Spatial-temporal variability of *Mytilus galloprovincialis* Lamarck 1819 populations and their accumulated sediment in Northern Portugal

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Mytilus galloprovincialis is an ecosystem engineer that provides habitat and generates environmental heterogeneity, increasing local biodiversity. Moreover, it is an economically important species representing 14% of the global production of marine bivalves. Natural drivers and the increase of anthropogenic pressures, such as sediment stress, influence its populations on rocky shores. The objective of this study was to explore the spatial-temporal patterns of different *M. galloprovincialis* attributes along North of Portugal. For that purpose, six rocky shores were selected and sampled six times along the year 2019. The percentage of cover, density, spat density, condition index, clump thickness, size classes and clump sediment content were considered. Results showed the lack of seasonality in *M. galloprovincialis* along the North coast of Portugal. However, density, spat stage, clump thickness, condition index and size classes showed some variability among dates and shores. The percentage cover and sediment content only significantly differed among shores. Our results indicated an absence of seasonality for all the studied variables, probably because temperature was always within the optimum range for this species and the abundance of food supply in the study area independently of the season. The accumulated sediment on mussel clumps did not show any temporal variability with only significant differences among shores. The accumulated sediment was composed mainly by medium and coarse sand and it was correlated with mussel average size, condition index, but especially with the mussel clump thickness.

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19 Abstract

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21 environmental heterogeneity, increasing local biodiversity. Moreover, it is an economically
22 important species representing 14% of the global production of marine bivalves. Natural drivers
23 and the increase of anthropogenic pressures, such as sediment stress, influence its populations on
24 rocky shores. The objective of this study was to explore the spatial-temporal patterns of different
25 *M. galloprovincialis* attributes along North of Portugal. For that purpose, six rocky shores were
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29 of Portugal. However, density, spat stage, clump thickness, condition index and size classes
30 showed some variability among dates and shores. The percentage cover and sediment content
31 only significantly differed among shores. Our results indicated an absence of seasonality for all
32 the studied variables, probably because temperature was always within the optimum range for
33 this species and the abundance of food supply in the study area independently of the season. The
34 accumulated sediment on mussel clumps did not show any temporal variability with only
35 significant differences among shores. The accumulated sediment was composed mainly by

36   medium and coarse sand and it was correlated with mussel average size, condition index, but
37   especially with the mussel clump thickness.
38   **Subjects** Ecology, Marine Biology
39   **Keywords** Ecosystem engineer, North east Atlantic, rocky shore, sediment stress.
40

Introduction

42   Mussels are important organisms in intertidal systems because they keep biodiversity, sheltering,
43   supporting and enhancing diverse assemblages of invertebrates (Leigh et al., 1987; Seed &
44   Suchanek, 1992; Seed, 1996) inducing physical changes in the substrate and providing suitable
45   space and resources for different species of animals and macroalgae (Thiel & Ullrich, 2002;
46   Loehle, 2004; Prado & Castilla, 2006; Borthagaray & Carranza, 2007). The Mediterranean
47   mussel *Mytilus galloprovincialis* Lamark, 1819 is one of the most frequent and abundant native
48   mussel species in the south Atlantic European and Mediterranean Sea rocky shores (Braby &
49   Somero, 2006). Recently, Lynch et al. (2020), have detected a northward range expansion of *M.*
50   *galloprocincialis* along Irish shores, probably as a result of global warming. Additionally, *M.*
51   *galloprovincialis* is also a widespread invasive species in other regions like South Africa (De
52   Moor & Bruton, 1988). Moreover, *M. galloprovincialis* is an economically important species
53   because of its high production (Guo et al., 2018). Because of that, it is vulnerable to recreational
54   and commercial harvesting (Smith & Murray, 2005). Aquaculture of marine bivalves accounts
55   14% of the global marine production (Wijsman et al., 2019). However, for mussels this practice,
56   requires the exploitation of wild populations, involving the collection of young mussels' larvae
57   directly from the water or harvesting of small mussels (0.5-2 cm) from intertidal and subtidal
58   beds (Consellería de Pesca, Marisqueo y Acuicultura, 2000; Cáceres-Martínez & Figueras, 2007;
59   Figueras, 2007). This practice affects not only mussel juveniles but also adult stocks because it
60   slows down the recovery of mussels (Harris et al., 2003), and thus it may influence the whole
61   communities associated with mussels (Veiga et al., 2020).
62   Natural populations of *M. galloprovincialis*, are under the effects of natural and anthropogenic
63   disturbances (Nicastro, McQuaid & Zardi, 2019), which can have a strong influence on natural
64   population dynamics (UNEP, 2006). Intertidal populations of *M. galloprovincialis* often live in
65   mechanically stressful environments, being affected by natural ecological drivers like changes of
66   temperature, salinity, concentration of suspended matter or phytoplankton (Braby & Somero,
67   2006; Zardi et al., 2008; Garner & Litvaitis, 2013; Araújo et al., 2020) and the presence of
68   filamentous algae that promote the larval colonization (Ceccherelli & Rossi, 1984). Among
69   anthropogenic disturbances, coastal urbanisation is one of the most persistent and increasing
70   threats due to an increase of ocean sprawl and high diversity of pollutants coming from industry
71   and domestic products (Todd et al., 2019). Coastal urbanisation has proved to have negative
72   effects on the abundance and size structure of intertidal *M. galloprovincialis* (Veiga et al., 2020).
73   Other anthropogenic disturbances like harvesting or trampling have also proved to have negative
74   effects on mussels populations (Smith & Murray, 2005). Among the multiple stressors that can
75   affect mussel populations, the sediment accumulated on rocky shores has been poorly studied.

76   Airoldi (2003) suggests that sediment can interfere in the development of mussel beds,
77   particularly the accumulation of sediment interferes with physical and biological processes that
78   lead to a reduction of suitable habitats (Airoldi, 2003). The main negative effect described for
79   sediment accumulation on mussel populations is the burial (e.g. Hutchison et al., 2016; Dos
80   Santos et al., 2018) but that effect can be different among mussel species in function of their
81   ability to emerge or resist burial (Zardi et al., 2008; Hutchison et al., 2016, 2020). Moreover, the
82   sediment can be a reservoir of contaminants that can result toxic for marine animals (Long et al.,
83   1996; Fichet, Radenac & Miramand, 1998). Finally, sediment accumulation can also modify the
84   services provided by mussels modifying the invertebrate assemblage diversity associated to
85   mussel beds and facilitating the colonisation of mussel beds by soft bottoms macro- and
86   meiobenthic species (e.g. Dos Santos et al., 2018).
87   Studies about patterns of variation in time and space of natural populations and assemblages are
88   a chief goal in ecology, especially when they include economically relevant species with a key
89   ecological role like *M. galloprovincialis* (Levin, 1992; Underwood & Chapman, 2000). The
90   understanding of variation in populations is essential to the management and conservation of
91   species because, as natural and anthropogenic processes like sediment accumulation may be
92   very variable in space and time, their effect on the population dynamics will also be very
93   variable (Andrew & Mapstone, 2006; Levin, 1992; Underwood, 1996; Benedetti-Cecchi, 2000;
94   Bertocci et al., 2012). Bivalve molluscs show high plasticity on their responses and adaptation to
95   local conditions (Bayne & Widdows, 1978; Widdows et al., 1984; Tedengren et al., 1990;
96   Navarro et al., 1991) so, their settlement and growth varies among regions, according to the local
97   environment, but it can also vary along the year in response to oceanographic natural oscillations
98   (Seed, 1976). In sedentary animals like mussels, their reproduction and growth are the only
99   mechanisms to sustain populations (Seed, 1976). Consequently, exogenous and endogenous
100 factors are crucial for controlling physiological rates and the reproduction (Orban et al., 2002;
101 Nsgarajan, Lea & Goss-Custard, 2006, Seed, 1976). Therefore, knowledge of the natural
102 variability in time and space is decisive to understand population dynamics (Underwood, 1981)
103 and for the management and conservation of the stocks of commercially exploited species, as
104 well as the services provided by those species.
105 Nowadays, there is a lack of information about the spatial-temporal variability of *M.*
106 *galloprovincialis* populations along the Atlantic coast of the Iberian Peninsula, where this
107 species plays key ecological and economical roles. Similarly, the ability of *M. galloprovincialis*
108 clumps to accumulate sediment on rocky shores is almost unexplored. The main aims of this
109 study are to fill these gaps of knowledge and to explore the spatial-temporal patterns of *M.*
110 *galloprovincialis,* and accumulated sediments on their clumps, along rocky shores in the North
111 of Portugal. Different variables will be considered: density, spat stage, percentage cover, clump
112 thickness, condition index and different size classes of mussels to achieve these objectives.
113 Moreover, the spatial-temporal patterns of sediment accumulation in mussel clumps and its
114 relationships with the mussel population attributes will be examined.
115

Materials & Methods

Study area

The study was done between January 2019 and December 2019 and included six rocky shores along 90 km of the Northern Portuguese coast: Aguda (N 41°04246', W 8°653254') it is an urban schist platform shore with significant natural/anthropogenic sediment input and close to an artificial seawall, Valadares (N 41°089167', W 8°658374') it is an urban schist platform shore with significant natural/anthropogenic sediment input, Cabo do Mundo (N 41°225741', W 8°717976') it is an urban granitic shore with gentle slope in a very industrial area, Carreço (N 41°742040', W 8°878418') it is a non-urban schist shore with gentle slope and significant natural sediment input, Forte do Cão (N 41°798244', W 8°874848') it is a non-urban granitic shore with gentle slope close to a storm-water outflow and Moledo (N 41°822605', W 8°874894') it is a non-urban granitic shore with gentle slope (Fig. 1). Along the Northern Portuguese coast, intertidal area varies from soft to hard bottoms but they mostly present a mixture of both substrates. Sampling was done during low tide in the mid tide level of the rocky shores, that typically is dominated by the species *M. galloprovincialis* (Veiga et al., 2020). In the North of Portugal, the spring – summer and the autumn – winter seasons are characterized by strong differences in mean monthly precipitation, air and water temperature, hydrodynamic conditions, wave height and storm frequency (Dias et al., 2002; Bertocci et al., 2012). The coastline is largely straight and is exposed to wave action, which varies strongly with seasons (Dias et al., 2002). In the spring – summer period the typical wave heights are between 1 and 3 m, with periods of 11-13 s (Dias et al., 2002) and swells direction generally is from W and NW. In the autumn - winter period, the waves can reach around 7 m with periods of 13-18 s (Dias et al., 2002). The tidal regime of the study area is semidiurnal with the largest spring tides of 3.5 - 4.0 m. Moreover, the studied area is subjected to a seasonal upwelling that provides nutrients and increases the primary production in the water column during spring and summer months (Lemos & Pires, 2004). Along the sampling year 2019, in the autumn – winter period, mean value of air temperature was 11.98º C, with values ranging between 3.31º C and 22.42º C. Mean precipitation was 77.51 mm, with values ranging between 34.5 mm and 145.75 mm, being December the month with more precipitation. In the spring – summer months, mean values of air temperature were 19.16º C, ranging between 4.13º C and 29.70º C. During these months, the mean precipitation was 31.03 mm, with values ranging between 3.3 mm and 117.2 mm (http://www.ipma.pt/pt/index.html). Monthly values for seawater temperature, salinity and wave height at the sampling area can be found in Figure 2. Values showed on Figure 2 were measured every 60 minutes by an oceanographic buoy (model Seawach) placed at 42.12ºN and 9.43ºW. Values of temperature and wave height were measured during 2019 but, for salinity there are many lacks of data for 2019 and thus, we included the data of 2018. All the data were obtained from the public repository of Puertos del Estado webpage (http://www.puertos.es/es-es/oceanografia/Paginas/portus.aspx).

Sampling

155   The sampling design included two seasons and three sampling dates within each season: spring -
156   summer (April, June and September) and autumn - winter (January, October and December). On
157   each of these dates, the six studied shores were visited, and at each shore, two sites separated by
158   10 s of meters were randomly selected. At each site, the percentage of mussel's cover was
159   calculated in four quadrats (50 x 50 cm). Cover was estimated by dividing each quadrat into 25
160   sub-quadrats of 10 x 10 cm, attributing a scale from 0, with an absence of mussels, to 4, when
161   all the quadrat (10 x 10 cm) were covered by mussels, and accumulation up the 25 estimates
162   (Dethier et al., 1993). In addition, four measures of mussel clump thickness were randomly taken
163   within each of the four 50 x 50 cm quadrats by introducing a rigid ruler until reaching the bottom
164   of the clump. Within each one of the 50 x 50 cm quadrats, one sample of 10 x 10 cm was
165   collected, by scraping all the mussels in this area, and stored in labelled bags. These samples
166   were preserved in a mixture of formalin 4% with rose of Bengal neutralised with sodium
167   tetraborate anhydrous (Borax). In the laboratory, samples were washed in a tower of sieves of
168   1000 μm, 500 μm, 250 μm, 125 μm and 63 μm mesh size. For each sample, twenty random
169   mussels from the 1000 μm sieve were separated to be measured with a calliper. Measured
170   mussels were grouped in the following size classes: Class 1: <10 mm, Class 2: 10-20 mm, Class
171   3: 20-30 mm, Class 4: 30-40 mm, Class 5: 40-50 mm and Class 6: >50 mm. Additionally, 10
172   mussels per replicate were opened with a surgical blade and the shell was separated from the soft
173   body. Afterwards, they were dried and weighed to calculate the condition index as the ratio
174   between soft tissues dry weight and the shell dry weight. Residues retained in the sieves of 500
175   μm and 1000 μm were sorted in a dissection microscope and all the mussels were collected and
176   counted. To evaluate mussels in the spat stage (i.e. mussels with size between 500 and 1000 μm),
177   as a proxy of recruitment, the number of mussels retained in the 500 μm mesh size was counted.
178   The amount of sediment retained at each mesh size (1000 μm, 500 μm, 250 μm, 125 μm and 63
179   μm) was evaluated by drying the sieve content at 65°C for about 12h and weighting.
180   **Data analyses**
181   Differences in the total density, spat density, percentage cover, mussel size classes and the
182   amount of sediment retained on mussel clumps (total and different sediment sizes) were
183   examined with analyses of variance (ANOVA). These analyses were based on a four way model
184   including Season (Se) with two 2 levels: autumn – winter and spring – summer, as a fixed
185   orthogonal factor, Date (Da) with 3 levels, as a random factor nested in Se, Shore (Sh) with 6
186   levels: Aguda, Valadares, Cabo do Mundo, Moledo, Carreço and Forte do Cão, as a fixed
187   orthogonal factor and Site (Si) with 2 levels, as a random factor nested in all the previous factors,
188   considering 4 replicates per site. ANOVA was also used to test for differences on thickness and
189   condition index, but these analyses were based on a five-way model, including all the factors
190   above mentioned and Plot (Pl), as an additional random factor, nested in Se x Da x Sh x Si, with
191   4 and 10 replicates for thickness and condition index, respectively. Cochran's C test was done to
192   test for homogeneity of variances. In some cases, when Cochran's C test was significant
193   (p<0.05) data were Ln(X+1) transformed with the objective of removing heterogeneity of
194   variances. When transformation was not possible, untransformed data were analysed and results

195 were considered only if significant at p<0.01, to compensate for the increased probability of type
196 I error (Underwood, 1997). Whenever ANOVA demonstrated significant differences (p<0.05) a
197 post hoc Student-Newman-Keuls (SNK) test was done to explore differences. Finally, in order to
198 explore the relationship between total sediment content and mussel descriptors, rank correlation
199 analyses were done for each descriptor. Due to the non-normal distribution of the data,
200 Spearman's rank correlation was used.
201
202 **Results**
203 **Spatial and temporal patterns of mussel descriptors**
204 ANOVA results for the percentage cover detected significant differences among Shores (Table
205 1). Post hoc analysis was not able to provide an alternative hypothesis, probably due to its lower
206 power (Underwood, 1997), (Fig. 3). For total and spat density, the interaction between shore and
207 date (Sh x Da) was significant (Table 1). Post hoc analysis for total density showed a
208 homogeneous pattern for the first three dates (Jan, Apr, Jun) but, significant differences were
209 detected in the last three months (Sep, Oct, Dec) (Fig. 4). Results for spat stage showed a similar
210 pattern as total density, but only Aguda showed significant differences in the last two months
211 (Oct, Dec) (Fig. 5).
212 Condition index and clump thickness showed significant differences for the interaction between
213 shore and date (Sh x Da) (Table 2). Post hoc analysis showed significant differences in the first
214 four months (Jan, Apr, Jun, Sep). On the other hand, in October, Valadares showed significantly
215 higher values than the remaining shores (Fig. 6). For bed thickness, post hoc analysis showed
216 significant differences in the first two months (Jan, Apr) for several shores (Fig. 7).
217 The size classes 1 and 3 did not show significant differences among seasons or shores (Table 3).
218 However, ANOVA detected significant differences for the interaction between shore and date
219 (Sh x Da) in Classes 2, 4, 5 and 6 (Table 3). The post hoc analyses showed significant
220 differences between shores in June and December for Class 2 (Fig. S1). For Class 4, significant
221 differences were detected in June and October (Fig. S2). For the Class 5, post hoc analysis
222 pointed out differences in January, April, September and December, (Fig. S3). For Class 6, post
223 hoc analysis showed significant differences in January, October. (Fig. S4).
224 The sediment content in clumps differed significantly among shores both for total sediment and
225 different sediment sizes (Table 4) (Fig. 8).
226 **Relationship between sediment content in clumps and different mussel attributes**
227 Spearman's rank correlations showed that total sediment content significantly increased with
228 mussel clumps thickness (R=0.551, p<0.01). Moreover, a significant positive correlation was
229 found between total sediment content and condition index (R=0.136, p<0.05) and with the
230 average mussel size (R=0.18, p<0.05) but the correlation coefficients were much lower than that
231 obtained for thickness. However, correlation between total sediment and cover (R=0.0356,
232 p>0.05), density (R=-0.05, p>0.05) or spat stage (R=-0.0345, p>0.05) were not significant.
233

Discussion

234
235 This study documented the lack of seasonality for all the studied descriptors in *M.*
236 *galloprovincialis* along the North coast of Portugal. However, significant differences were
237 shown on the term Sh x Da for density, spat stage, clump thickness, condition index and size
238 classes, demonstrating that drivers shaping these descriptors have limited effects at spatial (i.e.
239 shores) and temporal (i.e. date) scales. Moreover, percentage cover and sediment content on
240 mussel clumps showed significant differences just among shores indicating that the different
241 drivers that could influence these descriptors, have a constant effect along the explored time
242 scales (Season and Date), changing only at spatial scale.
243 The comparison of our results with previous studies is difficult due to the lack of information
244 about spatial-temporal variability of *M. galloprovincialis* populations in the Iberian Peninsula.
245 However, studies done in other regions (e.g. South-west England and Italian coast) demonstrated
246 differences between seasons for the condition index of *M. galloprovincialis* (Orban et al., 2002;
247 Ivankovic et al., 2005). Moreover, studies on benthic assemblage seasonality done in North of
248 Portugal were focused on tide pools (Rubal et al., 2011; Bertocci et al., 2012) and pointed out
249 that benthic assemblages (dominated by macroalgae) showed significant differences between
250 seasons. Results of these studies contrast with our findings for *M. galloprovincialis* suggesting
251 that drivers that shape mussel populations probably are different to those influencing tide pool
252 macroalgae assemblages. In contrast with our results, other invertebrates considered as
253 ecosystem engineers, such as *Sabellaria* worms (Gravina et al., 2018), showed seasonality with a
254 growing phase beginning in summer until fall, a degeneration phase in winter and spawning in
255 spring (Peharda et al., 2007; Gravina et al., 2018).
256 *Mytilus galloprovincialis* showed a homogenous pattern along time for percentage cover. The
257 absence of seasonality or other temporal variability in this descriptor suggests that mussels
258 occupy similar areas of rocky shores along the year, independently of the season and date. The
259 study by Boaventura and Re (2002), done along the Portuguese coast, showed that the
260 abundance of *M. galloprovincialis* declined from North to South of Portugal; this is in agreement
261 with the high values of the percentage cover found in our study. The percentage cover is
262 determined by the abundance and size of individuals, which is affected by growth, mortality and
263 recruitment (Roughgarden, Iwasa & Baxter, 1985; Petraitis, 1995). Therefore, results for the
264 percentage cover are in concordance with our results for density and spat stage that did not show
265 any seasonality. The constant amount of spat stage along the year suggests a constant recruitment
266 and spawning for *M. galloprovincialis* in the studied area. There are many studies about the
267 reproductive cycle of *M. galloprovincialis* showing contrasting conclusions (e.g. Seed, 1976;
268 Nsgarajan and Lea, 2006). Seed (1976) suggests that spawning in *Mytilus* is regulated by a
269 combination of external and internal factors but, the variation of seawater temperature is the
270 most crucial one and that low temperatures reached in winter and autumn can inhibit mussel
271 spawning. Seed (1976) pointed out that optimum seawater temperature for the genus *Mytilus*
272 ranges between 10º C and 20º C, which can influence not just the spawning but also the growth.
273 For the specie *M. galloprovincialis* the optimal temperature for the population growth rate ranges

274   between 13ºC and 18ºC (Yoann & Cédric, 2018). As temperature is different between regions
275   and may change considerably from year to year (Seed, 1976), the reproductive cycle of *M.*
276   *galloprovincialis* can present different seasonal patterns according to the studied region and even
277   among years. On the other hand, the study by Ceccherelli and Rossi (1984) does not exclude the
278   probability of spat stage occurs independently at different times along the whole year, with
279   different values among months. Therefore, *M. galloprovincialis* can present different
280   reproductive phenology at different regions (Ceccgerelli & Rossi, 1984). Constant recruitment
281   and reproduction along the year in our studied area is possible since seawater temperature is
282   around the optimum range described by Yoann & Cédric, 2018 during all year. The few
283   significant differences detected for total and spat abundance could be the result of local natural
284   or anthropogenic disturbances.
285   The condition index of mussels is affected through a variety of intrinsic and extrinsic factors, like
286   food availability, sea temperature, salinity and gametogenic cycle (Okumus & Stirling, 1998).
287   Many studies (e.g. Çelik et al., 2012) state that the condition index shows a seasonal variability;
288   achieving a maximum during gonadal development and decreases when spawning period starts.
289   However, other studies (e.g. Orban et al., 2002) showed that the condition index registered a
290   similar value along the year, in concordance with our results. The lack seasonal variability
291   suggest that mussels from north of Portugal do not have a defined period for gonadal
292   development and spawning. Therefore, mussels seem to be able to spawn along the whole year,
293   explaining in this way the constant recruitment that suggests the spat density results. As
294   percentage cover, clump thickness provides information about the habitat furnished by *M.*
295   *galloprovincialis* for the other species. The percentage cover gives information about the habitat
296   provided by *M. galloprovincialis* along the shore (horizontal) while thickness depends on the
297   accumulation of different layers of mussels, providing three-dimensional habitat (vertical). The
298   clump thickness of mussel populations in the intertidal is strongly influenced by wave action
299   (Zardi, McQuaid & Nicastro, 2007). Therefore, the magnitude of the hydrodynamic forces along
300   the year can affect the thickness of mussel clumps due to dislodgment of thick clumps during
301   storms (Zardi et al., 2006). Results showed that mussel clumps thickness differs among shores
302   and dates but not between seasons. Therefore, seasonal changes on wave height seems to play a
303   minor role in shaping the clump thickness since the wave height, in the studied area, has a clear
304   seasonal pattern (i.e. higher during Winter-Autumn) in contrast with our findings for clump
305   thickness. Therefore, observed differences among dates and shores may be the result of local
306   shoreline characteristics.
307   The size classes also showed absence lack of seasonality. The growth of mussels can be assessed
308   by the size, which usually is related to age, but it is also dependent on environmental conditions
309   (Seed, 1976). Peharda et al. (2007) showed that the growth of *M. galloprovincialis* is slow at
310   temperatures above 21ºC and at temperatures below 10ºC, but also found that food availability
311   can be an important driver for the growth of mussels. The lack of seasonal pattern on the
312   abundance of different size classes can be the result of a continuous recruitment and growth due
313   to optimal environmental conditions on the studied area. In general the lack of seasonal changes

314   on the *M. galloprovincialis* population on the studied area contrast with the seasonal changes on
315   water and air temperature, wave action or upwelling events related with the considered seasons.
316   However, the recorded changes on temperature in the North of Portugal are around the optimum
317   range of *M. galloprovincialis*. Moreover, Abrantes (1999) showed significant differences in the
318   phytoplankton biomass, the main food source for *M. galloprovincialis*, between August and
319   January along the coast of Portugal. Despite a reduction on the phytoplankton biomass during
320   winter, this reduction is not so marked as in the centre or south of Portugal (Abrantes, 1999).
321   Therefore, the availability of food during the winter in the north of Portugal may explain the high
322   percentage cover in the north observed by Boaventura et al. (2002) and the lack of seasonal
323   variability observed in our study.
324   However, significant differences were detected among shores or among shores and dates. These
325   differences could be caused by non-seasonal physical and biological processes such as trampling,
326   harvesting, pollution events, predation, or parasitism that could vary between dates and shores
327   independently of the season. For example, the effects of harvesting and trampling could also vary
328   among shores, for instance, in function of their accessibility to humans (Smith & Murray, 2005;
329   Rius, Kaehler & McQuaid, 2006; McPhee, 2017). However, differences in the morphology or the
330   orientation to wave exposure of the studied shores could be among plausible drivers for the
331   descriptors of percentage cover and sediment content that only showed significant differences
332   between shores.
333   Results of our study also showed a lack of variability on sediment accumulation along the two
334   studied temporal scales (i.e. season and date), although significant differences were found
335   between shores. Similar results were found in Argentina (Dos Santos et al., 2018) where no
336   seasonal pattern in the sediment accumulated on mussel beds was found. However, the amount
337   of sediment that reaches the shores can vary seasonally, as found by previous studies on South
338   Africa (Zardi et al., 2006) and Argentina (Dos Santos et al., 2018). Therefore, despite the
339   variable supply of sediments, results of our study and that by Dos Santos et al. (2018) suggest a
340   limited and constant capacity of mussel beds to retain sediment under natural conditions.
341   However, the ability to accumulate sediment showed significant differences among rocky shores
342   in our study. These results contrast with those found by Dos Santos et al. (2018) where no
343   significant differences were found on the sediment accumulated on mussel beds between their
344   studied sites. In our study we have considered a broader spatial scale than that in the study by
345   Dos Santos et al. (2018). Therefore, at each shore, local currents, bottom topography, tidal speed
346   and different sources of sediment may have resulted in the heterogeneous spatial pattern found.
347   Moreover, our results showed a positive relationship between sediment accumulation and mean
348   mussel size, condition index and clump thickness, however, the correlation coefficients of
349   average mussel size and condition index were very low and only clump thickness, with a
350   correlation coefficient above 0.5, may play a relevant role in shaping sediment accumulation.
351   Results also showed that 500 μm and 1000 μm sediment size categories were the most abundant
352   ones. This observation, is in agreement with the sediment size found in some northern
353   Portuguese sandy beaches (Veiga et al. 2014) suggesting that sandy beaches and rocky shores

354   receive sediment from the same or similar sources. It is also noticeable the low amount of 63 μm
355   sediment accumulated because burial by fine sediments induces higher mortality than burial by
356   coarse sediments (Hutchison et al., 2016). Moreover, Zardi et al. (2006) showed that *M.*
357   *galloprovincialis* has higher tolerance to burial than *Perna perna*, probably because its larger
358   palpial labs are more efficient sorting particles and avoiding gill damage.
359

360   ## Conclusions
361   The lack of seasonality and reduced temporal variability found for *M. galloprovincialis* in the
362   study area may be due to the optimal water temperature and food availability along the whole
363   year. The lack of temporal variability on the amount of sediment accumulated on mussel clumps
364   suggest constant input of sediment that only differs among shores and may be influenced by
365   clump thickness.
366

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371

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576

Significant differences for percentage cover, density and spat of *M. galloprovincialis* at the different studied temporal and spatial scales.

Table 1. Summary of univariate analyses of variance (ANOVA) for percentage cover, density and spat density of *M. galloprovincialis*. Significant differences indicated in bold. n.s.: not significant, $^{*}p<0.05$ $^{**}p<0.01$ $^{***}p<0.001$

1   Table 1. Summary of univariate analyses of variance (ANOVA) for percentage cover, density and spat density of *M. galloprovincialis*.

2   Significant differences indicated in bold. n.s.: not significant, *p<0.05 **p<0.01 ***p<0.001

Source of variation	df	%Cover		Density		Spat density		F versus
		MS	F	MS	F	MS	F	
Season=Se	1	1262.53	0.66	0.14	0.01	0.62	0.02	Da(Se)
Date(Se)=Da(Se)	4	1902.84	**7.14*****	10.07	**13.56*****	26.04	**20.39*****	Si(SexDaxSh)
Shore=Sh	5	1340.44	**2.86***	4.05	2.34	5.57	2.13	ShxDa(Se)
Site(Sh)=Si(SexDaxSh)	36	266.62	**2.55*****	0.74	**3.31*****	1.28	**3.14*****	Residual
SexSh	5	260.39	0.56	1.92	1.11	4.70	1.79	ShxDa(Se)
ShxDa(Se)	20	468.49	1.76	1.73	**2.33***	2.62	**2.05***	Si(SexDaxSh)
Residual	216	104.59		0.22		0.41		
Total	287							
Transform		none		Ln(X+1)		Ln(X+1)		
Cochran's Test		C=0.0702	n.s.	C=0.0829	n.s.	C=0.0820	n.s.	

Significant differences for condition index and clump thickness of *M. galloprovincialis* at the different studied temporal and spatial scales.

Table 2. Summary of univariate analyses of variance (ANOVA) for condition index and clump thickness of *M. galloprovincialis*. Significant differences indicated in bold. s.: significant; n.s.: not significant, [*]p<0.05 [**]p<0.01 [***]p<0.001

Table 2. Summary of univariate analyses of variance (ANOVA) for condition index and clump thickness of *M. galloprovincialis*.
Significant differences indicated in bold. s.: significant; n.s.: not significant, $^*p<0.05$ $^{**}p<0.01$ $^{***}p<0.001$

Source of variance	df	Condition Index		Clump Thickness		F versus
		MS	F	MS	F	
Season=Se	1	0.0028	0.12	0.0413	0.03	Da(Se)
Date(Se)=Da(Se)	4	0.0232	18.40***	1.4722	6.98***	Si(SexDaxSh)
Shore=Sh	5	0.0143	2.71*	2.6067	5.47**	ShxDa(Se)
Site(SexDaxSh)=Si(SexDaxSh)	36	0.0013	0.92	0.2109	3.55***	Pl(SexDaxShxSi)
Plot(SexDaxShxSi)=Pl(SexDaxShxSi)	216	0.0014	3.28***	0.0593	1.64***	Residual
SexSh	5	0.0011	0.20	0.2221	0.47	ShxDa(Se)
ShxDa(Se)	20	0.0053	4.17***	0.4767	2.26*	Si(SexDaxSh)
Residual	2592	0.0004		0.0362		
Total	2879					
Transformation		None		Ln(X+1)		
Cochran's Test		C=0.0744	s.	C=0.0398	n.s.	

Significant differences for different size classes of *M. galloprovincialis* at the different studied temporal and spatial scales.

Table 3. Summary of univariate analyses of variance (ANOVA) for different size classes of *M. galloprovincialis.* Significant differences indicated in bold. s.: significant; n.s.: not significant,

[*]p<0.05 [**]p<0.01 [***]p<0.001

3   Table 3. Summary of univariate analyses of variance (ANOVA) for different size classes of *M. galloprovincialis*. Significant
4   differences indicated in bold. s.: significant; n.s.: not significant, $^*p<0.05$ $^{**}p<0.01$ $^{***}p<0.001$

Source of variation	df	Class 1		Class 2		Class 3		Class 4		Class 5		Class 6		F versus
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	
Season=Se	1	0.68	0.83	0.70	0.19	0.59	0.01	0.08	0.07	0.06	0.95	0.59	0.01	Da(Se)
Date(Se)=Da(Se)	4	0.82	**9.79*****	3.75	**10.16*****	104.95	**8.25*****	1.13	1.29	0.06	0.54	48.98	**120.57*****	Si(SexDaxSh)
Shore=Sh	5	0.08	0.52	1.16	1.25	15.02	0.68	2.98	1.82	0.70	2.24	1.44	1.40	ShxDa(Se)
Site(Sh)=Si(SexDaxSh)	36	0.08	0.95	0.37	**2.49*****	12.72	**1.65***	0.87	**2.33*****	0.11	0.85	0.41	**2.45*****	Residual
SexSh	5	0.18	1.18	0.60	0.64	8.06	0.36	0.80	0.49	0.23	0.73	1.44	1.40	ShxDa(Se)
ShxDa(Se)	20	0.15	1.84	0.93	**2.53****	22.25	1.75	1.64	**1.88***	0.31	**2.82****	1.02	**2.52****	Si(SexDaxSh)
Residual	216	0.09		0.15		7.69		0.37		0.13		0.16		
Total	287													
Transformation		none		Ln(X+1)		none		Ln(X+1)		Ln(X+1)		none		
Cochran's Test		C=0.2500	s.	C=0.0622	n.s.	C=0.0584	n.s.	C=0.0636	n.s.	C=0.0761	n.s.	C=0.9161	s.	

Significant differences for sediment content of *M. galloprovincialis* clumps at the different studied temporal and spatial scales.

Table 4. Summary of univariate analyses of variance (ANOVA) for sediment content of *M. galloprovincialis* clumps. Significant differences indicated in bold. s.: significant; n.s.: not significant, $^*p<0.05$ $^{**}p<0.01$ $^{***}p<0.001$

1   Table 4. Summary of univariate analyses of variance (ANOVA) for sediment content of *M. galloprovincialis* clumps. Significant
2   differences indicated in bold. s.: significant; n.s.: not significant, *p<0.05 **p<0.01 ***p<0.001

Source of variation	df	63 µm		125 µm		250 µm		500 µm		1000 µm		Total		F versus
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F	
Season=Se	1	0.07	0.01	2.21	0.77	2.23	0.59	8.87	1.97	0.47	0.25	1.39	0.49	Da(Se)
Date(Se)=Da(Se)	4	5.37	**2.86***	2.86	2.50	3.80	1.41	4.50	2.03	1.90	1.31	2.84	1.49	Si(SexDaxSh)
Shore=Sh	5	14.11	**5.28****	5.04	**2.86***	24.21	**11.54*****	22.94	**6.28****	11.34	**5.51****	17.78	**7.42*****	ShxDa(Se)
Site(Sh)=Si(SexDaxSh)	36	1.88	**2.22*****	1.14	**3.13*****	1.99	**3.05*****	2.22	**2.82*****	1.45	**3.80*****	1.90	**3.68*****	Residual
SexSh	5	2.67	1.00	1.05	0.60	2.21	1.06	1.30	0.36	1.65	0.80	1.64	0.68	ShxDa(Se)
ShxDa(Se)	20	2.67	1.42	1.76	1.54	2.10	1.05	3.66	1.65	2.06	1.41	2.40	1.26	Si(SexDaxSh)
Residual	216	0.84		0.36		0.65		0.79		0.38		0.52		
Total	287													
Transformation		none		Ln(X+1)		Ln(X+1)		Ln(X+1)		Ln(X+1)		Ln(X+1)		
Cochran's Test		C=0.2446	s.	C=0.0789	n.s.	C=0.0564	n.s.	C=0.0691	n.s.	C=0.0521	n.s.	C=0.0590	n.s.	

Figure 1

Studied Area

Figure 1 – Location of the 6 studied shores along the Atlantic coast of Northern Portugal
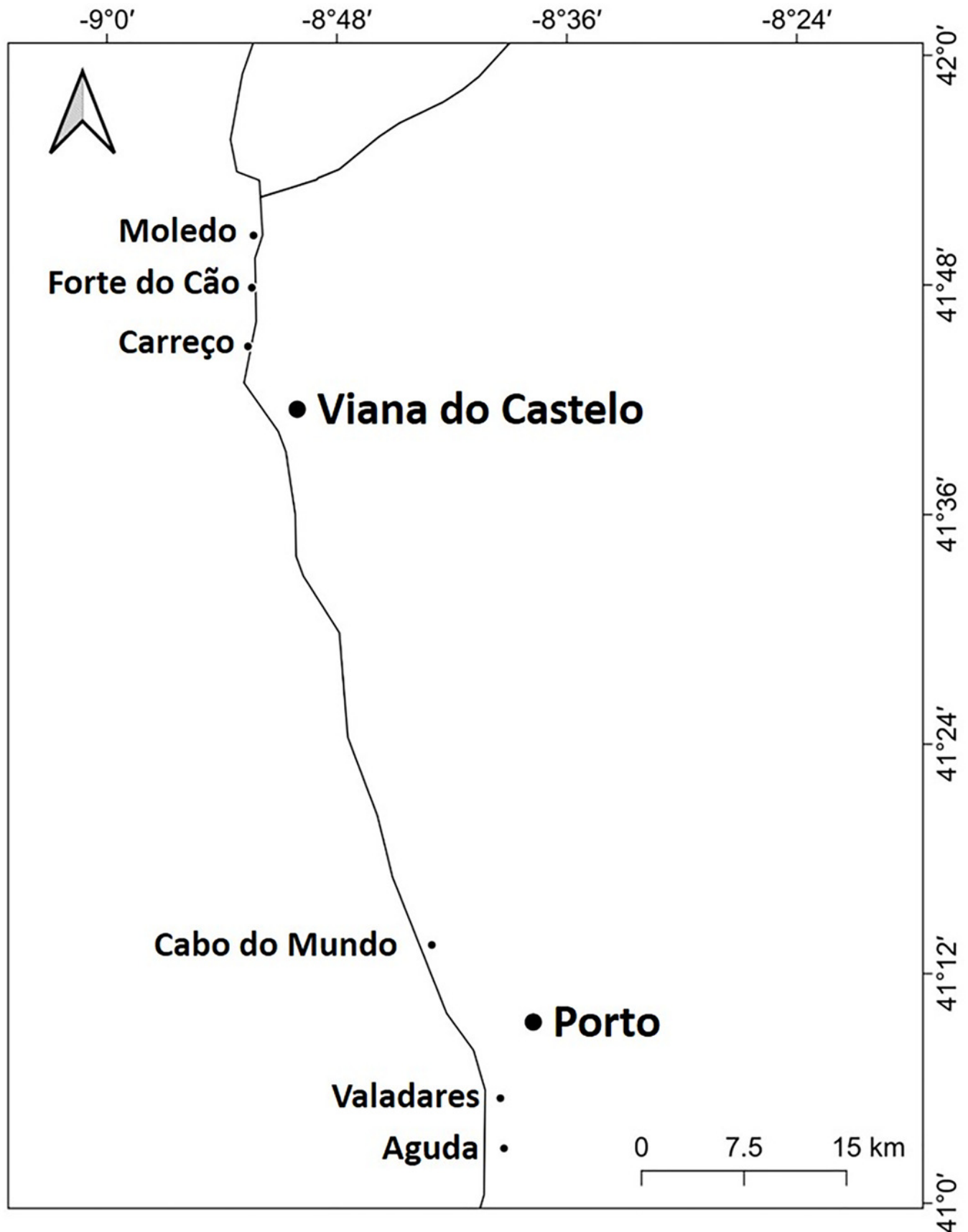
Figure 2

Environmental data

Figure 2 – **Annual variability of environmental variables registered along the year at the studied area.** (A) Temperature during 2019. Orange solid lines show the upper and lower limits of temperature tolerance for *M. galloprovincialis*. Blue solid lines show the upper and lower limits of optimal temperature for *M. galloprovincialis*. (B) Salinity during the year 2018. (C) Wave height during the year 2019. In all the figures dashed brown line represents maximum monthly values, black solid line represents average monthly values and dash and dot blue line represents minimum monthly values.
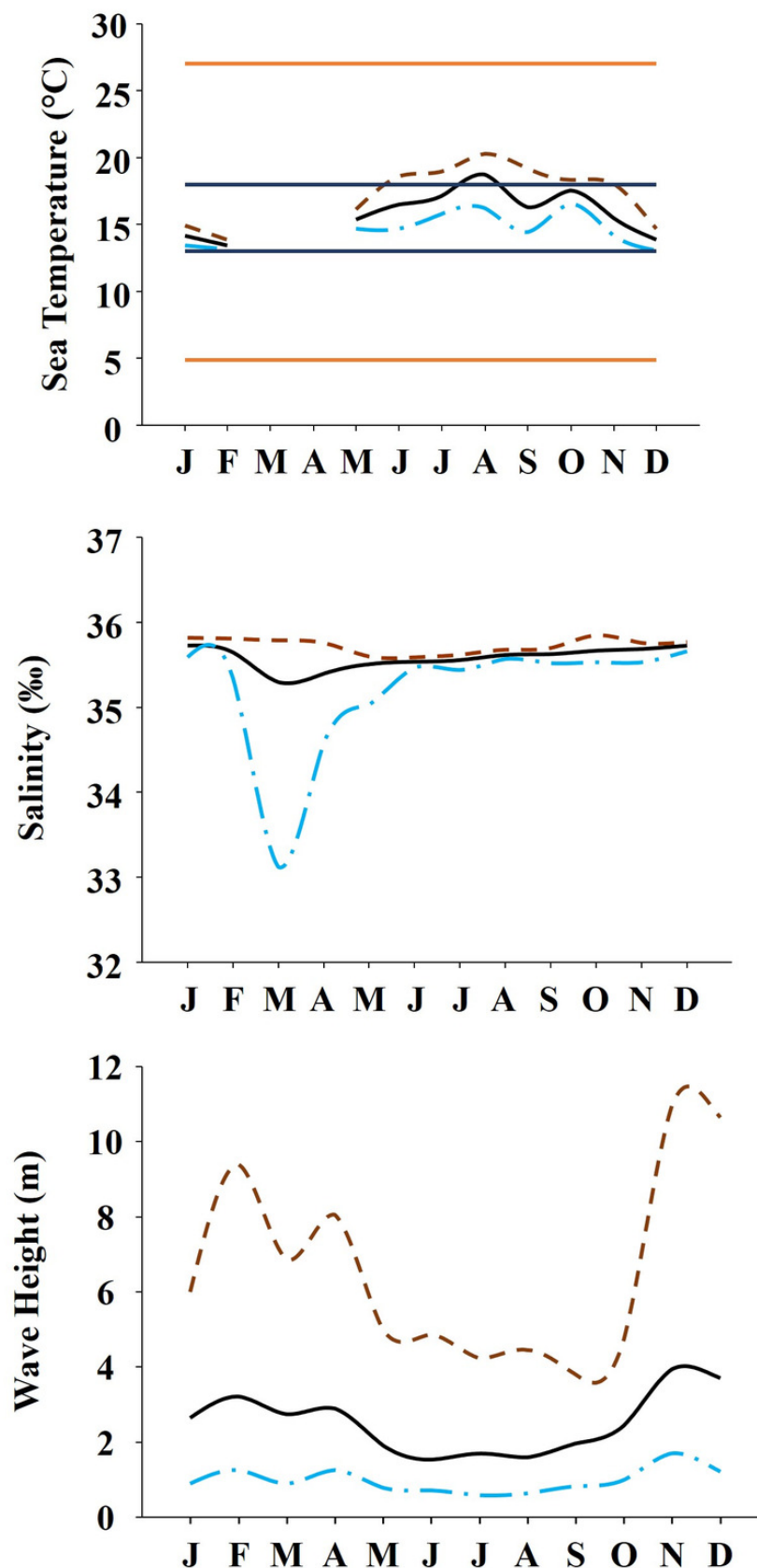
Figure 3

Percentage cover of *Mytilus galloprovincialis* at different studied shores.

Figure 3 –**Percentage cover of *Mytilus galloprovincialis* at different studied shores**.

Mean values (+ SE) of percentage cover in 50 x 50 cm.
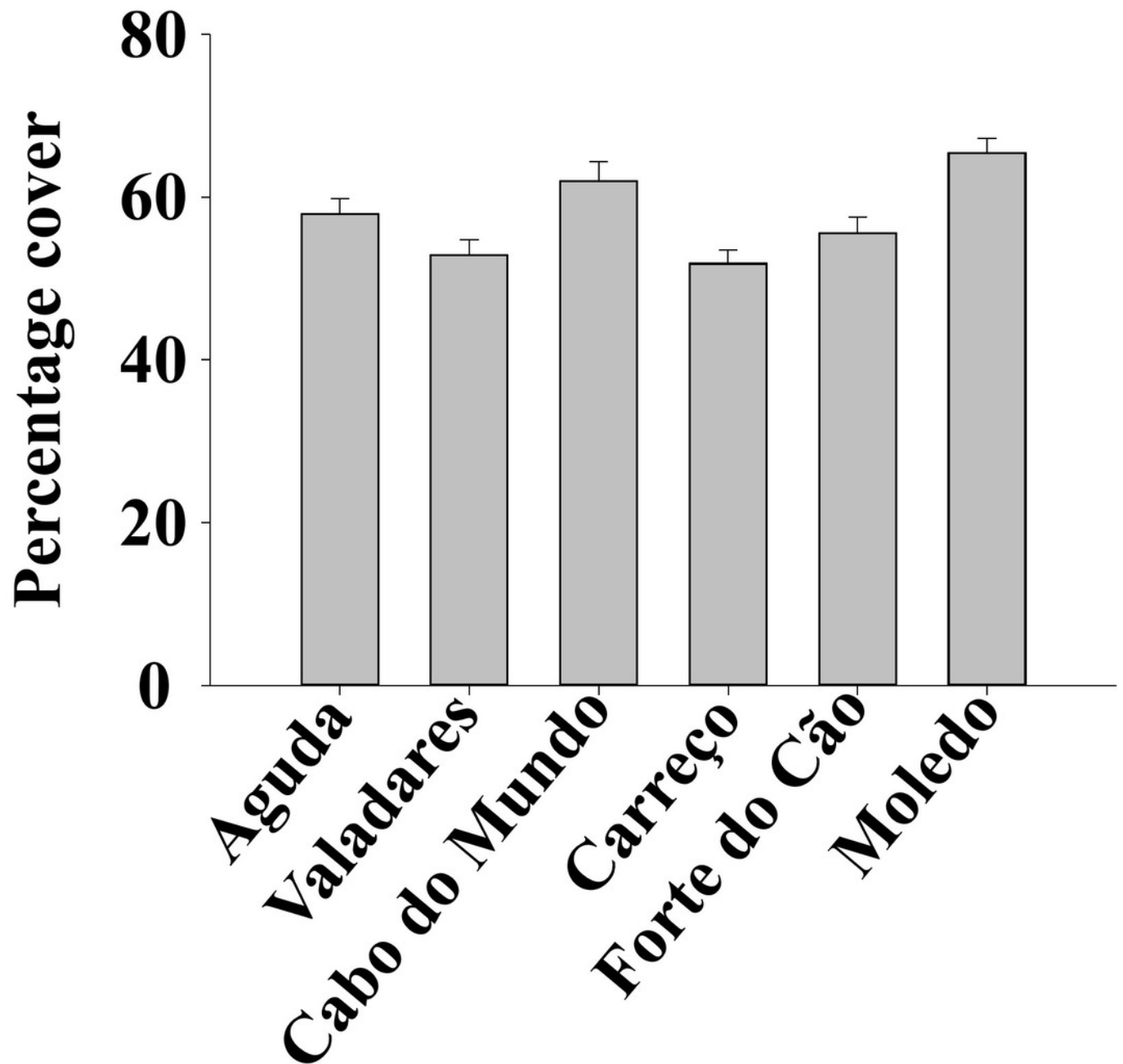
Figure 4

Significant differences of density of *Mytilus galloprovincialis* at different shores and dates.

Figure 4 – **Density of *Mytilus galloprovincialis* at different shores and dates**. Mean values (+ SE) of density (number of mussels per 10 cm^2). Different letters indicate significant differences between shores (P < 0.01) as detected by SNK test.
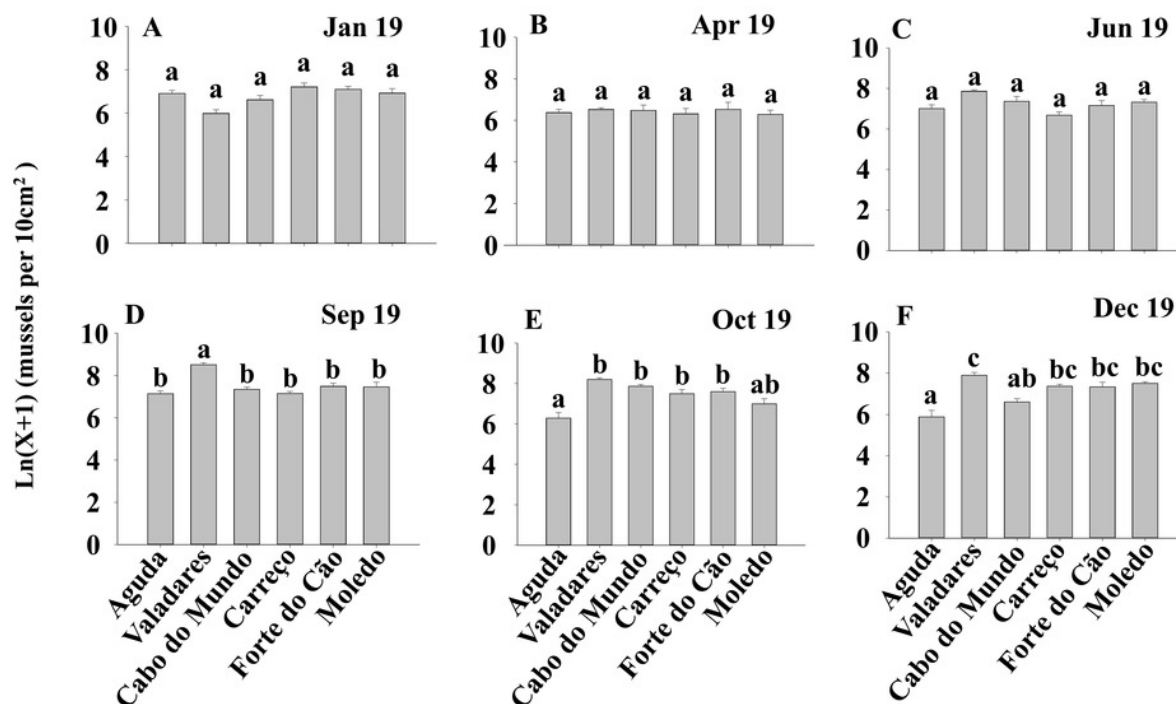
Figure 5

Density of *Mytilus galloprovincialis* in spat stage at different shores and dates.

Figure 5 – **Density of *Mytilus galloprovincialis* in spat stage at different shores and dates**. Mean values (+ SE) of mussels in spat stage (number of mussels with size between 500 and 1000 μm per 10 cm^2). Different letters indicate significant differences between shores ($P < 0.01$) as detected by SNK test.
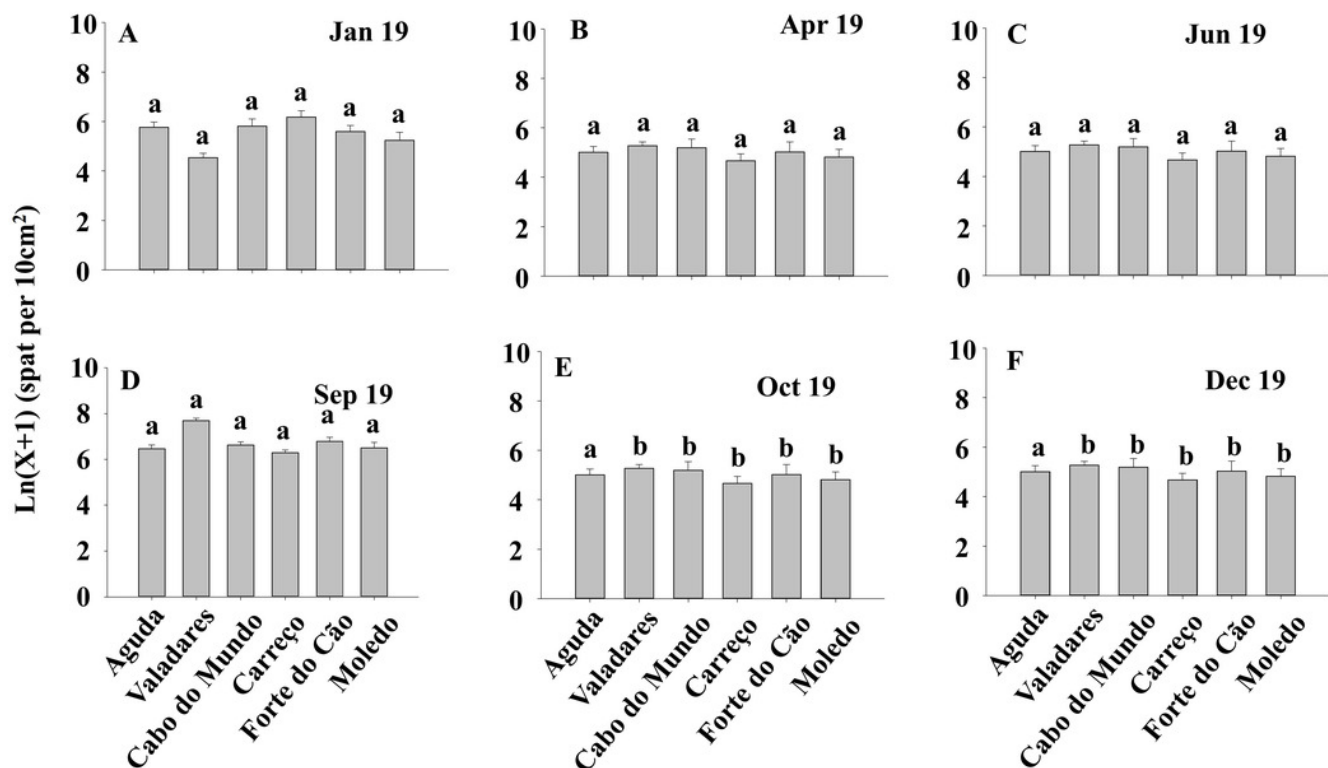
Figure 6

Condition index of *Mytilus galloprovincialis* at different shores and dates.

Figure 6 – **Condition index of *Mytilus galloprovincialis* at different shores and dates**. Mean values (+ SE) of conditionindex. Different letters indicate significant differences between shores (P < 0.01) as detected by SNK test.
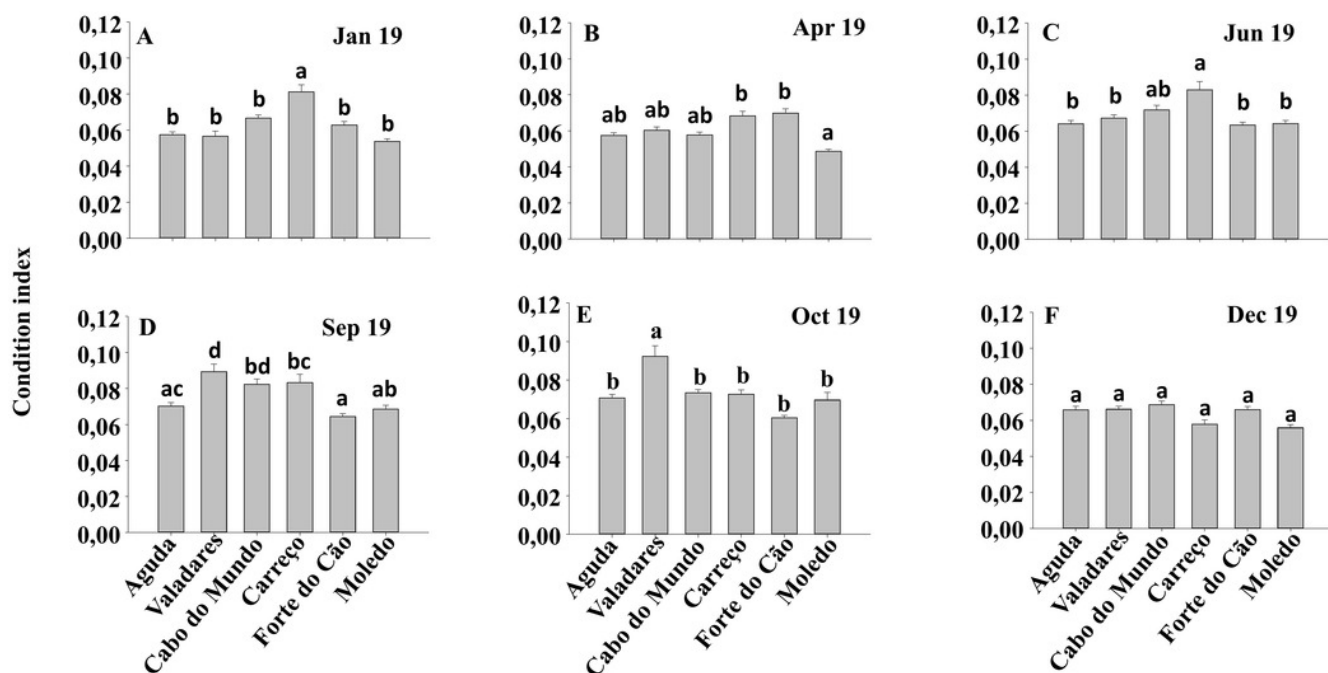
Figure 7

Clump thickness of *Mytilus galloprovincialis* at different shores and dates.

Figure 7 - **Clump thickness of *Mytilus galloprovincialis* at different shores and dates**. Mean values (+ SE) of clump thickness in cm. Different letters indicate significant differences between shores (P < 0.01) as detected by SNK test.
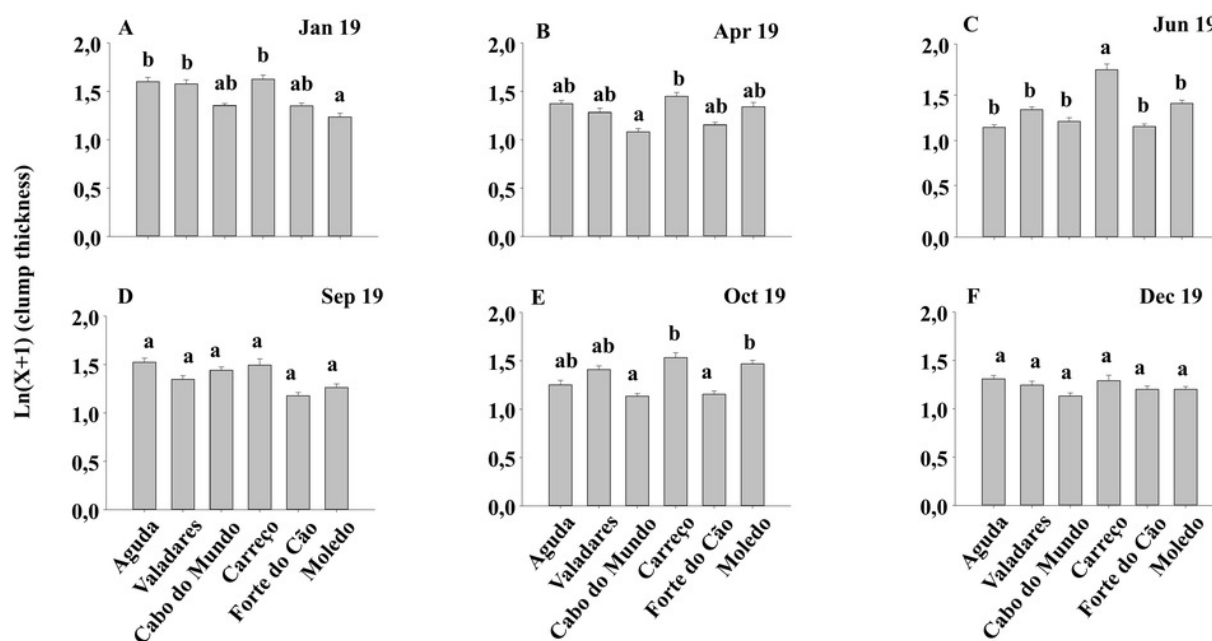
Figure 8

Sediment content of *Mytilus galloprovincialis* clumps at different shores

Figure 8 – **Sediment content of *Mytilus galloprovincialis* clumps at different shores**. Mean values (+ SE) of sediment content in grams. Different letters indicate significant differences between shores (P < 0.01) as detected by SNK test.