Almograve. Montedor = Valadares, P. Trovão, Consolação, Magoito, Cabo Raso, Foz and Alteirinhos.</p> <p>Valadares ≠ Consolação, Cabo Raso, Queimado, Almograve and Alteirinhos. Valadares = Montedor, P. Trovão, Magoito and Foz.</p> <p>P. Trovão ≠ Foz, Queimado and Almograve. P. Trovão = Montedor, Valadares, Consolação, Magoito, Cabo Raso and Alteirinhos.</p> <p>Consolação ≠ Valadares, Foz and Almograve. Consolação = Montedor, P. Trovão, Magoito, Cabo Raso, Queimado and Alteirinhos.</p> <p>Magoito ≠ Queimado and Almograve. Magoito = Montedor, Valadares, P. Trovão, Consolação, Cabo Raso, Foz and Alteirinhos.</p> <p>Cabo Raso ≠ Valadares, Foz and Almograve. Cabo Raso = Montedor, P. Trovão, Consolação, Magoito, Queimado and Alteirinhos.</p> <p>Foz ≠ P. Trovão, Consolação, Cabo Raso, Queimado, Almograve and Alteirinhos. Foz = Montedor, Valadares and Magoito.</p> <p>Queimado ≠ Montedor, Valadares, P. Trovão, Magoito, Foz and Almograve. Queimado = Consolação, Cabo Raso and Alteirinhos.</p> <p>Almograve ≠ Montedor, Valadares, P. Trovão, Consolação, Magoito, Cabo Raso, Foz, Queimado and Alteirinhos.</p> <p>Alteirinhos ≠ Valadares, Foz and Almograve. Alteirinhos = Montedor, P. Trovão, Consolação, Magoito, Cabo Raso and Queimado.</p>				

5.2. Spatial Variation in Macroinvertebrate Assemblages Structure

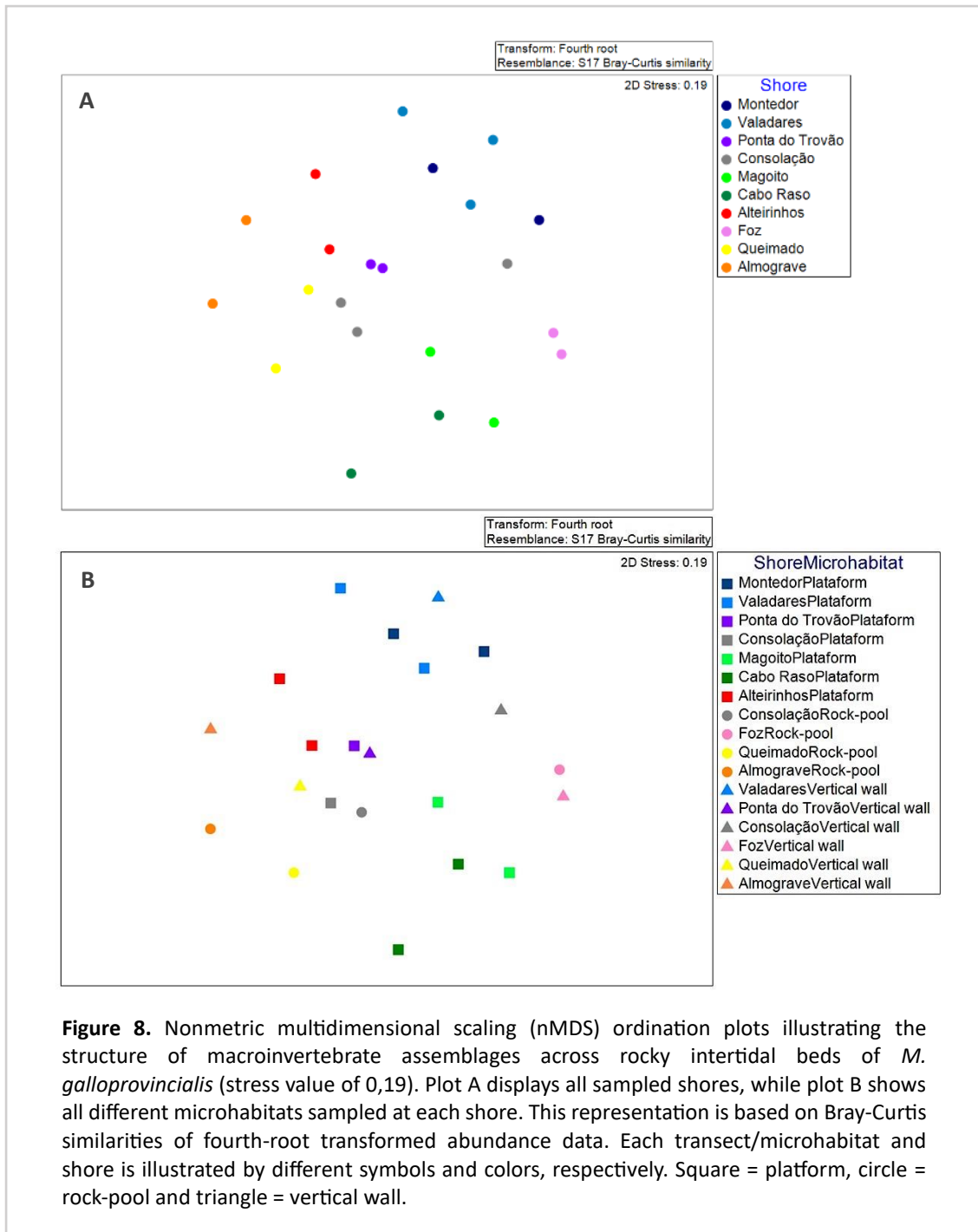
To investigate macroinvertebrate assemblages within intertidal mussel beds of *M. galloprovincialis* along the Portuguese coast, a preliminary small-scale study was conducted in the platform microhabitat of five shores to assess the variability between transects using PERMANOVA analysis (Table 5). The results revealed statistically significant variation between transects. However, pairwise tests performed within each shore consistently showed no

variation between transects across all shores, except for Montedor (p (Monte Carlo) = 0,049) and Alteirinhos (p (Monte Carlo) = 0,032). These exceptions, the northernmost and southernmost shores sampled in this study, respectively, exhibited significant differences between transects. Based on these results, and since the factor transect was not included in the analysis for rock-pool and vertical wall microhabitats (where data were collected from only one transect), we decided to exclude the factor transect from the PERMANOVA analyses of variation among shores and microhabitats (Table 6).

Table 5. Results of PERMANOVA and pairwise tests to assess changes in the structure of macroinvertebrate assemblages within rocky intertidal beds of *M. galloprovincialis* across two transects (T – T1 and T2) at each shore. Only data concerning the platform microhabitat were considered in this analysis. The dataset underwent a fourth root transformation and the analysis employed the Bray-Curtis similarity coefficient. df – degrees of freedom; MS – Mean Squares; Pairwise “≠” or “=” indicate factor levels with ($p < 0,05$) or without ($p > 0,05$) significant differences, respectively.

PERMANOVA table of results		Macroinvertebrate assemblages			
Source	df	MS	Pseudo-F	P(perm)	Unique perms
Shore	4	4.210,2	3,1659	0,0019	944
T (Shore)	5	1.329,9	2,6064	0,0002	9.886
Res	20	510,23			
Total	29				
Pairwise tests to factor T(Shore)	T1 = T2 on all shores (Valadares, Magoito and Cabo Raso), except at Montedor and Alteirinhos, where T1 ≠ T2.				

The patterns in the structure of macroinvertebrate assemblages among shores and microhabitats are illustrated through an nMDS ordination (Figures 8A and 8B, the latter being a copy of Figure 8A, but with symbols representing different microhabitats). For this analysis, average values were calculated per transect for the platform microhabitat, with each transect consisting of three replicates. In cases where multiple microhabitats (platforms, rock-pools, or vertical walls) were sampled in one transect, average values were calculated separately for each microhabitat, with three replicates per microhabitat. This approach was necessary because including all replicates sampled from each transect, microhabitat and shore resulted in a high stress value in the nMDS plot, indicating a poor representation of the data.



In the PERMANOVA analysis, a significant interaction was identified between factors Shore and Microhabitat (Table 6). For the platform microhabitat (seven shores), pairwise tests revealed significant differences among all shores, with the exception of a group formed by Montedor and Valadares, located in the North of Portugal, and a group formed by Ponta do Trovão and Consolação, located in the Central coast of Portugal. For the rock-pool microhabitat (four shores), Foz was found to differ significantly from all other shores, while the remaining

shores (Consolação, Queimado and Almograve) exhibited statistical similarity among themselves. Regarding the vertical wall microhabitat (six shores), no clear pattern was observed among shores. For instance, no differences were found between Queimado and Almograve. However, Queimado was considered similar to Ponta do Trovão and Consolação, whereas Almograve was significantly different from these shores. Concerning the factor Microhabitat, there were no statistical differences among microhabitats across all comparable shores, except for Consolação and Almograve where significant differences were detected between rock-pool and vertical wall microhabitats.

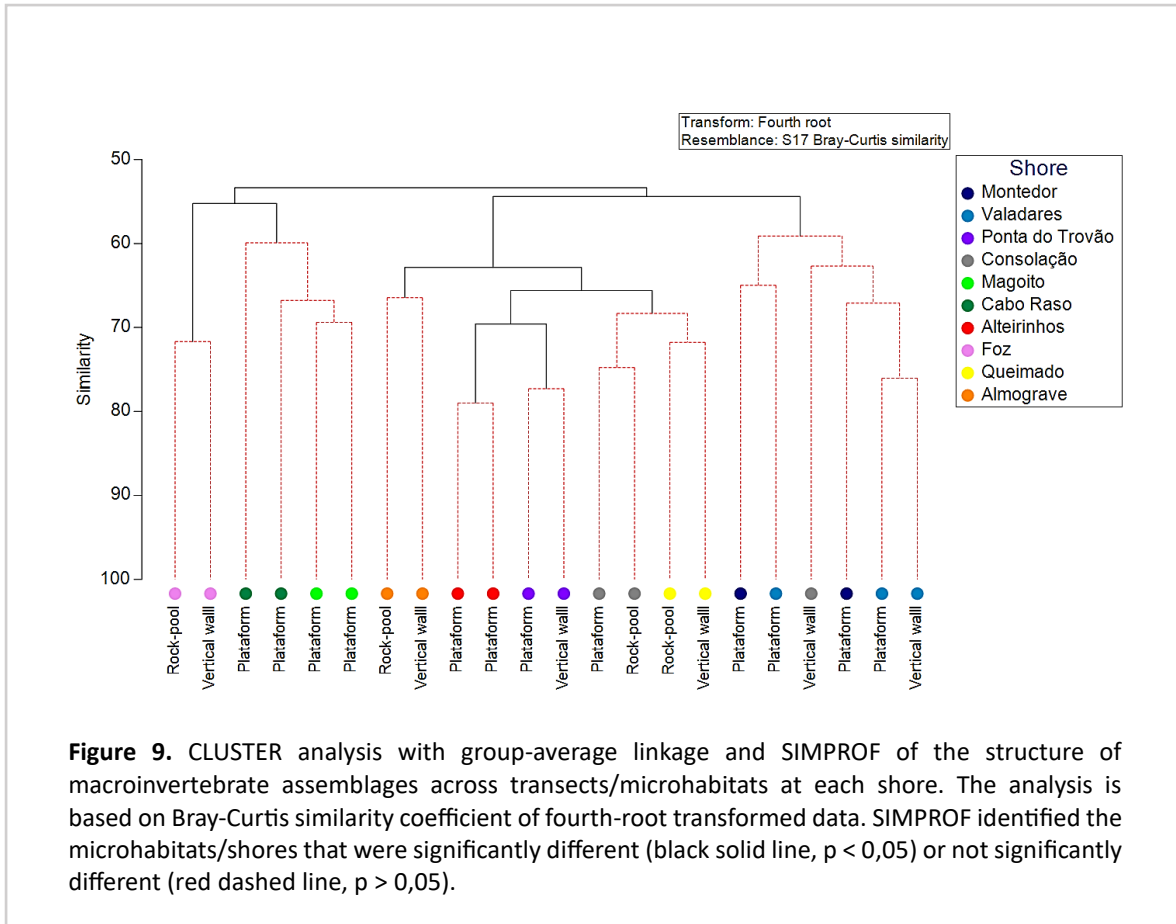
Table 6. Results of PERMANOVA assessing the variation of the macroinvertebrate assemblages structure within rocky intertidal beds of *M. galloprovincialis* in relation to factor Shore (S) and factor Microhabitat (M), along with pairwise tests for the significant interaction M x S. The analysis is based on Bray-Curtis similarity coefficient of fourth-root transformed data. df – degrees of freedom; MS – Mean Squares; Pairwise “≠” or “=” indicate factor levels with (p (Monte Carlo) < 0,05) or without (p (Monte Carlo) > 0,05) significant differences, respectively. *- not all microhabitats were sampled in all shores: seven shores with the platform microhabitat (Montedor, Valadares, P. Trovão, Consolação, Magoito, Cabo Raso, and Alteirinhos); four shores with the rock-pool microhabitat (Consolação, Foz, Queimado, and Almograve); and six shores with the vertical wall microhabitat (Valadares, P. Trovão, Consolação, Foz, Queimado, and Almograve).

PERMANOVA table of results		Macroinvertebrate assemblages			
Source	df	MS	Pseudo-F	P(perm)	Unique perms
M	2	2.194,6	3,874	0,0001	9.906
S	9	3.854,5	6,8041	0,0001	9.814
M x S*	5	949,09	1,6754	0,0043	9.865
Res	49	566,49			
Pairwise tests	<p>Within each microhabitat (platform): Montedor = Valadares and both ≠ from all other shores</p> <p>P. Trovão = Consolação and both ≠ from all other shores</p> <p>Magoito, Cabo Raso and Alteirinhos are ≠ from all other shores</p> <p>Within each microhabitat (rock-pool): Consolação = Queimado = Almograve and they are all ≠ from Foz</p> <p>Within each microhabitat (vertical wall): Valadares = Consolação. Valadares ≠ from all other shores</p> <p>P. Trovão = Consolação and Queimado. P. Trovão ≠ Valadares, Foz and Almograve</p> <p>Consolação = Valadares, P. Trovão, Foz and Queimado. Consolação ≠ Almograve</p> <p>Foz = Consolação. Foz ≠ Valadares, P. Trovão, Queimado and Almograve</p> <p>Queimado = P. Trovão, Consolação and Almograve. Queimado ≠ Valadares and Foz</p> <p>Almograve = Queimado. Almograve ≠ Valadares, P. Trovão, Consolação and Foz</p>				

Table 6. (continuation).

Pairwise tests	<p>Within each shore: platform = vertical wall in all comparable shores (Valadares, P. Trovão and Consolação)</p> <p>platform = rock-pool in the only comparable shore (Consolação)</p> <p>rock-pool = vertical wall in Foz and Queimado (2/4 comparable shores) and rock-pool ≠ vertical wall in Consolação and Almogrove (2/4 comparable shores)</p>
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This apparent pattern of greater variation among shores compared to the microhabitats within each shore is also visible in the nMDS plot (Figures 8A and 8B). In fact, the points representing the transects/microhabitats within each shore are generally closer to one another than those representing different shores, indicating that the structure of macroinvertebrate assemblages in microhabitats within the same shore is more similar than between different shores. However, given the relatively high stress value of 0,19 associated with this nMDS plot, a Hierarchical Agglomerative Clustering (HAC) was applied on the same similarity matrix, as recommended by Clarke (1993) (Figure 9). The Similarity Profile Routine (SIMPROF) was used in conjunction with the hierarchical cluster analysis. The resulting dendrogram and SIMPROF analysis demonstrated patterns similar to those observed in the nMDS plot (Figures 8A and 8B), suggesting that the structure of the macroinvertebrate assemblages is more associated to variation among shores rather than to differences between microhabitats. Furthermore, HAC with SIMPROF revealed seven statistically significant clusters/groups ($p < 0,05$): a northern/central group including transects/microhabitats sampled at Montedor (platform), Valadares (platform and vertical wall) and Consolação (vertical wall); a central group formed by Magoito and Cabo Raso (platform only); a central/southwestern group consisting of Consolação (platform and rock-pool) and Queimado (rock-pool and vertical wall); and individual shores, each including the different microhabitats sampled on that shore (Foz - rock-pool and vertical wall; Ponta do Trovão - platform and vertical wall; Almogrove - rock-pool and vertical wall; and Alteirinhos - platform).



The SIMPROF analysis identified clusters of shores/microhabitats that were either similar to or different from those revealed by the PERMANOVA analysis (see Figure 9 and Table 6, respectively). Particularly, both analyses consistently identified the group formed by the northern shores (Montedor and Valadares) and the individual shores represented by Foz and Alteirinhos. However, the results for other shores were less clear. For instance, although Cabo Raso and Magoito shores clustered together according to SIMPROF, significant differences were found between them in the PERMANOVA results. Conversely, Ponta do Trovão, Consolação and Queimado shores exhibited no significant differences between them according to PERMANOVA, a result that was not completely consistent with the SIMPROF analysis. Moreover, Almogrove did not present clear patterns in either analysis. SIMPROF considered it distinct from all other shores, while PERMANOVA found Almogrove similar to Queimado. However, we decided to treat Almogrove as a separate shore because, while Queimado showed similarities with Ponta do Trovão and Consolação in both PERMANOVA and SIMPROF analyses, Almogrove was consistently different from Ponta do Trovão and Consolação in the PERMANOVA results, except for rock-pools where Almogrove was similar to Consolação.

Therefore, in cases where conflicting patterns emerged between the two analyses, the PERMANOVA results were prioritized. Consequently, the following grouped and individual shores (listed from north to south) were considered: northern group (Montedor and Valadares); Peniche (Ponta do Trovão and Consolação) and Queimado group; Magoito; Cabo Raso; Foz; Almogrove; and Alteirinhos. To identify the taxa contributing the most to the dissimilarities between these grouped/individual shores, a SIMPER analysis was conducted (detailed results are provided in Appendix B). Given the large number of grouped/individual shores (seven in total), along with the numerous taxa contributing to the observed dissimilarities, we have focused our analysis on taxa that consistently appeared in the 50% SIMPER cut-off across all comparisons. The abundance of each of these taxa is represented on the nMDS in several Segmented Bubble Plots (Figure 10), which facilitate visualization of the SIMPER results (Appendix B). Whenever possible, Segmented Bubble Plots were organized to combine individual plots of taxa with closer taxonomic affinities (e.g. Bivalvia, Malacostraca, Gastropoda). The main patterns of variation in the taxa responsible for the observed differences between each shore or group of shores are described below.

Northern group (Montedor and Valadares)

Balanomorpha consistently stands out for its higher average abundance in the Northern group compared to all other grouped/individual shores. Besides Balanomorpha, the species *Mytilus galloprovincialis* and *Melarhaphes neritoides* were generally more abundant in the Northern group, though they were outnumbered on the southern shores, particularly at Almogrove and Alteirinhos. Conversely, *Lepidochitona cinerea*, *Mytilaster minimus*, Anthozoa and Syllidae were consistently less abundant in the North. Several species were absent from this region, including *Tanais dulongii*, *Acanthochitona crinita*, *Pachygrapsus marmoratus*, *Anoplodactylus virescens*, *Siphonaria pectinata*, *Cardita calyculata* and *Onchidella celtica*.

Peniche (Ponta do Trovão and Consolação) and Queimado group

The Peniche (Ponta do Trovão and Consolação) and Queimado group distinguished itself from the other grouped/individual shores by exhibiting a higher average abundance of Pyramidellidae, except for Almogrove, which displayed an even greater abundance. Additionally, this group consistently revealed a higher average abundance of the bivalves *Lasaea rubra* and *Mytilaster minimus*, except in the southernmost shores (Almogrove and Alteirinhos).

Furthermore, this group showed a greater abundance of *Tanais dulongii* and Nemertea, with *Tanais dulongii* being more abundant only in Cabo Raso and Nemertea being absent from several other shores. However, the average abundances for this group indicated a generally lower abundance of the gastropod *Steromphala umbilicalis*. *Jaera* sp. also showed a generally lower abundance, despite Ponta do Trovão appearing to have a substantial presence of this taxon as indicated by the Segmented Bubble Plot (Figure 10). Similarly, while the average abundance of *Patella ulyssiponensis* for the group is low, Queimado individually shows a significant presence of this taxon. These discrepancies arise because the SIMPER analysis uses average abundances across the three shores in the Peniche and Queimado group, leading to lower overall values when averaged with shores that have lower abundances. The analysis also suggested the absence of *Idotea* sp. in this specific group.

Magoito

The Magoito shore is most prominently distinguished by the consistently higher average abundance of the isopod *Idotea* sp. in all comparisons with other grouped/individual shores. Similarly, *Lepidochitona cinerea* and Anthozoa were also very abundant in this shore, with Anthozoa being more abundant only in Cabo Raso. Conversely, the species *Lasaea rubra* and *Melarhapha neritoides* were notably less abundant. Additionally, the families Pyramidellidae and Hyalidae generally exhibited lower average abundances in this shore compared to others. The polychaete belonging to the Syllidae family and the bivalve species *Mytilaster minimus* also recorded lower average abundances in this shore, as well as in other grouped/individual shores such as the Northern group, Cabo Raso and Foz (Figure 10). Several taxonomic groups were absent from Magoito, including the crab *Pachygrapsus marmoratus*, the gastropods *Siphonaria pectinata*, *Dikoleps cutleriana*, *Onchidella celtica* and *Limapontia depressa*, the bivalves *Tellimya ferruginosa* and *Cardita calyculata*, the polychaetes of the family Nereididae, the oligochaete of the family Naididae, the collembolan *Anurida maritima* and Nemertean.

Cabo Raso

Immediately adjacent to the south of Magoito is Cabo Raso. In the dissimilarity analysis between this shore and all other grouped/individual shores, several taxa emerged due to their consistently higher average abundances. Among them are *Tanais dulongii*, Anthozoa, *Pachygrapsus marmoratus*, *Patella ulyssiponensis* and *Anoplodactylus virescens*. Another important distinction for this shore was the consistently lower average abundances of the

gastropods *Mytilus galloprovincialis*, *Mytilaster minimus* and *Musculus costulatus* (all belonging to the family Mytilidae). It is important to highlight that the pycnogonid species *Phoxichilidium femoratum*, despite not appearing in the SIMPER results, was identified exclusively in the mussel beds of this shore. Cabo Raso also shared the absence of several taxa with Magoito, such as *Tellimya ferruginosa*, *Cardita calyculata*, *Dikoleps cutleriana*, *Onchidella celtica* and *Anurida maritima*. Additionally, the families Muricidae, Phyllodocidae and Naididae, as well as the species *Amphipholis squamata*, were absent from Cabo Raso.

Foz

Foz is generally characterized by having significantly fewer taxa compared to other grouped/individual shores. Among the taxa consistently identified in the SIMPER comparisons as being less abundant are *Mytilus galloprovincialis*, Hyalidae, Pyramidellidae, *Lasaea rubra* and *Lepidochitona cinerea*. *Pollicipes pollicipes* was the only species found to have a higher average abundance in Foz than in other grouped/individual shores. This distinction is further emphasized by the numerous taxa absences, including *Melarhaphes neritoides*, *Jaera* sp., *Idotea* sp., *Anurida maritima*, Nemertea, *Tanais dulongii*, *Tellimya ferruginosa*, *Dynamene bidentata*, *Anoplodactylus virescens*, *Dikoleps cutleriana*, *Limapontia depressa*, *Amphipholis squamata* and Naididae.

Almogrove

In contrast to Foz, Almogrove can be distinguished by its notably higher abundance and biodiversity. This shore appears to be a biodiversity hotspot, as it not only exhibits the highest taxonomic richness (number of taxa) of all grouped/individual shores (Figure 6), but also the highest average abundances of taxa among the groups compared in the SIMPER analysis (Appendix B). According to the SIMPER analysis, the most relevant taxa for explaining the differences between this shore and others, as well as the most consistently abundant, include several bivalves (*Lasaea rubra*, *Mytilus galloprovincialis*, *Mytilaster minimus*, *Hiatella arctica*, *Musculus costulatus*, *Tellimya ferruginosa* and *Cardita calyculata*), gastropods (Pyramidellidae, *Onchidella celtica*, *Dikoleps cutleriana*, *Melarhaphes neritoides* and *Sterromphala umbilicalis*), and polychaetes (Syllidae and Nereididae). Notably, the species *Pollicipes pollicipes*, which is more abundant in Foz as previously mentioned, and the oligochaete Naididae were absent in Almogrove.

Alteirinhos

Finally, for the southernmost sampled shore in this study, the primary differentiator that set this shore apart from the others was the significantly higher average abundance of the oligochaete Naididae. Another taxon that stood out on this shore was the collembolan species *Anurida maritima*, which was often more abundant here than on other grouped/individual shores where it was either absent or present in minimal numbers. Similarly to Almogrove, Alteirinhos also exhibited a diverse array of taxa with consistently higher average abundances, which can be consulted in more detail in Appendix B. This shore exhibited several absences, including Balanomorpha, Nemertea, *Patella ulyssiponensis*, *Pachygrapsus marmoratus*, *Hiatella arctica*, *Cardita calyculata*, *Limapontia depressa* and *Amphipholis squamata*.

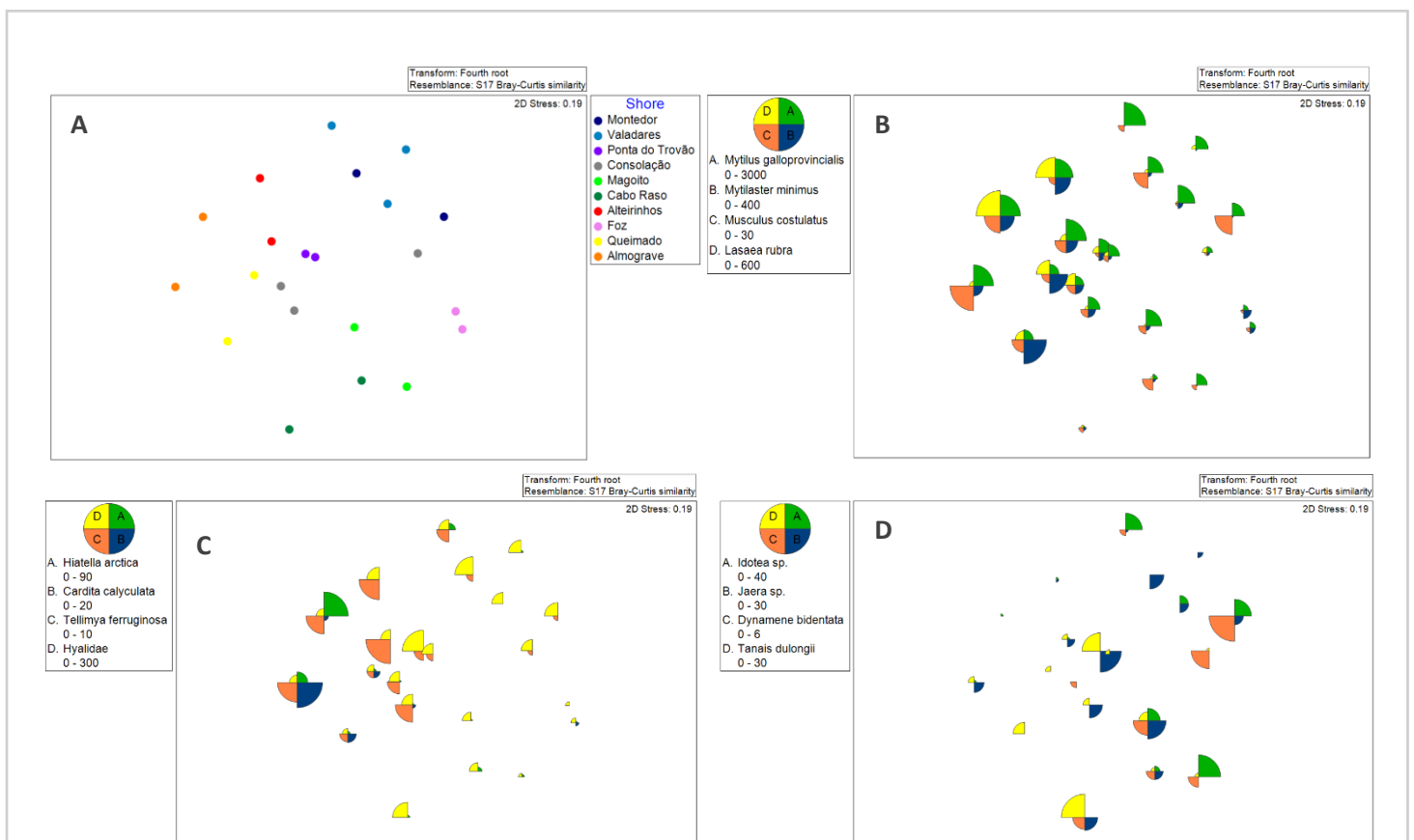


Figure 10 (A - D). Segmented bubble plots illustrating the distribution of the most consistent taxa from SIMPER comparisons. These plots are based on Bray-Curtis similarities of fourth-root transformed abundance data. Each circle is divided into segments, differentiated by color (legend provided on the left side of each map) and size, reflecting the relative abundance of each taxon within a sampled microhabitat of a particular shore. (A) nMDS ordination plot (reused from Figure 8) to facilitate the interpretation of shore distribution; (B) Distribution of Class Bivalvia, considering *Mytilus galloprovincialis* < 1 cm; (C) Distribution of Classes Bivalvia and Malacostraca (Hyalidae); (D) Distribution of Class Malacostraca.

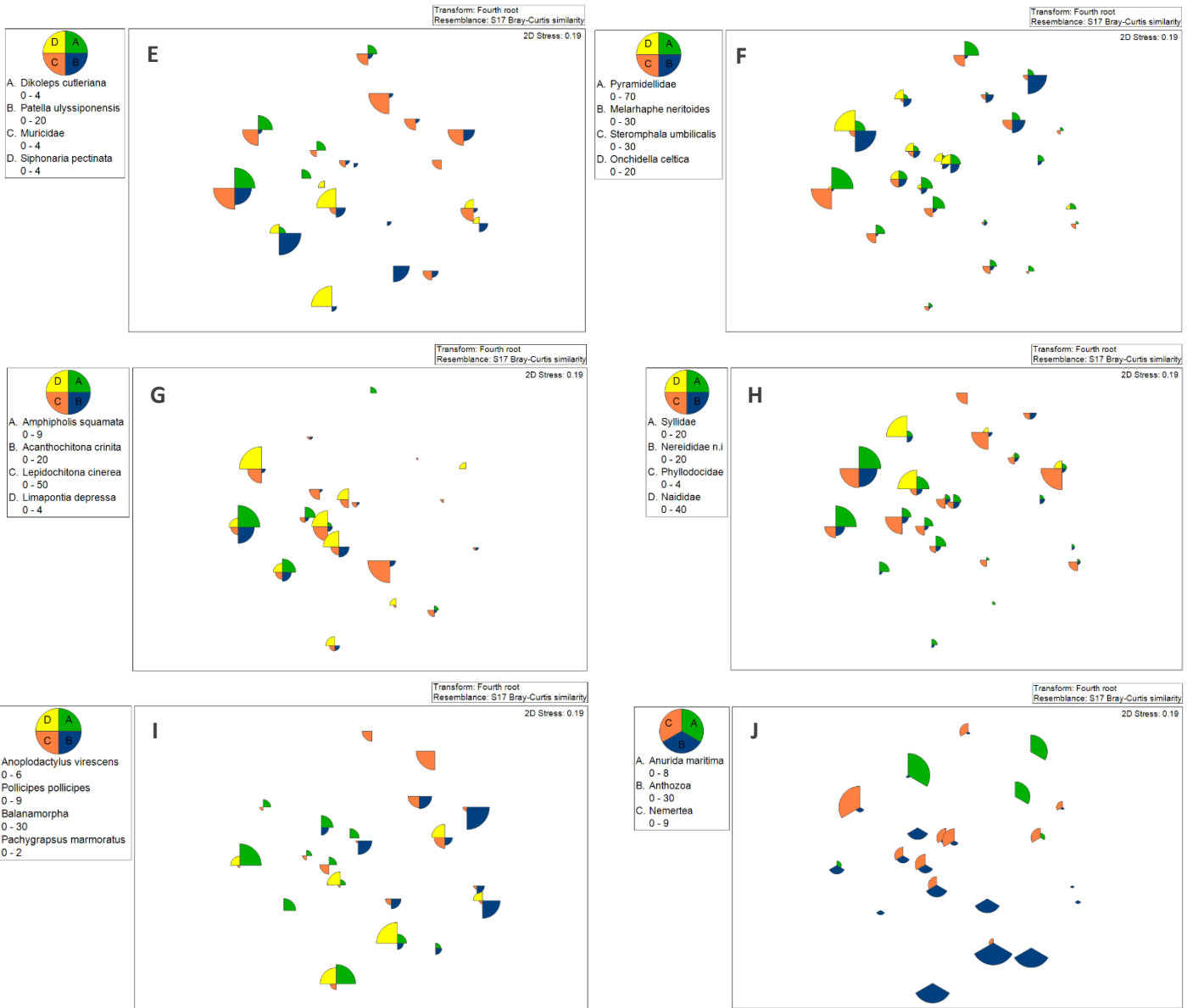


Figure 10 (E and J). Segmented bubble plots illustrating the distribution of the most consistent taxa from SIMPER comparisons. These plots are based on Bray-Curtis similarities of fourth-root transformed abundance data. Each circle is divided into segments, differentiated by color (legend provided on the left side of each map) and size, reflecting the relative abundance of each taxon within a sampled microhabitat of a particular shore. (E and F) Distribution of Class Gastropoda; (G) Distribution of Classes Ophiuroidea (*Amphipholis squamata*), Polyplacophora (*Lepidochitona cinerea* and *Acanthochitona crinita*) and Gastropoda (*Limapontia depressa*); (H) Distribution of Classes Polychaeta and Clitellata (subclass Oligochaeta, Naididae); (I) Distribution of Classes Pycnogonida (*Anoplodactylus virescens*), Thecostraca (*Pollicipes pollicipes* and *Balanomorpha*) and Malacostraca (*Pachygrapsus marmoratus*); (J) Distribution of Classes Hexapoda (*Anurida maritima*) and Anthozoa and Phylum Nemertea.

5.3. Relationship Between Macroinvertebrate Assemblages Structure and Predictor Variables

In the Distance based Linear Model (DistLM) analysis, marginal tests revealed significant contributions of each single predictor variable to the variation in the structure of macroinvertebrate assemblages ($p < 0,05$, results not shown). To determine the combination of predictor variables that best explain the overall variability, the “best” DistLM model building procedure was implemented, using the AIC criterion (Table 7). The overall best model, supported by a high R^2 value and a minimized AIC, included seven predictor variables: Shore, Total Replicate Wet Weight, Wet Material Weight ($> 500 \mu\text{m}$), Microhabitat, Mussel Length ($> 1 \text{ cm}$), SD Mussel Length ($> 1 \text{ cm}$) and Wet Sediment Weight ($> 200 \mu\text{m}$) ($R^2 = 0,67$; AIC = 382,33). The predictor variables selected in the model accounted for 67% of the variation in the structure of macroinvertebrate assemblages (Table 7). Shore emerged as the most important predictor variable, explaining 51% of the variation among mussel associated macroinvertebrate assemblages.

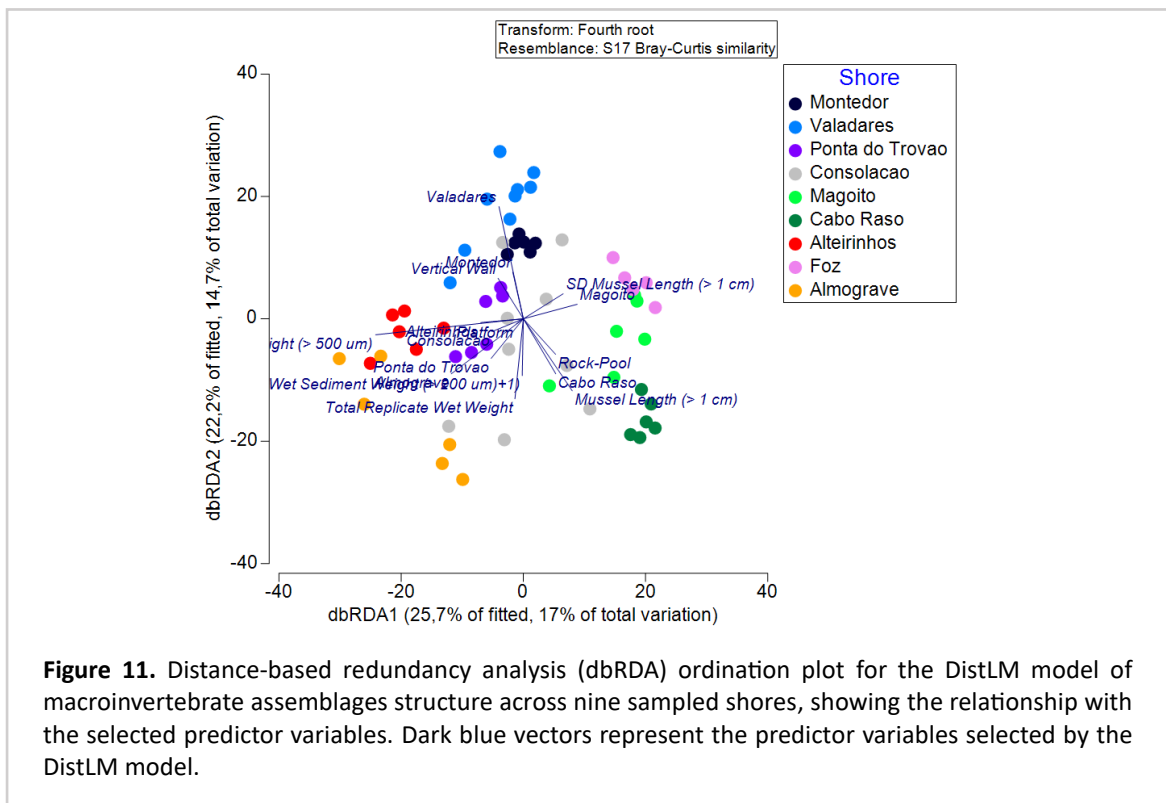
Table 7. Predictor variables selected through Distance-based Linear Model (DistLM) analysis using the BEST procedure based on the Akaike Information Criterion (AIC). The model identified the predictor variables that best explained the variation patterns in the structure of macroinvertebrate assemblages associated with rocky intertidal beds of *M. galloprovincialis*.

“BEST model”	Selected variables by order of selection (% of R^2 for cumulative groups of variables)
Seven variables: 67% in R^2 AIC: 382,33	1v: Shore (51%) 2v: 1v + Total Replicate Wet Weight (56%) 3v: 1v + Wet Material Weight ($> 500 \mu\text{m}$) + Microhabitat (60%) 4v: 3v + Mussel Length ($> 1 \text{ cm}$) (63%) 5v: 4v + SD Mussel Length ($> 1 \text{ cm}$) (65%) 6v: 5v + Wet Sediment Weight ($> 200 \mu\text{m}$) (66%) 7v: 6v + Total Replicate Wet Weight (67%)

The importance of the predictor variables selected by the DistLM model in explaining the variability of macroinvertebrate assemblages structure is illustrated in the corresponding dbRDA plot presented in Figure 11. The variability observed along the northern Portuguese shores (Montedor and Valadares) appeared to be more closely associated with local environmental conditions than with the quantitative predictor variables included in this study.

This is evident from the absence of any positive association between the quantitative predictor variable vectors in the dbRDA plot and these shores.

Although some local environmental conditions may also have contributed to variations in macroinvertebrate assemblages, for the central shores (specifically Magoito, Cabo Raso and Foz), the separation from the southwestern Portuguese ones (Almograve and Alteirinhos) in the dbRDA plot was attributed to differences in the complexity of mussel beds (Figure 11). The central shores were mainly characterized by larger mussels [e.g., “Mussel Length (> 1 cm)” at Magoito and Cabo Raso] or by mussel beds with greater size heterogeneity [e.g., “SD Mussel Length (> 1 cm)” at Foz]. In contrast, the southwestern shores were associated with higher sediment retention, as indicated by greater “Wet Sediment Weight (> 200 μm)” values at Almograve and Alteirinhos. In particular, Alteirinhos was strongly associated with the “Wet Material Weight (> 500 μm)” variable and further characterized by smaller and more uniform mussels. The patterns observed in the Consolação and Ponta do Trovão shores were less clear. These shores appeared to be associated with a combination of variables, as indicated by their intermixed positioning with other shores in the dbRDA plot (Figure 11).



The relative values of each quantitative predictor variable described in the previous paragraph can be further examined in the bubble plots presented in Figure 12. Although macroinvertebrate assemblages from Alteirinhos were associated with the “Wet Material Weight (> 500 μm)” variable in the dbRDA plot, this variable did not provide substantial additional insights beyond those already identified in the dbRDA plot. It appeared to be somewhat related to the macroinvertebrate assemblages abundance in each replicate, as well as to the larger sediment grains that might have been retained on the 500 μm sieve, thereby reinforcing the greater abundances and sediment retention observed along the southwestern shores (Almograve and Alteirinhos) (Figure 12A). For the “SD Mussel Length (> 1 cm)” variable (Figure 12B), Cabo Raso and, to a lesser extent, Foz stood out, displaying high heterogeneity in mussel shell sizes. Conversely, Alteirinhos, Magoito and Ponta do Trovão exhibited more homogeneous mussel beds.

Regarding the “Wet Sediment Weight (> 200 μm)” variable, in addition to the already mentioned pronounced tendency for sediment retention along the southwestern shores, the bubble plot in Figure 12C also illustrates the contrasting patterns observed at all other studied shores, except for Magoito, which also seemed to exhibit a significant capacity for sediment retention. Concerning the “Mussel Length (> 1 cm)” variable (Figure 12D), replicates collected in Cabo Raso, Magoito and Consolação presented larger-shelled mussels, while those from Ponta do Trovão and Alteirinhos harbored mussels with smaller shells.

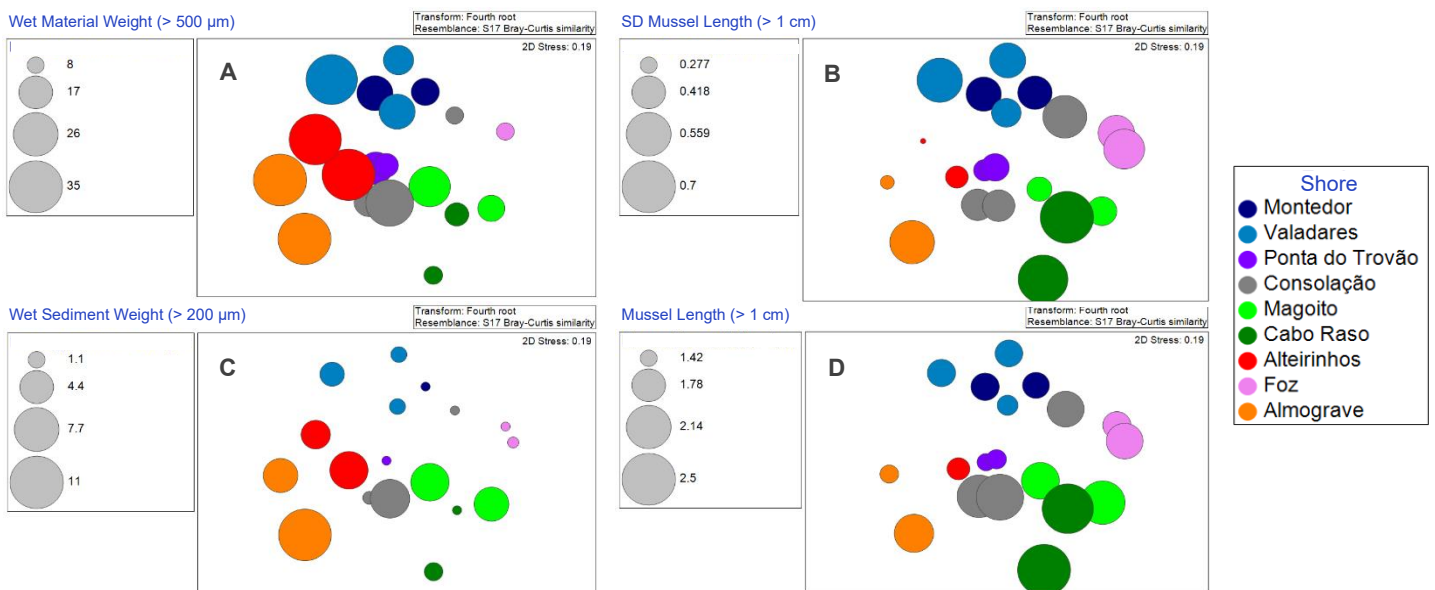


Figure 12. nMDS bubble plot representations illustrating the relative values of (A) Wet Material Weight (> 500 μm), (B) SD Mussel Length (> 1 cm), (C) Wet Sediment Weight (> 200 μm) and (D) Mussel Length (> 1 cm). The bubbles are overlaid on the 2D nMDS plot (stress value of 0,19) of macroinvertebrate assemblages associated with rocky intertidal beds of *M. galloprovincialis* at each sampled shore. This representation is based on Bray-Curtis similarities of fourth-root transformed abundance data.

6. Discussion

6.1. General Description of Biological Diversity

In this study, 66 replicates were sampled using 100 cm² quadrats, resulting in the identification of 72 taxa. Of these, 52 taxa were identified to the species level, corresponding to 72.2% of the total taxa. When compared with the global dataset on invertebrate abundance from rocky intertidal mussel beds reported by Cameron et al. (2024) in their Table 1, some interesting patterns emerge. For example, the South African survey, with a similar quadrat size (100 cm²) and a comparable sample size (N = 60), recorded 67 taxa and achieved a species-level identification percentage of 71.6%. This is very close to our findings, suggesting that the taxonomic richness and the level of species identification observed in our study align with those from South Africa.

In contrast, surveys performed on coasts such as Oregon (N = 30, 40 taxa), Nova Scotia (N = 90, 50 taxa) and Ireland (N = 15, 37 taxa) reported lower taxonomic richness and species identification percentages (65%, 64% and 64.9%, respectively). Note that our study, conducted in Portugal (NE Atlantic), can be more directly compared with regions sharing similar oceanographic boundaries, such as Ireland (NE Atlantic), Nova Scotia (NW Atlantic) and South Africa (SE Atlantic), than with those from distinct biogeographic regions like Oregon (NE Pacific). Moreover, at Almogrove, one of the ten sampled shores in our study, 48 taxa were identified from only six replicates, a number nearly as high as that reported for Nova Scotia and higher than that reported for Ireland, despite a much smaller sampling effort. These differences highlight how variations in sampling effort, local environmental conditions and biogeographic context can influence biodiversity estimates. Even so, our study appears to have been successful in capturing the biodiversity of rocky intertidal mussel beds, as evidenced by the relatively high overall richness and species-level identification rate.

Our findings also revealed a taxonomic composition dominated by Bivalvia, Malacostraca, Gastropoda, Polyplacophora and Polychaeta, which reflects patterns commonly observed in mussel bed associated assemblages. Mussel beds are recognized for hosting a core group of taxa worldwide. Cameron et al. (2024) noted that broader taxonomic groups, including those represented in our results, are consistently present across the majority of surveyed coasts, regardless of regional variations. Similarly, Seed (1996) and more recent studies, such as Arribas et al. (2014) and Veiga et al. (2022), also confirmed the predominance of these classes within mussel bed communities.

Seed (1996), in a review compiling data from various studies, observed that while species-specific variations can be largely influenced by biogeography, functionally similar species (often within the same family or genus) are frequently associated with distinct mytilid communities worldwide. For instance, this author highlighted species from the genera *Lasaea* (Lasaeidae), *Chthamalus* (Chthamalidae), *Perinereis* (Nereididae), *Hyalie* (Hyalidae) and *Typosyllis* (Syllidae) as common members of different rocky shore mytilid communities (see Table 1 in Seed, 1996). Our findings support this pattern, as we recorded species from these genera, namely *Lasaea rubra*, *Chthamalus montagui*, *C. stellatus*, *Perinereis marionii* and *P. oliveirae*, as well as species from the Syllidae and Hyalidae families. Additionally, several other taxa identified in our study, such as gastropods from the Pyramidellidae family, *Patella* spp., *Melarhaphe neritoides*, *Steromphala umbilicalis*, *Tanais dulongii*, as well as isopods from the genera *Jaera* and *Idotea*, along with polychaetes from the Phyllodocidae family, are also consistent with those commonly reported in similar studies (O'Connor & Crowe, 2007; Gestoso et al., 2013; Veiga et al. 2022; Torres, 2023).

Moreover, Seed (1996) noted that, although mussel communities exhibit high species richness and overall biodiversity, they are typically dominated by only a few very abundant species. This pattern is clearly reflected in our study, where, out of 72 recorded taxa, three stood out as the most dominant (besides *M. galloprovincialis* spat): Hyalidae amphipods (3.741 individuals), *Lasaea rubra* (4.325 individuals) and *Mytilaster minimus* (3.599 individuals). Also, a fair number of species identified in our mussel beds were still in their early life stages, including mollusks such as the gastropods *Patella* spp., *Steromphala umbilicalis* and *Nucella lapillus*. Juvenile chitons, particularly *Lepidochitona cinerea* and *Acanthochitona crinita*, were also recorded. This aligns with the well-established recognition of mussel beds as important nursery grounds for marine species (Gosselin & Chia, 1995; Silva et al., 2003; Mercegue et al., 2021; Seabra et al., 2019; Seabra et al., 2020).

In terms of taxonomic richness, in this study, marine mollusks had the highest richness (32 taxa), primarily driven by gastropods and bivalves. Arthropods ranked second (21 taxa), with malacostracan crustaceans being the main contributors. Annelids ranked third (12 taxa), particularly represented by polychaetes and oligochaetes (a subclass of the class Clitellata). While the ranking among these phyla varies, with mollusks being the richest in some studies (Arribas et al., 2014; Anu et al., 2017) and arthropods in others (Lintas & Seed, 1994; Borthagaray & Carranza, 2007), their dominance in these communities remains a recurring trend, regardless of geographic location or mussel species (Seed, 1996). Furthermore, chitons (Mollusca,

Polyplacophora), were relatively abundant in our study but contributed little to the overall taxonomic richness, a pattern also documented by Mercegue et al. (2021).

Another major result concerns taxonomic resolution. In this study, in most cases, each taxonomic family was generally represented by a single genus or species, leading to an almost direct correspondence between fine (to the lowest taxonomic level reachable) and coarse (family level) taxonomic resolutions (Figure 6), a pattern also observed by People (2006). The reason behind this outcome is unclear. Given the considerable amount of time required for species-level identification, especially in studies with large sample sizes such as this one, our results may provide empirical evidence for the potential benefits of adopting coarser taxonomic resolutions in future research. Depending on the study and its specific objectives, this approach could substantially reduce identification efforts, optimizing both time and resources without significant loss of information.

6.2. Spatial Variation in Macroinvertebrate Assemblages Structure

Spatial variability of macroinvertebrate assemblages associated with mussel beds was analyzed at multiple scales, including large-scale patterns among shores and small-scale patterns between transects within shores.

The PERMANOVA analysis detected significant differences between transects. However, pairwise tests indicated that these differences were limited to only two shores, Montedor and Alteirinhos. Since the majority of shores showed no significant variation and considering that the p-value for Montedor was marginally significant (p (Monte Carlo) = 0,049), we concluded that the structure of macroinvertebrate assemblages does not seem to substantially vary at the scale of a few meters. These findings are consistent with some studies (e.g., Lawrie & McQuaid, 2001; People, 2006), but contrast with others (e.g., Veiga et al., 2022). Although small-scale processes might be relevant, mussel bed assemblages from our study seem to be more strongly shaped by large-scale processes.

This interpretation is further reinforced by our results where shore emerged as the most important predictor variable shaping macroinvertebrate assemblages, accounting for 51% of the variation in the DistLM analysis. Similar patterns have been observed in other studies, such as Cole and McQuaid (2010), who found that regional effects were more important than the complexity of *M. galloprovincialis* beds in South Africa, and Sepúlveda et al. (2016), who notice

a north-south latitudinal gradient in faunal assemblages associated with the ribbed mussel (*Aulacomya atra*) along the South American coast.

Even so, it is important to keep in mind that microhabitats and physical characteristics of mussel beds do play a role in shaping macroinvertebrate assemblages (Delany et al., 1998; Bulleri et al., 2005; People, 2006; O'Connor & Crowe, 2007; Cole & McQuaid, 2010; Koivisto et al., 2011; Seabra et al., 2020; Veiga et al., 2022). Although their influence in our study appears to be secondary to that of the shore, some physical characteristics of mussel beds might be linked to shore variation (see section below). Nonetheless, we recognize that our microhabitat sampling design has limitations, particularly due to the uneven replication that was possible. For instance, Consolação was the only shore where a statistical comparison between platforms and rock-pools could be achieved. Ideally, a more balanced sampling design would be needed to make better-supported statements, but not all microhabitats with mussel beds were present in our sampled shores with proper relevance.

6.3. Biogeography, Habitat Complexity and Ecological Interactions in Shaping Macroinvertebrate Assemblages

The macroinvertebrate assemblage patterns observed in the mussel beds of the northern shores, Montedor and Valadares, appeared to be primarily shaped by broader biogeographic factors, while the assemblages on the remaining shores exhibited a stronger association with specific physical characteristics of the mussel beds. Nonetheless, at Ponta do Trovão and Consolação, the dbRDA analysis revealed overlapping influences from both mussel bed characteristics and biogeographic gradients, suggesting that these shores may serve as transitional zones where northern and central-southwestern assemblage patterns converge.

6.3.1. Northern Group (Montedor and Valadares)

Macroinvertebrate assemblages associated with *M. galloprovincialis* beds showed clear differences across latitudes, particularly between the northern group of shores and those in central and southwestern Portugal. Among all the predictor variables related to the physical characteristics of the mussel beds, none were strongly associated with the northern shores (Montedor and Valadares), as indicated by the dbRDA results. This suggests that the observed differences in macroinvertebrate assemblages were rather driven by broader biogeographic factors. Our findings were consistent with existing literature on the distribution patterns of rocky

shore organisms along the Portuguese coast, where biogeographic factors often played a significant role in shaping community structure (Boaventura et al., 2002). Seawater temperatures along the northern coast remain cold even during the summer season (De Azevedo & Franco, 2019), while temperatures along the southern coast are generally slightly higher due to the influence of warmer ocean currents (Santos, 1994 in Boaventura et al., 2002). According to Boaventura et al. (2002), there is a gradient along the Portuguese coast for many warm-water species, including the gastropods *Siphonaria pectinata* and *Onchidella celtica*, which are more abundant on the southern shores. Furthermore, the tanaid species *Tanais dulongii* also exhibits a geographic gradient in Portugal, being more associated with higher seawater temperatures (Pereira et al., 2006; Guerra-García & Sánchez, 2009). This gradient may help explain the absence of these species from the northern group in our study.

Conversely, while *M. galloprovincialis* was present along the entire Portuguese coast, Boaventura et al. (2002) found a progressive decline in its abundance from north to south. This finding aligns with our SIMPER analysis, which indicated a higher average abundance of mussel spat in the northern group as well. Although Boaventura et al. (2002) focused on the distribution of adult mussels, our analysis of mussel spat suggests that the greater presence of adults in the north is likely to enhance juvenile recruitment, a positive correlation also reported by McQuaid and Lindsay (2007). Furthermore, Boaventura et al. (2002) reported a north-to-south decline in the abundance of *Nucella lapillus*, a cold-water gastropod also recorded in this study. While adult individuals were easily identifiable, many juvenile specimens were at early developmental stages. To maintain taxonomic accuracy, these juveniles - though likely belonging to *Nucella lapillus* - were conservatively classified within the Muricidae family (see section 4.3). Our findings similarly reflect the pattern described by Boaventura et al. (2002), with Muricidae abundance being higher in the Northern group and decreasing southward, except in the southwestern shores (Almogrove and Alteirinhos), where a significant resurgence was observed. Numerous studies have documented a strong association between *Nucella* species and mussel beds, a logical association given that mussels are one of their primary prey items (Largen, 1967; Gosselin & Chia, 1995; Hunt & Scheibling, 1995; Boaventura et al., 2002; O'Connor & Crowe, 2007).

The order Balanomorpha also appeared to thrive in the local environmental conditions of the northern shores, contributing to the distinct separation of these shores from those further south. The species identified within this order included the barnacles *Chthamalus montagui*, *Chthamalus stellatus* and *Perforatus perforatus*. However, similar to the approach taken with the Muricidae family, individuals in this group were conservatively classified at the broader taxonomic level of Balanomorpha to ensure taxonomic accuracy. Barnacles tend to be

particularly abundant in wave-exposed habitats (Arribas et al., 2014). Although wave-exposure was not directly measured in our study, the higher abundance of Balanomorpha might be related to the greater wave-exposure conditions on the northern coast of Portugal, as described by Silva et al. (2018).

6.3.2. Magoito and Cabo Raso

Further south, along the Portuguese coastline, are the Magoito and Cabo Raso shores. Within these mussel beds, the class Anthozoa appears to have found favorable conditions for its establishment and thriving. This is consistent with reports from Boaventura et al. (2002), which noted a greater abundance of *Actinia* sp. (class Anthozoa) in the central regions of Portugal compared to the north and south. Additionally, Pereira et al. (2014) also documented the presence of two *Actinia* species at Cabo Raso and Mindelo (Sintra), the latter located just a few kilometers from Cabo Raso and Magoito. Despite identification efforts, specimens belonging to the class Anthozoa presented high levels of degradation, appearing as grayish, rounded soft bodies with few distinctive features. This indistinct morphology complicates the interpretation of their association with mussel beds on the central shores, as different species display unique resource preferences and habitat requirements. However, since Boaventura et al. (2002) and Pereira et al. (2014) both reported the presence of *Actinia* species in this region, it is possible that these unidentifiable gray individuals belong to this genus, although the identification remains uncertain.

It is well-documented in the literature that sea anemones may inhabit mussel beds (Sebens, 1982; Dittmann, 1990; Gargouri Ben Abdallah et al., 2013). Davenport et al. (2011) and Sebens (1982) highlighted the dual role of mussel beds as both a food source and habitat for intertidal anemone species. On the shores of Magoito and Cabo Raso, damaged mussels could provide a significant dietary resource for *Actinia* species. This scenario is supported by Davenport et al. (2011), who showed that crabs facilitate anemone feeding by cracking mussel shells. Such relationship is particularly relevant for Cabo Raso, where a higher presence of the crab species *Pachygrapsus marmoratus* has been recorded in our study. Furthermore, as observed by Sebens (1982) on the Pacific coast, the physical structure of mussel beds may offer shelter that supports recruitment and growth of juvenile anemones. Therefore, the mussel beds at Magoito and Cabo Raso may provide essential habitats for both feeding and protection, supporting the persistence of Anthozoa populations.

In terms of mussel bed characteristics, Magoito and Cabo Raso were distinguished by the larger size of their mussels. Several studies have examined the relationship between mussel size and the associated assemblages, reporting varied results. For instance, O'Connor and Crowe (2007) found that larger mussels tended to host a more abundant fauna. Conversely, Cole and McQuaid (2010) reported a negative correlation between average mussel size and macroinvertebrate abundance, indicating that larger mussels may support fewer individuals. Furthermore, both Veiga et al. (2022) and Sepúlveda et al. (2016) observed that the richness and abundance of associated macroinvertebrate assemblages varied independently of mussel size. Such inconsistencies possibly indicate that these interactions are not always straightforward but rather context dependent, that is, they may depend on other site-specific factors (Cole & McQuaid, 2010).

Nevertheless, O'Connor and Crowe (2007) also found that beds with larger mussels hosted associated organisms of greater proportions, which aligns with our findings. According to the SIMPER analysis, the taxa that contributed the most to the differences between assemblages at Magoito and Cabo Raso and those from other shores were generally larger-bodied species. At Magoito, these include isopods of the genus *Idotea* and the polyplacophoran *Lepidochitona cinerea*, while at Cabo Raso these include the crab *Pachygrapsus marmoratus*, the limpet *Patella ulyssiponensis*, the pygogonid species *Anoplodactylus virescens* and *Phoxichilidium femoratum*, as well as the tanaid *Tanais dulongii*.

O'Connor and Crowe (2007) and Torres et al. (2022) reported that *Idotea* species were frequently associated with mussel beds formed by larger individuals. It is plausible that larger-bodied species may prefer to inhabit these beds, as the increased interstitial space facilitates movement and foraging activities. Koivisto et al. (2011) also observed higher isopod abundance in both algal and sandy patches, a correlation that may help explain not only the presence of *Idotea* species, but also the overall abundance of isopods in Magoito. This shore is characterized by significant sediment retention within its mussel beds, along with the presence of macroalgae, as documented in unpublished pre-scraping photographs (described in Section 4.1).

The distribution of *P. ulyssiponensis* across our study shores appears to be shaped by both latitudinal gradients and specific microhabitat characteristics. Boaventura et al. (2002) reported a higher abundance of this species along the central coast of Portugal, a pattern that aligns well with our findings. However, *P. ulyssiponensis* is also noted for its southern distribution range (Christiaens, 1973 in Seabra et al., 2020), which aligns with its significant abundance at southwestern shores, particularly Queimado and Almogrove. The environmental conditions at

Cabo Raso, such as its high wave exposure (Boaventura et al., 2002), likely favor *P. ulyssiponensis* populations, especially juvenile patellids, which can be frequently found on wave-exposed rocks, often in association with mussels and algae (Guerra & Gaudencio, 1986; Silva et al., 2003; Seabra et al., 2023). Another aspect potentially contributing to the species abundance at Cabo Raso is the minimal sediment retention observed in its mussel beds. The intense wave action effectively washes away finer sediments, which can be beneficial since sediment stress is known to negatively impact limpet grazing activity and survival (Airoldi & Hawkins, 2007).

The high average abundance of *Pachygrapsus marmoratus* among the mussel beds at Cabo Raso could be explained by ecological interactions that align with its known feeding behaviors. Predation on mussels by intertidal crabs has already been documented (Navarrete & Castilla, 1988; Cannicci et al., 2002; Silva et al., 2009). According to Cannicci et al. (2002), *P. marmoratus* is a selective feeder with a diverse omnivorous diet, showing a preference for *M. galloprovincialis* and gastropods such as *Patella*, both of which are available in this shore. The presence of juvenile *P. ulyssiponensis* may attract these crabs, as smaller limpets become vulnerable to *P. marmoratus* predation when active outside the mussel beds. Silva et al. (2009) also noted that *P. marmoratus* exhibits a higher consumption of mussels on more exposed shores, which may further explain its dietary behavior at Cabo Raso. Additionally, mussel beds may even serve as refuge spaces, protecting these crabs from diurnal visual predators such as shorebirds (Ryer, 1987; Ellis et al., 2005, 2007).

Pycnogonids, or sea spiders, are frequently recorded in association with mussel beds (Dittmann, 1990; Lovely, 2005; Çinar et al., 2008; Jungerstam et al., 2014) and are well-known predators of cnidarians, including Anthozoa (Lebour, 1945; Genzano, 2002). At Cabo Raso, the high availability of Anthozoa likely contributes to the notable presence of pycnogonids, suggesting a predator-prey dynamic between these two taxa. In fact, our results indicate that the distribution patterns of the identified pycnogonids closely align with those of Anthozoa, reinforcing this potential ecological relationship.

Tanais dulongii, though often associated with mussel beds (Lintas & Seed, 1994; Adami et al., 2004; Çinar et al., 2020), appears to exhibit a strong association with algal turf habitats (Prathep et al., 2003; Pereira et al., 2006; Bamber et al., 2012). The high abundance of *T. dulongii* observed at Ponta do Trovão and Cabo Raso, both characterized by a substantial macroalgal presence within mussel beds (based on unpublished pre-scraping photographs), suggests that the availability of algal turf may play a critical role in shaping its distribution, as this species also utilizes algal resources as part of its diet (Rumbold et al., 2015). Moreover, the relatively low

sediment accumulation observed in mussel beds at both shores is consistent with prior findings, which indicate a negative correlation between *T. dulongii* abundance and sediment-rich conditions (Prathep et al., 2003). Together, these observations suggest that the distribution of *T. dulongii* along the Portuguese coast may be influenced not only by its distribution in warmer waters (as previously discussed), but also by the availability of suitable algal habitats and low sediment levels.

6.3.3. Foz

Located approximately 8 km north of Cabo Espichel, Foz is another shore marked by intense hydrodynamics and potential higher wave-exposure, conditions often associated with coastal promontories. These environmental conditions create a high-energy habitat particularly favorable for species associated with strong wave action, such as the stalked barnacle *Pollicipes pollicipes* (Barnes, 1996; Sousa et al., 2013; Fernandes et al., 2010; Cruz et al., 2022). Among all surveyed locations, Foz recorded the highest average abundance of *P. pollicipes*, making it an important discriminatory species associated with this shore.

P. pollicipes is predominantly intertidal and widely distributed along the Portuguese coast (Cruz et al., 2022). Despite not being commonly associated with mussel beds, *Pollicipes* species can settle in small gaps within these biogenic structures (Paine, 1974; Hoffman, 1989), as observed in our study. Here, the majority of individuals identified under microscope were juveniles attached to the peduncles of a few adults.

Another distinctive aspect of the Foz shore was the low biodiversity observed within its mussel beds, showing by far the lowest species richness and abundance among all shores. Here, the rocky intertidal landscape was characterized by small, isolated mussel patches with limited habitat connectivity (personal observation; unpublished data by David Mateus). The Equilibrium Theory of Island Biogeography (MacArthur & Wilson, 1967) provides a theoretical framework that supports these observations. According to this theory, smaller and more isolated “islands” (in this case, mussel patches) tend to sustain fewer species due to lower immigration and higher extinction rates. In line with this, both Seed (1996) and Koivisto et al. (2011) found a positive species-area relationship, where smaller patch sizes were associated with reduced species richness and abundance. Moreover, Brazeau’s (2009) study on community responses to different levels of isolation in dynamic habitats provides further empirical evidence supporting these theoretical predictions. This author demonstrated that habitat fragmentation in mussel beds led to the formation of isolated patches, limiting species dispersal and reducing both abundance and

richness. In Foz, the considerable distances between mussel patches likely hindered colonization and restricted the diversity of macroinvertebrate assemblages, emphasizing the importance of connectivity in maintaining ecological stability within intertidal habitats. Thus, our results suggest that small, isolated and hydrodynamically disturbed habitats may host lower overall diversity.

6.3.4. Almogrove

In the southwestern shores of Alentejo, Almogrove, unlike other shores where specific taxa accounted for the observed differences, revealed a generally higher abundance and richness of several taxa. Almogrove is characterized by a rocky intertidal zone with steep shale cliffs (Boaventura et al., 2002; Seabra et al., 2023). This geomorphological configuration increases substrate complexity, potentially creating a more heterogeneous intertidal landscape that supports a greater diversity of microhabitats and ecological niches, as suggested by Sebens (1991).

Mussel beds at Almogrove were relatively uniform, primarily consisting of medium-sized mussels. Since mussel size can shape the structure of associated macroinvertebrate assemblages (O'Connor & Crowe, 2007; Cole & McQuaid, 2010), this intermediate size range likely supports a greater diversity of associated taxa, providing a suitable microhabitat for species that are typically associated with either larger or smaller mussels. Furthermore, Veiga et al. (2022) found that more homogeneous mussel beds tend to support a broader range of fauna, likely due to their increased sediment retention capacity. This capacity arises from their compact and cohesive configuration, which reduces wave action and facilitates sediment accumulation (Iwasaki, 1995; Veiga et al., 2022). This findings align with other research, which has demonstrated that sediment retention in mussel beds strongly influences the structure of associated assemblages (Prado & Castilla, 2006; Koivisto et al., 2011; Torres, 2023). Given the high sediment content observed in samples from this shore, it is likely that increased sediment retention contributed to greater microhabitat heterogeneity, promoting the proliferation of infaunal species (Dos Santos et al., 2018).

In line with this observations, Koivisto et al. (2011) reported that bivalve abundance is often associated with mussel beds featuring greater sediment accumulation, a pattern also evident in Almogrove, where bivalves were especially abundant. Particularly, sediment trapping within mussel beds creates favorable microhabitats for species such as *Lasaea rubra* and *Hiatella arctica*, bivalves that are strongly associated with sediment-rich crevice environments (Kensler,

1964; Gosselin & Chia, 1995; Veiga et al., 2022; Torres, 2023). Likewise, other species thriving under this condition include the gastropods *Steromphala umbilicalis* and *Melarhappe neritoides* (Torres, 2023), both of which were also observed in high abundance at Almogrove. Sediment retention within mussel beds further benefits groups such as polychaetes and nemerteans. These organisms find suitable conditions in sediment-rich environments, an association well-documented in multiple studies (Kensler, 1964; Koivisto et al., 2011; Gestoso et al., 2013; Torres, 2023).

Although Torres (2023) noted a general association of the Muricidae and Pyramidellidae families with low-sediment environments, both families were found in abundance within Almogrove's mussel beds. This distribution pattern may stem from the fact that these families include predators and parasites, respectively, whose occurrence is likely more influenced by the availability of prey or hosts than by sediment conditions (Hunt & Scheibling, 1995; Burrows et al., 2009; Huntley et al., 2021; Torres et al., 2022).

Overall, the results from Almogrove support the idea that mussel beds with a homogeneous structure and high sediment retention create favorable microhabitats for species adapted to sediment-rich environments, thus promoting a diverse faunal community. The patterns observed on this shore emphasize how both biotic and abiotic conditions shape the coexistence of multiple species, each occupying its own ecological niche within the mussel bed (epifauna, mobile species and infauna).

6.3.5. Alteirinhos

Following patterns similar to those observed at Almogrove, the mussel beds at Alteirinhos demonstrated a strong capacity for sediment retention. However, while Almogrove showed a greater overall macroinvertebrate diversity, the mussel beds at Alteirinhos – characterized by their homogeneous structure, predominantly consisting of smaller mussels – displayed a distinct faunal composition, largely marked by the high abundance of oligochaetes from the Naididae family. The higher abundance of this family in Alteirinhos, compared to other shores, may indicate not only increased sedimentation levels (Torres, 2023), but also substantial organic enrichment (Giere & Pfannkuche, 1982). This pattern suggests that these worms may benefit from the accumulation of organic matter in the sediments, a process likely intensified by the biodeposition of faeces and pseudofaeces from mussels (Tsuchiya, 1980; Kautsky & Evans, 1987; Dittmann, 1990; Norling & Kautsky, 2007; Ysebaert et al., 2009). This enrichment might create an ideal environment for oligochaetes, which, unlike polychaetes, are more tolerant to

hypoxic and anoxic conditions often associated with organically enriched sediments (Hunter & Arthur, 1978; Giere & Pfannkuche, 1982; Ysebaert et al., 2009). However, given that the organic matter content in the sediments was not measured in this study, future research should aim to quantify this variable in mussel beds to better understand the relationship between organic enrichment and associated biological assemblages.

Another taxa that stood out at Alteirinhos was the springtail *Anurida maritima*. Kensler (1964) provided a detailed description of crevice habitats in the western Mediterranean region and their associated fauna, where *A. maritima* was abundantly found. Individuals of this species commonly shelter inside empty barnacle shells and feed on decomposing organic matter, including animal remains (Imms, 1906; Kensler, 1964; Christian, 1989). Gut content analysis have confirmed a preference for animal-based diets, though occasional ingestion of vegetable matter has also been noted (Imms, 1906; Christian, 1989). Overall, *A. maritima* seems to rely on the availability of dead organic material for sustenance. Additionally, as the distribution of this species has been described as strongly related to the availability of shelter (Kensler, 1964; Christian, 1989) and a preference for fine-grained substrates (Christian, 1989), the mussel beds at Alteirinhos may create similar conditions. These homogeneous mussel beds, dominated by smaller individuals, may retain finer sediments and potentially accumulate more organic matter within the compact spaces of the mussel matrix. This combination of fine-grained substrates, organic enrichment, and protection during both high and low tides likely supports the persistence of *A. maritima* on this shore.

7. Challenges and Future Recommendations

While this study provides valuable insights into the distribution, composition and relationships between taxa and the surrounding biotic and abiotic conditions, certain aspects could have been approached differently to better support our findings. For instance, measuring the organic matter content in the sediments would increase our understanding of how this variable may shape mussel bed associated assemblages, particularly species such as oligochaetes. Additionally, perhaps the most important improvement for future research would be the inclusion of a temporal analysis to determine whether the observed species distributions represent consistent patterns over time or merely snapshot occurrences.

This study also faced some inevitable limitations. The need for advanced taxonomic skills posed a particular challenge, as identifying some taxa to the species level often required

specialized knowledge that was not always readily available. Also, like many studies of this nature, challenges arose when adapting theoretical designs to the practical reality of fieldwork. For instance, as mentioned throughout the study, the sampling design aimed to include all three microhabitats across each of the studied shores for ideal comparisons, something that was not consistently achievable. Similarly, full mussel coverage within the 10 x 10 cm quadrat was not always possible, as coverage varied between replicates. Finally, understanding how the physical and biological characteristics of mussel beds, along with the environmental conditions of specific shores, shape the associated biota is a demanding task by itself. Establishing such connections involves careful consideration of multiple factors, including the specific resource requirements of each taxon.

8. Final Considerations

Mussel beds are commonly exploited by humans for consumption, trade or as a source of fishing bait, which may include the mussels themselves or organisms from their associated fauna. Yet, this oversimplifies the role of these biogenic habitats, neglecting the vital ecological functions they perform. Thus, in addition to the objectives and hypotheses outlined, this study seeks to bridge the gap between scientific understanding and public perception by providing empirical evidence of how these organisms can create entire ecosystems by themselves that support a diverse array of marine fauna. As the Senegalese forest engineer Baba Dioum stated in his 1968 speech at the General Assembly of the International Union for Conservation of Nature (IUCN), people only care for what they love and only love what they understand. This study highlights the beauty and balance of nature so it may be better understood, appreciated and ultimately protected. As part of a master's thesis in Natural Resources Management and Conservation, it also sheds light on how mandatory it is to consider ecosystem engineers, such as mussels, as priority species in conservation efforts. Poor management of these habitats can potentially lead to the collapse of entire ecological networks (some of which were discussed in the previous section), resulting in significant biodiversity loss. Therefore, raising public awareness and ensuring the conservation of mussel beds through sustainable environmental policies are crucial steps in preserving the health of coastal ecosystems and their natural resources.

9. References

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10. Appendixes

Appendix A: List of taxa identified in the study. Taxa are identified to the lowest possible taxonomic level (in bold). Whenever an Order is undefined, the lowest classification within the Class and Family levels (e.g., infraclass, superfamily) is provided.

Phylum	Class	Order	Family	Genus / Species	
Annelida	Clitellata (subclass Oligochaeta)	Tubificida	Naididae		
		Polychaeta	Eunicida	Lumbrineridae	
	Phyllodocida		Nereididae	<i>Perinereis marionii</i>	
					<i>Perinereis oliveirae</i>
		Phyllodocidae		<i>Eulalia viridis</i>	
			Syllidae	<i>Trypanosyllis zebra</i>	
			Polynoidae		
		(Infraclass Canalipalata)	Sabellariidae	<i>Sabellaria alveolata</i>	
		Sabellida	Sabellidae	<i>Amphiglena mediterranea</i>	
			Oweniidae		
			Serpulidae		
		(Infraclass Scolecida)	Orbiniidae		
Arthropoda	Hexapoda	(Subclass Collembola)	Neanuridae	<i>Anurida maritima</i>	
	Malacostraca	Amphipoda	Ampeliscidae		
			Aoridae		
			Hyalidae		
			Stenothoidae		
			Isopoda	Idoteidae	<i>Idotea sp.</i>
				Janiridae	<i>Jaera sp.</i>
				Munnidae	<i>Munna minuta</i>
				Sphaeromatidae	<i>Campecopea hirsuta</i>
					<i>Campecopea lusitanica</i>
					<i>Dynamene bidentata</i>
			Decapoda	Grapsidae	<i>Pachygrapsus marmoratus</i>
				Pilumnidae	<i>Pilumnus hirtellus</i>
		Tanaidacea	Tanaididae	<i>Tanais dulongii</i>	
Ostracoda	Podocopida	Cypridae	<i>Herpetocypris reptans</i>		
Pycnogonida	Pantopoda	Phoxichilidiidae	<i>Anoplodactylus virescens</i>		

	Thecostraca	Pollicipedomorpha	Pollicipedidae	<i>Phoxichilidium femoratum</i>
		Balanomorpha	Balanidae	<i>Pollicipes pollicipes</i>
			Chthamalidae	<i>Perforatus perforatus</i>
				<i>Chthamalus montagui</i>
				<i>Chthamalus stellatus</i>
Equinodermata	Echinoidea	Camarodonta	Parechinidae	<i>Paracentrotus lividus</i>
	Holothuroidea	Dendrochirotida	Cucumariidae	<i>Pawsonia saxicola</i>
	Ophiuroidea	Amphilepidida	Amphiuridae	<i>Amphipholis squamata</i>
Mollusca	Bivalvia	Cardiida	Cardiidae	
		Carditida	Carditidae	<i>Cardita calyculata</i>
		Myida	Corbulidae	<i>Varicorbula gibba</i>
		Adapedonta	Hiatellidae	<i>Hiatella arctica</i>
		Galeommatida	Lasaeidae	<i>Lasaea rubra</i>
				<i>Tellimya ferruginosa</i>
		Lucinida	Lucinidae	<i>Loripes orbiculatus</i>
		Mytilida	Mytilidae	<i>Leiosolenus aristatus</i>
				<i>Musculus costulatus</i>
				<i>Mytilaster minimus</i>
				<i>Mytilus galloprovincialis</i>
	Gastropoda	(Superfamily Acteonoidea)	Acteonidae	<i>Acteon tornatilis</i>
		Littorinimorpha	Barleeiidae	<i>Barleeia unifasciata</i>
			Littorinidae	<i>Littorina saxatilis</i>
				<i>Melarhapha neritoides</i>
			Tateidae	<i>Potamopyrgus antipodarum</i>
			Velutinidae	
			Naticidae	
		Ellobiida	Ellobiidae	<i>Melampus sp.</i>
		(Superfamily Plakobranchoidea)	Limapontiidae	<i>Limapontia depressa</i>
		Neogastropoda	Muricidae	<i>Nucella lapillus</i>
		(Superfamily Omalogyroidea)	Omalogyridae	<i>Omalogyra atomus</i>
		Systemommatophora	Onchidiidae	<i>Onchidella celtica</i>
		(Superfamily Patelloidea)	Patellidae	<i>Patella depressa</i>

				<i>Patella ulyssiponensis</i>
				<i>Patella vulgata</i>
		Siphonariida	Siphonariidae	<i>Siphonaria pectinata</i>
		Trochida	Skeneidae	<i>Dikoleps cutleriana</i>
			Trochidae	<i>Steromphala umbilicalis</i>
		(Superfamily Pyramidelloidea)	Pyramidellidae	
	Polyplacophora	Chitonida	Acanthochitonidae	<i>Acanthochitona crinita</i>
			Tonicellidae	<i>Lepidochitona cinerea</i>
Platyhelminthes	Turbellaria	Polycladida	Leptoplanidae	<i>Leptoplana tremellaris</i>
Cnidaria	Anthozoa			
Porifera	Demospongiae			
Nemertea				

Appendix B: Results from the SIMPER analysis with a cumulative contribution cut-off of 50%. Taxa with null average abundances, whose cumulative contributions exceed the 50% cut-off, are included below the red line. In each comparison, the cell with the higher average abundance is colored blue for the grouped/individual shores on the left and gray for the grouped/individual shores on the right.

Taxa	Av. Abund. (Northern group)	Av. Abund. (Peniche and Queimado group)	Contrib. %	Cum. %
<i>Lasaea rubra</i>	0,91	2,30	5,26	5,26
<i>Mytilaster minimus</i>	1,06	2,43	5,02	10,28
<i>Mytilus galloprovincialis</i>	5,74	4,45	2,00	15,27
<i>Lepidochitona cinerea</i>	0,07	1,33	4,31	19,58
Balanomorpha	1,16	0,56	3,40	22,99
<i>Jaera</i> sp.	0,86	0,54	3,18	26,17
Syllidae	0,23	1,03	3,11	29,27
Anthozoa	0,13	0,97	3,11	32,38
<i>Musculus costulatus</i>	0,92	0,87	2,92	35,29
<i>Steromphala umbilicalis</i>	0,95	0,59	2,84	38,13
Pyramidellidae	1,24	1,76	2,83	40,96
Hyalidae	2,88	2,53	2,73	43,69
<i>Melarhappe neritoides</i>	1,13	0,94	2,72	46,41
<i>Tanais dulongii</i>	0,00	0,79	2,70	49,11
<i>Patella ulyssiponensis</i>	0,66	0,53	2,64	51,75
<i>Idotea</i> sp.	0,80	0,00	2,60	
<i>Acanthochitona crinita</i>	0,00	0,53	1,73	
Taxa	Av. Abund. (Northern group)	Av. Abund. (Magoito)	Contrib. %	Cum. %
Anthozoa	0,13	1,98	7,35	7,35
<i>Lepidochitona cinerea</i>	0,07	1,81	6,71	14,06
<i>Idotea</i> sp.	0,80	1,83	5,62	19,68
<i>Melarhappe neritoides</i>	1,13	0,20	4,28	23,96
Hyalidae	2,88	1,95	4,09	28,06
Balanomorpha	1,16	0,43	3,95	32,01
<i>Jaera</i> sp.	0,86	0,94	3,76	35,76
<i>Lasaea rubra</i>	0,91	0,67	3,58	39,34
Pyramidellidae	1,24	0,87	3,54	42,89
<i>Mytilaster minimus</i>	1,06	1,25	3,31	46,20
<i>Mytilus galloprovincialis</i>	5,74	5,30	3,26	49,46
<i>Patella depressa</i>	0,99	1,80	3,20	52,65
Taxa	Av. Abund. (Northern group)	Av. Abund. (Cabo Raso)	Contrib. %	Cum. %
<i>Mytilus galloprovincialis</i>	5,74	2,50	10,37	10,37
Anthozoa	0,13	2,21	6,75	17,12
<i>Tanais dulongii</i>	0,00	1,31	3,90	21,01

Balanomorpha	1,16	0,43	3,24	24,25
<i>Melarhappe neritoides</i>	1,13	0,39	3,16	27,41
<i>Pachygrapsus marmoratus</i>	0,00	0,93	3,07	30,48
<i>Lasaea rubra</i>	0,91	1,48	3,04	33,52
Pyramidellidae	1,24	0,94	2,95	36,46
<i>Musculus costulatus</i>	0,92	0,76	2,83	39,29
<i>Patella ulyssiponensis</i>	0,66	1,20	2,77	42,07
<i>Jaera</i> sp.	0,86	1,33	2,75	44,82
<i>Anoplodactylus virescens</i>	0,00	0,92	2,74	47,56
<i>Idotea</i> sp.	0,80	0,42	2,71	50,27
Phyllodocidae	0,75	0,00	2,40	
Muricidae	0,73	0,00	2,27	
<i>Siphonaria pectinata</i>	0,00	0,67	2,04	
Taxa	Av. Abund. (Northern group)	Av. Abund. (Foz)	Contrib. %	Cum. %
<i>Mytilus galloprovincialis</i>	5,74	3,35	10,60	10,60
Hyalidae	2,88	1,60	5,78	16,38
<i>Mytilaster minimus</i>	1,06	2,24	5,66	22,04
<i>Melarhappe neritoides</i>	1,13	0,00	5,34	27,38
Pyramidellidae	1,24	0,77	4,29	31,67
Balanomorpha	1,16	0,53	4,25	35,92
<i>Pollicipes pollicipes</i>	0,35	0,92	4,12	40,04
<i>Lasaea rubra</i>	0,91	0,86	3,87	43,91
<i>Jaera</i> sp.	0,86	0,00	3,70	47,61
<i>Musculus costulatus</i>	0,92	0,50	3,56	51,17
<i>Idotea</i> sp.	0,80	0,00	3,28	
<i>Anurida maritima</i>	0,49	0,00	2,31	
Taxa	Av. Abund. (Northern group)	Av. Abund. (Almograve)	Contrib. %	Cum. %
<i>Lasaea rubra</i>	0,91	3,44	6,38	6,38
<i>Mytilaster minimus</i>	1,06	3,01	4,79	11,17
<i>Hiatella arctica</i>	0,41	2,33	4,71	15,88
<i>Lepidochitona cinerea</i>	0,07	1,80	4,30	20,18
Syllidae	0,23	1,74	3,87	24,05
Pyramidellidae	1,24	2,38	2,98	27,03
<i>Acanthochitona crinita</i>	0,00	1,22	2,89	29,92
<i>Musculus costulatus</i>	0,92	1,97	2,85	32,77
<i>Onchidella celtica</i>	0,00	1,15	2,85	35,62
<i>Cardita calyculata</i>	0,00	1,21	2,81	38,42
<i>Dikoleps cutleriana</i>	0,13	1,21	2,66	41,08
<i>Mytilus galloprovincialis</i>	5,74	6,54	2,63	43,72
Nereididae	0,57	1,45	2,62	46,34
<i>Melarhappe neritoides</i>	1,13	1,24	2,56	48,89

<i>Tellimya ferruginosa</i>	0,38	1,28	2,50	51,40
<i>Anoplodactylus virescens</i>	0,00	0,92	2,14	
Taxa	Av. Abund. (Northern group)	Av. Abund. (Alteirinhos)	Contrib. %	Cum. %
<i>Lasaea rubra</i>	0,91	3,29	8,65	8,65
<i>Mytilaster minimus</i>	1,06	3,25	7,94	16,58
Naididae	0,46	2,16	6,31	22,89
<i>Tellimya ferruginosa</i>	0,38	1,66	4,66	27,55
Balanomorpha	1,16	0,00	4,17	31,72
Syllidae	0,23	1,31	3,96	35,68
<i>Lepidochitona cinerea</i>	0,07	1,17	3,95	39,63
<i>Onchidella celtica</i>	0,00	1,05	3,73	43,36
<i>Mytilus galloprovincialis</i>	5,74	6,39	3,51	46,87
Anthozoa	0,13	0,98	3,25	50,12
Taxa	Av. Abund. (Peniche and Queimado group)	Av. Abund. (Magoito)	Contrib. %	Cum. %
<i>Idotea</i> sp.	0,00	1,83	6,74	6,74
<i>Lasaea rubra</i>	2,30	0,67	5,94	12,68
<i>Mytilaster minimus</i>	2,43	1,25	4,68	17,36
<i>Mytilus galloprovincialis</i>	4,45	5,30	3,97	21,33
Anthozoa	0,97	1,98	3,84	25,17
<i>Lepidochitona cinerea</i>	1,33	1,81	3,63	28,80
Pyramidellidae	1,76	0,87	3,49	32,28
<i>Jaera</i> sp.	0,54	0,94	3,41	35,69
Syllidae	1,03	0,17	3,31	39,00
Hyalidae	2,53	1,95	3,27	42,27
<i>Melarhappe neritoides</i>	0,94	0,20	3,08	45,36
Nemertea	0,81	0,00	2,98	48,34
<i>Tanais dulongii</i>	0,79	0,66	2,82	51,16
Nereididae	0,73	0,00	2,59	
Taxa	Av. Abund. (Peniche and Queimado group)	Av. Abund. (Cabo Raso)	Contrib. %	Cum. %
<i>Mytilus galloprovincialis</i>	4,45	2,50	6,68	6,68
Anthozoa	0,97	2,21	4,41	11,09
<i>Mytilaster minimus</i>	2,43	1,28	4,05	15,14
<i>Jaera</i> sp.	0,54	1,33	3,75	18,89
<i>Tanais dulongii</i>	0,79	1,31	3,73	22,62
<i>Patella ulyssiponensis</i>	0,53	1,20	3,59	26,21
Pyramidellidae	1,76	0,94	3,34	29,55
<i>Lasaea rubra</i>	2,30	1,48	3,27	32,82
<i>Pachygrapsus marmoratus</i>	0,15	0,93	2,89	35,71
<i>Musculus costulatus</i>	0,87	0,76	2,73	38,44

<i>Steromphala umbilicalis</i>	0,59	0,98	2,69	41,13
Hyalidae	2,53	2,72	2,68	43,81
Nemertea	0,81	0,17	2,67	46,48
<i>Anoplodactylus virescens</i>	0,38	0,92	2,65	49,13
<i>Melarhappe neritoides</i>	0,94	0,39	2,63	51,76
Taxa	Av. Abund. (Peniche and Queimado group)	Av. Abund. (Foz)	Contrib. %	Cum. %
<i>Lasaea rubra</i>	2,30	0,86	5,72	5,72
<i>Mytilus galloprovincialis</i>	4,45	3,35	4,99	10,70
<i>Lepidochitona cinerea</i>	1,33	0,20	4,71	15,42
Hyalidae	2,53	1,60	4,63	20,05
Pyramidellidae	1,76	0,77	4,45	24,50
<i>Melarhappe neritoides</i>	0,94	0,00	3,94	28,44
<i>Patella ulyssiponensis</i>	0,53	0,96	3,64	32,08
<i>Pollicipes pollicipes</i>	0,20	0,92	3,62	35,70
Nemertea	0,81	0,00	3,48	39,18
<i>Mytilaster minimus</i>	2,43	2,24	3,41	42,59
Syllidae	1,03	0,33	3,35	45,94
Anthozoa	0,97	0,36	3,35	49,29
<i>Tanais dulongii</i>	0,79	0,00	3,19	52,47
<i>Tellimya ferruginosa</i>	0,60	0,00	2,27	
Taxa	Av. Abund. (Peniche and Queimado group)	Av. Abund. (Almograve)	Contrib. %	Cum. %
<i>Mytilus galloprovincialis</i>	4,45	6,54	5,77	5,77
<i>Hiatella arctica</i>	0,26	2,33	5,58	11,35
<i>Lasaea rubra</i>	2,30	3,44	4,58	15,93
<i>Steromphala umbilicalis</i>	0,59	1,66	3,22	19,15
<i>Musculus costulatus</i>	0,87	1,97	3,05	22,20
<i>Mytilaster minimus</i>	2,43	3,01	2,94	25,14
Syllidae	1,03	1,74	2,93	28,07
<i>Dikoleps cutleriana</i>	0,14	1,21	2,92	30,99
<i>Cardita calyculata</i>	0,38	1,21	2,85	33,84
<i>Onchidella celtica</i>	0,45	1,15	2,85	36,70
<i>Patella ulyssiponensis</i>	0,53	1,11	2,77	39,46
<i>Melarhappe neritoides</i>	0,94	1,24	2,71	42,18
Muricidae	0,15	1,12	2,71	44,89
Nereididae	0,73	1,45	2,63	47,51
<i>Acanthochitona crinita</i>	0,53	1,22	2,53	50,04
Taxa	Av. Abund. (Peniche and Queimado group)	Av. Abund. (Alteirinhos)	Contrib. %	Cum. %
Naididae	0,05	2,16	7,95	7,95
<i>Mytilus galloprovincialis</i>	4,45	6,39	7,48	15,44
<i>Lasaea rubra</i>	2,30	3,29	5,29	20,72

<i>Mytilaster minimus</i>	2,43	3,25	4,76	25,48
<i>Tellimya ferruginosa</i>	0,60	1,66	4,21	29,69
<i>Jaera</i> sp.	0,54	0,78	3,28	32,97
<i>Onchidella celtica</i>	0,45	1,05	3,28	36,25
Nemertea	0,81	0,00	3,12	39,37
<i>Anurida maritima</i>	0,05	0,79	3,08	42,45
Anthozoa	0,97	0,98	2,96	45,41
<i>Tanais dulongii</i>	0,79	0,39	2,85	48,26
<i>Steromphala umbilicalis</i>	0,59	0,62	2,64	50,90
Balanomorpha	0,56	0,00	2,20	
<i>Patella ulyssiponensis</i>	0,53	0,00	1,89	
Taxa	Av. Abund. (Magoito)	Av. Abund. (Cabo Raso)	Contrib. %	Cum. %
<i>Mytilus galloprovincialis</i>	5,30	2,50	10,92	10,92
<i>Idotea</i> sp.	1,83	0,42	6,05	16,96
<i>Lepidochitona cinerea</i>	1,81	0,83	5,02	21,98
<i>Tanais dulongii</i>	0,66	1,31	4,32	26,30
<i>Jaera</i> sp.	0,94	1,33	4,04	30,34
<i>Lasaea rubra</i>	0,67	1,48	3,77	34,12
<i>Pachygrapsus marmoratus</i>	0,00	0,93	3,77	37,89
Hyalidae	1,95	2,72	3,50	41,38
<i>Anoplodactylus virescens</i>	0,17	0,92	3,23	44,61
Pyramidellidae	0,87	0,94	3,07	47,67
<i>Steromphala umbilicalis</i>	0,33	0,98	3,06	50,74
<i>Siphonaria pectinata</i>	0,00	0,67	2,50	
Taxa	Av. Abund. (Magoito)	Av. Abund. (Foz)	Contrib. %	Cum. %
<i>Idotea</i> sp.	1,83	0,00	9,15	9,15
<i>Mytilus galloprovincialis</i>	5,30	3,35	9,06	18,21
Anthozoa	1,98	0,36	7,83	26,04
<i>Lepidochitona cinerea</i>	1,81	0,20	7,74	33,78
<i>Mytilaster minimus</i>	1,25	2,24	5,36	39,13
<i>Jaera</i> sp.	0,94	0,00	3,96	43,09
Pyramidellidae	0,87	0,77	3,93	47,02
<i>Dynamene bidentata</i>	0,80	0,00	3,46	50,49
<i>Tanais dulongii</i>	0,66	0,00	2,99	
Taxa	Av. Abund. (Magoito)	Av. Abund. (Almograve)	Contrib. %	Cum. %
<i>Lasaea rubra</i>	0,67	3,44	6,85	6,85
<i>Mytilaster minimus</i>	1,25	3,01	4,35	11,21
<i>Hiatella arctica</i>	0,53	2,33	4,33	15,53
Syllidae	0,17	1,74	3,94	19,47
<i>Idotea</i> sp.	1,83	0,33	3,75	23,22
Pyramidellidae	0,87	2,38	3,63	26,85
Nereididae	0,00	1,45	3,46	30,31
<i>Mytilus galloprovincialis</i>	5,30	6,54	3,28	33,59

<i>Steromphala umbilicalis</i>	0,33	1,66	3,18	36,77
<i>Melarhappe neritoides</i>	0,20	1,24	2,99	39,76
<i>Tellimya ferruginosa</i>	0,00	1,28	2,97	42,73
<i>Dikoleps cutleriana</i>	0,00	1,21	2,92	45,66
<i>Onchidella celtica</i>	0,00	1,15	2,80	48,45
<i>Cardita calyculata</i>	0,00	1,21	2,75	51,20
<i>Limapontia depressa</i>	0,00	0,90	2,17	
Nemertea	0,00	0,85	2,12	
Taxa	Av. Abund. (Magoito)	Av. Abund. (Alteirinhos)	Contrib. %	Cum. %
<i>Lasaea rubra</i>	0,67	3,29	8,94	8,94
Naididae	0,00	2,16	7,20	16,13
<i>Mytilaster minimus</i>	1,25	3,25	6,91	23,04
<i>Tellimya ferruginosa</i>	0,00	1,66	5,52	28,56
<i>Idotea</i> sp.	1,83	0,33	5,16	33,72
<i>Mytilus galloprovincialis</i>	5,30	6,39	4,13	37,84
Syllidae	0,17	1,31	3,90	41,74
Anthozoa	1,98	0,98	3,66	45,41
<i>Lepidochitona cinerea</i>	1,81	1,17	3,66	49,07
<i>Melarhappe neritoides</i>	0,20	1,28	3,64	52,71
Nereididae	0,00	1,06	3,53	
<i>Onchidella celtica</i>	0,00	1,05	3,45	
<i>Anurida maritima</i>	0,00	0,79	2,74	
Taxa	Av. Abund. (Cabo Raso)	Av. Abund. (Foz)	Contrib. %	Cum. %
Anthozoa	2,21	0,36	7,96	7,96
<i>Jaera</i> sp.	1,33	0,00	5,29	13,25
<i>Tanais dulongii</i>	1,31	0,00	5,09	18,34
Hyalidae	2,72	1,60	4,68	23,02
<i>Mytilaster minimus</i>	1,28	2,24	4,15	27,16
<i>Mytilus galloprovincialis</i>	2,50	3,35	4,05	31,22
Pyramidellidae	0,94	0,77	3,60	34,82
<i>Anoplodactylus virescens</i>	0,92	0,00	3,58	38,40
<i>Pachygrapsus marmoratus</i>	0,93	0,17	3,56	41,96
<i>Pollicipes pollicipes</i>	0,33	0,92	3,45	45,41
<i>Musculus costulatus</i>	0,76	0,50	3,11	48,53
<i>Lepidochitona cinerea</i>	0,83	0,20	3,09	51,62
<i>Dynamene bidentata</i>	0,59	0,00	2,44	
Taxa	Av. Abund. (Cabo Raso)	Av. Abund. (Almograve)	Contrib. %	Cum. %
<i>Mytilus galloprovincialis</i>	2,50	6,54	9,00	9,00
<i>Lasaea rubra</i>	1,48	3,44	4,51	13,51
<i>Mytilaster minimus</i>	1,28	3,01	3,85	17,36
<i>Hiatella arctica</i>	0,76	2,33	3,54	20,90
Pyramidellidae	0,94	2,38	3,28	24,18
Nereididae	0,17	1,45	2,97	27,15

Anthozoa	2,21	0,93	2,94	30,09
Syllidae	0,70	1,74	2,90	33,00
<i>Musculus costulatus</i>	0,76	1,97	2,82	35,82
<i>Tellimya ferruginosa</i>	0,00	1,28	2,76	38,58
<i>Dikoleps cutleriana</i>	0,00	1,21	2,70	41,28
<i>Melarhappe neritoides</i>	0,39	1,24	2,60	43,88
<i>Onchidella celtica</i>	0,00	1,15	2,59	46,47
<i>Cardita calyculata</i>	0,00	1,21	2,55	49,02
<i>Tanais dulongii</i>	1,31	0,42	2,55	51,57
Phyllodoceidae	0,00	1,14	2,53	
Muricidae	0,00	1,12	2,44	
<i>Amphipholis squamata</i>	0,00	0,83	1,76	
Taxa	Av. Abund. (Cabo Raso)	Av. Abund. (Alteirinhos)	Contrib. %	Cum. %
<i>Mytilus galloprovincialis</i>	2,50	6,39	11,35	11,35
Naididae	0,00	2,16	6,31	17,65
<i>Mytilaster minimus</i>	1,28	3,25	5,77	23,42
<i>Lasaea rubra</i>	1,48	3,29	5,42	28,84
<i>Tellimya ferruginosa</i>	0,00	1,66	4,84	33,68
Anthozoa	2,21	0,98	3,77	37,45
<i>Patella ulyssiponensis</i>	1,20	0,00	3,52	40,97
<i>Tanais dulongii</i>	1,31	0,39	3,33	44,30
<i>Onchidella celtica</i>	0,00	1,05	3,03	47,32
<i>Pachygrapsus marmoratus</i>	0,93	0,00	2,76	50,08
<i>Anurida maritima</i>	0,00	0,79	2,40	
<i>Hiatella arctica</i>	0,76	0,00	2,08	
Taxa	Av. Abund. (Foz)	Av. Abund. (Almogrove)	Contrib. %	Cum. %
<i>Mytilus galloprovincialis</i>	3,35	6,54	7,91	7,91
<i>Lasaea rubra</i>	0,86	3,44	6,54	14,45
<i>Hiatella arctica</i>	0,17	2,33	5,34	19,78
<i>Lepidochitona cinerea</i>	0,20	1,80	4,04	23,82
Pyramidellidae	0,77	2,38	3,96	27,78
Syllidae	0,33	1,74	3,76	31,54
<i>Musculus costulatus</i>	0,50	1,97	3,61	35,15
<i>Melarhappe neritoides</i>	0,00	1,24	3,27	38,42
Nereididae	0,33	1,45	3,06	41,48
<i>Tellimya ferruginosa</i>	0,00	1,28	3,05	44,53
<i>Dikoleps cutleriana</i>	0,00	1,21	3,01	47,54
<i>Steromphala umbilicalis</i>	0,53	1,66	2,77	50,31
<i>Pollicipes pollicipes</i>	0,92	0,00	2,26	
<i>Limapontia depressa</i>	0,00	0,90	2,24	
Nemertea	0,00	0,85	2,20	
<i>Anoplodactylus virescens</i>	0,00	0,92	2,15	
Taxa	Av. Abund. (Foz)	Av. Abund. (Alteirinhos)	Contrib. %	Cum. %

<i>Mytilus galloprovincialis</i>	3,35	6,39	10,80	10,80
<i>Lasaea rubra</i>	0,86	3,29	8,78	19,59
Naididae	0,00	2,16	7,71	27,29
<i>Tellimya ferruginosa</i>	0,00	1,66	5,91	33,20
<i>Melarhaphe neritoides</i>	0,00	1,28	4,54	37,74
Hyalidae	1,60	2,72	4,02	41,76
<i>Mytilaster minimus</i>	2,24	3,25	3,73	45,48
<i>Lepidochitona cinerea</i>	0,20	1,17	3,69	49,17
Syllidae	0,33	1,31	3,47	52,64
<i>Patella ulyssiponensis</i>	0,96	0,00	3,38	
<i>Anurida maritima</i>	0,00	0,79	2,95	
Taxa	Av. Abund. (Almogrove)	Av. Abund. (Alteirinhos)	Contrib. %	Cum. %
<i>Hiatella arctica</i>	2,33	0,00	6,70	6,70
Naididae	0,00	2,16	6,25	12,95
<i>Lasaea rubra</i>	3,44	3,29	4,16	17,11
<i>Cardita calyculata</i>	1,21	0,00	3,34	20,45
<i>Steromphala umbilicalis</i>	1,66	0,62	3,20	23,65
<i>Patella ulyssiponensis</i>	1,11	0,00	3,20	26,85
<i>Dikoleps cutleriana</i>	1,21	0,20	3,00	29,84
Muricidae	1,12	0,17	2,89	32,74
Pyramidellidae	2,38	1,37	2,85	35,59
<i>Acanthochitona crinita</i>	1,22	0,33	2,83	38,42
Phyllodocidae	1,14	0,17	2,83	41,25
<i>Patella depressa</i>	1,86	0,95	2,69	43,94
<i>Melarhaphe neritoides</i>	1,24	1,28	2,62	46,56
<i>Limapontia depressa</i>	0,90	0,00	2,61	49,17
Syllidae	1,74	1,31	2,58	51,76
Nemertea	0,85	0,00	2,55	
<i>Amphipholis squamata</i>	0,83	0,00	2,29	

Appendix C: Photographic records of some macroinvertebrates specimens or parts of them identified in the sampled mussel beds. Photos captured through a dissecting microscope, with magnification ranging from 10x to 40x and no scale included.

Nereididae



Orbiniidae



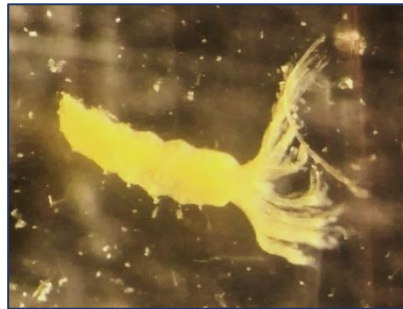
Phyllodocidae



Sabellaridae



Sabellidae



Syllidae



Anurida maritima



Herpetocypris reptans



Hyalidae



Idotea sp.



Jaera sp.



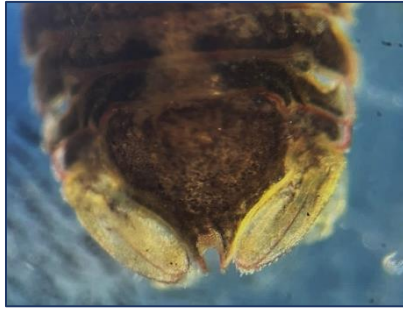
Campeopea hirsuta



Campecopea lusitanica



Dynamene bidentata



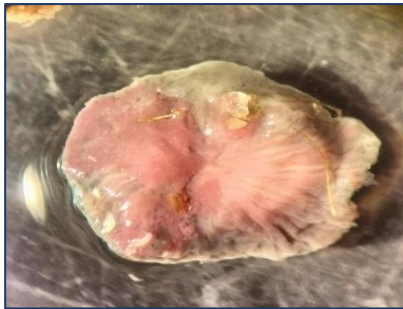
Pachygrapsus marmoratus



Tanais dulongii



Anthozoa



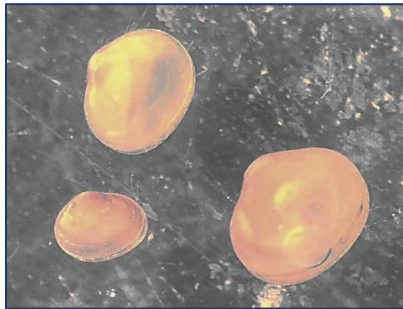
Amphipholis squamata



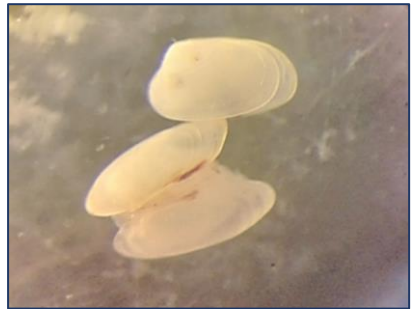
Cardita calyculata



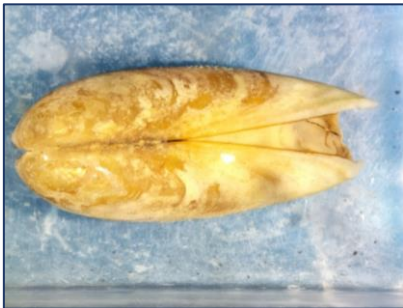
Lasaea rubra



Tellimya ferruginosa



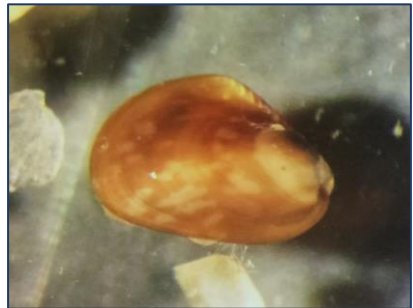
Leiosolenus aristatus



Musculus costulatus



Mytilaster minimus



Barleeia unifasciata



Pyramidellidae



Melampus sp. (larval stage)



Limapontia depressa



Littorina saxatilis



Melarhaphe neritoides



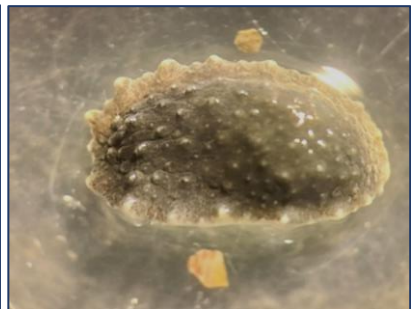
Nucella lapillus



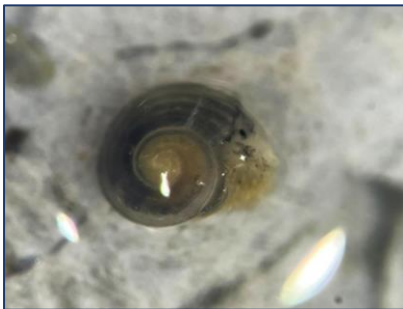
Omalogyra atomus



Onchidella celtica



Dikoleps cutleriana



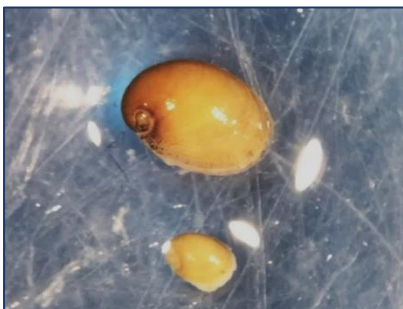
Potamopyrgus antipodarum



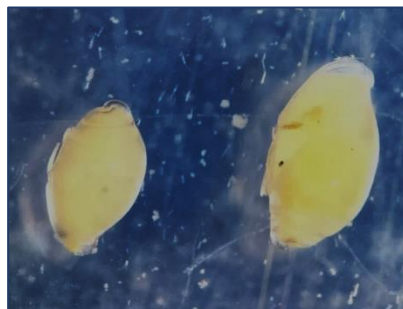
Steromphala umbilicalis



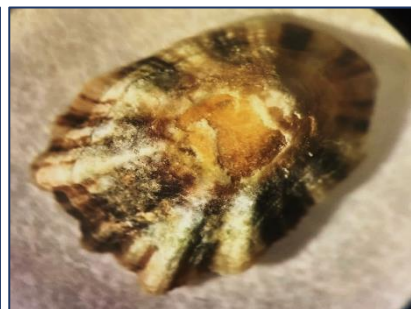
Velutinidae



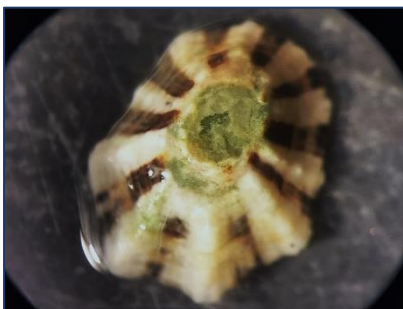
Acteon tornatilis



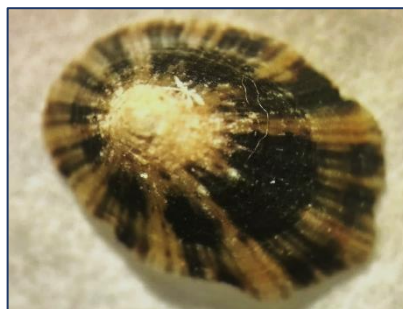
Patella depressa



Patella ulyssiponensis



Patella vulgata



Siphonaria pectinata



Acanthochitona crinita



Lepidochitona cinerea

