Marine Environmental Research 219 (2026) 108116

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: www.elsevier.com/locate/marenvrev

Effects of sediment on a rocky intertidal habitat-forming species and its harboured invertebrate assemblages

Puri Veiga [a,b,*], Ana Catarina Torres [a,b], Isabel Sousa-Pinto [a,b], Marcos Rubal [c]

[a] CIIMAR/CIMAR LA, Interdisciplinary Centre of Marine and Environmental Research, University of Porto, Terminal de Cruzeiros do Porto de Leixões, Matosinhos, 4450-208, Portugal
[b] Department of Biology, Faculty of Sciences, University of Porto, Rua do Campo Alegre s/n, Porto, 4169-007, Portugal
[c] Centre of Molecular and Environmental Biology (CBMA/ARNET), Department of Biology, University of Minho, Braga, 4710-057, Portugal

ARTICLE INFO

Keywords:
North-east atlantic
North Portugal
Mussels
Mytilus galloprovincialis
Macrofauna
Sedimentation

ABSTRACT

Sedimentation in rocky shores occurs through natural processes, but it is rising globally due to anthropogenic activities. However, few studies have assessed sediment effects on habitat-forming species and its harboured assemblages. To fill this knowledge gap, the mussel *Mytilus galloprovincialis* was considered as model habitat-forming to evaluate differences associated with varying sediment loads on mussel density and its invertebrate assemblages harboured. Field data were obtained at two non-urban intertidal rocky shores in the Northern Portuguese coast. First, the relationship between sediment load in mussel clumps and the associated invertebrate assemblages was examined in terms of abundance, richness, Pielou and Shannon indexes and multivariate structure. Then, mussel clumps with low and high sediment load were selected at each rocky shore to test differences on density and size of mussels and assemblage descriptors between them.

Sediment on mussels was composed by very coarse and coarse sand and showed a patchy distribution, but density and size of mussels were unaffected by sediment. Our results suggest significant effects of sediment on invertebrate assemblage associated with mussels specifically, decreasing evenness and heterogeneity of assemblages by favouring species tolerant to sediment (annelids, copepods and nematodes) and reducing the abundance of grazers and *Nucella lapillus*. As grazers and *N. lapillus* are considered keystone species, changes on them may trigger cascading effects on rocky shore ecosystems.

Our results highlight that even sedimentation derived from natural processes may impact intertidal biodiversity, which should be considered when managing coastal interventions specially in the current global change framework that probably will exacerbate sedimentation.

1. Introduction

Intertidal rocky habitats support biologically diverse and productive assemblages (Branch and Steele, 2001; Benedetti-Cecchi and Trussell, 2014), but they are amongst the most physically harsh habitats on Earth (Tomanek and Helmuth, 2002). Their position at the land–sea boundary exposes local assemblages to extreme fluctuations of physical conditions derived from the gradient between marine and terrestrial conditions (Branch and Steele, 2001). At the same time, they are easily accessible to humans and are exposed to many anthropogenic activities and disturbances (Thompson et al., 2002; Kunze et al., 2021).

Sedimentation is among the most prevalent and growing disturbance on rocky shores (Airoldi, 2003; Schiel and Gunn, 2019). Sediments can reach intertidal rocky shores due to natural processes such as river flows and cliff erosion (Thompson et al., 2002; Airoldi, 2003). However, the most common natural process that contribute to sediment inputs to intertidal rocky shores is the resuspension and transport of sediments from nearby habitats (beaches and subtidal areas) by wind, currents and waves (Airoldi, 2003). Natural sedimentation can be intensified by weather extreme events (e.g., storms, floods), which are becoming more common in the current scenario of global change (Scavia et al., 2002; Kooistra et al., 2025). Furthermore, sediment load in coastal habitats is rising globally as result of anthropogenic activities being expected to increase in the future (Thompson et al., 2002; Balata et al., 2007).

* Corresponding author. CIIMAR/CIMAR LA, Interdisciplinary Centre of Marine and Environmental Research, University of Porto, Terminal de Cruzeiros do Porto de Leixões, 4450-208, Matosinhos, Portugal.
E-mail address: puri.sanchez@fc.up.pt (P. Veiga).

https://doi.org/10.1016/j.marenvres.2026.108116
Received 18 February 2026; Received in revised form 10 May 2026; Accepted 11 May 2026
Available online 15 May 2026
0141-1136/© 2026 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

Nowadays sedimentation is of primary concern for coastal ecosystem functioning since the scale and extent of anthropogenic sedimentation frequently overdo that from natural processes [e.g. (Lazo et al., 2025; GESAMP, 1994),].

Sedimentation in rocky shores can emerge from direct anthropogenic alterations in the nearby coastal landscape such as industrial and domestic discharges, mining activities, infrastructure constructions (e.g., roads, bridges, harbours), dredging and beach nourishment (Airoldi, 2003; Magris and Ban, 2019). Nevertheless, human activities often influence sediment input to rocky shores indirectly by advancing soil erosion, altering the shoreline and river basins, which modify hydrodynamics and bottom features (Magris and Ban, 2019; Miller et al., 2002). Recent research points out that the instalment of offshore renewable energy devices (wind, wave and tidal) will also increase sedimentation in coastal habitats (Rezaei et al., 2023).

In this context, the increase of sediment deposition in coastal areas is perceived as a great threat to biodiversity worldwide (Magris and Ban, 2019; United Nations Environmental Programme, 1995). Rocky shores are amongst the habitats potentially most sensitive to sedimentation since once deposited, sediment can directly bury, smother, abrade and/or scour sessile and vagile organisms, which are the majority on rocky intertidal shores (Airoldi, 2003; Atalah and Crowe, 2010; Anderson et al., 2008a; Hutchison et al., 2020; Vaselli et al., 2008). Moreover, it can indirectly modify habitats and interplays with other physical and biological factors, namely reducing light or oxygen (Magris and Ban, 2019; Miller et al., 2002) and changing species interactions such as reducing grazing and competition (Engledow and Bolton, 1994; Airoldi and Hawkins, 2007). Previous studies have found sediment impacts on settlement, recruitment, growth and survival of taxa, eventually favouring sediment tolerant species against the most sensitive ones (Minchinton and Fels, 2013; Atalah and Crowe, 2010; Dos Santos et al., 2018). Regarding diversity, previous studies have found adverse effects of sediment determined by the dominance of sediment tolerant species (Airoldi, 2003; Engledow and Bolton, 1994). However, other studies reported a positive effect of sediment on diversity due to increased habitat heterogeneity (Thompson et al., 2002; Prado and Castilla, 2006).

Habitat-forming species (e.g., seaweeds, bivalves, corals) are common and in many cases dominant on intertidal rocky shores globally (Veiga et al., 2020; King et al., 2025) and they offer protection from abiotic and biotic pressures (Arribas et al., 2013; Cameron et al., 2024). Therefore, they play critical functions being considered biodiversity hotspots (Cameron et al., 2024; Veiga et al., 2022a; Torres et al., 2022). Many of these species are able of trapping sediment and shape sediment distribution (transport and deposition) in intertidal shores (Cameron et al., 2024; Airoldi and Virgilio, 1998; Crowe et al., 2004), but quantitative data are still very scarce (Airoldi, 2003).

The most noticeable habitat-forming species on exposed or moderately exposed intertidal shores along the south of the European Atlantic and Mediterranean coasts is the mussel, *Mytilus galloprovincialis* Lamarck, 1819 (Veiga et al., 2022a; Ramos-Oliveira et al., 2021). Previous studies demonstrated that mussel beds are exposed to high mortality rates as consequence of sediment scouring and burial and by the high content of suspended sediment in water (Anderson et al., 2008a; Dos Santos et al., 2018; Hutchison et al., 2016). However, effects of sediment on mussels are depend on burial duration, sediment grain size and mussel species; for instance, *M. edulis* Linnaeus, 1758 is able of emerging from burial (Hutchison et al., 2016, 2020). Moreover, Zardi et al. (2008) found a negative correlation between sediment load and attachment capacity to substrate in two mussel species (*M. galloprovincialis* and *Perna perna* (Linnaeus, 1758)). Therefore, sediment indirectly makes mussels more susceptible to removal by other disturbances.

At the same time, mussel clumps are recognised for accumulating large amounts of sediments (Cameron et al., 2024; Crowe et al., 2004; Ramos-Oliveira et al., 2021). Different studies in South Africa and Argentina pointed out that sediment load on rocky intertidal assemblages is seasonal, being maximum in autumn (Anderson et al., 2008a; Dos Santos et al., 2018; Zardi et al., 2008). However, mussel clumps kept up consistent sediment loads over a year despite temporal variations in sediment deposition (Dos Santos et al., 2018). Likewise, retained sediment in mussel clumps in Northern Portugal was not significantly different between dates and seasons (Ramos-Oliveira et al., 2021), suggesting a constant capacity of mussel beds to retain sediment and supporting the hypothesis that mussels play an important role on coastal sediment dynamics. However, the capacity of biological factors to shape the occurrence and distribution of sediments on rocky coasts has been widely overlooked (Airoldi, 2003).

Sediment included in mussel clumps is considered a structural component and can shape the structure of mobile and sessile assemblages harboured by mussel clumps (Airoldi, 2003; Cameron et al., 2024; Crowe et al., 2004). However, effects of sediment on invertebrate assemblages associated with mussel clumps have been scarcely studied (Dos Santos et al., 2018) and quantitative data from field observations on the sediment amount accumulated are still scarce (Airoldi, 2003). Recent losses of habitat-forming species such as mussel beds due to anthropogenic factors (King et al., 2025; Fields and Silbiger, 2022; Montie and Thomsen, 2023) have advocated the necessity to understand drivers shaping their associated assemblages. More research is required to ascertain effects of increasing sediment loads on intertidal rocky assemblages.

The present study aimed to improve our knowledge on how sediment load deposited over *M. galloprovincialis* clumps influences mussel density and size, and its hosted invertebrate assemblages on exposed rocky intertidal shores in the north Portuguese coast. A field approach was used to provide realistic and quantitative data of sediment load on mussels and its influence on intertidal biodiversity. The following working hypotheses were tested: 1) there is a relationship between sediment load with mussel density and the abundance (N), richness (S), Pielou (J') and Shannon indexes (H') and the multivariate structure of associated invertebrate assemblages; 2) density and size of mussels, N, S, J' and H' are lower on mussel clumps with high sediment load than on clumps with low sediment; 3) the multivariate structure of invertebrate assemblage differs between mussel clumps with high and low sediment load and it is more homogenous in clumps with high sediment load.

2. Material and methods

2.1. Study area

This study was done at two intertidal rocky shores, separated about 2 km, in the northern Portuguese coast (NW of Iberian Peninsula): Âncora (41°49′25.93″ N; 8°52′27.42″ W) and Moledo (41°50′28.81″ N; 8°52′32.30″ W), which are similarly exposed to the dominant W and NW swell. The coastal landscape includes hard and sedimentary bottoms, and it often results in a patchy combination of both. This area and harboured benthic assemblages on hard and sedimentary bottoms were explicitly described in previous research [e.g. (Rubal et al., 2014; Veiga et al., 2013, 2014, 2017),]. Studied rocky shores are granitic with gentle slope and are exposed to prevalent north-westerly waves and winds. They shield small resident populations (<50 000 total inhabitants) and they do not present great commercial or industrial plants so they can be considered non-urban shores (Veiga et al., 2022b). The tidal regime is semidiurnal, with the maximum height above chart datum ranging between 3.5 and 4.0 m. Moreover, the study area is subjected to seasonal upwelling that provides nutrients and increases the primary production in the water column (Lemos and Pires, 2004).

The study was done at the mid intertidal level (between 1.5 m and 2 m above Chart Datum) where *M. galloprovincialis* is the most conspicuous species (Veiga et al., 2020; Torres et al., 2022), whereas tidepools are dominated by macroalgae (Rubal et al., 2014).

2.2. Sampling design and sample processing

Sampling was done in August 2018. At each rocky shore (i.e., Âncora and Moledo), six plots (2 × 2 m), spaced few meters apart, were marked in the *M. galloprovincialis* beds, with >80% of mussel cover. Three replicates of 10 × 10 cm were randomly collected, spaced dozens of cm apart, per plot and shore. In replicates, mussel cover was 100% and macroalgae were absent. All mussels and associated fauna within each quadrat were scraped, stored in a labelled plastic bag and preserved in buffered formalin 4 % with rose Bengal until further study.

In the laboratory, each replicate was washed through a tower of 5 sieves of declining mesh size (i.e., 1 mm, 0.5 mm, 0.25 mm, 0.125 mm and 0.063 mm). In order to calculate the amount and grain-size composition of sediment accumulated in mussel beds, sediment retained in each sieve was dried at 60 °C for 24 h and then weighed. Mussels retained in each sieve were counted to obtain the total mussel density (number of individuals per 100 cm^2). To test the effect of sediment load on the diversity and structure of invertebrate assemblages on mussel beds, all invertebrates retained in the 1- and 0.5-mm sieves were sorted and identified to the lowest taxonomic level (species whenever possible). Moreover, twenty random mussels were separated to measure their shell length with vernier callipers (±0.1 mm).

2.3. Data analyses

Data were analysed by means of univariate and multivariate techniques using PRIMER 6 and PERMANOVA+ and SPSS28. To test the working hypotheses two different experiments were done.

2.3.1. Experiment 1. Relationship between sediment load, mussel density and the structure of associated invertebrate assemblages

To explore the relationship between univariate response variables (i.e., mussel density, N, S, H′ and J′) and total sediment load on mussel clumps, rank correlation analyses were done. Due to the non-normal distribution of the data, Spearman's rank correlation was used.

A Distance-based linear model (DISTLM) (Anderson, 2002) was also carried out to quantify the percentage of variability on the multivariate invertebrate assemblage associated with *M. galloprovincialis* (response variable) explained by each sediment grain sizes retained in mussel clumps (predictor variables): very coarse sand (>1 to ≤2 mm), coarse sand (<0.5 to ≤1 mm), medium sand (>0.25 to ≤0.5 mm), fine sand (>0.125 to ≤0.25 mm) and very fine sand (>0.063 to ≤0.125 mm). This analysis was based on Bray-Curtis similarity (data square root transformed) with 9999 permutations of residuals. R^2 routine was used as a selection criterion, and the contribution of each independent variable was described by the amount of explained variation. All analyses were based on a 'forward' selection procedure (Anderson et al., 2008b).

Draftsman plots were previously done to check the skewness of different sediment grain sizes and data were Log (x+1) transformed before DISTLM (Anderson, 2002). Total sediment showed a strong correlation with very coarse and coarse sands (r = 0.98 and 0.96, respectively). As this meant that they are redundant variables, total sediment was removed from the analysis.

2.3.2. Experiment 2. Effects of high versus low sediment load on mussel density and the structure of invertebrate assemblages associated with mussel clumps

As dominant sediment grain sizes, very coarse and coarse sands, showed a strong correlation with total sediment, the later was considered in this experiment. According to results achieved in experiment 1, five replicates with high sediment load (>100 g) and 5 replicates with low sediment load (<30 g) were selected at each rocky shore (i.e., Âncora and Moledo).

All univariate (mussel density, N, S, H′ and J′) and multivariate data were analysed using a two-way mixed model design with Shore (Sh) as a random orthogonal factor with two levels (Âncora and Moledo) and sediment load (Se) as a fixed orthogonal factor with two levels (Low and High), considering five replicates per Sh and Se. Analyses of variance (ANOVA) were done to test for differences between sediment load on total mussel density and N, S, H′ and J′ of invertebrate assemblages associated with mussel clumps. Previously to ANOVA, normality of data was checked by Shapiro–Wilk test and Cochran's C tests were done to check for homogeneity of variances. When relevant, Student-Newman-Keuls (SNK) tests were used for post-hoc comparisons of means for levels of factors involved in significant interactions. Permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001) based on a Bray-Curtis similarity matrix (square root transformed) was used to analyse differences in the composition of invertebrate assemblages associated with mussel clumps depending on their sediment load. PERMANOVA was also used to analyse differences in mussel size. When the number of unique permutations was low, Monte Carlo P-values were considered (Anderson et al., 2008b).

In order to test whether differences of assemblages between clumps with low and high sediment load were due to different multivariate dispersion between groups rather than in the location of centroids, the PERMDISP procedure was used (Anderson, 2006). Multivariate patterns were illustrated by non-metric multidimensional scaling (nMDS) ordination based on replicates per shore. PERMDISP was also used to test differences on multivariate invertebrate assemblage heterogeneity between mussel clumps with high and low sediment load.

The SIMPER procedure (Clarke, 1993) was used to determine the contribution (δi%) of each taxon to the Bray-Curtis dissimilarity between assemblages on mussel clumps with low and high sediment load (δi). The ratio δi/SD(δi) was used to quantify the consistency of the contribution of a particular taxon to the average dissimilarity in all pair-wise comparisons of samples between clumps with low and high sediment load. Values ≥ 1 indicated a high degree of consistency (Clarke and Gorley, 2015).

3. Results

3.1. Sediment load in mussel clumps

The total mean sediment load (±SE) in mussel clumps ranged between 2.60 ± 0.64 and 155.77 ± 24.71 g × 100 cm^2 in Âncora and 15.96 ± 0.28 and 362.46 ± 116.67 g × 100 cm^2 in Moledo (Fig. 1). Regarding sediment grain sizes, very coarse and coarse sands were the dominant components (~73% in Âncora and ~86% in Moledo; Fig. 1). As silt and clay content was negligible, only sand was included in the study.

3.2. Relationship between sediment load with mussel density and the structure of invertebrate assemblages associated with mussel clumps

Sediment load was not significantly correlated with mussel density (Fig. 2). Values of N and S associated with mussel clumps significantly increased with sediment load (Fig. 2). However, negative significant correlations were detected between sediment load and H′ and J' indexes (Fig. 2).

Distance-based linear models pointed out that medium sand, coarse sand and fine sand explained >50% of the variation in the multivariate structure of invertebrate assemblages associated with mussel clumps (Table 1).

3.3. Effects of high versus low sediment load on mussel density and the structure of associated invertebrate assemblages

Mussel density and taxon richness of invertebrates associated with mussel beds were not significantly different between clumps with high and low sediment load (Table 2; Fig. 3). Similarly, mussel size was not significantly different between clumps with high and low sediment load (Table 3; Fig. 3).

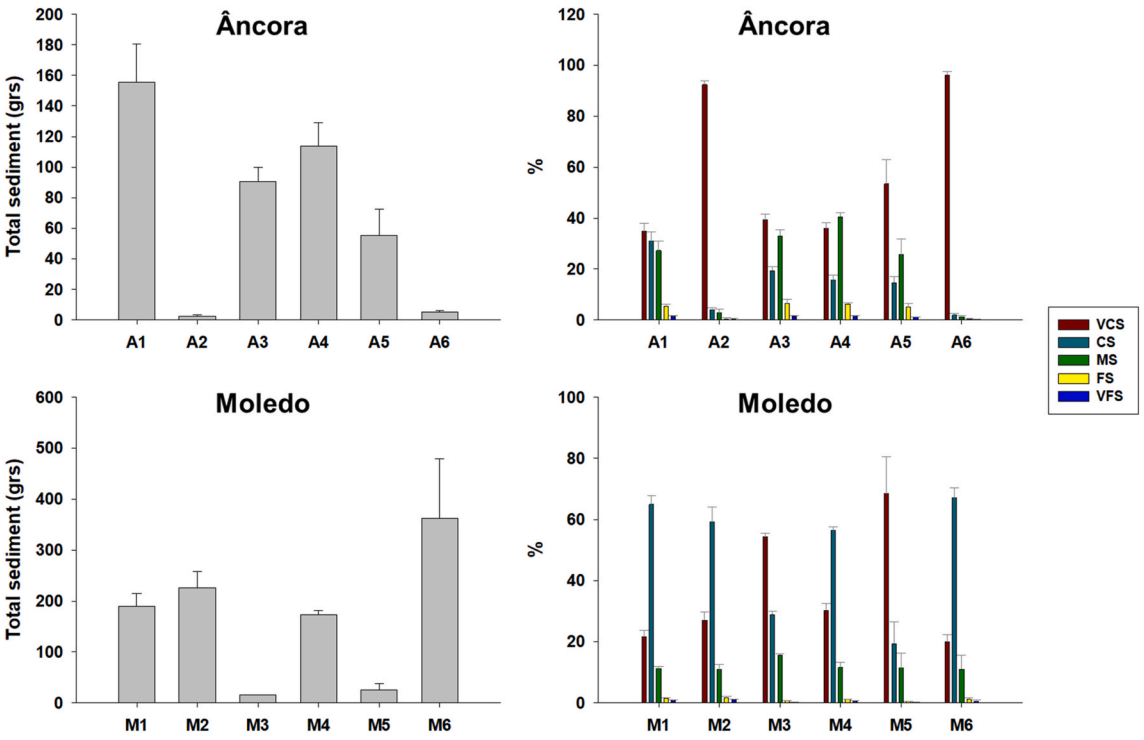


Fig. 1. Mean total (±SE, n = 3) sediment load and % of sediment grain sizes (VCS = very coarse sand, 1-2 mm; CS = coarse sand, 0.5-1 mm; MD = medium sand, 0.25-0.5 mm; FS = fine sand, 0.125-0.25 mm; VFS = very fine sand 0.063-0.125 mm) in different mussel plots (1-6) and shores (A = Âncora and M = Moledo).

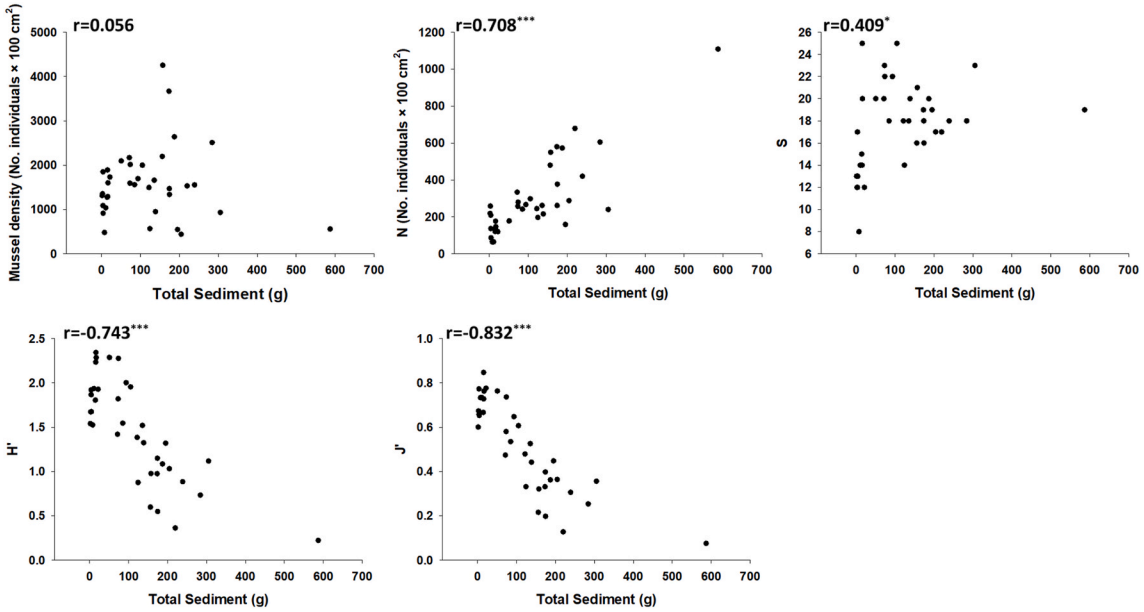


Fig. 2. Spearman rank's correlations (r) between total sediment load in mussel clumps and abundance (N), taxa richness (S) and Margalef (H′) and Pielou (J′) indexes of invertebrate assemblages associated with mussel clumps. *: $p < 0.05$; ***: $p < 0.001$.

However, N showed higher values in clumps with high sediment load, but only in Moledo (Table 2; Fig. 3). Values of H′ and J′ were higher in clumps with low sediment load in both studied shores (Table 2; Fig. 3).

The multivariate structure of invertebrate assemblage associated with mussel beds also showed significant differences for Shore × Sediment load interaction (Table 4). The nMDS ordination disclosed a clear separation between mussel clumps with high and low sediment load (Fig. 4). Moreover, the PERMDISP analysis for the interaction Shore × Sediment load ($F = 1.0023$, $p = 0.366$) indicated that the dispersion of replicates did not provide a significant contribution to the observed differences. However, PERMDISP analysis for the factor sediment load ($F = 4.915$, $p = 0.032$) indicated that the dispersion of assemblages on mussel clumps with low sediment load was significantly greater (i.e., more heterogenous) than that on high sediment load (i.e., more homogenous) (Fig. 5).

SIMPER analysis pointed out that the dissimilarity between high and low sediment loads was higher than that between rocky shores. Bray-

Table 1
Results of DistLM carried out to ascertain the role of different sediment grain sizes, considering forward-selection of variables, where amount explained by each variable added to model is conditional on variables already in the model (i.e., those variables listed above it) on the multivariate structure of invertebrate assemblages associated with *Mytilus galloprovincialis*. %Var: percentage of variance in species data explained by that variable; Cum. %: cumulative percentage of variance explained. Variables significantly related to faunal assemblages indicated in bold. Very coarse sand (1-2 mm), coarse sand (0.5-1 mm), medium sand (0.25-0.5 mm), fine sand (0.125-0.25 mm) and very fine sand (0.063-0.125 mm).

Variable	%Var	*Pseudo-F*	p	Cum (%)
Medium sand	39.90	22.57	**0.000**	39.902
Coarse sand	7.13	4.45	**0.000**	47.036
Fine sand	4.51	2.98	**0.004**	51.544
Very coarse sand	2.69	1.82	0.059	54.232
Very fine sand	1.21	0.82	0.610	55.442

Curtis dissimilarity between low and high sediment load was 71.72% in Âncora and 72.78% in Moledo whereas dissimilarity between Âncora and Moledo was 38.35% at high sediment load and 47.38% at low sediment load. Moreover, SIMPER analysis identified 25 taxa as main responsible for differences on invertebrate assemblages associated with mussel beds between clumps with high and low sediment load, which showed an average dissimilarity of 72% in both studied shores (Âncora and Moledo). Collectively, these taxa contributed more than 90% to the total dissimilarity. The contribution to the percentage of dissimilarity of 16 taxa was consistent between Âncora and Moledo. Ten of these taxa, nematodes; the annelids: *Eulalia clavigera* (Audouin and Milne Edwards, 1833), *Syllis pulvinata* (Langerhans, 1881) and Oligochaetes; the molluscs: *Hiatella arctica* (Linnaeus, 1767), *Lasea rubra* (Montagu, 1803), *Runcina* sp. and *Steromphala umbilicalis* (da Costa, 1778); and the arthropods: Copepods and Chironomids reached higher abundance in clumps with high sediment load. The remaining 6 taxa, 2 molluscs (*Nucella lapillus* (Linnaeus, 1758) and *Patella depressa* Pennant, 1777) and 4 arthropods (*Apohyale stebbingi* (Chevreux, 1888), *Hyale* spp., *Idotea neglecta* G. O. Sars, 1897 and *Jaera (Jaera) praehirsuta* Forsman, 1949) reached higher abundance in clumps with low sediment load.

4. Discussion

This study suggests significant effects of sediment load on invertebrate assemblage associated with *M. galloprovincialis* clumps. Specifically, an increase in retained sediment correlated with a decreased assemblage evenness and heterogeneity. In this way, our results contribute to improve the understanding how biodiversity harboured by a key habitat-forming species is modified by sediment load as a prevalent and increasing stressor (Thompson et al., 2002; Atalah and Crowe, 2010; Drakard et al., 2025).

Sediment load on mussel beds in our study ranged from ~260 to 36000 g × m^2. Most of our values were above sediment treatments (i.e., 500, 1000 and 2000 g × m^2) considered by Airoldi and Hawkins (2007) to mirror sediment loads on urban rocky coasts and testing their effects on *Patella vulgata* Linnaeus, 1758. However, rocky shores included in our study are far from urban areas (Rubal et al., 2014; Veiga et al., 2022b). In this way, sediment accumulated on mussel beds in our study probably derives from natural processes. Moreover, our results indicated that sediment on mussel clumps was composed mainly by very coarse and coarse sands. Similar results were found by Ramos-Oliveira et al. (2021) when assessing spatio-temporal variability of sediment accumulated in *M. galloprovincialis* beds in Northern Portugal. Previous studies done on intertidal and subtidal soft bottom in the study area also showed the dominance of these grain size classes (Veiga et al., 2014, 2017), suggesting that sediment retained in mussel clumps in the current study is probably transported from nearby sedimentary areas or from the same source.

Table 2
ANOVA examining effects of sediment load on mussel density, total number of individuals (N), total number of taxa (S), Shannon diversity index (H') and Pielou evenness index (J') of invertebrate assemblages associated with *Mytilus galloprovincialis*. df: degrees of freedom; MS: mean squares; *F*: F-ratio. Significant effects are indicated in bold.

Source of variation	df	Mussel density			N			S			H'			J'		
		MS	*F*	p	MS	*F*	p	MS	*F*	p	MS	*F*	p	MS	*F*	p
Shore (Sh)	1	1320980.00	5.68	**0.03**	27825.80	4.20	0.057	28.80	2.91	0.107	0.001	0.01	0.920	0.006	1.28	0.275
Sediment load (Se)	1	68445.00	0.18	0.746	173724.80	2.74	0.346	24.20	0.72	0.553	3.898	3.77	0.303	0.627	8.87	0.206
Sh × Se	1	384753.80	1.65	0.217	63393.80	9.56	**0.007**	33.80	3.41	0.083	1.033	20.21	**0.000**	0.071	14.52	**0.002**
Residual	16	232754.90			6630.85			9.90			0.051			0.005		
Total	19															
Transformation		none			none			none			none			none		
Cochran's test		$C = 0.32$	ns		$C = 0.61$	ns		$C = 0.59$	ns		$C = 0.35$	ns		$C = 0.33$	ns	

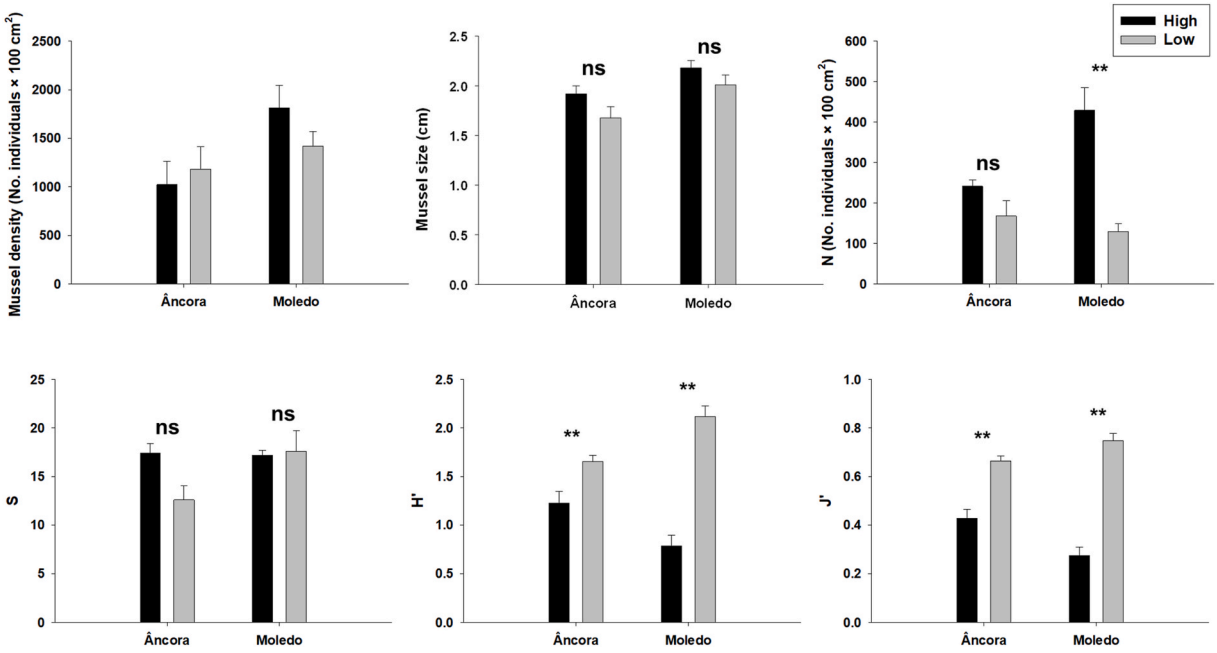


Fig. 3. Mean (±SE) mussel density and size, abundance, richness and Margalef and Pielou indexes of invertebrate assemblages associated with mussel clumps characterised by high (>100 g) and low (<30 g) sediment load at two studied shores. For all variables n = 5 except for mussel size (n = 100). n.s = not significant; ** = $p < 0.01$.

Table 3
PERMANOVA examining effects of sediment load on size of *Mytilus galloprovincialis*. df: degrees of freedom; MS: mean squares. P(MC) = p-value calculated by Monte Carlo method.

Source of variation	df	MS	*Pseudo-F*	p	Unique permutations	p (MC)
Shore (Sh)	1	1966.3	0.96	0.505	9950	
Sediment load (Se)	1	1503.8	0.71	0.501	3	0.684
Sh × Se	1	2116.3	1.03	0.441	9930	
Residual	16	649.6				
Total	19					

Table 4
PERMANOVA examining effects of sediment load on the structure of the invertebrate assemblage associated with *Mytilus galloprovincialis* (Data square root transformed). df: degrees of freedom; MS: mean squares. P(MC) = p-value calculated by Monte Carlo method.

Source of variation	df	MS	*Pseudo-F*	p	Unique permutations	p (MC)
Shore (Sh)	1	2082.50	3.21	**0.001**	9930	
Sediment load (Se)	1	19064.00	8.40	0.249	3	**0.031**
Sh × Se	1	2270.50	3.50	**0.000**	9944	
Residual	16	649.63				
Total	19					

Our sediment values were higher than those retained by turf-forming algae (86-924 g × m^2) (Airoldi and Virgilio, 1998). Values within the range provided in our study were also found within beds of *P. perna* and *M. galloprovincialis* in South Africa (4444 - 14 444 g × m^2) (Zardi et al., 2008) and of *Brachidontes rodriguezii* (A. d'Orbigny, 1846) beds in Argentina (19 630 - 23 230 g × m^2) (Dos Santos et al., 2018). However, our results revealed a higher variation on mussel sediment load (by two orders of magnitude) compared to other studies (Dos Santos et al., 2018; Zardi et al., 2008). Sediment deposition on rocky shores is spatially patchy, generating a sediment mosaic that diverges in size and may influence its effect as disturbance and modify resource availability (e.g., habitat, light, oxygen) (Airoldi, 1998). Although the capacity of biological factors to shape the occurrence and distribution of sediments on rocky coasts has been widely overlooked (Airoldi, 2003), the thickness of mussel clumps is positively correlated to sediment load (Ramos-Oliveira et al., 2021). Crowe et al. (2004) suggest that smaller mussels may trap a greater volume of sediment per unit of area. However, differences in mussel size between clumps with high and low sediment load were not detected in our study. Although not considered here, differences in mussel clump thickness could have contributed to patchy distribution of sediment. In fact, Widdows et al. (2002) demonstrated experimentally, that one day after depositing 6 cm of sediment over a mussel bed, the mussel aggregation restructured to elevate mussels and drop sediment level. Therefore, mussels seem to play an important role in sediment dynamics by trapping and stabilising sediment analogously to previous evidence reported for turf-forming algae (Airoldi and Virgilio, 1998).

Mussel mortality driven by sediment burial is widely documented [e.g., 18,24,35]. Our results, instead, revealed that mussel density was not affected by sediment load, leading to rebut our first and second hypotheses regarding mussel density. Similarly, the abundance of *Xenostrobus inconstans* (Dunker, 1856) in rocky shores of Australia was also not influenced by sediment addition (Minchinton and Fels, 2013). However, *B. rodriguezii* abundance was higher in sites less exposed to sand and its mortality increased 50% under experimental sediment burial (Dos Santos et al., 2018). Since sediment loads in (Dos Santos et al., 2018) are within our study's range, differences in sediment load did not appear to cause the lack of effect on mussel density. On one hand, mussel mortality increases with burial duration and burial by finer sediment fractions (Hutchison et al., 2016). Considering the sediment granulometry in our study, (very coarse and coarse sand), this could explain its negligible effect on mussel density. On the other hand, some mussel species (e.g., *M. edulis*) are capable of emerging from burial, particularly in coarser sediments under high energy environments (Hutchison et al., 2016, 2020), such as in our study area. This can potentially to explain the absence of differences on mussel density between high and low sediment loads. However, manipulative experiments will be necessary to disentangle this issue.

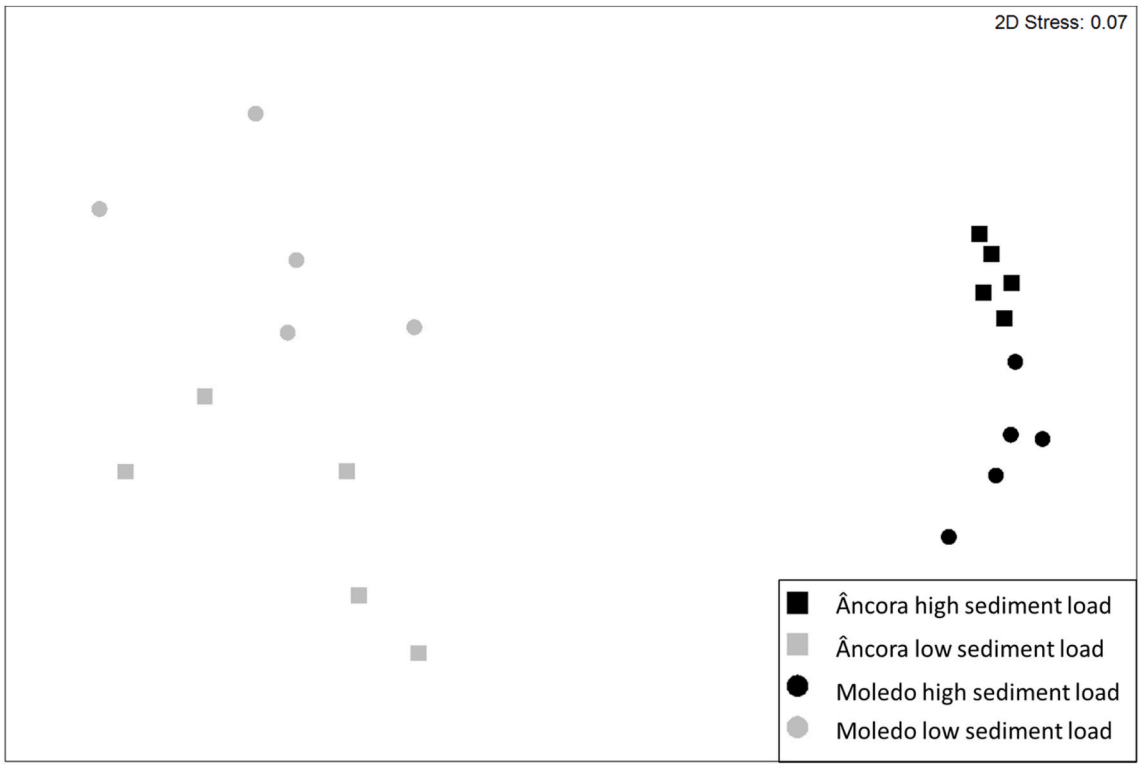


Fig. 4. nMDS ordination of invertebrate assemblages in clumps with high (>100 g) and low (<30 g) sediment load, based on Bray-Curtis similarities of square-root transformed abundances at two studied shores.

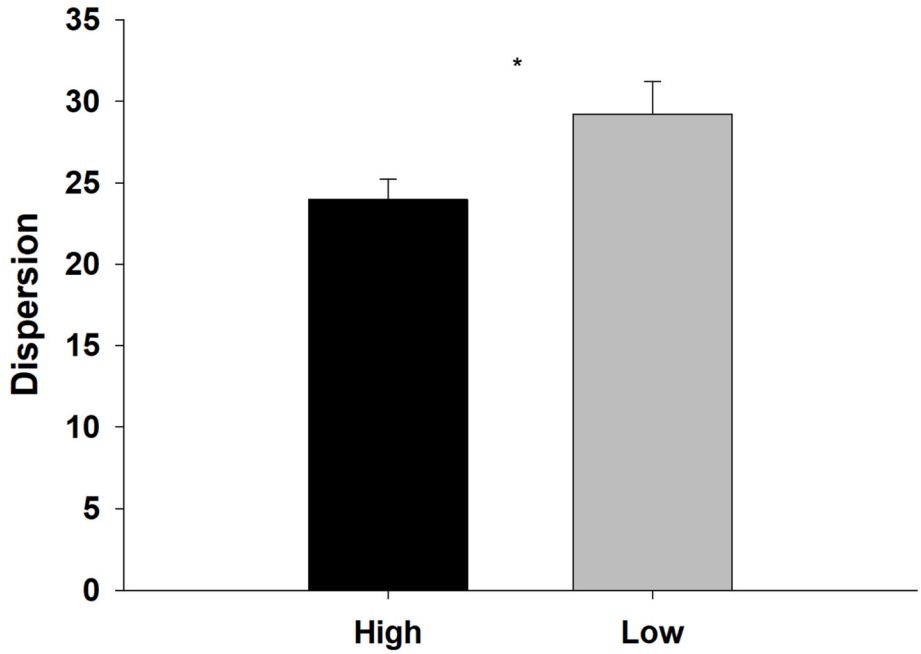


Fig. 5. Mean (±SE, n = 10) of dispersion (distance from mean) of invertebrate assemblages in clumps with high (>100 g; in black) and low (<30 g; in grey) sediment load, based on Bray-Curtis similarities of square-root transformed abundances. *: $p < 0.05$.

Our study also tested if there was a relationship between sediment accumulated in mussel clumps and the structure of their invertebrate assemblages. Results of experiment 1 confirmed this since sediment load was positively correlated with N and S. Similarly, abundance (Prado and Castilla, 2006) and richness of invertebrates on mussels (Arribas et al., 2013) increase with sediment load retained in mussel beds. This could be explained with the fact that the presence of sediment can increase complexity of the habitat provided by mussels (Thompson et al., 2002; Prado and Castilla, 2006). Particularly, the abundance and richness of soft-bottom organisms is favoured by sediment load on mussels (Airoldi, 2003; Crowe et al., 2004; O'Connor and Crowe, 2007). However, the correlation coefficient for S ($r = 0.409$), although significant, was lower than that for N ($r > 0.7$). Results of the experiment 2, pointed out no differences on S and higher values of N on mussel clumps with greater

sediment load. However, sediment effect on N was dependent on shore being significant only in one of the studied shores. Therefore, our second hypothesis was not supported by findings for S and N.

On the other hand, significant negative correlations for H′ and J′ indexes with sediment load ($r > 0.7$) were also found. Likewise, H′ and J′ reached significant higher values on mussel clumps with lower sediment load regarding those with higher sediment load. Thus, the first and second hypotheses were supported on the basis of the findings for H′ and J'. As H′ and J' englobe the number of taxa, but also the evenness, our results suggest that the sediment content can promote the number of individuals on mussel clumps, but also that the repartition of these individuals among different species is less equitable in clumps with greater sediment load. Dos Santos et al. (Dos Santos et al., 2018) also documented lower diversity and evenness of invertebrate assemblages on mussels in sites more affected by sand. Consistently, Engledow and Bolton (1994) documented that sand influenced algal diversity via equitability rather than species richness due to the increasing abundance of species tolerant to sediment, which become dominant under greater sediment load.

Regarding the whole invertebrate assemblage, >50% of its variability was explained by sediment content on mussel clumps supporting our first hypothesis regarding the relationship of multivariate assemblage and sediment. In the same way, invertebrate assemblage differed between mussel clumps with high and low sediment load. Mussel clumps with high sediment load showed a greater similarity and homogeneity of assemblages than those with low sediment load. In this way, our third hypothesis was supported. Our results match with those found by Balata et al. (2007), who documented that sediment reduced the dissimilarity between assemblages of algae and invertebrates. The increased similarity among assemblages under high sediment load mostly occurred by changes in the abundance of some taxa. Specifically, annelids, copepods, nematodes and the molluscs *L. rubra* and *S. umbilicalis* reached greater abundances on mussel clumps with higher sediment load. Nematodes and copepods are adapted to live among sediment interstices, so they probably benefited from the presence of coarse sands on mussels (Giere, 2009). Dos Santos et al. (Dos Santos et al., 2018) also found greater abundance of annelids on mussel clumps buried by sand. Some taxa as annelids or small bivalves (such as *L. rubra*) benefit from sediment biodeposits retained on mussel beds (Arribas et al., 2013). Magris and Ban (2019) in a meta-analysis documented a strong positive effect of sediment on annelids, explained by sediment containing food resources for suspension- and detritus-feeding annelids.

However, crustacean species (*I. neglecta*, *Hyale* spp. and *J. praehirsuta*) and the molluscs *P. depressa* and *N. lapillus* reached greater abundances on mussel clumps with low sediment load. The negative influence of sedimentation on grazer abundance such as *P. depressa* has been widely tested in observational and experimental studies [e.g., 22,23]. Sediment impacts on grazers include movement and attachment weakness, but also a reduction on feeding activity directly rising mortality or indirectly by altering and/or reducing food resources (algal assemblages) on rocky shores (Atalah and Crowe, 2010; Airoldi and Hawkins, 2007). Therefore, sediment effects could also be related to feeding preferences and resource availability. Although feeding preferences of isopods and amphipods are poorly understood and are flexible (Ingólfsson and Agnarsson, 2003), *Hyale* spp. and *Idotea neglecta* prefer grazing on mature algae (McBane and Croker, 1983; Jormalainen et al., 2001) and *Jaera* spp. prefers microalgae (Sjöberg, 1967). Therefore, sediment increasing on mussel clumps probably reduces feeding activity of these crustacean species. In contrast, the mollusc *S. umbilicalis*, that feeds on microalgae and epiphytic diatoms (Da Rosa et al., 2026), reached greater abundance on clumps with high sediment load. This pattern could be explained by biotic interactions since *S. umbilicalis* could probably take advantage of the lower numbers of grazers on mussels with high sediment load.

The dog whelk (*N. lapillus*), it is an important predator in intertidal rocky shores where it usually feeds on barnacles and mussels (Burrows and Hughes, 1991) and exerts a strong top-down control on intertidal ecosystems (Trussell et al., 2003; Contolini et al., 2020). When foraging, it moves short distances and attacks its preys by drilling or injecting a paralysing agent, followed by extraction of flesh through the drill hole or from between the opened shell valves (Hughes, 1986). Handling each prey items take from several hours to days. In this way, *N. lapillus* requires hard rocky substrates for attachment and to search preys. Sediment could modify the substratum, weakening its movement and attachment strength and directly prompting the removal of adults, juveniles and their egg capsules or indirectly influence its feeding (Tyler-Walters et al., 2007).

As in our study, Atala and Crowe (Atalah and Crowe, 2010) also documented that sediment effects are characterised by a compromise between tolerant and sensitive species, which shape alterations in assemblage structure. Minchinton and Fels (2013) also verified that increasing sedimentation led to changes in the composition of assemblages, favouring species that tolerate or are facilitated by sediment and those species more flexible in terms of habitat, such as nematodes, copepods and annelids in our study.

Our results provided evidence that sediment has potential to cause changes in the structure of invertebrate assemblages associated with an important habitat-forming species such as *M. galloprovincialis* in exposed intertidal rocky shores. Primarily, sediment load reduces the evenness and heterogeneity of invertebrate assemblages, favouring those species tolerant to sediment (annelids, copepods and nematodes) and reducing the abundance of grazers and *N. lapillus*. Considering that there is an extensive body of literature showing that keystone species as grazers and *N. lapillus* are able of shaping the structure of rocky shores assemblages [e.g. (Menge, 2000; Jenkins et al., 2005; Gilson and McQuaid, 2023),] changes on these species derived by sediment load as here reported could trigger cascading effects on rocky shore ecosystems although more research will be needed to test this issue.

Our results highlight that even sedimentation derived from natural processes has potential ecological impacts for intertidal biodiversity, which should be considered when managing coastal areas (e.g., engineering projects, dredging activities). Sea level rise, increased storminess and changes in sediment supply because of nourishments are expected to increase sedimentation in the future (Scavia et al., 2002; Kooistra et al., 2025). In this way, sediment effects on benthic assemblages could be exacerbated in the current scenario of globate change and more research is needed to minimise impacts of this stressor in coastal communities.

Funding

This research was partially funded by national funds through FCT - Fundação para a Ciência e a Tecnologia, I.P., and by the European Commission's Recovery and Resilience Facility, within the scope of UID/04423/2025 (https://doi.org/10.54499/UID/04423/2025), UID/PRR/04423/2025 (https://doi.org/10.54499/UID/PRR/04423/2025), and LA/P/0101/2020 (https://doi.org/10.54499/LA/P/0101/2020). This study had also the support of FCT through the project "Contrato-Programa" UID/04050/2025 funded by FCT I.P (https://doi.org/10.54499/UID/04050/2025). and the project LA/P/0069/2020 granted to the Associate Laboratory ARNET. P. Veiga was hired through the 'Regulamento do Emprego Cientifico e Tecnologico—RJEC'(https://doi.org/10.54499/2023.08939.CEECIND/CP2848/CT0002). M. Rubal is funded by FCT, under the Scientific Employment Stimulus - FCT-Tenure (2023.11245.TENURE.012).

CRediT authorship contribution statement

Puri Veiga: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft. **Ana Catarina Torres:** Data curation, Investigation,

Visualization, Writing – review & editing. **Isabel Sousa-Pinto:** Funding acquisition, Project administration, Resources, Supervision, Writing – review & editing. **Marcos Rubal:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – review & editing.

Declaration of competing interest

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

Acknowledgements

We are grateful to two anonymous referees for all the helpful comments and suggestions, which greatly improved this paper.

Data availability

Data will be made available on request.

References

Airoldi, L., 1998. Roles of disturbance, sediment stress, and substratum retention on spatial dominance in algal turf. Ecology 79, 2759–2770. https://doi.org/10.1890/0012-9658(1998)079[2759:RODSSA]2.0.CO;2.

Airoldi, L., 2003. The effects of sedimentation on rocky coast assemblages. Oceanogr. Mar. Biol. Annu. Rev. 41, 161–236.

Airoldi, L., Hawkins, S.J., 2007. Negative effects of sediment deposition on grazing activity and survival of the limpet *Patella vulgata*. Mar. Ecol. Prog. Ser. 332, 235–240. https://doi.org/10.3354/meps332235.

Airoldi, L., Virgilio, M., 1998. Responses of turf-forming algae to spatial variations in the deposition of sediments. Mar. Ecol. Prog. Ser. 165, 271–282. https://doi.org/10.3354/meps165271.

Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26, 32–46. https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x.

Anderson, M.J., 2002. DISTLM v.2: a FORTRAN Computer Program to Calculate a Distance-based Multivariate Analysis for a Linear Model. Department of Statistics, University of Auckland.

Anderson, M.J., 2006. Distance-based tests for homogeneity of multivariate dispersions. Biometrics 62, 245–253. https://doi.org/10.1111/j.1541-0420.2005.00440.x.

Anderson, M.J., Gorley, R.N., Clarke, K.R., 2008b. PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth, England, pp. 1–214.

Anderson, R.J., Anderson, D.R., Anderson, J.S., 2008a. Survival of sand-burial by seaweeds with crustose bases or life-history stages structures the biotic community on an intertidal rocky shore. Bot. Mar. 51, 10–20. https://doi.org/10.1515/BOT.2008.006.

Arribas, L.P., Bagur, M., Klein, E., Penchaszadeh, P.E., Palomo, M.G., 2013. Geographic distribution of two mussel species and associated assemblages along the northern argentinean coast. Aquat. Biol. 18, 91–103. https://doi.org/10.3354/ab00495.

Atalah, J., Crowe, T.P., 2010. Combined effects of nutrient enrichment, sedimentation and grazer loss on rock pool assemblages. J. Exp. Mar. Biol. Ecol. 388, 51–57. https://doi.org/10.1016/j.jembe.2010.03.005.

Balata, D., Piazzi, L., Benedetti-Cecchi, L., 2007. Sediment disturbance and loss of beta diversity on subtidal rocky reefs. Ecology 88, 2455–2461. https://doi.org/10.1890/07-0053.1.

Benedetti-Cecchi, L., Trussell, G., 2014. Rocky intertidal communities. In: Bertness, M., Bruno, J., Silliman, B., Stachowicz, J. (Eds.), Marine Community Ecology and Conservation. Oxford University Press, pp. 203–225.

Branch, G.M., 2001. Rocky shores. In: Steele, J.H. (Ed.), Encyclopedia of Ocean Sciences. Academic Press, pp. 2427–2434. https://doi.org/10.1006/rwos.2001.0086.

Burrows, M.T., Hughes, R.N., 1991. Optimal foraging decisions by dogwhelks, *Nucella lapillus* (L.): influences of mortality risk and rate-constrained digestion. Funct. Ecol. 5, 461–475. https://doi.org/10.2307/2389628.

Cameron, N.M., Scrosati, R.A., Valdivia, N., Meunier, Z.D., 2024. Global taxonomic and functional patterns in invertebrate assemblages from rocky-intertidal mussel beds. Sci. Rep. 14, 26. https://doi.org/10.1038/s41598-023-50549-8.

Clarke, K.R., 1993. Nonparametric multivariate analyses of changes in community structure. Aust. J. Ecol. 18, 117–143. https://doi.org/10.1111/j.1442-9993.1993.tb00438.x.

Clarke, K.R., Gorley, R.N., 2015. PRIMER *v7:* User Manual/Tutorial. PRIMER-E.

Contolini, G.M., Reid, K., Palkovacs, E.P., 2020. Climate shapes population variation in dogwhelk predation on foundational mussels. Oecologia 192, 553–564. https://doi.org/10.1007/s00442-019-04591-x.

Crowe, T.P., Smith, E.L., Donkin, P., Barnaby, D.L., Rowland, S.J., 2004. Measurements of sublethal effects on individual organisms indicate community-level impacts of pollution. J. Appl. Ecol. 41, 114–123. https://doi.org/10.1111/j.1365-2664.2004.00882.x.

Da Rosa, V.C., Copertino, M.S., Santos, R., Martínez-Crego, B., 2026. Bottom-up and top-down effects on the epiphytic diatom communities of the seagrass *Zostera noltei* H. J. Exp. Mar. Biol. Ecol. 594, 152147. https://doi.org/10.1016/j.jembe.2025.152147.

Dos Santos, E.P., Carcedo, M.C., Zotelo, C., Fiori, S.M., 2018. Effects of erosion-accretion processes on a community dominated by *Brachidontes rodriguezii* (Mollusca: mytilidae) on a rocky outcrop of the South Atlantic coast. J. Mar. Syst. 187, 146–155. https://doi.org/10.1016/j.jmarsys.2018.07.006.

Drakard, V.F., Hollarsmith, J.A., Stekoll, M.S., 2025. Climate-related sediment load has severe impacts on the early life-stages of commercially important high-latitude kelp species. J. Exp. Mar. Biol. Ecol. 592, 152128. https://doi.org/10.1016/j.jembe.2025.152128.

Engledow, H.R., Bolton, J.J., 1994. Seaweed α-diversity within the lower eulittoral zone in Namibia: the effects of wave action, sand inundation, mussels and limpets. Bot. Mar. 37, 267–276. https://doi.org/10.1515/botm.1994.37.3.267.

Fields, J.B., Silbiger, N.J., 2022. Foundation species loss alters multiple ecosystem functions within temperate tidepool communities. Mar. Ecol. Prog. Ser. 683, 1–19. https://doi.org/10.3354/meps13978.

GESAMP, 1994. Anthropogenic influences on sediment discharge to the coastal zone and environmental consequences. Rep. Stud. GESAMP 52, 1–67.

Giere, O., 2009. Meiobenthology: the Microscopic Motile Fauna of Aquatic Sediments. Springer-Verlag.

Gilson, A.R., McQuaid, C., 2023. Top-down versus bottom-up: grazing and upwelling regime alter patterns of primary productivity in a warm-temperate system. Ecology 104, e4180. https://doi.org/10.1002/ecy.4180.

Hughes, R.N., 1986. A Functional Biology of Marine Gastropods. Croom-Helm, London.

Hutchison, Z.L., Green, D.H., Burrows, M.T., Jackson, A.C., Wilson, B., Last, K.S., 2020. Survival strategies and molecular responses of two marine mussels to gradual burial by sediment. J. Exp. Mar. Biol. Ecol. 527, 151364. https://doi.org/10.1016/j.jembe.2020.1513642020.

Hutchison, Z.L., Hendrick, V.J., Burrows, M.T., Wilson, B., Last, K.S., 2016. Buried alive: the behavioural response of the mussels, *Modiolus modiolus* and *Mytilus edulis* to sudden burial by sediment. PLoS One 11 (3), e0151471. https://doi.org/10.1371/journal.pone.0151471.

Ingólfsson, A., Agnarsson, I., 2003. Amphipods and isopods in the rocky intertidal: dispersal and movements during high tide. Mar. Biol. 143, 859–866. https://doi.org/10.1007/s00227-003-1132-6.

Jenkins, S.R., Coleman, R.A., Santina, P.D., Hawkins, S.J., Burrows, M.T., Hartnoll, R.G., 2005. Regional scale differences in the determinism of grazing effects in the rocky intertidal. Mar. Ecol. Prog. Ser. 287, 77–86. https://doi.org/10.3354/meps287077.

Jormalainen, V., Honkanen, N., Heikkilae, N., 2001. Feeding preferences and performance of a marine isopod on seaweed hosts: cost of habitat specialization. Mar. Ecol. Prog. Ser. 220, 219–230. https://doi.org/10.3354/meps220219.

King, N.G., Teagle, H., Hawkins, S.J., Smale, D.A., 2025. Foundation species loss alters algal community structure and dynamics at a trailing range edge. J. Ecol. 113, 3858–3872. https://doi.org/10.1111/1365-2745.70199.

Kooistra, T.J., Witbaard, R., Bouma, T.J., Pearson, S.G., Bijleveld, A.I., van der Heide, T., Franken, O., Soetaert, K., 2025. Coarsening coasts: quantifying sensitivity of benthic communities to sandification. Estuar. Coast Shelf Sci. 320, 109303. https://doi.org/10.1016/j.ecss.2025.109303.

Kunze, C., Wölfelschneider, M., Rölfer, L., 2021. Multiple driver impacts on rocky intertidal systems: the need for an integrated approach. Front. Mar. Sci. 8, 667168. https://doi.org/10.3389/fmars.2021.667168.

Lazo, P., Aguilar, G., Arróspide, C., 2025. Extreme human-induced pocket beach growth on a rocky coast. Sci. Rep. 15, 6283. https://doi.org/10.1038/s41598-025-87197-z.

Lemos, R.T., Pires, H.O., 2004. The upwelling regime off the west Portuguese coast, 1941–2000. Int. J. Climatol. 24, 511–524. https://doi.org/10.1002/joc.1009.

Magris, R.A., Ban, N.C., 2019. A meta-analysis reveals global patterns of sediment effects on marine biodiversity. Global Ecol. Biogeogr. 28, 1879–1898. https://doi.org/10.1111/geb.12990.

McBane, C.D., Croker, R.A., 1983. Animal-algal relationships of the amphipod *Hyale nilssoni* (Rathke) in the rocky intertidal. J. Crustac Biol. 3, 592–601. https://doi.org/10.1163/193724083X00256.

Menge, B.A., 2000. Top-down and bottom-up community regulation in marine rocky intertidal habitats. J. Exp. Mar. Biol. Ecol. 250, 257–289. https://doi.org/10.1016/S0022-0981(00)00200-8.

Miller, D.C., Muir, C.L., Hauser, O.A., 2002. Detrimental effects of sedimentation on marine benthos: what can be learned from natural processes and rates? Ecol. Eng. 19, 211–232. https://doi.org/10.1111/geb.12990.

Minchinton, T.E., Fels, K.J., 2013. Sediment disturbance associated with trampling by humans alters species assemblages on a rocky intertidal seashore. Mar. Ecol. Prog. Ser. 472, 129–140. https://doi.org/10.3354/meps10120.

Montie, S., Thomsen, M.S., 2023. Long-term community shifts driven by local extinction of an iconic foundation species following an extreme marine heatwave. Ecol. Evol. 13, e10235. https://doi.org/10.1002/ece3.10235.

O'Connor, N.E., Crowe, T.P., 2007. Biodiversity among mussels: separating the influence of sizes of mussels from the ages of patches. J. Mar. Biol. Assoc. U. K. 87, 551–557. https://doi.org/10.1017/S0025315407050503.

Prado, L., Castilla, J.C., 2006. The bioengineer *Perumytilus purpuratus* (Mollusca: bivalvia) in central Chile: biodiversity, habitat structural complexity and environmental heterogeneity. J. Mar. Biol. Assoc. U. K. 86, 417–421. https://doi.org/10.1017/S0025315406013282.

Ramos-Oliveira, C., Sampaio, L., Rubal, M., Veiga, P., 2021. Spatial-temporal variability of *Mytilus galloprovincialis* Lamarck 1819 populations and their accumulated

sediment in northern Portugal. PeerJ 9, e11499. https://doi.org/10.7717/peerj.11499.
Rezaei, F., Contestabile, P., Vicinanza, D., Azzellino, A., 2023. Towards understanding environmental and cumulative impacts of floating wind farms: lessons learned from the fixed-bottom offshore wind farms. Ocean Coast Manag. 243, 106772. https://doi.org/10.1016/j.ocecoaman.2023.106772.
Rubal, M., Veiga, P., Reis, P.A., Bertocci, I., Sousa-Pinto, I., 2014. Effects of subtle pollution at different levels of biological organisation on species-rich assemblages. Environ. Pollut. 191, 101–110. https://doi.org/10.1016/j.envpol.2014.04.019.
Scavia, D., Field, J.C., Boesch, D.F., Buddemeier, R.W., Burkett, V., Cayan, D.R., Fogarty, M., Harwell, M.A., Howarth, R.W., Mason, C., Reed, D.J., Royer, T.C., Sallenger, A.H., Titus, J.G., 2002. Climate change impacts on US coastal and marine ecosystems. Estuaries 25, 149–164. https://doi.org/10.1007/BF02691304.
Schiel, D.R., Gunn, T.D., 2019. Effects of sediment on early life history stages of habitat-dominating fucoid algae. J. Exp. Mar. Biol. Ecol. 516, 44–50. https://doi.org/10.1016/j.jembe.2019.04.005.
Sjöberg, B., 1967. On the ecology of the *Jaera albifrons* group (Isopoda). Sarsia 29, 321–348. https://doi.org/10.1080/00364827.1967.10411093.
Thompson, R.C., Crowe, T.P., Hawkins, S.J., 2002. Rocky intertidal communities: past environmental changes, present status and predictions for the next 25 years. Environ. Conserv. 29, 168–191. https://doi.org/10.1017/S0376892902000115.
Tomanek, L., Helmuth, B., 2002. Physiological ecology of rocky intertidal organisms: a synergy of concepts. Integr. Comp. Biol. 42, 771–775. https://doi.org/10.1093/icb/42.4.771.
Torres, A.C., Rubal, M., Costa-Garcia, R., Sousa-Pinto, I., Veiga, P., 2022. Differences in the structure and diversity of invertebrate assemblages harbored by an intertidal ecosystem engineer between urban and non-urban shores. J. Mar. Sci. Eng. 10, 242. https://doi.org/10.3390/jmse10020242.
Trussell, G.C., Ewanchuk, P.J., Bertness, M.D., 2003. Trait-mediated effects in rocky intertidal food chains: predator risk cues alter prey feeding rates. Ecology 84, 629–640. https://doi.org/10.1890/0012-9658(2003)084[0629:TMEIRI]2.0.CO;2.
Tyler-Walters, H., 2007. *Nucella lapillus* Dog whelk. In: Tyler-Walters, H., Hiscock, K. (Eds.), Marine Life Information Network: Biology and Sensitivity Key Information Reviews, [on-line]. Plymouth: Marine Biological Association of the United Kingdom. https://doi.org/10.17031/marlinsp.1501.1.
United Nations Environmental Programme, 1995. Global Biodiversity Assessment. UNEP Nairobi: Cambridge University Press.
Vaselli, S., Bertocci, I., Maggi, E., Benedetti-Cecchi, L., 2008. Effects of mean intensity and temporal variance of sediment scouring events on assemblages of rocky shores. Mar. Ecol. Prog. Ser. 364, 57–66. https://doi.org/10.3354/meps07469.
Veiga, P., Moreira, J., Sampaio, L., Rubal, M., 2022b. Influence of urbanization on patterns of variability of *Mytilus galloprovincialis* populations. Water 14, 1570. https://doi.org/10.3390/w14101570.
Veiga, P., Moreira, J., Sampaio, L., Troncoso, J.S., Rubal, M., 2022a. Effects of habitat homogenisation on assemblages associated with mussel clumps. PLoS One 17 (6), e0269308. https://doi.org/10.1371/journal.pone.0269308.
Veiga, P., Ramos-Oliveira, C., Sampaio, L., Rubal, M., 2020. The role of urbanisation in affecting *Mytilus galloprovincialis*. PLoS One 15 (5), e0232797. https://doi.org/10.1371/journal.pone.0232797.
Veiga, P., Redondo, W., Sousa-Pinto, I., Rubal, M., 2017. Relationship between structure of macrobenthic assemblages and environmental variables in shallow sublittoral soft bottoms. Mar. Environ. Res. 129, 396–407. https://doi.org/10.1016/j.marenvres.2017.07.002.
Veiga, P., Rubal, M., Cacabelos, E., Maldonado, C., Sousa-Pinto, I., 2014. Spatial variability of macrobenthic zonation on exposed sandy beaches. J. Sea Res. 90, 1–9. https://doi.org/10.1016/j.seares.2014.02.009.
Veiga, P., Rubal, M., Vieira, R., Arenas, F., Sousa-Pinto, I., 2013. Spatial variability in intertidal macroalgal assemblages on the North Portuguese coast: consistence between species and functional group approaches. Helgol. Mar. Res. 67, 191–201. https://doi.org/10.1007/s10152-012-0315-2.
Widdows, J., Lucas, J.S., Brinsley, M.D., Salkeld, P.N., Staff, F.J., 2002. Investigation of the effects of current velocity on mussel feeding and mussel bed stability using an annular flume. Helgol. Mar. Res. 56, 3–12. https://doi.org/10.1007/s10152-001-0100-0.
Zardi, G.I., Nicastro, K.R., McQuaid, C.D., Erlandsson, J., 2008. Sand and wave induced mortality in invasive (*Mytilus galloprovincialis*) and indigenous (*Perna perna*) mussels. Mar. Biol. 153, 853–858. https://doi.org/10.1007/s00227-007-0857-z.