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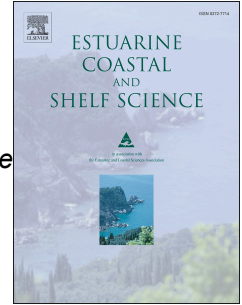
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**Credit author statement**

**Simão Correia:** Formal analysis, Investigation, Writing – Original draft.

**Luísa Magalhães:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – Review & Editing.

**Rosa Freitas:** Conceptualization, Methodology, Resources, Supervision.

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1 **Large scale patterns of trematode parasite communities infecting**  
2 ***Cerastoderma edule* along the Atlantic coast from Portugal to Morocco**

3

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13

14 **Abstract**

15 In this study, spatial sampling was performed from North Portugal to South Morocco to  
16 analyse trematode communities of the widespread bivalve *Cerastoderma edule*, host of  
17 several trematode species. From the twelve trematode species found in this study, nine  
18 were present in multiple aquatic systems demonstrating high trematode dispersal ability,  
19 driven by the presence of all the hosts. Multivariate analysis related to trematode  
20 communities in cockles clustered: 1) Portuguese aquatic systems influenced by cold waters,  
21 leading to low trematode abundance; 2) coastal systems characterized by dominance of  
22 trematode *Parvatrema minutum* and muddy sediments; 3) lagoons (or bays) with high  
23 oceanic influence and high trematode diversity. These findings suggested that, besides host  
24 species presence, temperature is an important trigger for parasite infection, with coastal  
25 upwelling operating as a shield against trematode infection in Portugal and masking

26 latitudinal gradients. Results highlighted the possible consequences of thermal modification  
27 mediated by oceanographic global circulation change on cockle populations.

28

29 **Keywords**

30           Cockle; Spatial survey; Host-parasite system; Abiotic drivers; Coastal waters;  
31 Community composition

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## 32           **1. Introduction**

33           Coastal aquatic systems are known for their high diversity and importance to  
34 populations of migratory and resident species (Levin et al., 2001). These aquatic systems  
35 have high economic value providing many natural resources and settlement sites for human  
36 population (Basset et al., 2013). In these ecosystems, a considerable part of the animal  
37 biological diversity are parasitic species, corresponding approximately, to 2/5 of eukaryotic  
38 total species richness (Dobson et al., 2008; Hudson et al., 2006). These parasites are also  
39 ubiquitous in every free-living community. However, they remain neglected in most global  
40 community analyses. In terms of functional diversity, parasites play a key structuring role in  
41 communities, providing information about the ecosystem functioning (Hudson et al., 2006;  
42 Marcogliese, 2004; Dairain et al., 2019). They impose adverse effects on their hosts  
43 phenotype and health (Marcogliese, 2004) which may result into high mortality at population  
44 scale (Curtis, 1995; Fredensborg et al., 2005; O'Connell-Milne et al., 2016). At higher scale,  
45 they induce significant impact on environmental functions (Thomas et al., 1999),  
46 exacerbated in a climate change framework (Mouritsen et al. 2005, Marcogliese 2008).  
47 Thus, parasites are considered ecosystem engineers by interfering with the host local  
48 population and consequently affecting the value and impact of these species in the  
49 ecosystem (Thomas et al., 1999). This role is magnified when the host species itself is also  
50 an ecosystem engineer (Dairain et al., 2019).

51           In coastal waters, including bays, estuaries and coastal lagoons, trematodes are the  
52 most abundant and common macroparasites (Lauckner, 1983; Roberts et al., 2009). They  
53 have a complex and heteroxenous life cycle, infecting more than one host species to  
54 complete their life cycle (Bartoli and Gibson, 2007) with alternation between asexual  
55 multiplication and sexual reproduction phases (Whitfield, 1993). The typical trematode life  
56 cycle includes a free-living larva (miracidium) that hatches from the egg and infects first  
57 intermediate hosts, most of the time a mollusc. At this stage, the parasite transforms into a  
58 mother sporocyst that will develop, depending on the trematode species, into a mature  
59 sporocyst or into redia. Within the sporocysts or rediae, cercariae free-living stages develop

60 by asexual multiplication. Cercariae will emerge from the first host and reach the second  
61 intermediate host, an invertebrate or a vertebrate species depending on the trematode  
62 species. The cercariae penetrate the second intermediate host and metamorphose into  
63 metacercariae. The cycle is complete when the parasitized second intermediate host is  
64 predated by the final host, a vertebrate species. Then, each metacercaria transforms into an  
65 adult form that will reproduce sexually and produce eggs (Bartoli and Gibson, 2007; Esch,  
66 2002; Roberts et al., 2009).

67         The complex life cycle described here, shows not only how important host diversity is  
68 in the distribution of trematode parasites, but also highlights that environmental parameters  
69 must have a key role in the modulation of parasite population dynamics, especially by their  
70 impact on infective free-living larvae transmission and infection success (Anderson and  
71 Sukhdeo, 2010; de Montaudouin et al., 2016a, 2016b; Koprivnikar and Poulin, 2009; Studer  
72 and Poulin, 2013). Indeed, a greater host diversity is usually reflected in a greater diversity  
73 of parasites, particularly for those with complex life cycles (Sukhdeo and Sukhdeo, 2004)  
74 and in the same sense, a higher abundance of suitable hosts increases the abundance and  
75 prevalence of parasites in the ecosystem (Combes, 1991). As an example, Hechinger and  
76 Lafferty (2005) found a positive correlation between bird communities composition (the final  
77 hosts of several trematode species) and trematode communities composition in a snail host.  
78 Similarly, Thieltges and Reise (2007) demonstrated higher metacercariae abundance (the  
79 trematode parasitic stage occurring in the second intermediate host) positively correlated to  
80 an increase in abundance and diversity of the higher trophic level host communities. On the  
81 other hand, higher host density can also promote a dilution effect and therefore decrease the  
82 parasite burden in a specific host (Buck et al., 2017; Magalhães et al., 2016; Mouritsen et  
83 al., 2003). Concerning the abiotic environmental factors, different conditions of temperature  
84 (Achiorno and Martolirelli, 2016; de Montaudouin et al., 2016a), salinity and pH (Koprivnikar  
85 et al., 2010, 2014; Mouritsen, 2002; Studer and Poulin, 2013), among others, can also have  
86 an influence on trematode dynamics (Wilson et al., 2002). As an example, a higher cercariae  
87 emission from the first intermediate host is related to an increase on the water temperature

88 (de Montaudouin et al., 2016a) and consequently a higher trematode infectivity (Thieltges  
89 and Rick, 2006). Favourable salinity conditions have been reported to benefit, as well,  
90 trematode emergence from the first intermediate host (Koprivnikar et al., 2014; Lei and  
91 Poulin, 2011).

92 Bivalves (along with several other molluscs) are suitable and frequent first and/or  
93 second intermediate hosts for trematode parasites (Lauckner, 1983), especially because  
94 they are easily invaded by trematodes free-living stages through their suspension-feeding  
95 activity. *Cerastoderma edule*, the edible cockle, is among the most common and widely  
96 distributed bivalve species of the northeast Atlantic coast, from Norway (Dabouineau and  
97 Ponsero, 2011) to Mauritania (Honkoop et al., 2008). Cockles are extensively commercially  
98 exploited presenting therefore high socio-economic value. Besides, cockles display a crucial  
99 ecological role, linking primary producers to higher trophic levels (key species) and acting as  
100 ecosystem engineer (Ciutat et al., 2006; Morgan et al., 2013; Rakotomalala et al., 2015).  
101 This bivalve species acts as first and/ or second intermediate host of several trematode  
102 species (de Montaudouin et al., 2009; Longshaw and Malham, 2013) and, when compared  
103 to other bivalves, parasitic communities of cockles are particularly diverse and abundant. For  
104 these reasons, cockles and their associated trematode fauna are a good model to study  
105 host/parasite interactions (e.g. de Montaudouin et al., 2009; Lauckner, 1983; Thieltges et al.,  
106 2006).

107 The often so called Latitudinal Diversity Gradient, describing that species richness  
108 increases from the poles to the tropics, is a pattern widely recognized and applicable to  
109 many terrestrial and marine species (Hillebrand, 2004). However, the causes that determine  
110 this gradient are not yet fully understood, with hypotheses that go from higher migration  
111 rates to the tropics (Jablonski et al., 2006) and/ or a lower climate variation that allows the  
112 accumulation of species (Guo and Ricklefs, 2000), to the greater opportunity of species to  
113 specialize due to the high productivity and environmental stability, characteristic of tropical  
114 habitats (Harrison and Cornell, 2008; Mittelbach et al., 2007). Nonetheless, when referring to  
115 parasitic species, the knowledge is more limited and the observation of latitudinal patterns,



116 especially in the case of parasites with complex life cycles, it is not so evident (Poulin and  
117 Leung, 2011; Stephens et al., 2016). Despite the recent study efforts on latitudinal patterns  
118 of parasites (Poulin and Morand, 2004; Studer et al., 2013; Thieltges et al., 2009, 2011;  
119 Torchin et al., 2015), results are usually conflicting. For instance, Rohde and Heap (1998)  
120 observed an increase in the diversity and abundance of monogenean parasites towards the  
121 tropics, however, in the same study, no latitudinal gradient was observed for digenean  
122 parasites. Studer et al. (2013) have not found evidences of latitudinal patterns when working  
123 with the cockle *Austrovenus stutchburyi* and trematodes as host-parasite model, while  
124 Poulin and Mouritsen (2003) have demonstrated an increase of trematode diversity in a snail  
125 intermediate host at higher latitudes. An opposite pattern was observed by Thieltges et al.  
126 (2009) for trematode communities infecting a crustacean host.

127         The present study aimed to provide, for the first time, a large spatial survey of  
128 trematode communities infecting *Cerastoderma edule* in the southern range of its distribution  
129 area, i.e. from the North of Portugal to the South of Morocco. The tested hypotheses were:  
130 1) trematode communities follow a latitudinal gradient driven by abiotic latitudinal-related  
131 factors and 2) trematode communities abundance and/ or diversity is dependent on the type  
132 of studied system (lagoon vs. estuary vs. bay).

133

## 134 **2. Material and Methods**

### 135 *2.1 Study Area*

136 The present study was conducted in a total of seventeen semi-diurnal tidal marine  
137 systems distributed along Portugal and Morocco coastline (Figure 1). Six aquatic systems  
138 were sampled in Portugal from July to October 2016: the Ria de Aveiro coastal lagoon,  
139 Óbidos coastal lagoon, Albufeira coastal lagoon, Sado estuary, Mira estuary and Ria  
140 Formosa coastal lagoon. In Morocco, eleven aquatic systems were sampled from November  
141 2007 to January 2008: the Tahaddart estuary, Loukkos estuary, Merja Zerga coastal lagoon,  
142 Sebou estuary, Oum Er Rbia estuary, Sidi Moussa coastal lagoon, Oualidia coastal lagoon,  
143 Souss estuary, Chbika estuary, Khnifiss coastal lagoon and Dakhla bay.

144 Through literature review, information on annual variation of water temperature and  
145 salinity for each sampled aquatic system at each respective sampled year (whenever  
146 possible) was obtained and gathered in Table 1.

147 Throughout this manuscript, the term 'coastal lagoon' is used when referring to  
148 coastal water bodies, connected to the ocean through one or more inlets and separated by a  
149 barrier. The lagoons vary from oligohaline to hypersaline conditions (Gooch et al., 2015).  
150 'Estuaries' were considered as semi-enclosed coastal water bodies, that have a connection  
151 with the open sea and within which seawater is measurably diluted with fresh water derived  
152 from land drainage (Pritchard, 1967). When in the presence of large bodies of water that  
153 enters through the coast and are intimately connected to an ocean by a wide entrance, the  
154 term 'bay' was used (UN, 1982).

155

### 156 *2.2 Field sampling and parasite identification*

157 At each sampling area, sediment samples were collected to perform grain size  
158 analysis following the method described by Quintino et al. (1989). Silt and clay fraction (fine  
159 particles with diameter below 63  $\mu\text{m}$ ) were assessed by wet sieving and the remaining

160 fractions (sand and gravel) were determined by sieving through a column of five sieves with  
161 decreasing mesh sizes (2.00, 1.00, 0.50, 0.250 and 0.125 mm).

162 Cockles were collected in the intertidal zone (with exception of Óbidos lagoon) using  
163 six quadrats (0.25 m<sup>2</sup> each) randomly placed along a 100 m parallel to the water transect  
164 and by sieving the sediment through a 1-mm mesh. The number of cockles per square  
165 meter (density) was then estimated. In the Óbidos lagoon, a subtidal area where the quadrat  
166 method was impossible to perform, samples were collected with a hand dredge and cockle  
167 density (d) was calculated following the equation:

$$d(\text{ind. m}^{-2}) = \frac{n}{a \times t \times l}$$

168 where “n” corresponds to the total number of cockles collected; “a” to the hand  
169 dredge area (m<sup>2</sup>); “t” the mean number of trawls (mean number of times the dredge was  
170 dragged in the sediment per launch); and “l” the total number of launches.

171 Shell length (SL) of each cockle was measured to the lowest mm with a calliper.  
172 From each aquatic system, according to availability, a variable number (between 11 and 65)  
173 of adult cockles (23 – 30 mm) were dissected. In Albufeira lagoon and Mira estuary, due to  
174 low abundance of cockles from this length class, twenty cockles representing the SL of each  
175 area (16 – 31 mm and 8 – 18 mm, respectively) were dissected. Cockle flesh was squeezed  
176 between two glass slides and observed under a stereomicroscope. All trematodes were  
177 identified to the species level following de Montaudouin et al. (2009) identification key.

178 Parasite abundance (mean number of trematode metacercariae per cockle),  
179 prevalence (percentage of infected cockles by trematode species) and trematode species  
180 richness (number of trematode species present) were calculated according to Bush et al.  
181 (1997).

182

### 183 *2.3 Data analysis*

184 To test the influence of latitude (independent variable) on the variation of trematode  
185 species richness (TSR), trematode total prevalence (TTP) and trematode mean abundance

186 (TMA) (dependent variables), individual regression analyses were performed using the  
187 SPSS v.25 software.

188 The Chbika estuary, due to the lack of abiotic information, was excluded from all the  
189 following multivariate analyses and used only on trematodes descriptive information.

190 The data matrix with the abundance of trematode per site [abundance per trematode  
191 species metacercariae x sampling site] was square root transformed and the Bray-Curtis  
192 (Legendre and Legendre, 1998) similarity calculated between sites. To identify the biological  
193 affinity groups, the resemblance matrix was then analysed using a hierarchical clustering  
194 analysis tool. The affinity groups were characterized according to environmental and  
195 biological features by calculating the mean value of annual maximum and minimum water  
196 temperature, annual maximum and minimum water salinity, median grain-size, cockle  
197 density at sampling time and by calculating the rarefaction index, i.e. an estimation of the  
198 trematode species diversity through standardization of the number of samples (Gotelli and  
199 Colwell, 2001). Differences in terms of trematode metacercariae abundance were then  
200 tested among affinity groups, type of aquatic system (lagoons vs estuaries) and  
201 geographical position (north vs. south of strait of Gibraltar). Differences were tested using  
202 permutational multivariate analysis of variance (Anderson et al., 2008) following unrestricted  
203 permutation of the raw data (9999 permutations) and the calculation of type III sums of  
204 squares. Similarity Percentages (SIMPER) were used to characterize the type of aquatic  
205 system and the geographical position by the species that most contributed to the  
206 dissimilarity between groups. Affinity groups differences were visualized through Principal  
207 Coordinates Ordination analysis (PCO) after a distance among centroids resemblance  
208 (Clarke and Warwick, 2001). The abiotic variables that were highly correlated (Spearman  $\rho >$   
209  $|0.7|$ ) to samples ordination were represented as superimposed vectors in the PCO graph.

210 To model the relationship and provide quantitative measures of abiotic and biotic  
211 data (annual maximum and minimum water temperature, annual maximum and minimum  
212 water salinity and median grain-size and cockle density) on metacercariae community of  
213 each aquatic system, a Distance-based linear model (DistLM) was performed (Anderson et

214 al., 2008). The results were obtained using appropriate permutation (9999 permutations) and  
215 following the step-wise method and Akaike information criterion (AICc). This criterion  
216 balances between data fitness and the most parsimonious model (the model with lower  
217 power loss). Thus, it is considered the best model, among the possible ones, the one  
218 showing the lowest AIC (Symonds and Moussalli, 2011). Distances among aquatic systems  
219 were visualized through a dbRDA plot.

220 All multivariate analyses were performed using the PRIMER v.6 software.

221

### 222 **3. Results**

#### 223 *3.1 Trematode species richness, prevalence and abundance*

224 During this study, 398 cockles were dissected, 280 were infected by a total of twelve  
225 trematode species. *Bucephalus minimus* and *Monorchis parvus* infecting cockles as first  
226 intermediate host, *Gymnophalus choledochus* using cockles as first and second  
227 intermediate host and nine species of trematodes at metacercariae stage, i.e. infecting  
228 cockles as second intermediate host, *Curtuteria arguinae*, *Diphterostomum brusinae*,  
229 *Himasthla continua*, *H. elongata*, *H. interrupta*, *H. quissetensis*, *Parvatrema minutum*,  
230 *Psilostomum brevicolle* and *Renicola roscovitus* (Table 2).

231 *P. minutum* was the most prevalent and abundant trematode species, representing  
232 approximately 90 % of total metacercariae abundance. This species was found in twelve out  
233 of the seventeen sampled systems and therefore throughout the whole sampled latitudinal  
234 gradient. *H. elongata* was exclusively found in three aquatic systems located north of 38 °N  
235 (northern Portuguese aquatic systems) whereas, *H. continua* was only present in five  
236 aquatic systems located south of 35 °N. *R. roscovitus* was the rarest and the least abundant  
237 species, represented by 1 metacercariae identified in the Óbidos lagoon (Figure 2; Table 4).  
238 *C. arguinae*, *H. quissetensis* (representing 5 % of total trematode abundance) and *P.*  
239 *brevicolle* were common in several aquatic systems south of 37 °N, found in the two aquatic  
240 systems nearest to the north Atlantic Ocean – Mediterranean transition (strait of Gibraltar, 36

241 °N) and in several aquatic systems south of this biogeographical barrier (Figure 2). *G.*  
242 *choledochus*, *D. brusinae* and *H. interrupta*, all the other species infecting cockles as second  
243 intermediate host, showed low abundance, representing each less than 1.5 % of total  
244 abundance (Figure 3).

245 Overall, trematode species richness (TSR, considering all identified trematode  
246 species) increased linearly from north to south but accounting for only 22% of the total  
247 variation ( $R^2 = 0.22$ ). When excluding Chbika and Sebou, two small estuaries that displayed  
248 the lowest species richness in this study (1 trematode species each), the linear model fitted  
249 better with latitude, explaining 61% of total variation (Table 3).

250 Trematode total prevalence (TTP, considering all identified trematode species)  
251 decreased with the latitude as demonstrated by the quadratic equation that explained 82%  
252 of the TTP variety ( $R^2 = 0.82$ ; Table 3). The Óbidos lagoon (39 °N, Portugal) showed the  
253 lowest TTP value (6%) whereas, almost every aquatic system south of 36 °N presented  
254 100% of TTP (except Loukkos estuary, 35 °N) (Table 4).

255 Trematode mean abundance (TMA, considering trematode species infecting cockles  
256 as second intermediate host) did not follow significantly any model. Nonetheless, a higher  
257 TMA was observed in the central zone of the total extent of the sampled area in comparison  
258 to the aquatic systems located at the northern and southern edges of the total area sampled  
259 in this study. The Óbidos lagoon (39 °N, Portugal) presented the lowest TMA ( $0.03 \pm 0.17$   
260 metacercariae.cockle<sup>-1</sup>) whereas, Oum Er Rbia (33 °N, Morocco) presented the highest TMA  
261 ( $820 \pm 595$  metacercariae.cockle<sup>-1</sup>).

262

### 263 3.2 Multivariate analysis

264 Cluster analysis, at a similarity distance of 70%, allowed to assemble the different  
265 areas in three affinity groups (Figure 4A): group A, subdivided into A1 composed by  
266 Tahaddart, Loukkos, Sebou and Souss estuaries and A2 composed by Merja Zerga lagoon,  
267 Oum Er Rbia estuary and Khnifiss lagoon; group B, divided in B1 composed by Sidi Moussa

268 and Oualidia lagoons and group B2, splitted into B2.1 composed by Dakhla bay and B2.2  
269 composed by all Portuguese systems (Ria de Aveiro lagoon, Óbidos lagoon, Albufeira  
270 lagoon, Sado estuary, Mira estuary and Ria Formosa lagoon). Cockle density showed to be  
271 significantly higher in group B1 and lower in group B2.1. Sediment median grain-size was  
272 significantly higher in group B2.2 and lower in group B2.1 (Table 5). Concerning water  
273 physico-chemical characterization, all descriptors showed no significant differences among  
274 the affinity groups. Nevertheless, group A1 displayed the highest values of maximum and  
275 minimum water temperature while, group B2.2 registered the lowest values for the same  
276 variables. Maximum and minimum water salinity presented the highest values for group B2.1  
277 and the lowest for groups B1 and B2.2, respectively (Table 5).

278 The obtained affinity groups were represented on the PCO ordination graph (Figure  
279 4B). The axis 1 of the PCO explained 59% of the total variation, separating the group A  
280 which is composed by the majority of the aquatic systems south of 36 °N and classified as  
281 estuaries (positive side of the axis) from the group B2 (negative side of the axis), that  
282 comprises all aquatic systems north of 36 °N, considered as costal lagoons, and the  
283 southernmost sampled aquatic system (Dakhla bay, 23 °N). PERMANOVA results confirmed  
284 a significant difference between sites located North and South from the Gibraltar strait  
285 (PERMANOVA: 240.37,  $p < 0.001$ ) mostly driven by the presence of *P. minutum* and *H.*  
286 *quissetensis* (Table 6) and a significant difference between estuaries and coastal lagoons  
287 (PERMANOVA: 38.94,  $p < 0.001$ ) particularly dependent also on *P. minutum* and *H.*  
288 *quissetensis* (Table 6). Minimum water temperature and cockle density presented a positive  
289 correlation to this axis and sediment median grain-size a negative correlation. In turn, axis 2  
290 described 27% of total variation dividing group B2.2 and group A, both in the positive side of  
291 the axis, from group B1 in the negative side of the axis. The geographical position (north vs.  
292 south) in relation to the strait of Gibraltar (36 °N) showed again an important effect on these  
293 groups separation that was also driven by cockle density (negative correlation).

294           The best model obtained through the DistLM analysis included the variables  
295 sediment median grain-size and cockle density as predictors of trematode community  
296 composition, explaining 42 % of the total variation ( $R^2 = 0.42$ ). When transposed to the  
297 dbRDA plot, axis 1 (representing 29 % of total variation), led by the differences in terms of  
298 median grain size, separated the aquatic systems north of the strait of Gibraltar (Portuguese  
299 aquatic systems) from the southern (Moroccan) aquatic systems with the exception of Sidi  
300 Moussa coastal lagoon and Merja Zerga estuary. Axis 2 (explaining 13 % of total variation)  
301 was positively correlated to cockle density separating two coastal lagoons of Morocco (Sidi  
302 Moussa and Oualidia coastal lagoons) and Oum Er Rbia estuary from the other aquatic  
303 systems (Figure 5).



#### 304 4. Discussion

305 Trematode parasites can have a significant impact on population dynamics of their  
306 hosts, implying modification on host growth (Wegeberg and Jensen, 2003) or inducing  
307 higher mortalities rates (Desclaux et al., 2004), which highlights the importance to study  
308 host-parasite interactions. This study is among the few reports on large-scale trematode  
309 communities infecting cockles (e.g. de Montaudouin et al., 2009; Magalhães et al., 2015)  
310 and represents the first large-scale assessment of latitudinal gradient (and abiotic related  
311 factors) as a driver of trematode communities composition in *Cerastoderma edule* as a host  
312 model. In addition, this is the first exhaustive study on trematode species composition in  
313 Moroccan cockles.

314 There are sixteen trematode species infecting *Cerastoderma edule* in its  
315 distributional range that use this bivalve as first and/ or second intermediate host (de  
316 Montaudouin et al., 2009). In the present study, a total of 12 species were identified along  
317 the whole sampled latitudinal gradient. Nine (*Bucephalus minimus*, *Curtuteria arguinae*,  
318 *Diptherostomum brusinae*, *Gymnophallus choledochus*, *Himasthla continua*, *H. interrupta*, *H.*  
319 *quissetensis*, *Psilostomum brevicolle* and *Parvatrema minutum*) showed a great dispersal  
320 ability, since they were present in a wide range, i.e. along the sampled latitudes, possibly  
321 related to migration of birds and fish which are trematode final hosts (Feis et al., 2015). For a  
322 trematode species, to complete its life cycle, the three intermediate/final host species should  
323 be present in the same aquatic system (Bustnes and Galaktionov, 1999). Nonetheless,  
324 biogeographical barriers, such as oceans in the case of continental species, are among the  
325 most important factors contributing to isolation and prevention of species exchange among  
326 regions (Cox and Moore, 1980; Ricklefs and Schluter, 1993).

327 In the present study, the strait of Gibraltar (36 °N), a known geographical barrier,  
328 showed some influence on trematode communities, dividing the observed trematode species  
329 in three different categories. The first category gathers seven trematode species (*Monorchis*  
330 *parvus*, *Bucephalus minimus*, *Psilostomum brevicolle*, *Gymnophallus choledochus*,

331 *Parvatrema minutum*, *Curtuteria arguinae* and *Himasthla interrupta*) for which there is no  
332 influence of the biogeographical barrier (*i.e.* Gibraltar) and which occurrence is mediated by  
333 the predominant presence of the intermediate hosts in the sampled area (*Peringia ulvae*,  
334 *Scrobicularia plana*, *Gobius* spp., among others (cf. Table 2)). In this study *H. continua* was  
335 only found south of Gibraltar (36 °N), however, its published distribution (de Montaudouin et  
336 al., 2009) places this species in this ubiquitous group of parasites. The life cycle of *C.*  
337 *arguinae*, is unknown (Desclaux et al., 2006) preventing any hypothesis concerning the link  
338 with first intermediate and final hosts distribution. *M. parvus* was only observed at the  
339 Portuguese coast, still this isolated occurrence is more likely related to the fact that  
340 trematodes infecting first intermediate host, usually display very low prevalence (Granovitch  
341 and Johannesson, 2000; Islam et al., 2009; Tigga et al., 2014). Indeed, *M. parvus* has been  
342 previously recorded along the whole studied latitudinal gradient (de Montaudouin et al.,  
343 2009). The second category, contrastingly, gathers two trematode species with a Southern  
344 distribution, *Diptherostomum brusinae* and *H. quissetensis*, possibly mediated by the  
345 biogeographical barrier and first intermediate host, *Tritia reticulata*, an abundant gastropod  
346 in southern areas, from France to Morocco (but its actual northern latitude corresponds to  
347 Baltic Sea (Pizzolla, 2005). Thirdly, *H. elongata* and *Renicola roscovitus* displayed a  
348 Northern distribution likewise their first intermediate host *Littorina littorea*, a marine  
349 gastropod that inhabits the intertidal zone from the White Sea to Gibraltar, on the Atlantic  
350 east coast (Johannesson, 1988). Thus, this study confirms that at this latitudinal scale, the  
351 distribution of the trematode species is mainly driven by the occurrence of the first  
352 intermediate host (de Montaudouin and Lanceleur, 2011; Thieltges, 2007; Thieltges et al.,  
353 2009), considering that final hosts have generally a wider distribution area (Magalhães et al.,  
354 2015).

355 Trematode species richness (TSR) and trematode total prevalence (TTP) increased  
356 towards south (from 40 °N to 23 °N). This latitudinal dependent pattern of TSR follows the  
357 same trend described for benthic macrofaunal diversity which show higher values with

358 decreasing latitudes (Macpherson, 2002; Martins et al., 2013; Roy et al., 2004). However,  
359 this pattern was not observed in the case of Chbika and Sebou estuaries, located at 28 °N  
360 and 34 °N, respectively, that presented the lowest TSR.

361 Chbika is not a permanent estuary ('Oued'), which might induce lower macrofaunal  
362 and parasite diversity. Conversely, the Sebou river is one of the biggest North African rivers,  
363 crossing several riverside populations and then impacted by several anthropogenic  
364 activities, including agricultural activities (Perrin et al., 2014). The constant use of pesticides  
365 and fertilizers by the agricultural activities, plus the connection with untreated sewage from  
366 peripheral cities, result in very pollutant loads that contaminate the river to its estuary (Perrin  
367 et al., 2014). This presumable poor health and ecological status of this ecosystem might be  
368 inducing a low trematode parasites diversity, opposing to the latitudinal trend. Indeed,  
369 trematodes, especially free-living stages, are sensitive to water disturbance, reducing their  
370 survival, preventing transmission between hosts (Pietroock and Marcogliese, 2003;  
371 Koprivnikar et al., 2007) and can be used as indicators of retrograde condition (MacKenzie,  
372 1999). Therefore, our results showed that such as free-living species, parasitic fauna seems  
373 to follow a latitudinal gradient of decreasing species richness from tropical to extra-tropical  
374 areas, one of the oldest recognized ecological patterns (Wright et al., 1993; Willig et al.,  
375 2003). This latitudinal pattern is usually not clear for communities of parasites with complex  
376 life cycles (Poulin and Leung, 2011; Studer et al., 2013) due to the complexity of host/  
377 parasite interactions, but also because these cycles (and in particular infection success  
378 stage) depend on several abiotic factors, including anthropogenic stressors (Rohr et al.,  
379 2008; Altman and Byers, 2014).

380 Among abiotic factors, temperature is one of the strongest drivers of trematode  
381 activity (propagule dispersal, survival, infection (Thieltges and Rick, 2006)) as well as of host  
382 infection levels (higher values observed during the warmer seasons (Goater, 1993; Desclaux  
383 et al., 2004)). As an example, in Arcachon bay, a synchrony was observed between  
384 parasites emergence from the first intermediate host and the infection in the second

385 intermediate host when water temperature was above 15 °C (de Montaudouin et al., 2016a).  
386 In the case of the present study, the minimum water temperature of the aquatic systems  
387 south of 36 °N was around 15°C, 3 °C above north of 36 °N. This temperature difference can  
388 explain why Morocco displays higher TTP and TMA than Portugal. In fact, this study showed  
389 that abundance and prevalence of trematode communities presented higher values in  
390 ecosystems characterized by higher maximum water temperature (affinity group A). In  
391 contrast, all the northern sampled areas (Portuguese aquatic systems located north of the  
392 strait of Gibraltar) were all gathered in the same affinity group (group B2.2) characterized by  
393 the lowest trematode abundance and prevalence. The Portuguese coast proximity to an  
394 upwelling front and consequent occurrence of cold vertical currents (Queiroz et al., 2012)  
395 may operate as a shield against trematode infection.

396 In the present study, the discrimination of the trematode assemblages was also  
397 explained by the cockle density, the sediment median grain-size and the type of aquatic  
398 system, some of these factors being possible confounding. Cockles density was higher in  
399 the studied areas characterized by higher maximum temperature. This can result either from  
400 increased recruitment success (Gam et al., 2010; Magalhães et al., 2016) or from better  
401 conditions in terms of food quality and quantity. Nevertheless, the system presenting the  
402 highest cockle density (Sidi Moussa lagoon) was also the system with one of the lowest  
403 trematode abundance suggesting that when a certain density threshold is passed, cercariae  
404 are diluted among second intermediate host and consequent lower mean metacercariae  
405 infection is observed, as previously highlighted by Magalhães et al. (2016).

406 The type of aquatic system (estuaries, lagoons or bays) showed also to be  
407 determinant for the trematode community composition. There was a clear separation  
408 between three particular areas South of 36 °N, that presented higher trematode biodiversity:  
409 Oualidia and Sidi Moussa lagoon, and Dakhla bay corresponding to group B1 and B2.1,  
410 respectively. These areas are classified as coastal lagoons (group B1) or bays (group B2.1)  
411 and therefore characterized by higher oceanic influence and hydrodynamics (Kjerfve and

412 Magill, 1989) and lower water temperature variations, especially Dakhla bay which is located  
413 in the interaction between the Canary stream and the subtropical ridge currents (Orbi et al.,  
414 1999). Leung et al. (2009) and Mouritsen and Poulin (2005) referred that these combinations  
415 of characteristics are usually related to higher trematode diversity and abundance, which  
416 was confirmed by our results (the highest rarefaction indices were found in affinity groups B1  
417 and B2.1). Additionally, coastal lagoons tend to be shallower compared to estuaries (Kjerfve,  
418 1986). This enables light to penetrate up to the bottom, allowing benthic plants to thrive  
419 (higher productivity) (Kennish and Paerl, 2010) which could lead to an increase of benthic  
420 communities (first hosts of trematode species) diversity and abundance. As previously  
421 discussed, higher hosts diversity and abundance is usually correlated to higher trematode  
422 diversity (Hechinger and Lafferty, 2005).

423         Cockles from Óbidos lagoon, located 40 °N, displayed extreme values of infection,  
424 with the lowest TTP and TMA registered. Most of the hosts of the trematode species found  
425 in this study have been previously reported in this lagoon (e.g. Carvalho et al., 2011;  
426 Lourenço, 2006), however this aquatic system presented the lowest values of water  
427 temperature, showing once again the great importance that water temperature has on  
428 trematode infection. Besides, this system also has the peculiarity that cockles were collected  
429 in a subtidal position. Despite this assumption is based on only one sampling point, these  
430 results could suggest that cockles tidal position can also be a driver of trematode infection.  
431 In fact, similar results were found by Gam et al. (2008) in Merja Zerga coastal lagoon  
432 (Morocco) where cockles living in subtidal zones presented lower trematode infection than  
433 intertidal sympatric specimens. This was interpreted as a differential distance to upstream  
434 intertidal first intermediate host.

435         The temporal gap and the seasonal differences among some of the samples could of  
436 course bias our spatial analysis. However, at these scales, we assume that spatial effects  
437 (17° in latitude corresponding to approx. 3,000 km) are stronger than temporal effects (8  
438 years), once trematode composition at a given site is often stable at multiannual scale. As  
439 an illustration, de Montaudouin et al. (2012) showed that trematode communities of

440 Arcachon bay, France, were the same after 8 years, the same temporal gap as in this study,  
441 due to environmental stability along time. In the same direction, in the Ria de Aveiro coastal  
442 lagoon, one of the sampled systems, diversity of trematode was equivalent after 6 years  
443 (Freitas et al., 2014; Russell-Pinto et al., 2006). On the other hand, concerning seasonal  
444 differences, actually, trematode abundance (infecting cockles as second host) follows a  
445 seasonal pattern, increasing their infections during the warmer seasons, contrary to what is  
446 observed in the colder seasons (Desclaux et al., 2004; Goater, 1993). This could mean a  
447 positive influence of the results (in terms of infection intensity) in the Portuguese aquatic  
448 systems (systems sampled during summer). However, due to the low trematode abundance  
449 on the Portuguese systems, seasonal effects are not so evident (Magalhães et al., 2018).  
450 Moreover, the present study findings demonstrated a higher trematode abundance on  
451 Moroccan aquatic systems (winter samples), which means that seasonal effects were not  
452 exacerbated. Finally, we believe that the present findings are of high impact because of the  
453 interest in trematode communities knowledge improvement in each sampled area and each  
454 country.

455

## 456 **5. CONCLUSION**

457 The present study showed that at the studied scale, trematode abundance and  
458 prevalence in cockles seemed to follow a latitudinal pattern. This latitudinal gradient of  
459 trematode, however, was more related to temperature than to latitude. In fact, the type of  
460 aquatic system, namely coastal lagoons or bays, also demonstrated to have an impact,  
461 correlated with the oceanic influence. Nevertheless, the occurrence of trematode species is  
462 only possible when all the hosts of that species were present in the ecosystem.

463 Furthermore, the obtained results highlighted the ubiquity of trematode parasites in  
464 the different aquatic systems and alert to a possible change on the trematode fauna  
465 composition and abundance in cockle populations driven by thermal modification mediated  
466 by oceanographic global circulation. Besides global temperature monitoring, it is then  
467 imperative to incorporate trematodes communities assessment in ecological studies, due to

468 their highly integrative significance, to better predict potential negative impact on host  
469 populations and communities sustainability. Nonetheless, due to the seasonal and temporal  
470 differences between sampling efforts it is important to perform more studies to fully  
471 comprehend what drives trematode communities in a latitudinal gradient, along with studies  
472 that support temporal consistency in trematode communities.

473

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**Fig. 1** Study area. Geographical location of the 17 aquatic systems distributed along the Portuguese and Moroccan coastlines. Sampling sites: 1 - Ria de Aveiro; 2 - Óbidos lagoon; 3 - Albufeira lagoon; 4 - Sado estuary; 5 - Mira estuary; 6 - Ria Formosa; 7 - Tahaddart estuary; 8 - Loukkos estuary; 9 - Merja Zerga lagoon; 10 - Sebou estuary; 11 - Oum Er Rbia estuary; 12 - Sidi Moussa lagoon; 13 - Oualidia lagoon; 14 - Souss estuary; 15 - Chbika estuary; 16 - Khnifiss lagoon and 17 - Dakhla bay.

**Fig. 2** Latitudinal distribution of the 12 trematode species found in *Cerastoderma edule*. Dashed line: Strait of Gibraltar. Grey bar: Presumable distributional range.

**Fig. 3** Trematode mean abundance per aquatic system for the two most representative species, *Parvatrema minutum* (black bar) and *Himasthla quissetensis* (dark grey bar), and for the other cercariae (light grey bar).

**Fig. 4** Cluster analysis based on trematode parasites communities in seventeen aquatic systems from Portugal and Morocco (**A**) and Principal coordinates ordination (PCO) showing the variables that better explained samples distribution (**B**). MGS: Sediment median grain-size; M Temp: Maximum annual water temperature; density: cockle density. Sampling sites: 1 - Ria de Aveiro; 2 - Óbidos lagoon; 3 - Albufeira lagoon; 4 - Sado estuary; 5 - Mira estuary; 6 - Ria Formosa; 7 - Tahaddart estuary; 8 - Loukkos estuary; 9 - Merja Zerga lagoon; 10 - Sebou estuary; 11 - Oum Er Rbia estuary; 12 - Sidi Moussa lagoon; 13 - Oualidia lagoon; 14 - Souss estuary; 15 - Chbika estuary; 16 - Khnifiss lagoon and 17 - Dakhla bay.

**Fig. 5** Distance-based redundancy analysis plot and the correlated variables that explained aquatic systems distribution based on trematode abundance. Sampling sites: 1 - Ria de Aveiro; 2 - Óbidos lagoon; 3 - Albufeira lagoon; 4 - Sado estuary; 5 - Mira estuary; 6 - Ria Formosa; 7 - Tahaddart estuary; 8 - Loukkos estuary; 9 - Merja Zerga lagoon; 10 -

Sebou estuary; 11 - Oum Er Rbia estuary; 12 - Sidi Moussa lagoon; 13 - Oualidia lagoon; 14 - Souss estuary; 15 - Chbika estuary; 16 - Khnifiss lagoon and 17 - Dakhla bay.

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**Table 1.** Characterization of each sampled area in terms of type of aquatic system (1 = lagoon; 2 = estuary; 3 = bay), latitude (LAT), longitude (LON), surface area (km<sup>2</sup>), maximum annual water temperature (M Temp, °C), minimum annual water temperature (m Temp, °C), maximum annual water salinity (M Sal), minimum annual water salinity (m Sal) and sediment median grain-size (MGS, mm). ND – no data

System	Type	LAT (N)	LON (W)	Surface Area (km <sup>2</sup> )	M Temp	m Temp	M Sal	m Sal	MGS	References
Ria Aveiro	1	40°38'	8°44'	83.0	22.0	15.0	28.0	12.0	0.277	Dias et al., 2000 Lillebø et al., 2015
Óbidos	1	39°24'	9°12'	7.0	22.0	10.0	37.0	26.0	0.392	Malhadas et al., 2009 Oliveira et al., 2006
Albufeira	1	38°30'	9°10'	1.3	22.5	11.0	36.0	31.0	0.404	Fortunato et al., 2014
Sado	2	38°28'	8°50'	240.0	21.9	13.8	36.0	10.9	0.304	Bao et al., 1999 Martins et al., 2001
Mira	2	37°43'	8°46'	16.0	22.5	12.0	35.0	27.0	0.353	Silva et al., 2006
Ria Formosa	1	36°58'	7°52'	170.0	26.0	12.0	36.5	13.0	0.326	Gamito and Erzini, 2005
Tahaddart	2	35°46'	5°42'	10.0	26.0	13.0	41.0	21.0	0.194	Achab, 2011
Loukkos	2	35°07'	06°00'	72.0	27.0	15.0	34.0	22.0	0.203	Geawhari et al., 2014
Merja Zerga	1	34°51'	06°16'	27.0	28.0	11.0	35.0	27.0	0.272	Gam et al., 2010
Sebou	2	34°16'	06°39'	17.5	30.0	16.0	35.0	12.0	0.219	Haddout et al., 2015
Oum Er Rbia	2	33°28'	08°34'	1.5	25.0	15.0	35.0	30.0	0.146	Khalki and Moncef, 2007
Sidi Moussa	1	32°54'	08°49'	4.2	27.0	15.0	33.0	22.0	0.273	Maanan et al., 2004
Oualidia	1	32°45'	08°30'	3.0	21.0	16.0	36.0	28.0	0.181	Hilmi et al., 2005
Souss	2	30°21'	09°35'	16.0	25.0	19.0	39.0	35.0	0.202	Anaijar et al., 2008

Chbika	2	28°14'	11°42'	0.2	ND	ND	ND	ND	0.184	
Khnifiss	1	28°03'	12°15'	65.0	22.0	16.0	38.0	34.0	0.150	Semlali et al., 2012
Dakhla	3	23°45'	15°50'	400.0	26.0	14.0	39.5	37.0	0.120	Zidane et al., 2018

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**Table 2.** Digenean trematode species found in *Cerastoderma edule* from the Atlantic coasts of Portugal and Morocco with indication of the hosts involved in their life cycle. Adapted from de Montaudouin et al. (2009). \*: Probable final host of *Curtuteria arguinae*.

Trematode species	1 <sup>st</sup> intermediate host	2 <sup>nd</sup> intermediate host	Final host
<i>Bucephalus minimus</i>	<i>Cerastoderma edule</i>	<i>Pomatoschistus</i> spp.	<i>Dicentrarchus labrax</i>
<i>Monorchis parvus</i>	<i>Cerastoderma edule</i>	<i>Cerastoderma edule</i>	<i>Diplodus</i> spp.
<i>Gymnophalus choledochus</i>	<i>Cerastoderma edule</i>	<i>Cerastoderma edule</i>	Water birds
<i>Curtuteria arguinae</i>	Unidentified species	<i>Cerastoderma edule</i>	Water birds (*)
<i>Diptherostomum brusinae</i>	<i>Tritia reticulata</i>	<i>Cerastoderma edule</i>	<i>Blennius</i> , <i>Sargus</i> , <i>Symphodus</i> , <i>Oblata</i>
<i>Himasthla continua</i>	<i>Peringia</i> spp.	<i>Cerastoderma edule</i>	Water birds
<i>Himasthla elongata</i>	<i>Littorina littorea</i>	<i>Cerastoderma edule</i>	Water birds
<i>Himasthla interrupta</i>	<i>Peringia</i> spp.	<i>Cerastoderma edule</i>	Water birds
<i>Himasthla quissetensis</i>	<i>Tritia reticulata</i>	<i>Cerastoderma edule</i>	Water birds
<i>Parvatrema minutum</i>	<i>Scrobicularia plana</i>	<i>Cerastoderma edule</i>	<i>Haemotopus ostralegus</i>
<i>Psilostomum brevicolle</i>	<i>Peringia</i> spp.	<i>Cerastoderma edule</i>	Water birds
<i>Renicola roscovitus</i>	<i>Littorina littorea</i>	<i>Cerastoderma edule</i>	Water birds

**Table 3.** Results of the regression analyses performed to test the influence of latitude (independent variable) on trematode species richness (TSR) and total trematode prevalence (TTP) in *Cerastoderma edule*. SE: standard error. w/o: without. Sampling sites: Se – Sebou estuary; Ch – Chbika estuary.

	Predictors	Estimate	SE	p - value	R <sup>2</sup>
<b>Trematode species richness (TSR)</b>					
	Constant	11.265	3.272	0.004	
	Latitude	-0.225	0.096	0.034	
	Model		1.164	0.034	0.217
<b>Trematode species richness (TSR)</b> (w/o Se & Ch)					
	Constant	14.501	2.344	<0.001	
	Latitude	-0.307	0.068	0.001	
	Model		1.164	0.001	0.608
<b>Total Trematode Prevalence (TTP)</b>					
	Constant	-4.158	1.454	0.013	
	Latitude	0.371	0.091	0.001	
	Latitude <sup>2</sup>	-0.007	0.001	<0.001	
	Model		0.136	<0.001	0.821

**Table 4.** Prevalence of trematode parasites infecting cockle populations in the aquatic systems of Portugal and Morocco. Sampling sites: RA - Ria de Aveiro; OB - Óbidos lagoon; AL - Albufeira lagoon; SA - Sado estuary; MI - Mira estuary; RF - Ria Formosa; TA - Tahaddart estuary; LO - Loukkos estuary; MZ - Merja Zerga lagoon; SE - Sebou estuary; OR - Oum Er Rbia estuary; SM - Sidi Moussa lagoon; OA - Oualidia lagoon; SO - Souss estuary; CH - Chbika estuary; KH - Khnifiss lagoon and DA - Dakhla bay. N: number of dissected cockles.

		<i>B. minimus</i>	<i>M. parvus</i>	<i>G. choledochus</i>	<i>D. brusinae</i>	<i>H. continua</i>	<i>H. elongata</i>	<i>H. interrupta</i>	<i>H. quissetensis</i>	<i>C. arguinae</i>	<i>P. brevicolle</i>	<i>P. minutum</i>	<i>R. roscovitus</i>	Total parasite Prevalence
Portugal	RA (n=65)	-	-	-	-	-	11	-	-	-	-	26	-	35
	OB (n=35)	3	-	-	-	-	-	-	-	-	-	-	3	6
	AL (n=20)	-	40	-	20	-	10	-	-	-	-	-	-	55
	SA (n=21)	-	-	-	-	-	48	5	-	-	-	-	-	52
	MI (n=20)	-	-	50	-	-	-	-	-	-	5	-	-	55
	RF (n=25)	-	-	-	4	-	-	-	36	20	4	8	-	48
Morocco	TA (n=13)	8	-	-	15	54	-	-	-	-	-	100	-	100
	LO (n=20)	10	-	-	10	-	-	-	-	-	-	90	-	90
	MZ (n=20)	-	-	-	30	-	-	-	70	100	-	100	-	100

SE (n=17)	-	-	-	-	-	-	-	-	-	-	100	-	100
OR (n=20)	-	-	-	-	80	-	65	-	-	45	95	-	100
SM (n=15)	7	-	-	47	-	-	100	100	100	13	67	-	100
OA (n=20)	5	-	-	30	-	-	75	100	100	20	-	-	100
SO (n=20)	-	-	5	-	10	-	60	-	-	-	95	-	100
CH (n=11)	-	-	-	-	-	-	-	-	-	-	100	-	100
KH (n=20)	10	-	5	85	100	-	60	-	-	45	100	-	100
DA (n=36)	-	-	-	92	47	-	39	-	75	25	11	-	100



**Table 5.** Characterization of each affinity group in terms of maximum annual water temperature (M Temp, °C), minimum annual water temperature (m Temp, °C), maximum annual water salinity (M Sal), minimum annual water salinity (m Sal), sediment median grain size (MGS, mm), cockles density (ind.m<sup>-2</sup>) and Rarefaction index for a standardized number of 10 individuals (ES(10)). Significant differences among affinity groups are represented with different letters ( $p < 0.05$ ). Sampling sites: RA - Ria de Aveiro; OB - Óbidos lagoon; AL - Albufeira lagoon; SA - Sado estuary; MI - Mira estuary; RF - Ria Formosa; TA - Tahaddart estuary; LO - Loukkos estuary; MZ - Merja Zerga lagoon; SE - Sebou estuary; OR - Oum Er Rbia estuary; SM - Sidi Moussa lagoon; OA - Oualidia lagoon; SO - Souss estuary; CH - Chbika estuary; KH - Khnifiss lagoon and DA - Dakhla bay.

<b><i>Affinity groups</i></b>	<b>Sampling areas</b>	<b>M Temp</b>	<b>m Temp</b>	<b>M Sal</b>	<b>m Sal</b>	<b>MGS</b>	<b>Cockle density</b>	<b>ES (10)</b>
<i>A1</i>	TA, LO, SE, SO	27.0 ± 2.2	15.8 ± 2.5	37.3 ± 3.3	22.5 ± 9.5	0.2 ± 0.0 <sup>a</sup>	404 ± 457 <sup>a</sup>	1.0
<i>A2</i>	MZ, OR, KH	25.0 ± 3.0	14.0 ± 2.6	36.0 ± 1.7	30.3 ± 3.5	0.2 ± 0.1 <sup>a,b</sup>	1643 ± 2267 <sup>a,b</sup>	1.3
<i>B1</i>	SM, OA	24.0 ± 4.2	15.5 ± 0.7	34.5 ± 2.1	25.0 ± 4.2	0.2 ± 0.1 <sup>a,b</sup>	6092 ± 1114 <sup>b</sup>	2.4
<i>B2.1</i>	DA	26.0	14.0	39.5	37.0	0.1 <sup>b</sup>	15 <sup>c</sup>	2.4
<i>B2.2</i>	RA, OB, AL, SA, MI, RF	22.8 ± 1.6	12.3 ± 1.8	34.8 ± 3.4	20.0 ± 9.0	0.3 ± 0.0 <sup>c</sup>	135 ± 304 <sup>a</sup>	1.0

**Table 6.** Results of the Similarity Percentages (SIMPER) used to characterize the type of aquatic systems (coastal lagoons vs. estuaries) and the geographical position (northern systems vs. southern systems) by the trematode species (of *Cerastoderma edule*) that most contributed to dissimilarity between groups.

	<b>Species</b>	<b>Average abundance group 1</b>	<b>Average abundance group 2</b>	<b>Dissimilarity Contribution (%)</b>
<b>Coastal lagoons (1) vs Estuaries (2)</b>	<i>Parvatrema minutum</i>	5.42	12.22	69.28
	<i>Himasthla quissetensis</i>	1.70	0.00	8.76
	<i>Himasthla interrupta</i>	0.66	0.29	4.64
	<i>Curtuteria arguinae</i>	0.91	0.00	3.83
	<i>Himasthla elongata</i>	0.05	0.13	3.74
	<b>Species</b>	<b>Average abundance group 1</b>	<b>Average abundance group 2</b>	<b>Dissimilarity Contribution (%)</b>
<b>Northern systems (1) vs Southern systems (2)</b>	<i>Parvatrema minutum</i>	0.84	13.15	58.62
	<i>Himasthla quissetensis</i>	0.06	1.81	10.26
	<i>Dipheterostomum brusinae</i>	0.04	1.04	9.12
	<i>Curtuteria arguinae</i>	0.00	1.30	8.48
	<i>Himasthla interrupta</i>	0.01	0.99	6.02

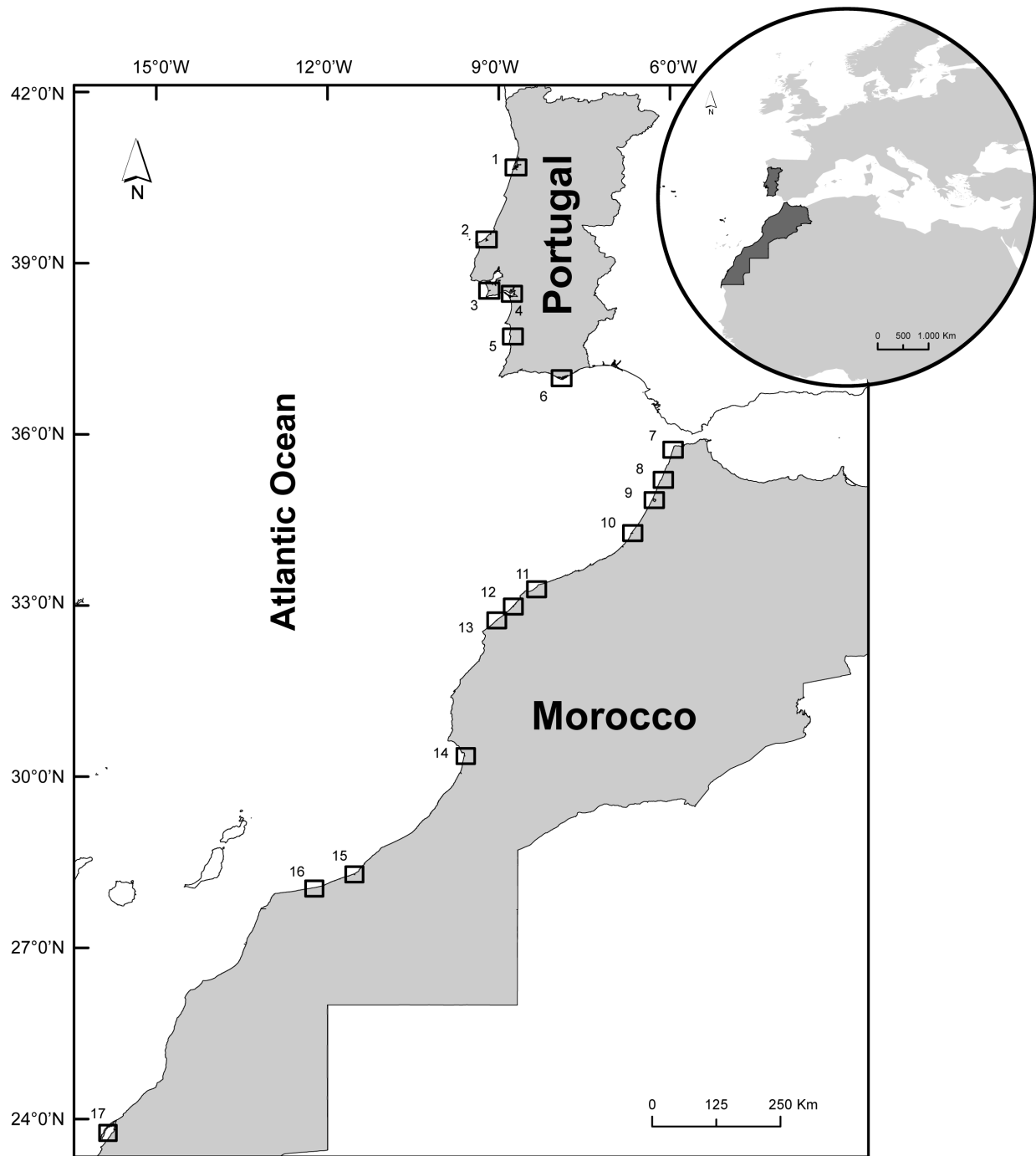


Figure 2

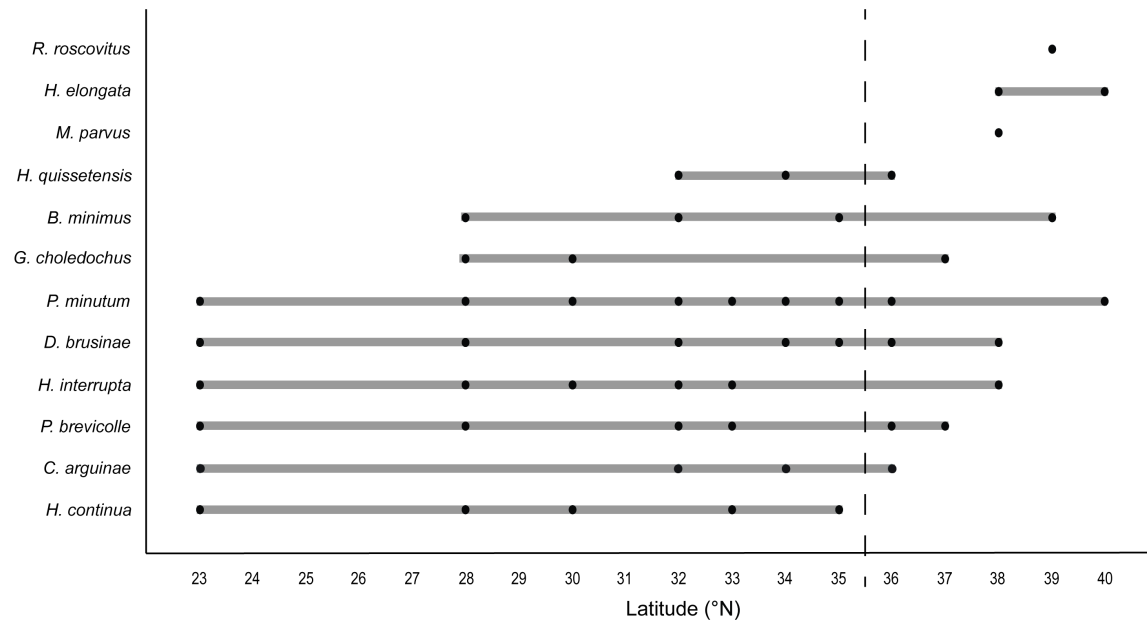


Figure 3

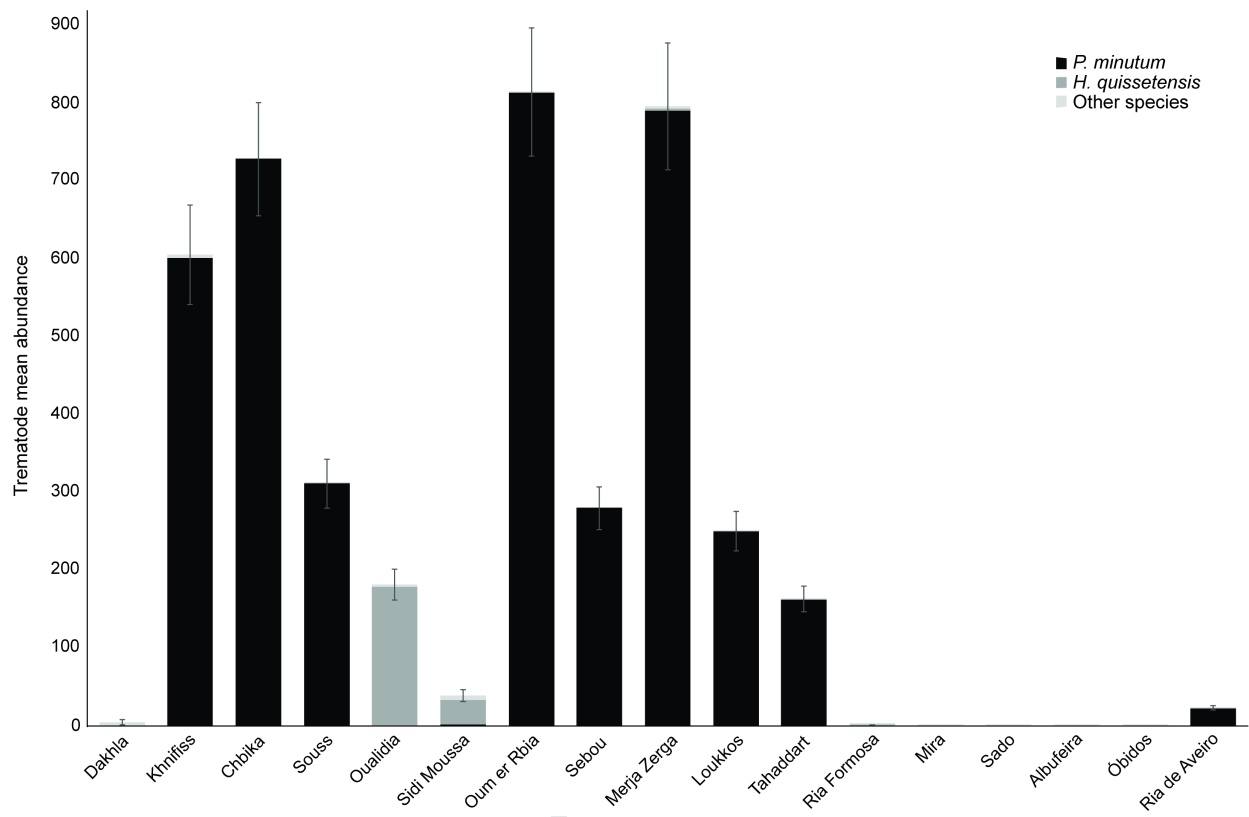
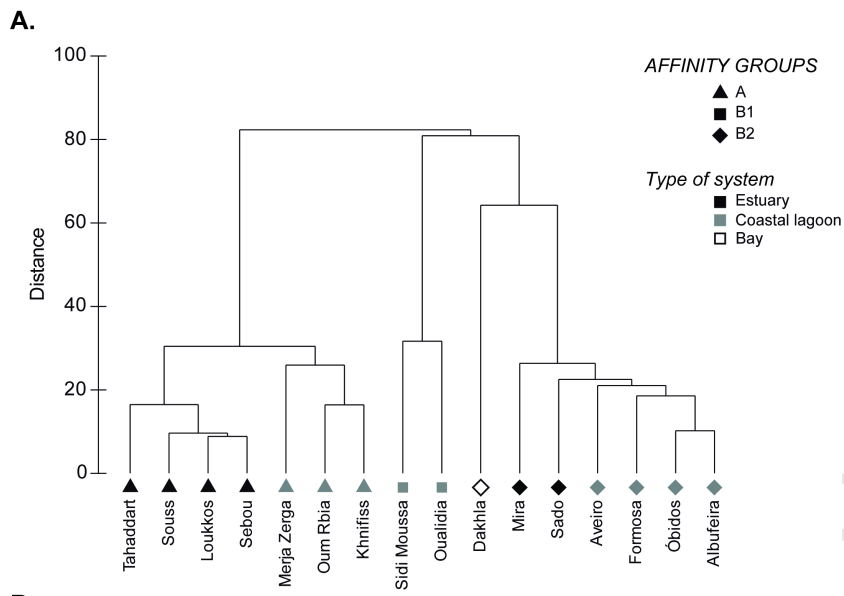


Figure 4



**B.**

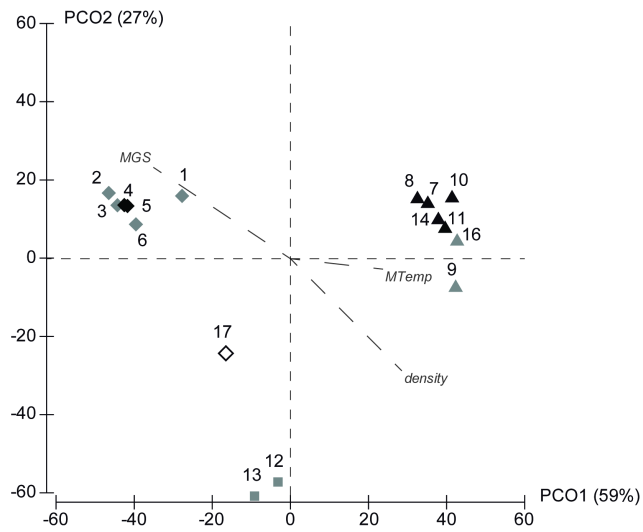
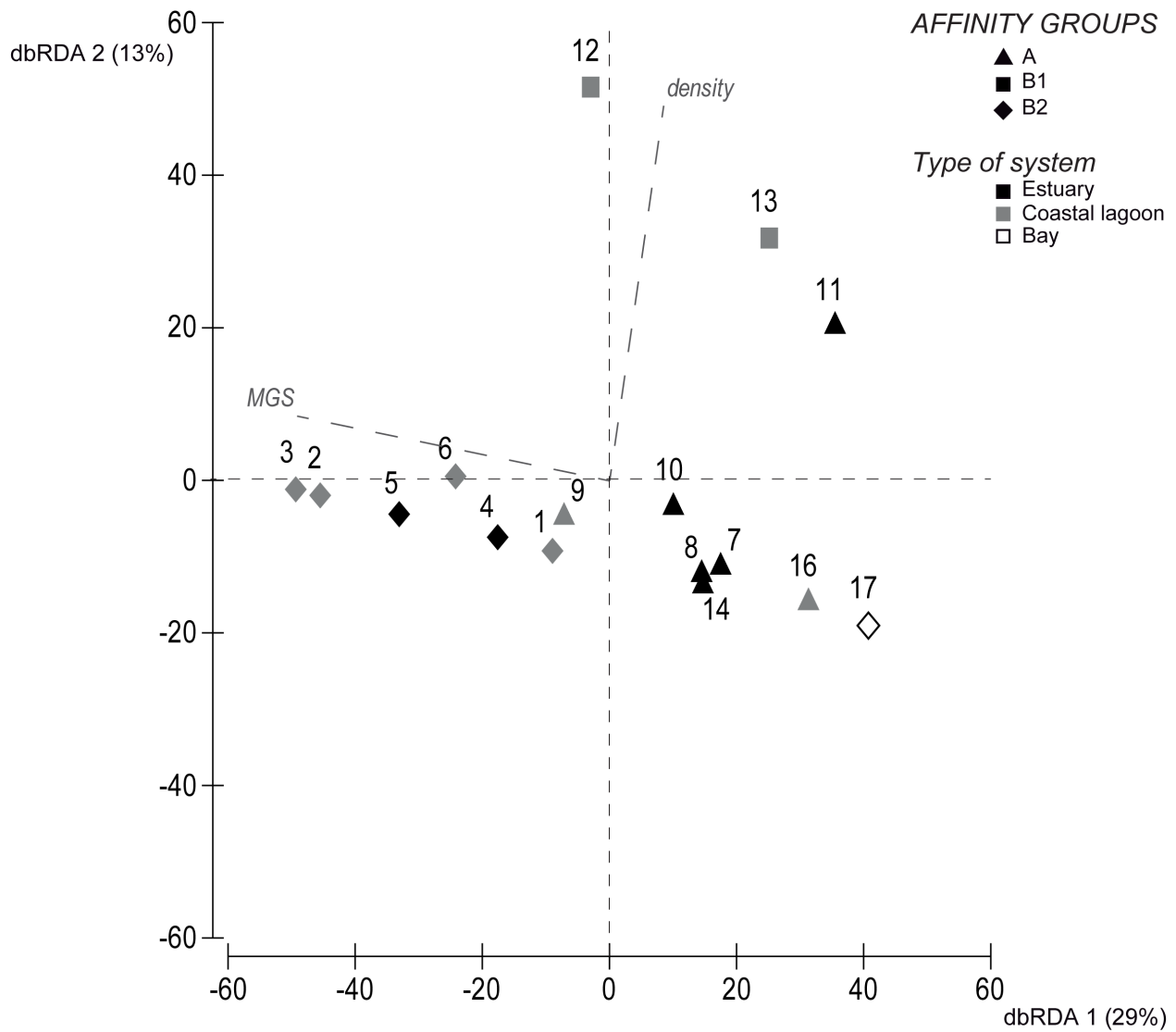


Figure 5



1 **Highlights**

2 Trematode diversity in the southern distribution area of *Cerastoderma edule*.

3 Trematode species occurrence driven by the presence of the first intermediate host.

4 Trematode prevalence and abundance was positively correlated to temperature.

5 At large scale, cockle density positively influences trematode abundance.

6 Systems under buffered environmental variations presented higher trematode  
7 abundance.

8 Cockle density influences positively trematode abundance within certain values



**Declaration of interests**

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

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: