



Short-term effects of trampling on intertidal *Mytilus galloprovincialis* beds

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ABSTRACT

Human trampling represents one of the main anthropogenic pressures in the rocky intertidal. This habitat includes many ecosystem engineers such as mussels that provide biogenic habitat and multiple services. This research assessed potential impacts of human trampling on beds of the mussel, *Mytilus galloprovincialis*, on NW shores of Portugal. To test for direct effects of trampling on mussels and indirect effects on the associated assemblages, three treatments were applied: control (untouched beds), low and high intensity of trampling. Effects of trampling were dependent on the taxa. Thus, values of shell length of *M. galloprovincialis* were greater under the highest intensity of trampling while abundances of Arthropoda, Mollusca and *Lasaea rubra* showed the opposite pattern. Moreover, total number of taxa and abundances of Nematoda and Annelida showed higher values under low trampling intensity. The implications of these results to manage human use in areas with ecosystem engineers are discussed.

1. Introduction

Marine ecosystems provide crucial goods and services to humanity (Selig et al., 2019); however, over the last decades anthropogenic activities have deeply affected and degraded marine ecosystems (Halpern et al., 2008), with consequences to human well-being (Worm et al., 2006). This is especially evident in intertidal rocky shores, where a great variety of anthropogenic activities and disturbances coalesce, mainly by their position at the land–sea interface and by being areas easily accessible to humans (Thompson et al., 2002; Kunze et al., 2021).

Rocky intertidal habitats host exclusive and diverse ecosystems and many of their species show considerable ecological, economic and social value (Seitz et al., 2014; Kunze et al., 2021). Among these, ecosystem engineers (e.g., canopy macroalgae, mussels, oysters) are especially relevant because they provide biogenic habitat and enhance local biodiversity (e.g., Milazzo et al., 2004; Araújo et al., 2009; Arribas et al., 2014; Çinar et al., 2020; Veiga et al., 2022a). They also play a major role in ecosystems by their capacity to structure assemblages and influence ecological processes (Jones et al., 1994). In this way, intertidal rocky shores are frequented by many visitors during low tide periods for recreational purposes (Lucas and Smith, 2016; Mendez et al., 2017; Stevčić et al., 2018). However, visitor activities can have negative effects on

benthic intertidal organisms by controlling and interfering the species composition, reducing their abundance, diversity and reproductive output, altering their size structure, and when affecting ecosystem engineers, they can even modify the functioning and structure of ecosystems (Lucas and Smith, 2016; Micheli et al., 2016; Mendez et al., 2017; Stevčić et al., 2018). The attractiveness of coastal areas as desired tourism destination or for local recreational uses, coupled with coastal population increase, have contributed to enhance the impact of leisure activities on intertidal assemblages, currently a major concern (Crowe et al., 2000; Thompson et al., 2002).

Trampling is one of the most common human disturbances on intertidal rocky shores (e.g., Plicanti et al., 2016; Mendez et al., 2018, 2019). It is linked to commercial and recreational activities, such as the simple exploration of the area, gathering bait for angling and collecting live and dead organisms (e.g., Brosnan and Crumrine, 1994; Smith and Murray, 2005; Casu et al., 2006; Araújo et al., 2009; Stevčić et al., 2018). Most of previous studies testing effects of trampling have focused on algae (Keough and Quinn, 1998; Schiel and Taylor, 1999; Milazzo et al., 2004; Araújo et al., 2009) and sessile invertebrates (Smith and Murray, 2005; Long et al., 2011; Santos et al., 2015; Mendez et al., 2018), and generally point out to a reduction in their density and cover. Some studies have tested trampling effects on ecosystem engineers (e.g.,

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Brosnan and Crumrine, 1994; Milazzo et al., 2004; Smith and Murray, 2005; Araújo et al., 2009; Mendez et al., 2018, 2019); however, the effects of trampling on faunal assemblages associated with ecosystem engineers have been poorly explored (but see Beauchamp and Gowing, 1982; Van De Werfhorst and Pearse, 2007) and mobile fauna has been particularly overlooked (but see Plicanti et al., 2016).

Trampling can directly affect benthic communities by dislodging or crushing individuals (Povey and Keough, 1991; Brosnan and Crumrine, 1994; Smith and Murray, 2005) and indirectly influence biological interactions between species, for instance, leading to changes in physiological performance (Barradas et al., 2018) or in the vulnerability to predation (Cintra-Buenrostro, 2007). This is particularly obvious when trampling affects ecosystem engineers because it can directly influence them (e.g., abundance, size) and indirectly promoting changes in their associated assemblages' structure. Therefore, trampling impacts can ultimately trigger cascade effects in the structure of the entire community altering the habitat complexity, physical environment, light conditions, temperature, hydrodynamics, sedimentation and biotic interactions (McCook and Chapman, 1991; Platt and Connell, 2003).

Previous studies have indicated that trampling effects on rocky shores are largely conditioned by the duration, frequency and intensity of the disturbance but also by the local structure of the rocky habitat, including previous disturbances and features of the affected community (e.g., Povey and Keough, 1991; Brosnan and Crumrine, 1994; Araújo et al., 2009; Long et al., 2011; Mendez et al., 2017, 2019). This makes it difficult to implement management strategies that could mitigate trampling effects, because efficient measures for one area or particular target assemblages could not be effective for other sites or assemblages (Sarmiento et al., 2013).

The Mediterranean mussel, *Mytilus galloprovincialis* Lamarck, 1819, is one of the most conspicuous and dominant ecosystem engineers on exposed or moderately exposed intertidal shores along the south of the European Atlantic and Mediterranean coasts (Ramos-Oliveira et al., 2021). It modifies the local environment and provides secondary substratum and structurally complex three-dimensional habitat for many species (e.g., O'Connor and Crowe, 2007; Gestoso et al., 2013; Arribas et al., 2014; Çinar et al., 2020; Veiga et al., 2022a). Moreover, it plays a relevant role as link between benthos and phytoplankton (Kautsky and Evans, 1987), and as an active filter-feeder is able to improve water quality (Musella et al., 2020). Besides its ecological relevance, it is also an economically important marine resource, severely exploited in many European countries for human consumption (Rius and Cabral, 2004).

A loss of mussel cover in response to trampling was generally reported in previous studies (Brosnan and Crumrine, 1994; Smith and Murray, 2005; Van De Werfhorst and Pearse, 2007; Smith et al., 2008; Mendez et al., 2017, 2018). Furthermore, differences in size-structure of mussel populations, biomass and density were also found in more trampled/visited sites (Smith and Murray, 2005; Smith et al., 2008). Recent studies also showed differences in the response of mussel populations to trampling between exposed and sheltered conditions (Mendez et al., 2019) and urban and non-urban shores (Veiga et al., 2020; Torres et al., 2022; Veiga et al., 2022b).

The sandy shores of northern Portugal are intensely visited in summer for recreational uses while rocky shores are intermittently frequented for shellfish harvesting activities throughout the year (Araújo et al., 2009). The goal of this study was to examine direct and indirect effects of human trampling on *M. galloprovincialis* beds and their associated macrobenthic assemblages. A manipulative experiment was done considering unmanipulated controls and two treatments corresponding to two different intensities of trampling to test hypotheses on the vulnerability of mussel beds in northern Portugal. Specifically, the direct impact was measured in terms of variation in density, size, condition index and accumulated sediment in mussel clumps, whereas the indirect impact was estimated as changes in the structure of the whole associated faunal assemblage and in the abundance of the main taxa. Likewise, this study also aims to provide empirical data to support management and

conservation actions on the Portuguese coast, and potentially to analogous coastlines and ecosystem engineers, with the final aim of ensuring the sustainable use of these ecologically relevant but vulnerable organisms.

2. Materials and methods

2.1. Study area

This experiment was set up on the 25th of May 2021 on the intertidal rocky shore at Cabo do Mundo (41.2257410°N; 8.7179760°W) in the north of Portugal. This rocky granitic shore has a gentle slope, is exposed to prevailing north-westerly winds and waves and is characterized by a semi-diurnal tidal regime, with the maximum height above chart datum ranging between 3.5 and 4.0 m. Mussel beds are dominant on the exposed substratum at mid-tidal level where tidepools are dominated by macroalgae (Rubal et al., 2014). Different studies were previously done in this shore and people were rarely observed around.

2.2. Sample collection and processing

The experiment was designed after information provided by previous studies done on mussel beds in the area. Thus, spatial replication was done at the scales with the highest degree of variability, i.e. 10s of centimetres (among replicates) and 10s of meters (among sites) (Veiga et al., 2022b). Selection of experimental patches of mussels was done depending on whether each patch was extensive enough to allow people walking on them in order to emulate trampling properly; however, each treatment could not be replicated on each selected patch because of limitations in mussel beds sizes. Therefore, two sites separated by 10s of meters were selected. At each site, three paths (10s of centimetres apart), at mid intertidal level (between 1.5 m and 2 m above Chart Datum) and parallel to the shoreline were marked, each 10 m long and 0.5 m wide. Each of the three paths was randomly assigned to one of the three treatments considered: control treatment (i.e., no trampling), low trampling treatment (trampled 15 times) and high trampling treatment (trampled 30 times) (Fig. S1). Trampling intensities were chosen considering previous studies (e.g., Araújo et al., 2009). The different trampling treatments were done in one day (25.05.2021) always by the same person (about 70 kg in weight) wearing rubber boots. Each path was marked at the corners with labelled screws. During the trampling treatments and posterior sampling, the perimeter of each path was marked using tape measures. Samples were collected after one tidal cycle (i.e., 26.05.2021) following previous studies that also tested short term effects of trampling (e.g., Povey and Keough, 1991; Casu et al., 2006; Sarmiento et al., 2013; Nicastro et al., 2019). For each site and treatment, three samples of 10 × 10 cm were randomly collected within the centre of each path to avoid any border effect (Fig. S1). 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. In the laboratory, each sample was washed through a tower of 5 sieves of descending mesh size, i.e., 1000 µm, 500 µm, 250 µm, 125 µm and 63 µm, respectively. In order to calculate the amount and grain-size composition of sediment present on mussel beds, sediment retained in each sieve was dried at 65 °C for 12 h and then weighed. Mussels also retained in each sieve were sorted and counted to obtain the total mussel density. Furthermore, following the methodology used in previous studies (Ramos-Oliveira et al., 2021; Veiga et al., 2022b), the number of mussels retained in the 500 µm sieve was used to evaluate mussel density in the spat stage (i.e., mussels with sizes between 500 and 1000 µm) that can be considered as a proxy of recruitment. Moreover, twenty random mussels, obtained from the 1000 µm sieve, were separated to measure their shell length with vernier callipers (±0.1 mm). Finally, ten mussels per replicate were used to determine the condition index, defined as the ratio between soft tissue dry weight and shell dry weight.

To explore the effect of trampling on the diversity and structure of

macrobenthic assemblages on mussel beds, all animals retained in the 1000 and 500 μm sieves were sorted and identified to the lowest taxonomic level (species whenever possible).

2.3. Data analysis

All univariate and multivariate data were analysed using a two-way mixed model design with Trampling intensity (Ti) as a fixed orthogonal factor with three levels (Control, Low and High) and Site (Si) as a random orthogonal factor with two levels and three replicates per Ti and Si. Analyses of variance (ANOVA) were done to test for differences between trampling intensity on total and spat mussel density, total sediment content in mussel clumps, condition index and shell length. ANOVA was also used to test for differences among trampling intensities on the total number of individuals (N), total number of taxa (S), Shannon diversity index (H') values, and abundances of the three most abundant species and major taxa associated with *Mytilus galloprovincialis*. Cochran's C tests were previously done to check for homogeneity of variances, and when the test was significant ($p < 0.05$) data were $\text{Ln}(x + 1)$ transformed to remove heterogeneity. When ANOVA indicated significant differences ($p < 0.05$) among trampling intensities, a post hoc Student-Newman-Keuls (SNK) test was done to explore for differences among different treatments.

Permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001) based on a Bray-Curtis dissimilarity matrix (square root transformed) was used to analyze the multivariate structure of macrobenthic assemblages associated with mussel clumps. Multivariate patterns were illustrated by non-metric multidimensional scaling (nMDS) ordination.

3. Results

3.1. Effect of trampling on *M. galloprovincialis* attributes

Total density, spat density, condition index and sediment content of *M. galloprovincialis* clumps showed no significant differences among control and trampling treatments (Table 1). However, mean mussel shell length was significantly larger under the highest intensity of trampling compared to lower intensity and control treatments (Table 1; Fig. 1A).

3.2. Effect of trampling on assemblages associated with *M. galloprovincialis*

A total of 4608 individuals (1676 in control, 2219 in low intensity and 713 in high intensity of trampling) and 43 taxa (33 in control, 37 in low intensity and 30 in the high intensity of trampling) were found (Table S1). The numerically dominant taxa were Oligochaeta (31 % of the total individuals), followed by Nematoda (25 %) and the bivalve *Lasaea rubra* (18 %) (Table S1). In the control treatment, these three taxa showed similar numerical dominance ranging between 23 % for *L. rubra* and 21 % for oligochaetes. However, in low intensity of trampling, oligochaetes were clearly the dominant taxa (41 %) followed by nematodes

(24 %) and *L. rubra* (17 %) while in the high intensity of trampling, nematodes were the most abundant taxa (37 %) followed by oligochaetes (20 %) and *L. rubra* (9 %). The remaining taxa accounted for <8 % (Table S1). Four species were exclusively associated with the control treatment whereas 6 species were found only in low intensity of trampling and one in the high intensity of trampling (Table S1).

The composition of the whole macrofaunal assemblages was not significantly affected by the trampling intensity (Table 2; Fig. 2), neither were the total number of individuals (N) or Shannon diversity index (H') values (Table 3; Fig. 1B, D). The total number of taxa (S) showed significant larger values in the low intensity of trampling compared to the high intensity treatment (Table 3; Fig. 1C).

Among the numerically dominant taxa, abundance of nematodes was significantly larger in the low intensity of trampling compared to the higher intensity treatment (Table 4; Fig. 3A). Oligochaetes and *L. rubra* were not significantly affected by trampling (Table 4). However, a general trend of smaller abundances for each taxon was found under high trampling compared to the control and low intensity treatments while oligochaetes showed non-significant but greater abundances under low intensity trampling (Fig. 3B, C).

When the main major Phyla (Annelida, Arthropoda and Mollusca) were considered, total abundances of annelids and molluscs were not significantly affected by trampling (Table 5). However, arthropods were significantly fewer in numbers in high trampling compared to the control and low intensity treatments (Table 5; Fig. 4B).

4. Discussion

Pressure on marine ecosystems derived from human activity is increasingly making it necessary to understand their impacts to improve applied management on coastal areas and dealing with hazards resulting from multiple human uses (Korpinen et al., 2021). Trampling is one of the most frequent human disturbances on intertidal rocky shores (Plicanti et al., 2016; Mendez et al., 2018, 2019) but has been less studied than other sources of disturbance, particularly in the Atlantic (e.g., Sampaio et al., 2022). For instance, in Portuguese rocky shores, Araújo et al. (2009) indicated that high trampling intensity is able to severely reduce the abundance of the algae *Ascophyllum nodosum* and *Fucus vesiculosus*. Moreover, Plicanti et al. (2016) reported that even low trampling intensities reduced the percentage cover of intact reefs of the annelid ecosystem engineer *Sabellaria alveolata*, but it did not alter the structure of their associated assemblages.

4.1. Trampling effects on *M. galloprovincialis*

Trampling directly affects mussels by the crushing of individuals or by the weakening of the byssus attachment to the rocks, which can cause dislodgment and making them less resilient to other disturbances such as high wave action during vigorous hydrodynamics or storms (Povey and Keough, 1991; Brosnan and Crumrine, 1994; Smith and Murray, 2005). The present findings suggest that smaller mussels are more vulnerable to trampling because shell length was significantly greater under high

Table 1

ANOVA examining significant differences in total density, spat density, sediment content, condition index and shell length of *M. galloprovincialis*. df: degrees of freedom; MS: mean squares; F: F-ratio; ns: not significant; s: significant *: $p < 0.05$. Relevant significant differences are indicated in bold (i.e., including fixed factors).

Source of variation	df	Total density		Spat density		Sediment content		df	Condition index		df	Shell length	
		MS	F	MS	F	MS	F		MS	F		MS	F
Trampling intensity (Ti)	2	130,619.40	2.19	5798.00	0.06	94.88	0.13	2	0.0000	0.16	2	0.0726	27.05*
Site (Si)	1	577,454.22	2.33	406,501.39	3.07	2775.80	6.19*	1	0.0003	0.95	1	0.0031	0.12
Tr x Si	2	59,705.72	0.24	93,942.89	0.71	709.21	1.58	2	0.0001	0.19	2	0.0027	0.10
Residual	12	248,024.50		132,621.94		448.27		174	0.0003		354	0.0265	
Total	17							179			359		
Transformation		None		None		None			None			$\text{Ln}(x + 1)$	
Cochran's test		C = 0.58	ns	C = 0.61	ns	C = 0.31	ns		C = 0.51	s		C = 0.25	ns

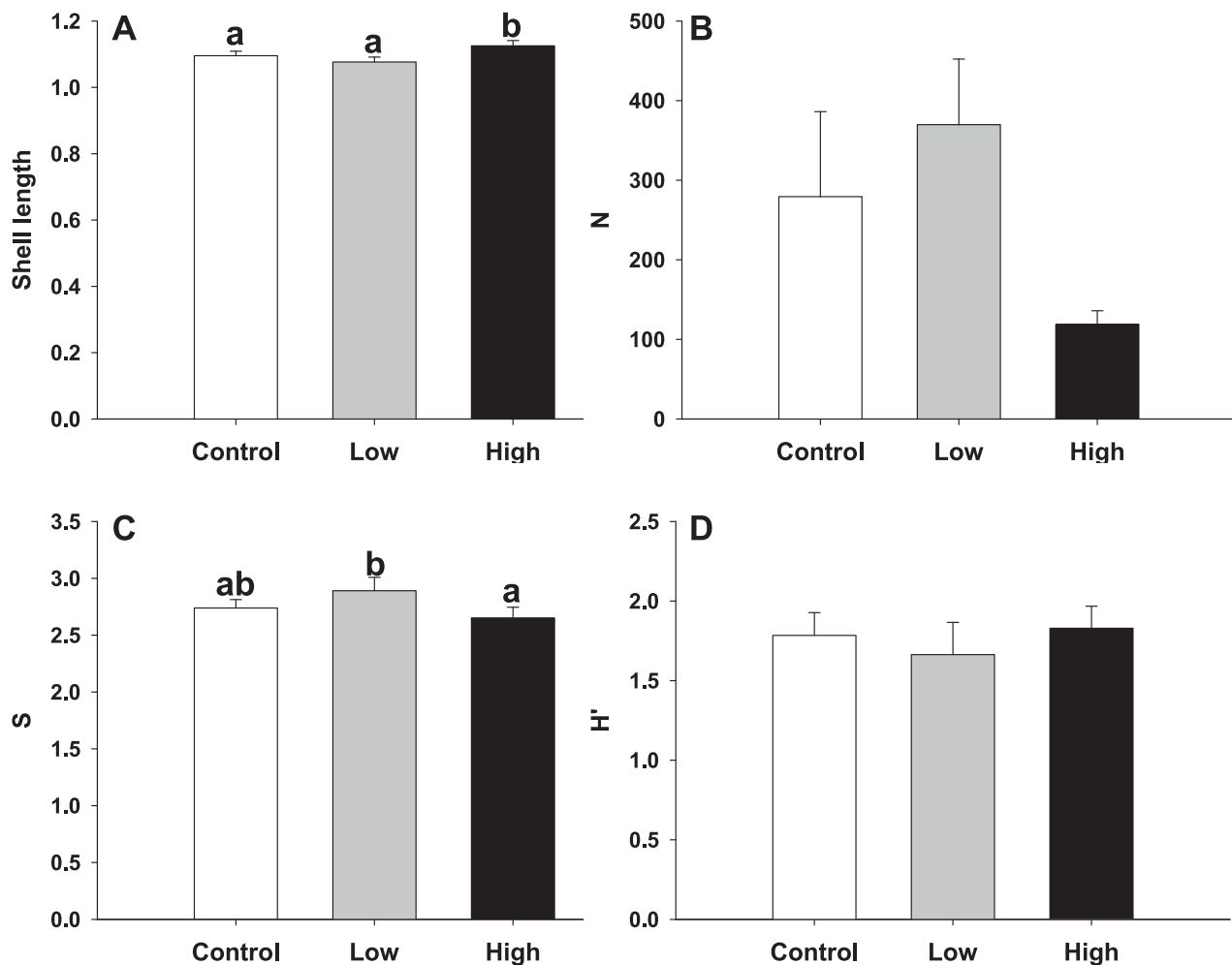


Fig. 1. Mean (+SE) mussel shell length (A), total number of individuals (B), total number of taxa (C) and Shannon diversity index (H') values (D) of macrofauna associated with *Mytilus galloprovincialis*. Dissimilar letters indicate significant differences (SNK test, *: $p < 0.05$). Data transformed to $\ln(X + 1)$ in A and C.

Table 2

PERMANOVA examining significant differences in the structure of the total assemblage associated with *Mytilus galloprovincialis* (Data square root transformed). df: degrees of freedom; MS: mean squares.

Source of variation	df	Total assemblage		
		MS	Pseudo-F	Unique perms
Trampling intensity (Ti)	2	1554.700	1.969	60
Site (Si)	1	2014.800	7.749	999
Tr x Si	2	789.410	0.685	997
Residual	12	1152.100		
Total	17			

trampling intensity. In the same area, mussel shell length varies significantly at the scale of site (Ramos-Oliveira et al., 2021) and most of its variability occurs at the scale of quadrat (Veiga et al., 2022b). However, present results showed significant differences only between treatments and it seems unlikely that these could be an artefact caused by random distribution of mussel size. A more plausible explanation could be that attachment and shell strength often increase with body size (Hunt and Scheibling, 2001; Beadman et al., 2003; Aguilera et al., 2017), making larger mussels more resistant to trampling (Micheli et al., 2016; Mendez et al., 2019). For instance, *Mytilus californianus* showed that individuals <10 mm in length were less abundant at the most trampled site (Goldstein, 1992). However, Beauchamp and Gowing (1982) found that *M. californianus* size was unaffected by trampling and Smith et al. (2008)

reported a smaller mean length in sites submitted to a higher level of human visitation. Our study and that by Goldstein (1992) are exclusively focused on trampling while Smith et al. (2008) included also all other activities linked to human visitation, including harvesting that targets on larger mussels (Crowe et al., 2000; Rius and Cabral, 2004; Smith and Murray, 2005).

Decrease in mussel cover is also commonly associated with trampling (Van De Werfhorst and Pearse, 2007; Mendez et al., 2017, 2019), even under low intensity (Micheli et al., 2016). However, our results showed no influence of trampling on total and spat density, similarly to that reported in *M. californianus* (Beauchamp and Gowing, 1982). Mendez et al. (2018) noticed a decline in cover immediately after trampling disturbance; in this way, our sampling - a day after proceeding with the experimental trampling treatments - should not have influenced the results. The highest loss of mussels may occur when they are loosely packed (Brosnan and Crumrine, 1994; Smith and Murray, 2005). However, in our study mussels were arranged in multi-layered clumps tightly packed that are less vulnerable to trampling (Brosnan and Crumrine, 1994). Moreover, Mendez et al. (2019) compared mussel clumps from wave-exposed and sheltered sites and found that the former were more resilient to trampling because they showed a greater degree of attachment and compressive strength. In this sense, our experiment was done in an area highly exposed to the wave action and this could explain the resistance of mussel clumps to trampling in terms of density, at least in the short term. However, long-term effects of trampling cannot be excluded (see Povey and Keough, 1991; Keough and Quinn, 1998; Schiel

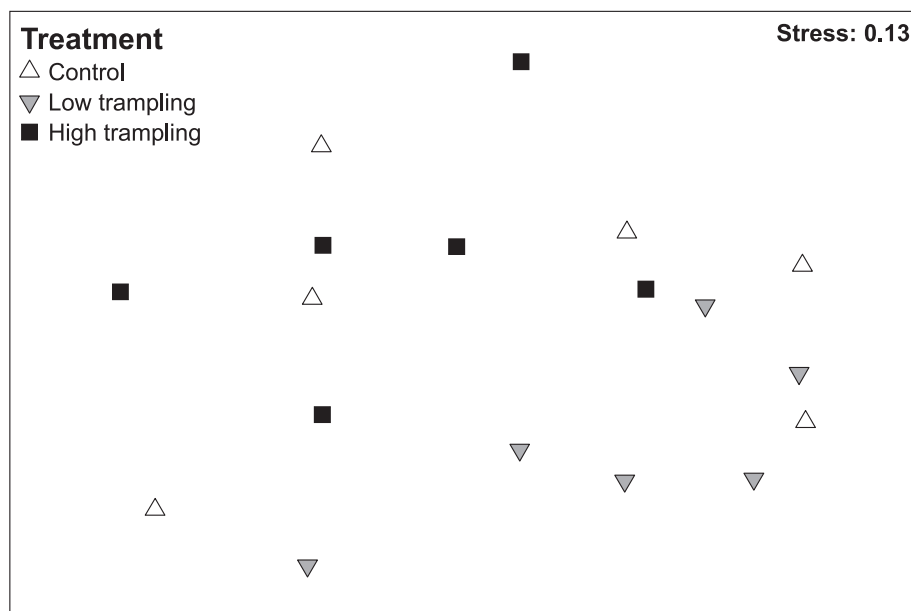


Fig. 2. nMDS ordination of macrobenthic assemblages based on Bray-Curtis similarities of square-root transformed abundances.

Table 3

ANOVA examining significant differences in total number of individuals (N), total number of taxa (S) and Shannon diversity index (H') values of macrofaunal assemblages associated with *Mytilus galloprovincialis*. df: degrees of freedom; MS: mean squares; F: F-ratio; ns: not significant; *: $p < 0.05$. Relevant significant differences are indicated in bold (i.e., including fixed factors).

Source of variation	df	N		S		H'	
		MS	F	MS	F	MS	F
Trampling intensity (Ti)	2	96,951.500	10.28	0.088	20.46*	0.044	0.66
Site (Si)	1	2266.889	0.05	0.183	3.38	0.7651	6.05*
Tr x Si	2	9434.389	0.21	0.004	0.008	0.067	0.53
Residual	12	44,537.278		0.054			
Total	17						
Transformation		None		Ln(X + 1)		None	
Cochran's test		C = 0.5683	ns	C = 0.4883	ns	C = 0.4273	ns

Table 4

ANOVA examining significant differences in the total abundance of the three most important taxa associated with *Mytilus galloprovincialis*. df: degrees of freedom; MS: mean squares; F: F-ratio; ns: not significant; *: $p < 0.05$. Relevant significant differences are indicated in bold (i.e., including fixed factors).

Source of variation	df	Nematodes		Oligochaetes		<i>Lasaea rubra</i>	
		MS	F	MS	F	MS	F
Trampling intensity (Ti)	2	3108.389	20.05*	4.114	8.34	5742.389	2.88
Site (Si)	1	320.889	0.10	0.979	0.91	896.056	0.15
Tr x Si	2	155.056	0.05	0.493	0.46	1996.722	0.33
Residual	12	3086.222		1.071		5992.278	
Total	17						
Transformation		None		Ln(X + 1)		None	
Cochran's test		C = 0.379	ns	C = 0.407	ns	C = 0.403	ns

and Taylor, 1999; Araújo et al., 2012; Barradas et al., 2018).

4.2. Trampling effects on associated fauna

Biodiversity loss is nowadays considered as one of the most severe global environmental problems (Cardinale et al., 2012; Roe, 2019). In this framework, improving the knowledge about how human disturbances influence the role of engineering species as providers of biodiversity hotspots is key for marine ecosystems management. Mussel beds increase local biodiversity (e.g., Arribas et al., 2014; Çınar et al., 2020; Veiga et al., 2022a, 2022b) and, for instance, >100 invertebrate species were found among *M. galloprovincialis* in NW Iberian Peninsula (Veiga

et al., 2022a). In this way, trampling could also have indirect negative effects on the associated biota resulting in local biodiversity loss (Micheli et al., 2016; Mendez et al., 2019) but few studies have assessed such effects (but see Beauchamp and Gowing, 1982; Van De Werfhorst and Pearse, 2007). Our data indicated that total abundance, Shannon diversity index values and the structure of the whole assemblages associated with mussel beds were not affected by trampling. Smith et al. (2008) also found that the assemblage diversity associated to *M. californianus* beds did not significantly differ between areas with different levels of human visitation. Similarly, trampling did not affect the structure, total abundance and diversity of the assemblages associated with *Sabellaria alveolata* (Plicanti et al., 2016).

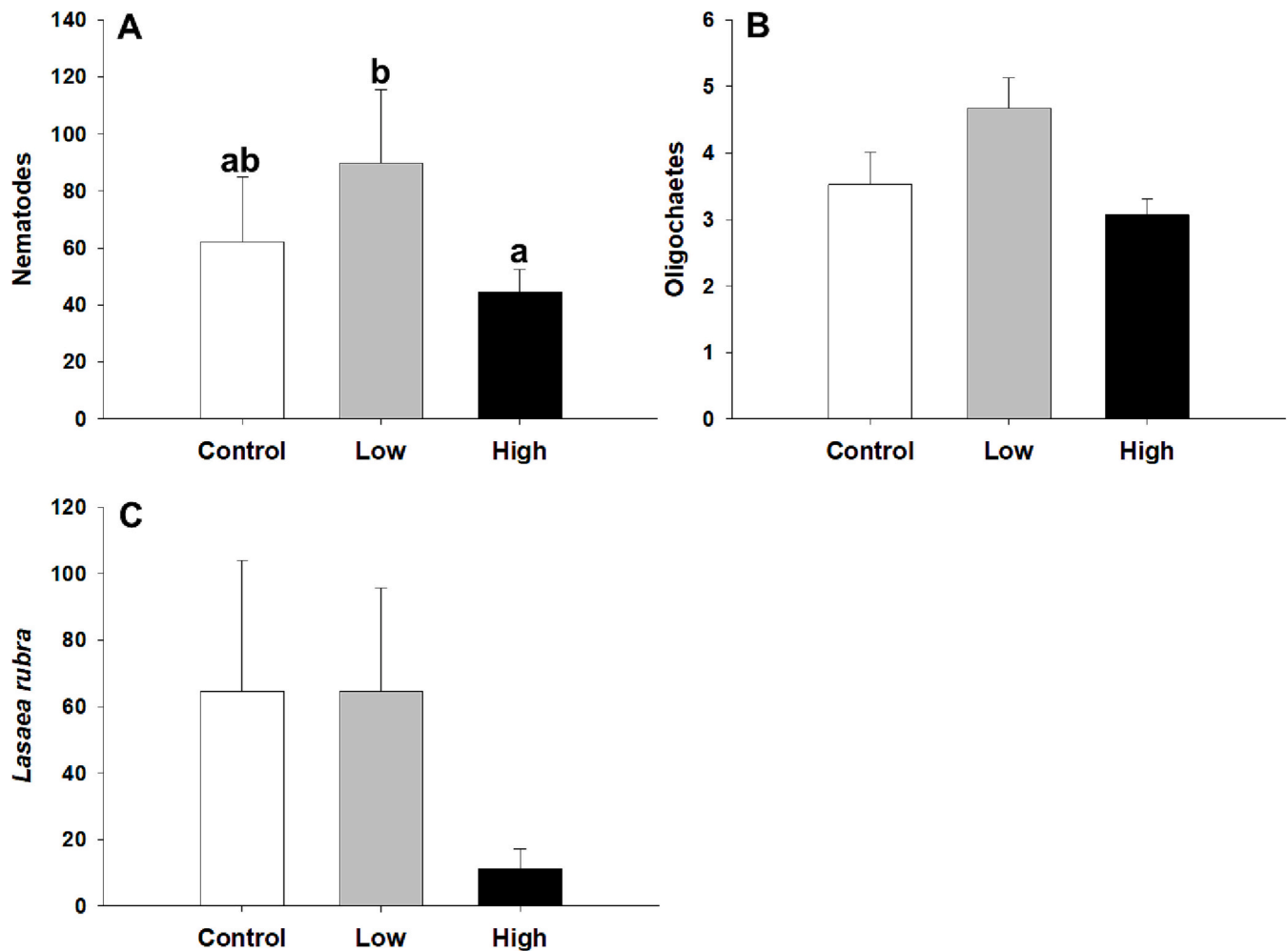


Fig. 3. Mean values (+SE) of total abundance of three dominant taxa associated with *Mytilus galloprovincialis*. Nematodes (A), Oligochaetes (B) and *Lasaea rubra* (C). Dissimilar letters indicate significant differences (SNK test, $p < 0.05$). Data transformed to $\ln(X + 1)$ in B.

Table 5

ANOVA examining significant differences in the total abundance of major macrofaunal taxa (Annelids, Arthropods and Molluscs) associated with *Mytilus galloprovincialis*. df: degrees of freedom; MS: mean squares; F: F-ratio; ns: not significant; *: $p < 0.05$. Relevant significant differences are indicated in bold (i.e., including fixed factors).

Source of variation	df	Annelids		Arthropods		Molluscs	
		MS	F	MS	F	MS	F
Trampling intensity (Ti)	2	4.161	9.24	1.758	20.85*	6066.667	3.34
Site (Si)	1	0.900	0.91	1.161	3.28	533.556	0.09
Tr x Si	2	0.450	0.46	0.084	0.024	1816.889	0.31
Residual	12	0.987		0.354		5819.778	
Total	17						
Transformation		$\ln(X + 1)$		$\ln(X + 1)$		None	
Cochran's test		$C = 0.416$	ns	$C = 0.427$	ns	$C = 0.363$	ns

Mobile fauna, as here investigated, are often considered resistant to trampling because of their capacity to move out from affected areas and then come back again after the disturbance ended (Casu et al., 2006; Micheli et al., 2016; Plicanti et al., 2016). However, the total number of species and the abundance of some taxa (i.e., nematodes, oligochaetes and Annelida) were larger at the lowest intensity of trampling while the abundance of arthropods, molluscs and the bivalve *L. rubra* was lower under high intensity. In addition, the identity of the numerically dominant taxa differed among treatments becoming nematodes and oligochaetes more abundant in trampling treatments with respect to the control. This suggests that effects of trampling are dependent on the taxa, in accordance with similar studies focused on assemblages on

macroalgae (Milazzo et al., 2004; Casu et al., 2006).

Beauchamp and Gowing (1982) indicated that the number of animal species associated with *M. californianus* was higher at the intermediate trampled site. This pattern is similar to our findings and supports the Intermediate Disturbance Hypothesis that predicts that the number of species peaks at an intermediate level of disturbance (in our study the treatment under low intensity of trampling) by the coexistence of competitive dominants and rapid colonizers, while diversity will be low at both extremes by the competitive exclusion and local extinction (Sousa, 1979; Svensson et al., 2007, 2012). Mendez et al. (2017) found that richness of sessile species was higher in trampled plots than in control ones but their data come from analyses of photographs that only

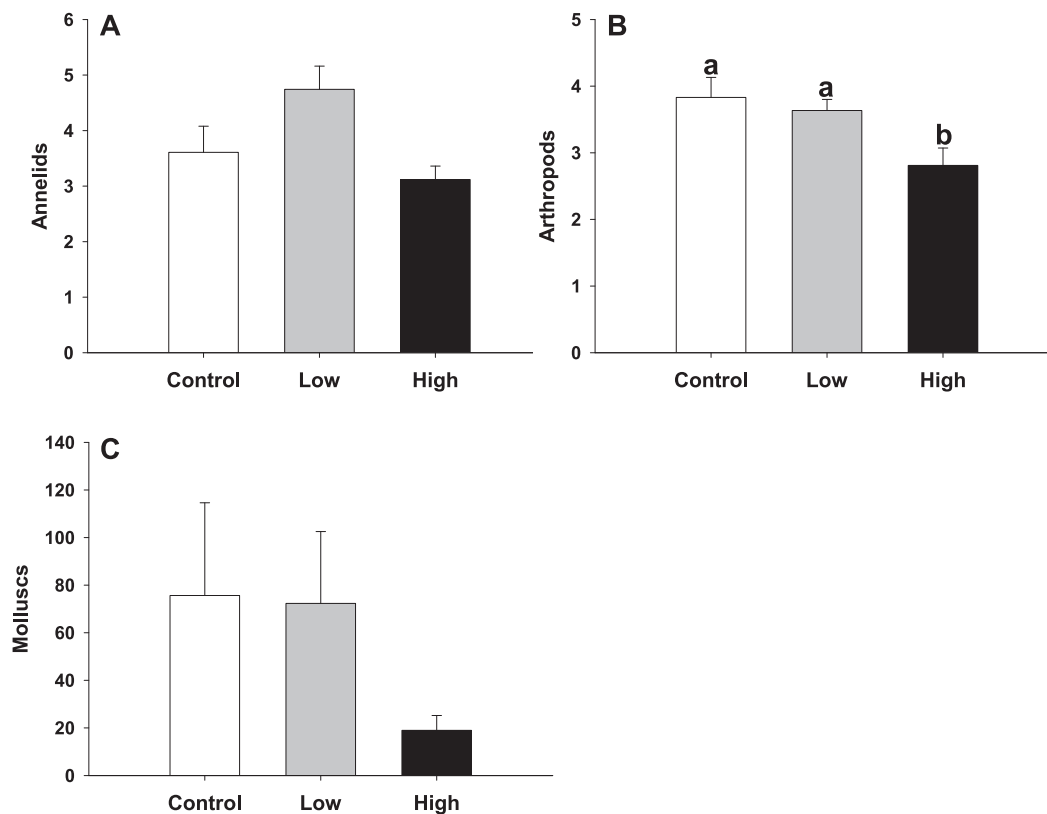


Fig. 4. Mean values (+SE) of total abundance of major macrofaunal taxa associated with *Mytilus galloprovincialis*: Annelids (A), Arthropods (B) and Molluscs (C). Dissimilar letters indicate significant differences (SNK test, *, $p < 0.05$). Data transformed to $\ln(X + 1)$ in A and B.

considered cover of sessile taxa. Contrarily, Van De Werfhorst and Pearse (2007) found that species richness was consistently higher at the least trampled site. These contrasting results could be due to differences on the timing, frequency and intensity of trampling among studies, as well as on differences in the native assemblages (Povey and Keough, 1991; Brosnan and Crumrine, 1994; Araújo et al., 2009; Long et al., 2011; Mendez et al., 2017, 2019).

Our findings also suggest that nematodes and annelids were favoured by intermediate disturbance because these taxa reached the highest abundance under low trampling. Furthermore, these taxa are typically linked to sediment (O'Connor and Crowe, 2007; Veiga et al., 2022a). Calcagno et al. (2012) found that disturbance resulted in the loss of the sediment layer trapped among *Mytilus chilensis* beds, thus affecting in turn their associated fauna. However, our study did not detect significant differences in the sediment content of *M. galloprovincialis* beds among trampling treatments and therefore this cannot explain the observed patterns for the aforementioned taxa. Oligochaetes associated with *M. galloprovincialis* also showed greater abundance in urban shores, where usually trampling is more frequent and intense (Torres et al., 2022). Contrarily, the bivalve *L. rubra*, Arthropoda and Mollusca showed lower numbers under high trampling. Likewise, numbers of *Lasaea cistula* inhabiting *M. californianus* beds were fewer at the most trampled sites (Beauchamp and Gowing, 1982; Goldstein, 1992) and *L. rubra* was less abundant on urban shores in comparison to non-urban ones (Torres et al., 2022). This pattern can be explained by the mostly sessile life style and the direct development reproductive strategy of *L. rubra* (McGrath and Foighil, 1986). Thus, mobile animals can recolonise faster the trampled-disturbed area from undisturbed adjacent zones during the following high tide than *L. rubra*.

Although little is known about the susceptibility of most taxa to trampling (Plicanti et al., 2016; Sampaio et al., 2022), the patterns of abundance of several taxa in our study match with those associated with other anthropogenic disturbances (e.g., pollution, harvesting). For

instance, free-living marine nematodes are useful indicators of environmental quality because many species persist when exposed to different perturbations (e.g., Ridall and Ingels, 2021; Franzo et al., 2022; Ng et al., 2022). In fact, nematodes were the taxa numerically dominant only under high trampling. Similarly, annelids (polychaetes and oligochaetes) respond positively to different anthropogenic stressors (e.g., Parapar et al., 2009; Glasby et al., 2021; Sampaio et al., 2022). Although oligochaetes and nematodes were not identified to species level, our data suggest that they seem tolerant to moderate trampling intensities. In contrast, arthropods and molluscs are often negatively affected by a number of disturbances (Lenihan et al., 2003, 2018; Sampaio et al., 2022). However, significant differences among trampling treatments were not detected apart from those regarding *L. rubra*. On the other hand, when higher taxonomical levels were considered (i.e., molluscs and arthropods), these taxa showed lower abundances under high trampling.

Our results showed that trampling, at the short term, is able to affect the size structure of *M. galloprovincialis* populations. Considering that the mussel is also a relevant shellfish resource, the effects of trampling on shell length could bring important economic consequences (Crowe et al., 2000; Rius and Cabral, 2004; Smith and Murray, 2005). In addition, richness of assemblages associated with mussels increased by moderate trampling and effects of trampling were dependent on taxa, i.e., nematodes and annelids in general seen tolerant while *L. rubra*, arthropods and molluscs seem sensitive to the disturbance. In any case, none of the taxa analysed showed their greatest abundances under high trampling.

5. Conclusions

Trampling influences *Mytilus galloprovincialis* and its associated assemblages in the short term. Moreover, major changes at the medium and long term cannot be discounted for this ecosystem engineer and associated biota that ultimately could affect further biological

interactions (Micheli et al., 2016; Mendez et al., 2017, 2018). Regarding the most sensitive taxa as found in our study (i.e., *L. rubra*, arthropods and molluscs), trampling impacts could persist for a long-term but future experiments are necessary to test this prediction. Therefore, trampling should be considered as a relevant disturbance on rocky intertidal areas when planning and implementing effective management actions able of mitigating the effects of anthropogenic activities. As tourism and casual intertidal visiting will certainly increase worldwide, trampling impacts will do as well (Mendez et al., 2017). On the other hand, mussels are mainly known as a food resource but people often ignore their relevant ecological role and the many benefits they provide (Veiga et al., 2021). In this way, preventive programs devoted to regulate visitor numbers, implementing educational activities and using informative panels to actively engage people about the importance of ecosystem engineers could be useful in rocky intertidal areas dominated by mussels and similar taxa (e.g., macroalgae, tube-building annelids).

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CRedit authorship contribution statement

Puri Veiga: Conceptualization, Methodology, Formal analysis, Investigation, Resources, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition. **Leandro Sampaio:** Methodology, Investigation, Writing – review & editing. **Juan Moreira:** Methodology, Investigation, Writing – review & editing. **Marcos Rubal:** Conceptualization, Methodology, Formal analysis, Investigation, Resources, Writing – review & editing, Supervision.

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.

Data availability

Data are available as supplementary material

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