Spatial-temporal variability of *Mytilus galloprovincialis* Lamarck 1819 populations and their accumulated sediment in Northern Portugal (#52360)

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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 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. Therefore, it is crucial to investigate its spatial and temporal patterns of variability because there is a lack of information about this species along the Iberian Peninsula. 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 temporal and spatial variability. 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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18

Abstract

20 *Mytilus galloprovincialis* is an ecosystem engineer that provides habitat and generates

21 environmental heterogeneity, increasing biodiversity. Moreover, it is an economically important

22 species representing 14% of the global production of marine bivalves. Natural drivers and the

23 increase of anthropogenic pressures, such as sediment stress, influence its populations on rocky

24 shores. Therefore, it is crucial to investigate its spatial and temporal patterns of variability

25 because there is a lack of information about this species along the Iberian Peninsula. The

26 objective of this study was to explore the spatial-temporal patterns of different *M.*

27 *galloprovincialis* attributes along North of Portugal. For that purpose, six rocky shores were

28 selected and sampled six times along the year 2019. The percentage of cover, density, spat

29 density, condition index, clump thickness, size classes and clump sediment content were

30 considered. Results showed the lack of seasonality in *M. galloprovincialis* along the North coast

31 of Portugal. However, density, spat stage, clump thickness, condition index and size classes

32 showed some temporal and spatial variability. The percentage cover and sediment content only

33 significantly differed among shores. Our results indicated an absence of seasonality for all the

34 studied variables, probably because temperature was always within the optimum range for this

35 species and the abundance of food supply in the study area independently of the season. The

36   accumulated sediment on mussel clumps did not show any temporal variability with only
37   significant differences among shores. The accumulated sediment was composed mainly by
38   medium and coarse sand and it was correlated with mussel average size, condition index, but
39   especially with the mussel clump thickness.
40   **Subjects** Ecology, Marine Biology
41   **Keywords** Ecosystem engineer, North east Atlantic, rocky shore, sediment stress.
42

Introduction

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

76   have negative effects on mussels populations (Smith & Murray, 2005). Among the multiple
77   stressors that can affect mussel populations, the sediment accumulated on rocky shores has been
78   poorly studied. Airoldi (2003) suggests that sediment can interfere in the development of mussel
79   beds, particularly the accumulation of sediment interferes with physical and biological processes
80   that lead to a reduction of suitable habitats (Airoldi, 2003). The main negative effect described
81   for sediment accumulation on mussel populations is the burial (e.g. Hutchison et al., 2016; Dos
82   Santos et al., 2018) but that effect can be different among mussel species in function of their
83   ability to emerge or resist burial (Zardi et al., 2008; Hutchison et al., 2016, 2020). Moreover, the
84   sediment can be a reservoir of contaminants that can result toxic for marine animals (Long et al.,
85   1996; Fichet, Radenac & Miramand, 1998). Finally, sediment accumulation can also modify the
86   services provided by mussels modifying the invertebrate assemblage diversity associated to
87   mussel beds and facilitating the colonisation of mussel beds by soft bottoms macro- and
88   meiobenthic species (e.g. Dos Santos et al., 2018).
89   Studies about patterns of variation in time and space of natural populations and assemblages are
90   a chief goal in ecology, especially when they include economically relevant species with a key
91   ecological role like *M. galloprovincialis* (Levin, 1992; Underwood & Chapman, 2000). The
92   understanding of variation in populations is essential to the management and conservation of
93   species because, as natural and anthropogenic processes like sediment accumulation may be
94   very variable in space and time, their effect on the population dynamics will also be very
95   variable (Andrew & Mapstone, 2006; Levin, 1992; Underwood, 1996; Benedetti-Cecchi, 2000;
96   Bertocci et al., 2012). Bivalve molluscs show high plasticity on their responses and adaptation to
97   local conditions (Bayne & Widdows, 1978; Widdows et al., 1984; Tedengren et al., 1990;
98   Navarro et al., 1991) so, their settlement and growth varies among regions, according to the local
99   environment, but it can also vary along the year in response to oceanographic natural oscillations
100   (Seed, 1976). In sedentary animals like mussels, their reproduction and growth are the only
101   mechanisms to sustain populations (Seed, 1976). Consequently, exogenous and endogenous
102   factors are crucial for controlling physiological rates and the reproduction (Orban et al., 2002;
103   Nsgarajan, Lea & Goss-Custard, 2006, Seed, 1976). Therefore, knowledge of the natural
104   variability in time and space is decisive to understand population dynamics (Underwood, 1981)
105   and for the management and conservation of the stocks of commercially exploited species, as
106   well as the services provided by those species.
107   Nowadays, there is a lack of information about the spatial-temporal variability of *M.*
108   *galloprovincialis* populations along the Atlantic coast of the Iberian Peninsula, where this
109   species plays key ecological and economical roles. Similarly, the ability of *M. galloprovincialis*
110   clumps to accumulate sediment on rocky shores is almost unexplored. The main aims of this
111   study are to fill these gaps of knowledge and to explore the spatial-temporal patterns of *M.*
112   *galloprovincialis,* and accumulated sediments on their clumps, along rocky shores in the North
113   of Portugal. Different variables will be considered: density, spat stage, percentage cover, clump
114   thickness, condition index and different size classes of mussels to achieve these objectives.

115   Moreover, the spatial-temporal patterns of sediment accumulation in mussel clumps and its

116   relationships with the mussel population atributes will be examined.

117

Materials & Methods

Study area

120   The study was done between January 2019 and December 2019 and included six rocky shores

121   along 90 km of the Northern Portuguese coast: Aguda (N 41°04246', W 8°653254'), Valadares

122   (N 41°089167', W 8°658374'), Cabo do Mundo (N 41°225741', W 8°717976'), Carreço (N

123   41°742040', W 8°878418'), Forte do Cão (N 41°798244', W 8°874848') and Moledo (N

124   41°822605', W 8°874894') (Fig. 1). Along the Northern Portuguese coast, intertidal area varies

125   from soft to hard bottoms but they mostly present a mixture of both substrates. Sampling was

126   done during low tide in the mid tide level of the rocky shores, that typically is dominated by the

127   species *M. galloprovincialis* (Veiga et al., 2020). In the North of Portugal, the spring – summer

128   and the autumn – winter seasons are characterized by strong differences in mean monthly

129   precipitation, air and water temperature, hydrodynamic conditions, wave height and storm

130   frequency (Dias et al., 2002; Bertocci et al., 2012). The coastline is largely straight and is

131   exposed to wave action, which varies strongly with seasons (Dias et al., 2002). In the spring –

132   summer period the typical wave heights are between 1 and 3 m, with periods of 11-13 s (Dias et

133   al., 2002) and swells direction generally is from W and NW. In the autumn - winter period, the

134   waves can reach around 7 m with periods of 13-18 s (Dias et al., 2002). The tidal regime of the

135   study area is semidiurnal with the largest spring tides of 3.5 - 4.0 m. Moreover, the studied area

136   is subjected to a seasonal upwelling that provides nutrients and increases the primary production

137   in the water column during spring and summer months (Lemos and Pires, 2004). Along the

138   sampling year 2019, in the autumn – winter period, mean value of air temperature was 11.98º C,

139   with values ranging between 3.31º C and 22.42º C. Mean precipitation was 77.51 mm, with

140   values ranging between 34.5 mm and 145.75 mm, being December the month with more

141   precipitation. In the spring – summer months, mean values of air temperature were 19.16º C,

142   ranging between 4.13º C and 29.70º C. During these months, the mean precipitation was 31.03

143   mm, with values ranging between 3.3 mm and 117.2 mm (http://www.ipma.pt/pt/index.html).

144   Monthly values for seawater temperature, salinity and wave height at the sampling area can be

145   found in Figure 2. Values showed on Figure 2 were measured every 60 minutes by an

146   oceanographic buoy (model Seawach) placed at 42.12ºN and 9.43ºW. Values of temperature and

147   wave height were measured during 2019 but, for salinity there are many lacks of data for 2019

148   and thus, we included the data of 2018. All the data were obtained from the public repository of

149   Puertos del Estado webpage (http://www.puertos.es/es-es/oceanografia/Paginas/portus.aspx).

Sampling

151   The sampling design included two seasons and three sampling dates within each season: spring -

152   summer (April, June and September) and autumn - winter (January, October and December). On

153   each of these dates, the six studied shores were visited, and at each shore, two sites separated by

154   10 s of meters were randomly selected. At each site, the percentage of mussel's cover was

155 calculated in four quadrats (50 x 50 cm). Cover was estimated by dividing each quadrat into 25
156 sub-quadrats of 10 x 10 cm, attributing a scale from 0, with an absence of mussels, to 4, when
157 all the quadrat (10 x 10 cm) were covered by mussels, and accumulation up the 25 estimates
158 (Dethier et al., 1993). In addition, four measures of mussel clump thickness were randomly taken
159 within each of the four 50 x 50 cm quadrats by introducing a rigid ruler until reaching the bottom
160 of the clump. Within each one of the 50 x 50 cm quadrats, one sample of 10 x 10 cm was
161 collected, by scraping all the mussels in this area, and stored in labelled bags. These samples
162 were preserved in a mixture of formalin 4% with rose of Bengal neutralised with sodium
163 tetraborate anhydrous (Borax). In the laboratory, samples were washed in a tower of sieves of
164 1000 μm, 500 μm, 250 μm, 125 μm and 63 μm mesh size. For each sample, twenty random
165 mussels from the 1000 μm sieve were separated to be measured with a calliper. Measured
166 mussels were grouped in the following size classes: Class 1: <10 mm, Class 2: 10-20 mm, Class
167 3: 20-30 mm, Class 4: 30-40 mm, Class 5: 40-50 mm and Class 6: >50 mm. Additionally, 10
168 mussels per replicate were opened with a surgical blade and the shell was separated from the soft
169 body. Afterwards, they were dried and weighed to calculate the condition index as the ratio
170 between soft tissues dry weight and the shell dry weight. Residues retained in the sieves of 500
171 μm and 1000 μm were sorted in a dissection microscope and all the mussels were collected and
172 counted. To evaluate mussels in the spat stage (i.e. mussels with size between 500 and 1000 μm),
173 as a proxy of recruitment, the number of mussels retained in the 500 μm mesh size was counted.
174 The amount of sediment retained at each mesh size (1000 μm, 500 μm, 250 μm, 125 μm and 63
175 μm) was evaluated by drying the sieve content at 65°C for about 12h and weighting.
176 **Data analyses**
177 Differences in the total density, spat density, percentage cover, mussel size classes and the
178 amount of sediment retained on mussel clumps (total and different sediment sizes) were
179 examined with analyses of variance (ANOVA). These analyses were based on a four way model
180 including Season (Se) with two 2 levels: autumn – winter and spring – summer, as a fixed
181 orthogonal factor, Date (Da) with 3 levels, as a random factor nested in Se, Shore (Sh) with 6
182 levels: Aguda, Valadares, Cabo do Mundo, Moledo, Carreço and Forte do Cão, as a fixed
183 orthogonal factor and Site (Si) with 2 levels, as a random factor nested in all the previous factors,
184 considering 4 replicates per site. ANOVA was also used to test for differences on thickness and
185 condition index, but these analyses were based on a five-way model, including all the factors
186 above mentioned and Plot (Pl), as an additional random factor, nested in Se x Da x Sh x Si, with
187 4 and 10 replicates for thickness and condition index, respectively. Cochran's C test was done to
188 test for homogeneity of variances. In some cases, when Cochran's C test was significant
189 (p<0.05) data were Ln(X+1) transformed with the objective of removing heterogeneity of
190 variances. When transformation was not possible, untransformed data were analysed and results
191 were considered only if significant at p<0.01, to compensate for the increased probability of type
192 I error (Underwood, 1997). Whenever ANOVA demonstrated significant differences (p<0.05) a
193 post hoc Student-Newman-Keuls (SNK) test was done to explore differences. Finally, in order to
194 explore the relationship between total sediment content and mussel descriptors, rank correlation

195 analyses were done for each descriptor. Due to the non-normal distribution of the data,
196 Spearman's rank correlation was used.

197

Results

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

229

Discussion

231 This study documented the lack of seasonality for all the studied descriptors in *M.*
232 *galloprovincialis* along the North coast of Portugal. However, significant differences were
233 shown on the term Sh x Da for density, spat stage, clump thickness, condition index and size
234 classes, demonstrating that drivers shaping these descriptors have limited effects at spatial (i.e.

235   shores) and temporal (i.e. date) scales. Moreover, percentage cover and sediment content on
236   mussel clumps showed significant differences just among shores indicating that the different
237   drivers that could influence these descriptors, have a constant effect along the explored time
238   scales (Season and Date), changing only at spatial scale.
239   The comparison of our results with previous studies is difficult due to the lack of information
240   about spatial-temporal variability of *M. galloprovincialis* populations in the Iberian Peninsula.
241   However, studies done in other regions (e.g. South-west England and Italian coast) demonstrated
242   differences between seasons for the condition index of *M. galloprovincialis* (Orban et al., 2002;
243   Ivankovic et al., 2005). Moreover, studies on benthic assemblage seasonality done in North of
244   Portugal were focused on tide pools (Rubal et al., 2011; Bertocci et al., 2012) and pointed out
245   that benthic assemblages (dominated by macroalgae) showed significant differences between
246   seasons. Results of these studies contrast with our findings for *M. galloprovincialis* suggesting
247   that drivers that shape mussel populations probably are different to those influencing tide pool
248   macroalgae assemblages. In contrast with our results, other invertebrates considered as
249   ecosystem engineers, such as *Sabellaria* worms (Gravina et al., 2018), showed seasonality with a
250   growing phase beginning in summer until fall, a degeneration phase in winter and spawning in
251   spring (Peharda et al., 2007; Gravina et al., 2018).
252   *Mytilus galloprovincialis* showed a homogenous pattern along time for percentage cover. The
253   absence of seasonality or other temporal variability in this descriptor suggests that mussels
254   occupy similar areas of rocky shores along the year, independently of the season and date. The
255   study by Boaventura and Re (2002), done along the Portuguese coast, showed that the
256   abundance of *M. galloprovincialis* declined from North to South of Portugal; this is in agreement
257   with the high values of the percentage cover found in our study. The percentage cover is
258   determined by the abundance and size of individuals, which is affected by growth, mortality and
259   recruitment (Roughgarden, Iwasa & Baxter, 1985; Petraitis, 1995). Therefore, results for the
260   percentage cover are in concordance with our results for density and spat stage that did not show
261   any seasonality. The constant amount of spat stage along the year suggests a constant recruitment
262   and spawning for *M. galloprovincialis* in the studied area. There are many studies about the
263   reproductive cycle of *M. galloprovincialis* showing contrasting conclusions (e.g. Seed, 1976;
264   Nsgarajan and Lea, 2006). Seed (1976) suggests that spawning in *Mytilus* is regulated by a
265   combination of external and internal factors but, the variation of seawater temperature is the
266   most crucial one and that low temperatures reached in winter and autumn can inhibit mussel
267   spawning. Seed (1976) pointed out that optimum seawater temperature for the genus *Mytilus*
268   ranges between 10º C and 20º C, which can influence not just the spawning but also the growth.
269   For the specie *M. galloprovincialis* the optimal temperature for the population growth rate ranges
270   between 13ºC and 18ºC (Yoann & Cédric, 2018). As temperature is different between regions
271   and may change considerably from year to year (Seed, 1976), the reproductive cycle of *M.*
272   *galloprovincialis* can present different seasonal patterns according to the studied region and even
273   among years. On the other hand, the study by Ceccherelli and Rossi (1984) does not exclude the
274   probability of spat stage occurs independently at different times along the whole year, with

275 different values among months. Therefore, *M. galloprovincialis* can present different
276 reproductive phenology at different regions (Ceccgerelli & Rossi, 1984). Constant recruitment
277 and reproduction along the year in our studied area is possible since seawater temperature is
278 around the optimum range described by Yoann & Cédric, 2018 during all year. The few
279 significant differences detected for total and spat abundance could be the result of particular
280 ==disturbances such as harvesting or trampling.==
281 The condition index of mussels is affected through a variety of intrinsic and extrinsic factors, like
282 food availability, sea temperature, salinity and gametogenic cycle (Okumus & Stirling, 1998).
283 Many studies (e.g. Çelik et al., 2012) state that the condition index shows a seasonal variability;
284 achieving a maximum during gonadal development and decreases when spawning period starts.
285 However, other studies (e.g. Orban et al., 2002) showed that the condition index registered a
286 similar value along the year, in concordance with our results. The lack seasonal variability
287 suggest that mussels from north of Portugal do not have a defined period for gonadal
288 development and spawning. Therefore, mussels seem to be able to spawn along the whole year,
289 explaining in this way the constant recruitment that suggest the spat density results. As
290 percentage cover, clump thickness provides information about the habitat furnished by *M.*
291 *galloprovincialis* for the other species. The percentage cover gives information about the habitat
292 provided by *M. galloprovincialis* along the shore (horizontal) while thickness depends on the
293 accumulation of different layers of mussels, providing three-dimensional habitat (vertical). The
294 clump thickness of mussel populations in the intertidal is strongly influenced by wave action
295 (Zardi, McQuaid & Nicastro, 2007). Therefore, the magnitude of the hydrodynamic forces along
296 the year can affect the thickness of mussel clumps due to dislodgment of thick clumps during
297 storms (Zardi et al., 2006). Results showed that mussel clumps thickness differs between shores
298 and dates but not between seasons. ==Therefore, the wave height seems to play a minor role in==
299 ==shaping the clump thickness since the wave height, in the studied area, has a clear seasonal==
300 ==pattern (i.e. higher during Winter-Autumn)in contrast with our findings for clump thickness.==
301 The size classes also showed absence lack of seasonality. The growth of mussels can be assessed
302 by the size, which usually is related to age, but it is also dependent on environmental conditions
303 (Seed, 1976). Peharda et al. (2007) showed that the growth of *M. galloprovincialis* is slow at
304 temperatures above 21ºC and at temperatures below 10ºC, but also found that food availability
305 can be an important driver for the growth of mussels. The lack of seasonal pattern on the
306 abundance of different size classes can be the result of a continuous recruitment and growth due
307 to optimal environmental conditions on the studied area. In general the lack of seasonal changes
308 on the *M. galloprovincialis* population on the studied area contrast with the seasonal changes on
309 water and air temperature, wave action or upwelling events related with the considered seasons.
310 However, the recorded changes on temperature in the North of Portugal are around the optimum
311 range of *M. galloprovincialis*. Moreover, Abrantes (1999) showed significant differences in the
312 phytoplankton biomass, the main food source for *M. galloprovincialis*, between August and
313 January along the coast of Portugal. Despite a reduction on the phytoplankton biomass during
314 winter, this reduction is not so marked as in the centre or south of Portugal (Abrantes, 1999).

315   Therefore, the availability of food during the winter in the north of Portugal may explain the high
316   percentage cover in the north observed by Boaventura et al. (2002) and the lack of seasonal
317   variability observed in our study.
318   However, significant differences were detected among shores or among shores and dates. These
319   differences could be caused by non-seasonal physical and biological processes such as trampling,
320   harvesting, pollution events, predation, or parasitism that could vary between dates and shores
321   independently of the season. For example, the effects of harvesting and trampling could also vary
322   among shores, for instance, in function of their accessibility to humans (Smith & Murray, 2005;
323   Rius, Kaehler & McQuaid, 2006; McPhee, 2017). However, differences in the morphology or the
324   orientation to wave exposure of the studied shores could be among plausible drivers for the
325   descriptors of percentage cover and sediment content that only showed significant differences
326   between shores.
327   Results of our study also showed a lack of variability on sediment accumulation along the two
328   studied temporal scales (i.e. season and date), although significant differences were found
329   between shores. Similar results were found in Argentina (Dos Santos et al., 2018) where no
330   seasonal pattern in the sediment accumulated on mussel beds was found. However, the amount
331   of sediment that reaches the shores can vary seasonally, as found by previous studies on South
332   Africa (Zardi et al., 2006) and Argentina (Dos Santos et al., 2018). Therefore, despite the
333   variable supply of sediments, results of our study and that by Dos Santos et al. (2018) suggest a
334   limited and constant capacity of mussel beds to retain sediment under natural conditions.
335   However, the ability to accumulate sediment showed significant differences among rocky shores
336   in our study. These results contrast with those found by Dos Santos et al. (2018) where no
337   significant differences were found on the sediment accumulated on mussel beds between their
338   studied sites. In our study we have considered a broader spatial scale than that in the study by
339   Dos Santos et al. (2018). Therefore, at each shore, local currents, bottom topography, tidal speed
340   and different sources of sediment may have resulted in the heterogeneous spatial pattern found .
341   Moreover, our results showed a positive relationship between sediment accumulation and mean
342   mussel size, condition index and clump thickness, however, the correlation coefficients of
343   average mussel size and condition index were very low and only clump thickness, with a
344   correlation coefficient above 0.5, may play a relevant role in shaping sediment accumulation.
345   Results also showed that 500 μm and 1000 μm sediment size categories were the most abundant
346   ones. This observation, is in agreement with the sediment size found in some northern
347   Portuguese sandy beaches (Veiga et al. 2014) suggesting that sandy beaches and rocky shores
348   receive sediment from the same or similar sources. It is also noticeable the low amount of 63 μm
349   sediment accumulated because burial by fine sediments induces higher mortality than burial by
350   coarse sediments (Hutchison et al., 2016). Moreover, Zardi et al. (2006) showed that *M.*
351   *galloprovincialis* has higher tolerance to burial than *Perna perna*, probably because its larger
352   palpial labs are more efficient sorting particles and avoiding gill damage.
353
354   **Conclusions**

355 The lack of seasonality and reduced temporal variability found for *M. galloprovincialis* in the
356 study area may be due to the optimal water temperature and food availability along the whole
357 year. The lack of temporal variability on the amount of sediment accumulated on mussel clumps
358 suggest constant input of sediment that only differs among shores and may be influcneced by
359 clump thickness.
360

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365 References

366 Abrantes F, Moita MT. 1999. Water column and recent sediment data on diatoms and
367   coccolithophorids off Portugal confirm sediment record of upwelling events. *Oceanologica*
368   22(3):319–336 DOI: 10.1016/S0399-1784(99)80034-6
369 Airoldi L. 2003. The effects of sedimentation on rocky coast assemblages. *Oceanography and*
370   *Marine Biology* 41:161–236 DOI: 10.1201/9780203180570-23
371 Andrew NL, Mapstone BD. 2006. Sampling and the description of spatial pattern in marine
372   ecology. *Oceanography and Marine Biology* 52: 39–90 DOI: 10.1016/0198-
373   0254(88)92605-2
374 Araújo J, Soares F, Medeiros A, Bandarra NM, Freire M, Falcão M, Pousão-Ferreira P. 2020.
375   Depth effect on growth and fatty acid profile of Mediterranean mussel (*Mytilus*
376   *galloprovincialis*) produced on a longline off south Portugal. *Aquaculture International* 28:
377   927–946 DOI:10.1007/s10499-019-00504-0
378 Bayne BL, Widdows J. 1978. The physiological ecology of two populations of *Mytilus edulis* L.
379   *Oecologia* 37,137–162 DOI: 10.1007/BF00344987
380 Benedetti-Cecchi L. 2000. Priority effects, taxonomic resolution, and the prediction of variable
381   patterns of colonisation of algae in littoral rock pools. *Oecologia* 123:265–274 DOI:
382   10.1007/s004420051013
383 Bertocci I, Araújo R, Incera M, Arenas F, Pereira R, Abreu H, Larsen K, Sousa-Pinto I. 2012.
384   Benthic assemblages of rock pools in northern Portugal : seasonal and between-pool
385   variability. *Scientia Marina* 76(4):781–789 DOI: 10.3989/scimar.03669.21
386 Boaventura D, Ré P, Fonseca LC, Hawkins SJ. 2002. Intertidal rocky shore communities of the
387   continental Portuguese coast : Analysis of distribution patterns. *Marine Ecology* 23(1):69–
388   90 DOI: 10.1046/j.1439-0485.2002.02758.x
389 Borthagaray AI, Carranza A. 2007. Mussels as ecosystem engineers: their contribution to species
390   richness in a rocky littoral community. *Acta Oecologica* 31:243–250 DOI:
391   10.1016/j.actao.2006.10.008

392 Braby CE, Somero GN. 2006. Ecological gradients and relative abundance of native (*Mytilus*
393   *trossulus*) and invasive *(Mytilus galloprovincialis*) blue mussels in the California hybrid
394   zone. *Marine Biology*148: 1249–1262 DOI: 10.1007/s00227-005-0177-0
395 Cáceres-Martínez J, Figueras A. 2007. Fijación de los juveniles del mejillón: fijación del
396   mejillón. In: Figueras A, ed. *Biología y Cultivo del Mejillón (Mytilus galloprovincialis) en*
397   *Galicia*. CSIC - CSIC Press (Spain) 72–93.
398 Ceccgerelli VU, Rossi R. 1984. Settlement , growth and production of the mussel *Mytilus*
399   galloprovincialis. *Marine Ecologic Progress Series* 16:173–184 DOI: 10.3354/meps016173
400 Çelik MY, Karayücel S, Karayücel I, Öztürk R, Eyüboglu B. 2012. Meat yield, condition index
401   and biochemical composition of mussels (*Mytilus galloprovincialis* Lamarck, 1819) in
402   Sinop, South of the Black Sea. *Journal of Aquatic Food Product Technology* 21:198–205
403   DOI: 10.1080/10498850.2011.589099
404 Consellería de Pesca, Marisqueo y Acuicultura. 2000. ORDEN de 26 de Octubre de 2000 por la
405   que se regula la extracción de semilla de mejillón en bancos naturales., pp. 15681–15684.
406   *Diario Oficial de Galicia* 228: 15681–15684
407   https://www.xunta.gal/dog/Publicados/2000/20001124/Anuncio15CB6_es.html (acessed 5
408   July 2020)
409 De Moor, IJ, Bruton, MN (Compilers). 1988. Atlas of alien and translocated indigenous aquatic
410   animals in southern Africa. National Scientific Programmes Unit: CSIR, SANSP Report
411   144, 1988, pp 317. Available at http://hdl.handle.net/10204/2416 (accessed 27 August
412   2020)
413 Dethier MN, Graham ES, Cohen S, Tear LM. 1993. Visual versus random-point percent cover
414   estimations: "objective" is not always better. *Marine Ecology Progress Series* 96:93–100
415   DOI: 10.3354/meps096093
416 Dias JMA, Gonzalez R, Garcia C, Diaz-del-Rio V. 2002. Sediment distribution patterns on the
417   Galicia-Minho continental shelf. *Oceanography* 52:215–231 DOI: 10.1016/S0079-
418   6611(02)00007-1
419 Dos Santos EP, Carcedo MC, Zotelo C, Fiori SM. 2018. Effects of erosion-accretion processes
420   on a community dominated by *Brachidontes rodriguezzi* (Mollusca: Mytilidae) on a rocky
421   outcrop of the South Atlantic coast. *Journal of Marine Systems* 187:146-155 DOI:
422   10.1016/j.jmarsys.2018.07.006
423 Fichet D, Radenac G, Miramand P. 1998. Experimental estudies of impacts of harbour sediments
424   resuspension to marine invertebrates larvae: bioavailability of Cd, Cu, Pb and Zn and
425   toxicity. *Marine Pollution Bulletin* 36(7–12): 509–518 DOI: 10.1016/S0025-
426   326X(97)00190-2
427 Figueras AJ. 2007. *Biología y Cultivo del Mejillón (Mytilus galloprovincialis) en Galicia*. CSIC -
428   CSIC PressGarner YL, Litvaitis MK. 2013. Effects of wave exposure, temperature and
429   epibiont fouling on byssal thread production and growth in the blue mussel, *Mytilus edulis*,
430   in the Gulf of Maine. *Journal of Experimental Marine Biology and Ecology* 446:52–56
431   DOI: 10.1016/j.jembe.2013.05.001

432 Gravina MF, Cardone F, Bonifazi A, Bertrandino MS, Chumienti G, Longo C, Marzano CN,
433   Moretti M, Lisco S, Moretti V, Corriero G, Giangrande A. 2018. *Sabellaria spinulosa* (
434   Polychaeta , Annelida) reefs in the Mediterranean Sea : Habitat mapping, dynamics and
435   associated fauna for conservation management. *Estuarine, Coastal and Shelf Science*
436   200:248–257 DOI: 10.1016/j.ecss.2017.11.017
437 Guo C, Chen Y, Li W, Xie S, Lek S, Li Z. 2018. Food web structure and ecosystem properties of
438   the largest impounded lake along the eastern route of China's South-to-North Water
439   Diversion Project. *Ecological Informatics* 43:174–184 DOI: 10.1016/j.ecoinf.2017.12.003
440 Harris J, Branch G, Sibiya C, Bill C. 2003. The Sokhulu subsistence mussel-harvesting project:
441   co-management in action. Chapter 4. In: Hauck M, Sowman M, eds. *Waves of Change:*
442   *coastal and fisheries co-management in Southern Africa*. Cape Town: UCT Press, 61–98.
443 Hutchison ZL, Green DH, Burrows MT, Jackson AC, Wilson B, Last KS. 2020. Survival
444   strategies and molecular responses of two marine mussels to gradual burial by sediment.
445   *Journal of Experimental Marine Biology and Ecology* 527:151364 DOI:
446   10.1016/j.jembe.2020.151364
447 Hutchison ZL, Hendrick VJ, Burriwa MT, Wilson B, Last KS. 2016. Buried Alive: The
448   behavioural response of the mussels, *Modiolus modiolus* and *Mytilus edulis* to dudden
449   burial by sediment. *PloS One* 11(3): e0151471 DOI: 10.1371/journal.pone.0151471
450 Instituto Português do Mar e da Atmosfera. Boletins Climatológicos. Available at
451   http://www.ipma.pt/pt/index.html (accessed 5 June 2020)
452 Ivankovic D, Pavicic J, Erk M, Filipovic-Marijic V, Raspor B. 2005. Evaluation of the *Mytilus*
453   *galloprovincialis* Lam. . digestive gland metallothionein as a biomarker in a long-term field
454   study : Seasonal and spatial variability. *Marine Pollution Bulletin* 50:1303–1313 DOI:
455   10.1016/j.marpolbul.2005.04.039.
456 Leigh ECJr, Paine RT, Quinn JF, Suchanek TH. 1987. Wave energy and intertidal productivity.
457   *Proceedings of the National Academy of Sciences of the United States of America* 84:1314–
458   1318 DOI: 10.1073/pnas.84.5.1314
459 Lemos RT, Pires H. 2004. The upwelling regime off the west Portuguese coast, 1941-2000.
460   *International Journal of Climatology* 24:511–524 DOI: 10.1002/joc.1009
461 Levin SA. 1992. The problem of pattern and scale in ecology. *Ecological society of America*
462   73:1943–1967 DOI: 10.2307/1941447
463 Loehle C. 2004. Challenges of ecological complexity. Ecological Complexity 1:3–6 DOI:
464   10.1016/j.ecocom.2003.09.001
465 Long ER, Robertson A, Wolfe DA, Hameedi J, Sloane GM. 1996. Estimates of the spatial extent
466   of sediment toxicity in major US estuaries. *Environmental Science & Technology* 30:3585–
467   3592 DOI: 10.1021/es9602758
468 Lynch SA, Coghlan A, Leary BO, Morgan E, Culloty SC. 2020. Northward establishment of the
469   mediterranean mussel *Mytilus galloprovincialis* limited by changing climate. *Biology*
470   *Invasions* 22:2725–2736 DOI: 10.1007/s10530-020-02294-6
471 McPhee DP. 2017. Urban recreational fisheries in the australian coastal zone: The sustainability

472   challenge. *Sustainability* 9:1–12 DOI: 10.3390/su9030422

473 Navarro E, Iglesias JIP, Camacho AP, Labarta U, Beiras R. 1991. The physiological energetics
474   of mussels (*Mytilus galloprovincialis* Lmk.) from diferent cultivation rafts in the Ria de
475   Arosa (Galicia,N.W. Spain). *Aquaculture*, 94:197–212 DOI: 10.1016/0044-8486(91)90118-
476   Q

477 Nicastro KR, McQuaid CD, Zardi GI. 2019. Between a rock and a hard place : combined effect
478   of trampling and phototrophic shell-degrading endoliths in marine intertidal mussels.
479   *Marine Biodiversity* 49:1581–1586 DOI: 10.1007/s12526-018-0924-3

480 Nsgarajan R, Lea SWG, Goss-Custard J. 2006. Seasonal variations in mussel , *Mytilus edulis* L .
481   shell thickness and strength and their ecological implications. *Journal of Experimental*
482   *Marine Biology and Ecology* 339:241–250 DOI: 10.1016/j.jembe.2006.08.001

483 Okumus I, Stirling HP. 1998. Seasonal variations in the meat weight, condition index and
484   biochemical composition of mussels (*Mytilus edulis* L.) in suspended culture in two Scottish
485   sea lochs. *Aquaculture* 159(3–4):249–261 DOI: 10.1016/S0044-8486(97)00206-8

486 Orban E, Lena G Di, Nevigato T, Casini I, Marzetti A, Caproni R. 2002. Seasonal changes in
487   meat content, condition index and chemical composition of mussels (*Mytilus*
488   *galloprovincialis*) cultured in two different Italian sites. *Food Chemistry* 77:57–65 DOI:
489   10.1016/S0308-8146(01)00322-3

490 Peharda M, Zupan I, Baveevié L, Frankié A, Klanjsflcek T. 2007. Growth and condition index of
491   mussel *Mytilus galloprovincialis* in experimental integrated aquaculture. *Aquaculture*
492   *Research* 38:1714–1720 DOI: 10.1111/j.1365-2109.2007.01840.x

493 Petraitis PS. 1995. The role of growth in maintaining spatial dominance by mussels (*Mytilus*
494   *edulis*). *Ecology* 76:1337–1346 DOI: 10.2307/1940940

495 Prado L, Castilla JC. 2006. The bioengineer *Perumytilus purpuratus* (Mollusca: Bivalvia) in
496   central Chile: biodiversity, habitat structural complexity and environmental heterogeneity.
497   *Jounal of the Marine Biological Association of the UK* 86:417–421 DOI:
498   10.1017/S0025315406013282

499 Rius M, Kaehler S, McQuaid CD. 2006. The relationship between human exploitation pressure
500   and condition of mussel populations along the south coast of South Africa. *South African*
501   *Journal of Science* 102:130–136

502 Roughgarden J, Iwasa Y, Baxter C. 1985. Demographic-theory for an openmarine population
503   with space-limited recruitment. *Ecology* 66:54–67 DOI: 10.2307/1941306

504 Rubal M, Veiga P, Vieira R, Sousa-Pinto I. 2011. Seasonal patterns of tidepool macroalgal
505   assemblages in the North of Portugal . Consistence between species and functional group
506   approaches. *Jornal of Sea Research* 66:187–194 DOI: 10.1016/j.seares.2011.07.003

507 Seed R. 1976. Ecology. In: Bayne BL ed. *Marine mussels: their ecology and physiology*.
508   Cambridge: Cambridge University Press, , 13–67.

509 Seed R. 1996. Patterns of biodiversity in the macro-invertebrate fauna associated with mussel
510   patches on rocky shores. *Jounal of the Marine Biological Association of the UK* 76:203–
511   210 DOI: 10.1017/S0025315400029131

512   Seed R, Suchanek TH. 1992. Population and community ecology of *Mytilus*. In: Gosling E, ed.
513   *The mussel Mytilus: ecology, physiology, genetics and culture*. London: Elsevier, , 87–169.
514   Smith JR, Murray SN. 2005. The effects of experimental bait collection and trampling on a
515   *Mytilus californianus* mussel bed in southern California. *Marine Biology* 147:699–706 DOI:
516   10.1007/s00227-005-1619-4
517   Tedengren M, Andrë C, Johannesson K, Kautsky N. 1990. Genotypic and phenotypic diferences
518   between Baltic and North Sea populations of *Mytilus edulis* evaluated through reciprocal
519   transplantations. III. *Physiology*. *Marine Ecology Progress Series* 59:221–227 DOI:
520   10.3354/meps059203
521   Thiel M, Ullrich N. 2002. Hard rock versus soft bottom: the fauna associated with intertidal
522   mussel beds on hard bottoms along the coast of Chile, and considerations on the functional
523   role of mussel beds. *Helgoland Marine Research* 56:21–30 DOI: 10.1007/s10152-001-
524   0098-3
525   Todd PA, Heery EC, Loke LHL, Thurstan RH, Kotze DJ, Swan C. 2019. Towards an urban
526   marine ecology: characterizing the drivers, patterns and processes of marine ecosystems in
527   coastal cities. *OIKOS* 128:1215–1242 DOI: 10.1111/oik.05946
528   Underwood AJ. 1981. Structure of a rocky intertidal community in New South Wales: patterns of
529   vertical distribution and seasonal changes. *Journal of Experimental Marine Biology and
530   Ecology* 51:57–85 DOI: 10.1016/0022-0981(81)90154-4
531   Underwood AJ. 1997. *Experiments in ecology: their logical design and interpretation using
532   analysis of variances*. Cambridge: Univeristy Press
533   Underwood AJ, Chapman MG. 1996. Scales of spatial patterns of distribution of intertidal
534   invertebrates. *Oecologia* 107:212–224 DOI: 10.1007/BF00327905
535   Underwood AJ, Chapman MG, Connell SD. 2000. Observations in ecology: you can't make
536   progress on processes without understanding the patterns. *Journal of Experimental Marine
537   Biology and Ecology* 250:97–115 DOI: 10.1016/S0022-0981(00)00181-7
538   UNEP 2006. Marine and coastal ecosystems and human wellbeing: A synthesis report based on
539   the findings of the Millennium Ecosystem Assessment. UNEP. Available at
540   https://www.unenvironment.org/resources/report/marine-and-coastal-ecosystems-and-
541   human-well-being-synthesis-report-based-findings (accessed 9 August 2020)
542   Veiga P, Ramos-Oliveira C, Sampaio L, Rubal M. 2020. The role of urbanisation in affecting
543   *Mytilus galloprovincialis*. *PLoS ONE* 15(5): e0232797. DOI: 10.1371/journal.pone.0232797
544   Widdows J, Donkin P, Salked PN, Cleary JJ, Lowe DM, Evans SV, Thompson PE. 1984.
545   Relative importance of environmental factors in determining physiological diferences
546   between two populations of mussels (*Mytilus edulis*). *Marine Ecology Progress Series*
547   17:33–47 DOI: 10.3354/meps017033
548   Wijsman JWM, Troost K, Fang J, Roncarati A. 2019. Global production of marine bivalves.
549   Trends and challenges. In: Smaal A, Ferreira J, Grant J, Petersen J, Strand Ø eds. *Goods
550   and services of marine bivalves*. Switzerland: Springer, Cham, 7–26. DOI: 10.1007/978-3-
551   319-96776-9_2

552 World sea temperatures. Portugal. Available at https://www.seatemperature.org/ (accessed 27
553   June 2020)

554 Yoann T, Cédric B. 2018. Assessing the sensivity of bivalve populations to global warming
555   using an individual-based modelling approach. *Global Change Biology* 24:4581–4597 DOI:
556   10.1111/gcb.14402

557 Zardi GI, McQuaid CD, Nicastro KR. 2007. Balancing survival and reproduction : seasonality of
558   wave action, attachment strength and reproductive output in indigenous *Perna perna* and
559   invasive *Mytilus galloprovincialis* mussels. *Marine Ecology Progress Series* 334:155–163
560   DOI: 10.3354/MEPS334155

561 Zardi GI, Nicastro KR, McQuaid CD, Erlandsson J. 2008. Sand and wave induced mortality in
562   invasive (*Mytilus galloprovincialis*) and indigenous (*Perna perna*) mussels. *Marine Biology*
563   153: 853–858 DOI: 10.1007/s00227-007-0857-z

564 Zardi GI, Nicastro KR, McQuaid CD, Rius M, Porri F. 2006. Hydrodynamic stress and habitat
565   partitioning between indigenous (*Perna perna*) and invasive (*Mytilus galloprovincialis*)
566   mussels : constraints of an evolutionary strategy. *Marine Biology* 150:79–88 DOI:
567   10.1007/S00227-006-0328-Y

568

Table 1(on next page)

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

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.	

3

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Table 2 (on next page)

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

Figure 2 –(A) Temperature at the studied area during the year 2019. (B) Salinity at the studied area during the year 2018. (C) Wave height at the studied area during the year 2019.

1

2   Table 2. Summary of univariate analyses of variance (ANOVA) for condition index and clump thickness of *M. galloprovincialis*.

3   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.	

4

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Table 3 (on next page)

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

1

2

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.	

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Table 4(on next page)

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

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 MS	63 µm F	125 µm MS	125 µm F	250 µm MS	250 µm F	500 µm MS	500 µm F	1000 µm MS	1000 µm F	Total MS	Total F	F versus
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.	

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Figure 1

Studied Area

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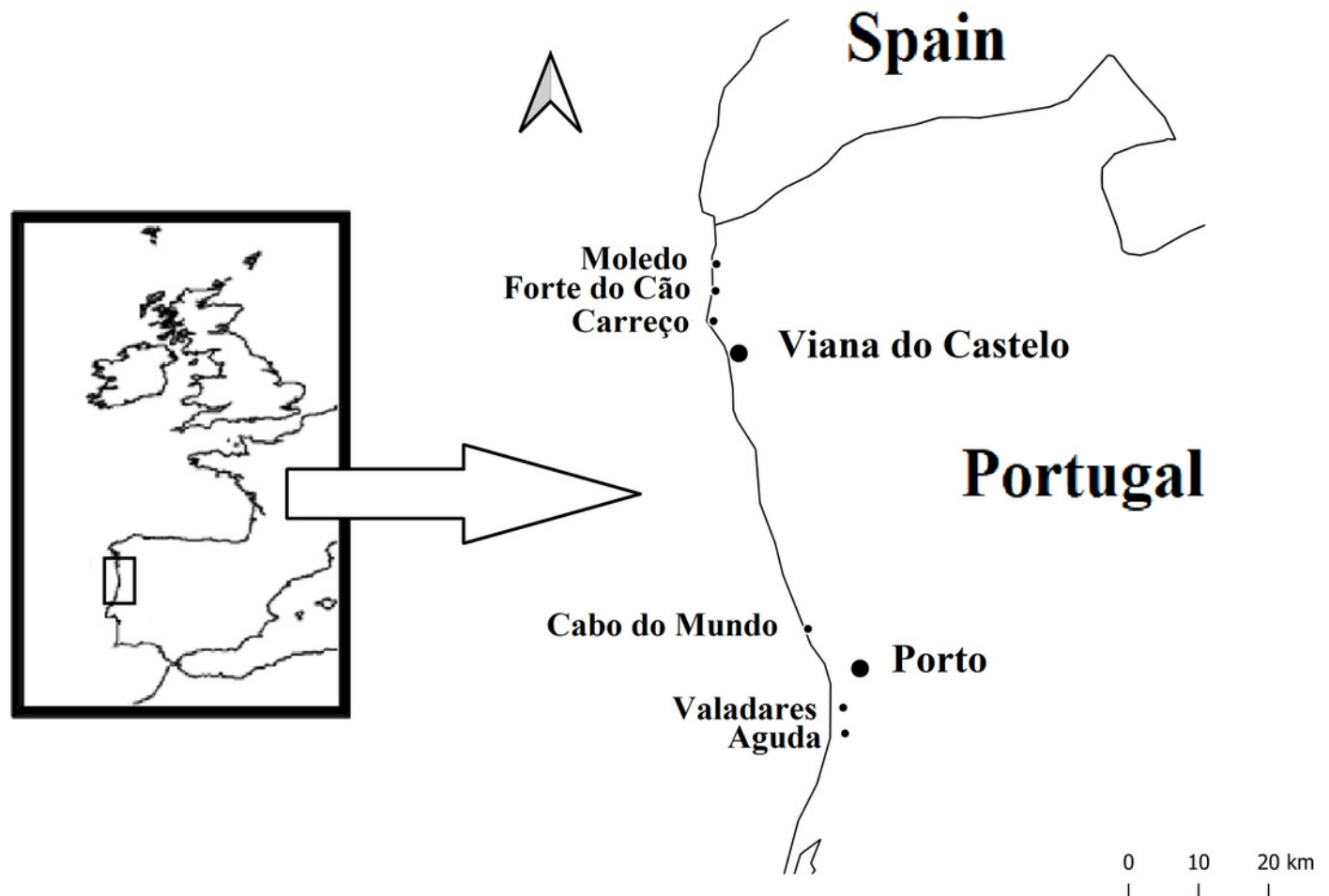
Figure 2

Environmental data

Figure 2 –(A) Temperature at the studied area during the year 2019. Red lines show the upper and lower limits of temperature tolerance for *M. galloprovincialis*. Green lines show the upper and lower limits of optimal temperature for *M. galloprovincialis*. (B) Salinity at the studied area during the year 2018. (C) Wave height at the studied area during the year 2019.
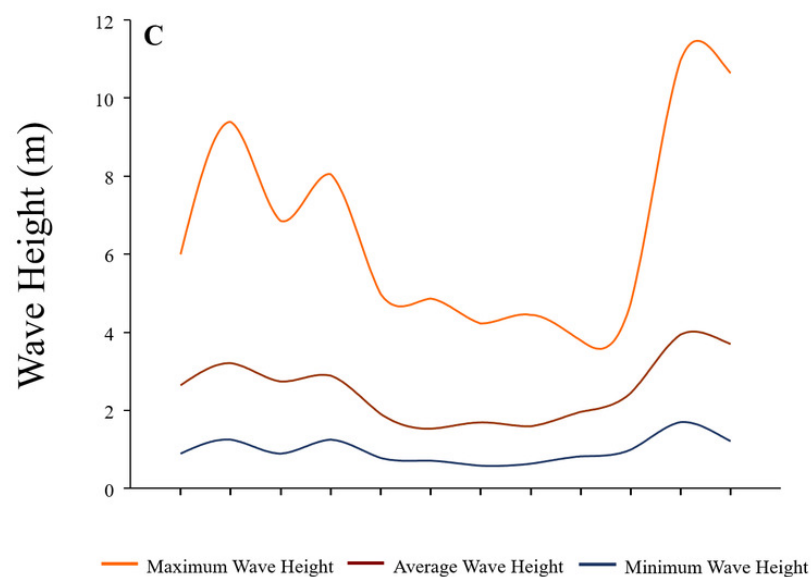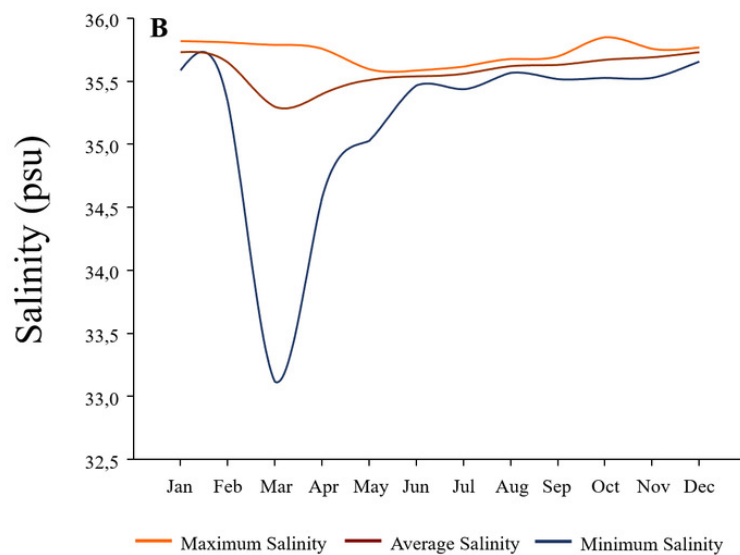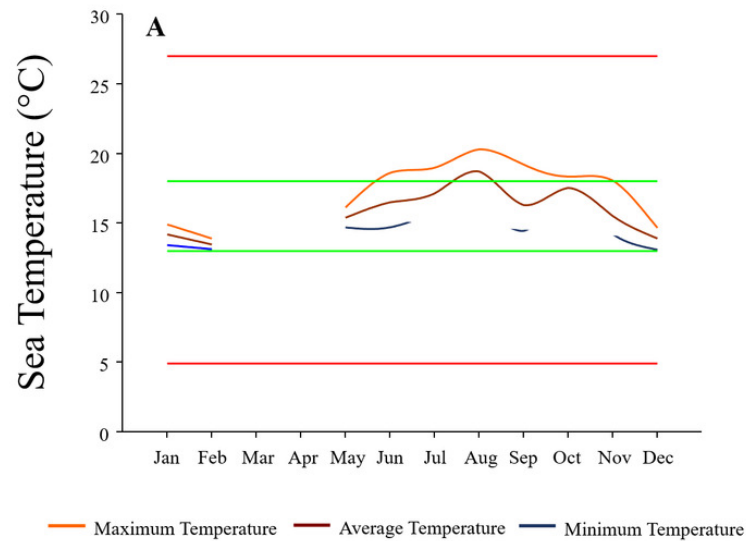
Figure 3

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

Figure 3 –**Percentage cover of *Mytilus galloprovincialis* at different studied shores**.
Meanvalues (+ SE) ofpercentage cover in 50 x 50 cm. Ag: Aguda, Va: Valadares, Cm: Cabo
do Mundo, Ca: Carreço, Fc: Forte do Cão, Mo: Moledo.
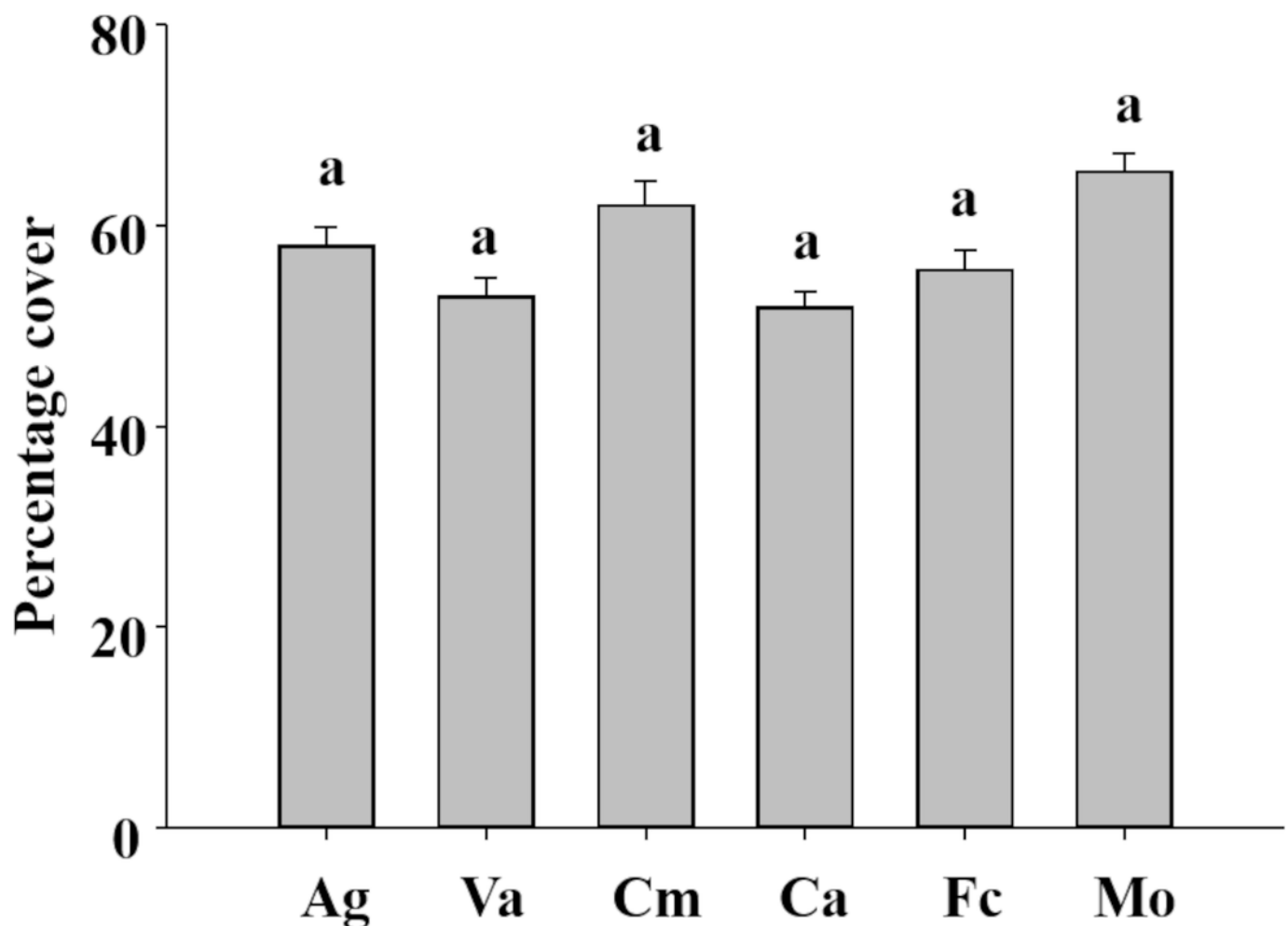
Figure 4

Significant differences of density of *Mytilus galloprovincialis* at different shores and dates.
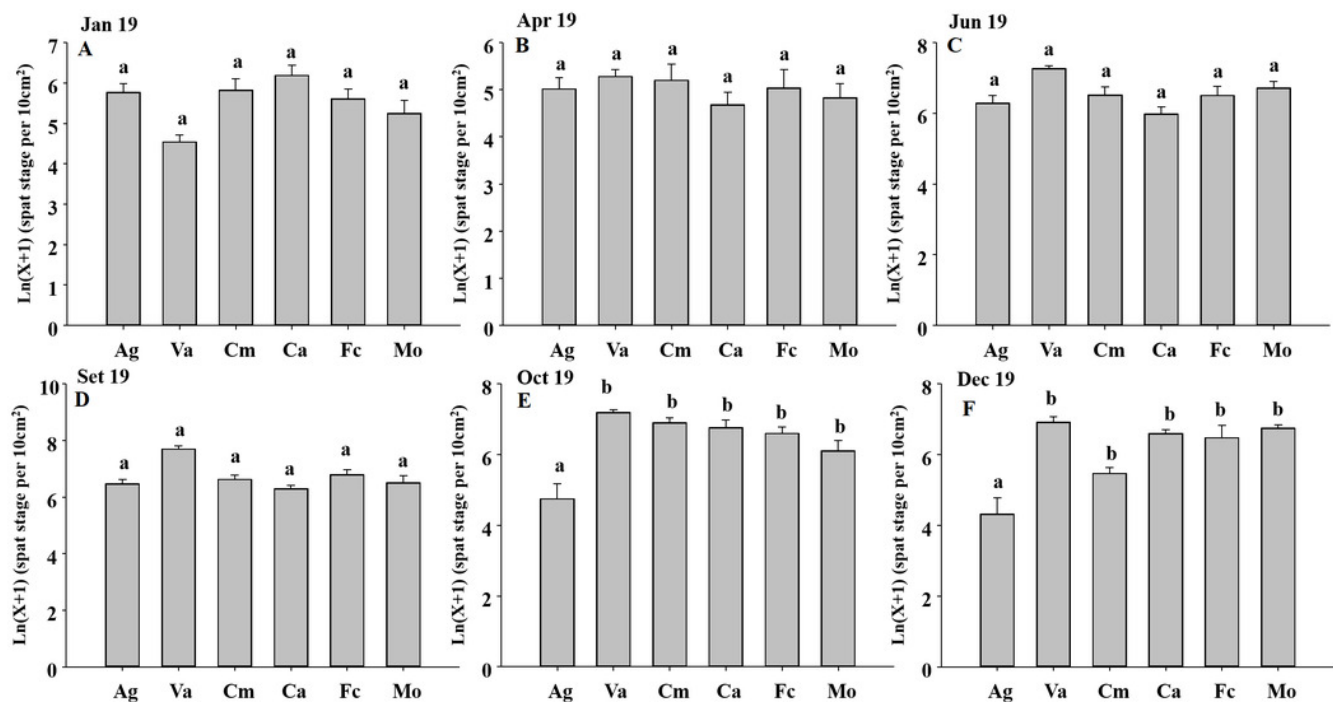
Figure 4 – **Density of *Mytilus galloprovincialis* at different shores and dates**. Mean values (+ SE) of density (number of mussels per 10 cm^2). Ag: Aguda, Va: Valadares, Cm: Cabo do Mundo, Ca: Carreço, Fc: Forte do Cão, Mo: Moledo. Different letters indicate significant differences between shores (P < 0.01) as detected by SNK test.
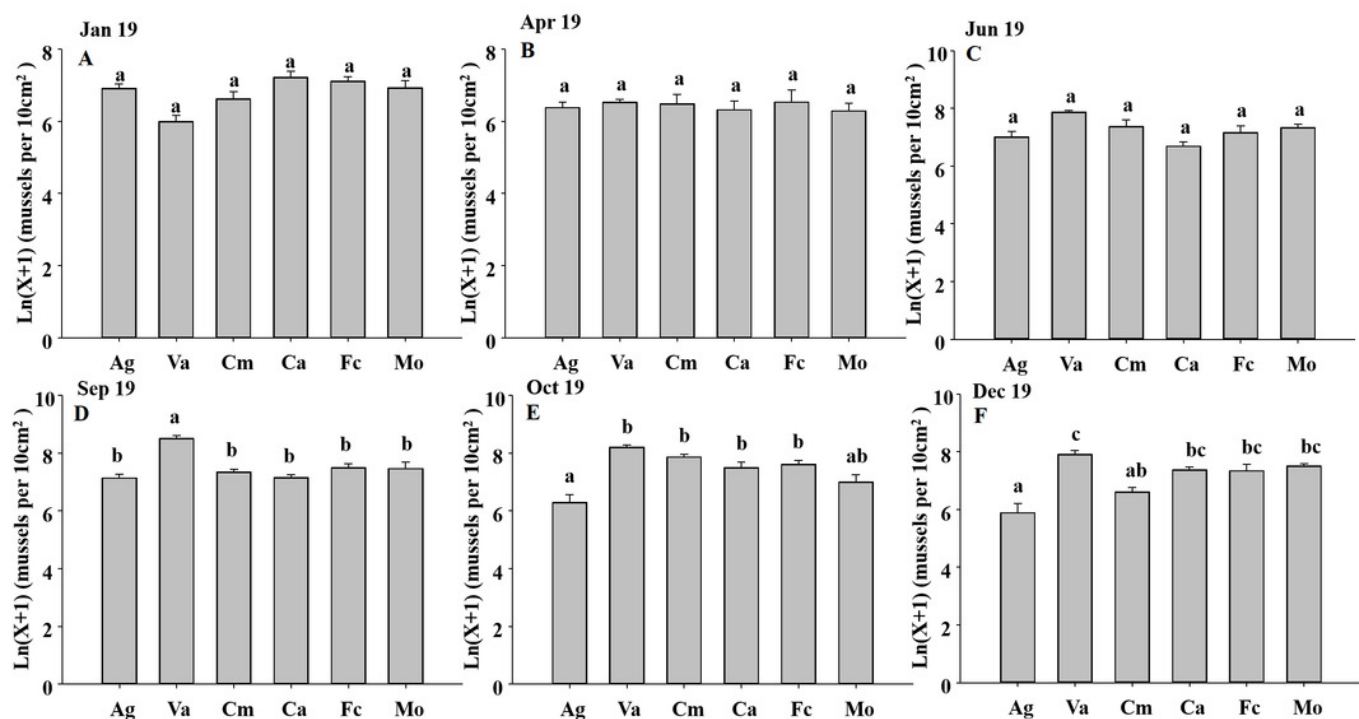
Figure 5

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). Ag: Aguda, Va: Valadares, Cm: Cabo do Mundo, Ca: Carreço, Fc: Forte do Cão, Mo: Moledo. Different letters indicate significant differences between shores (P < 0.01) as detected by SNK test.
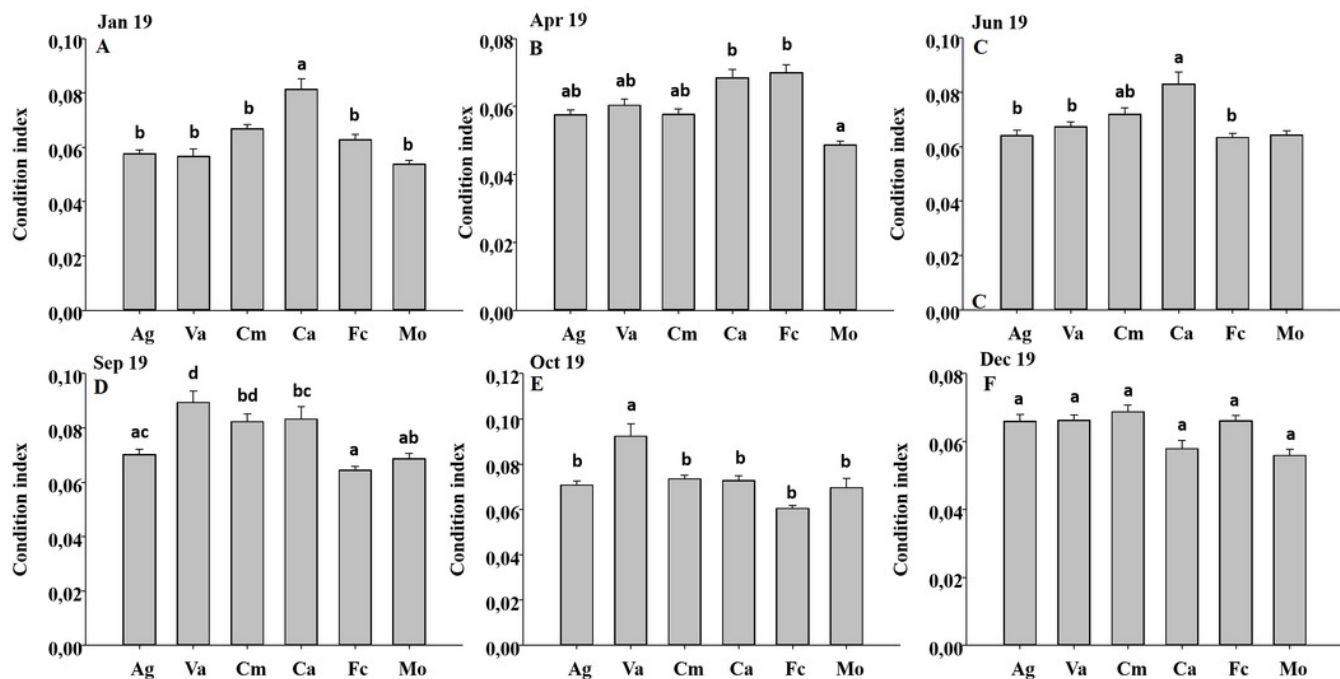
Figure 6

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

Figure 6 – **Condition index of *Mytilus galloprovincialis* at different shores and dates**. Meanvalues (+ SE) ofconditionindex. Ag: Aguda, Va: Valadares, Cm: Cabo do Mundo, Ca: Carreço, Fc: Forte do Cão, Mo: Moledo. Different letters indicate significant differences between shores (P < 0.01) as detected by SNK test.
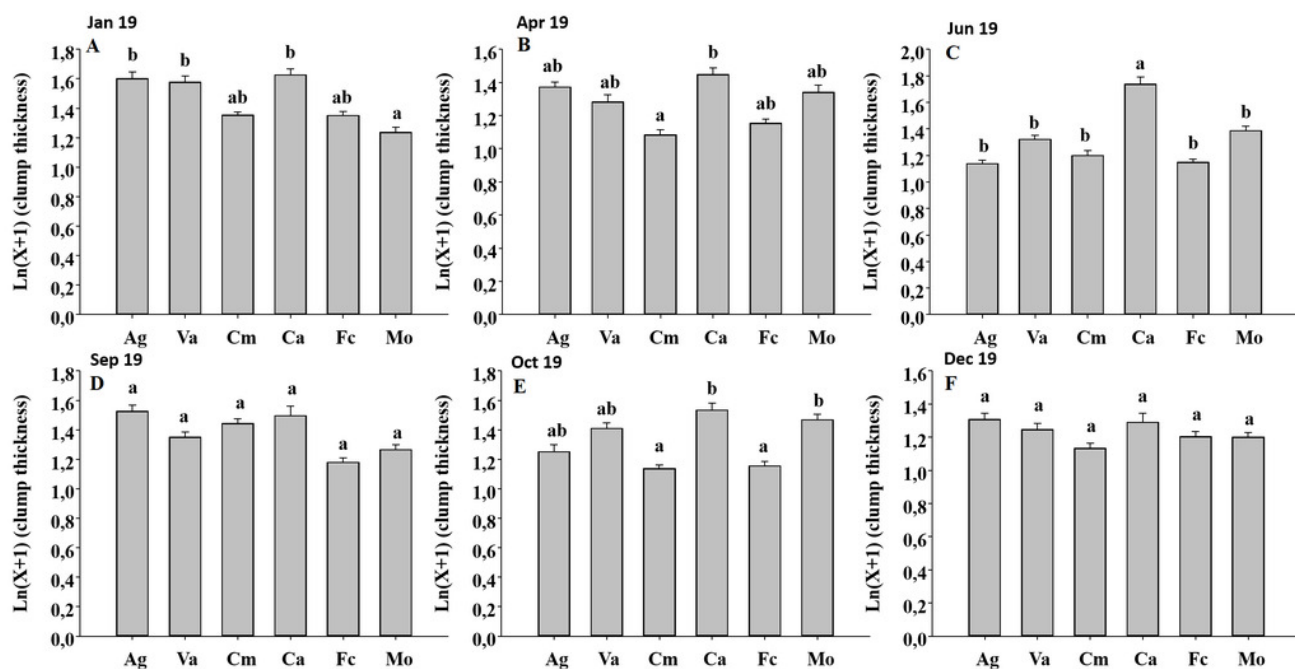
Figure 7

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

Figure 7 - **Clump thickness of *Mytilus galloprovincialis* at different shores and dates**. Meanvalues (+ SE) ofclumpthickness in cm. Ag: Aguda, Va: Valadares, Cm: Cabo do Mundo, Ca: Carreço, Fc: Forte do Cão, Mo: Moledo. 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**.
Meanvalues (+ SE) of sediment content in grams. Ag: Aguda, Va: Valadares, Cm: Cabo do
Mundo, Ca: Carreço, Fc: Forte do Cão, Mo: Moledo. Different letters indicate significant
differences between shores (P < 0.01) as detected by SNK test.