

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

Simão Correia^a, Luísa Magalhães^{a,*}, Rosa Freitas^a, Hocein Bazairi^c, Meriam Gam^c, Xavier de Montaudouin^b

^a Departamento de Biologia & CESAM, Universidade de Aveiro, 3810-193, Aveiro, Portugal

^b Université de Bordeaux, EPOC, UMR 5805 CNRS, 2, Rue Du Pr Jolyet, F-33120, Arcachon, France

^c Mohammed V University in Rabat, Faculty of Sciences, BioBio Research Center, BioEcoGen Laboratory, 4 Av. Ibn Battouta, B.P. 1014 RP, Rabat, Morocco

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In this study, spatial sampling was performed from north Portugal to south Morocco to analyse trematode communities of the widespread bivalve *Cerastoderma edule*, host of several trematode species. From the twelve trematode species found in this study, nine were present in multiple aquatic systems demonstrating high trematode dispersal ability, driven by the presence of all hosts. Multivariate analysis related to trematode communities in cockles clustered: 1) Portuguese aquatic systems influenced by cold waters, leading to low trematode abundance; 2) coastal systems characterized by dominance of trematode *Parvatrematium minutum* and muddy sediments; 3) lagoons (or bays) with high oceanic influence and high trematode diversity. These findings suggested that, besides host species presence, temperature is an important trigger for parasite infection, with coastal upwelling operating as a shield against trematode infection in Portugal and masking latitudinal gradients. Results highlighted the possible consequences of thermal modification mediated by oceanographic global circulation change on cockle populations.

1. Introduction

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

affecting the value and impact of these species in the ecosystem (Thomas et al., 1999). This role is magnified when the host species itself is also an ecosystem engineer (Dairain et al., 2019).

In coastal waters, including bays, estuaries and coastal lagoons, trematodes are the most abundant and common macroparasites (Lauckner, 1983; Roberts et al., 2009). They have a complex and heteroxenous life cycle, infecting more than one host species to complete their life cycle (Bartoli and Gibson, 2007) with alternation between asexual multiplication and sexual reproduction phases (Whitfield, 1993). The typical trematode life cycle includes a free-living larva (miracidium) that hatches from the egg and infects first intermediate hosts, most of the time a mollusc. At this stage, the parasite transforms into a mother sporocyst that will develop, depending on the trematode species, into a mature sporocyst or into redia. Within the sporocysts or rediae, cercariae free-living stages develop by asexual multiplication. Cercariae will emerge from the first host and reach the second intermediate host, an invertebrate or a vertebrate species depending on the trematode species. The cercariae penetrate the second intermediate host and metamorphose into metacercariae. The cycle is complete when the parasitized second intermediate host is predated by the final host, a vertebrate species. Then, each metacercaria transforms into an adult

* Corresponding author.

E-mail address: luisa.magalhaes@ua.pt (L. Magalhães).

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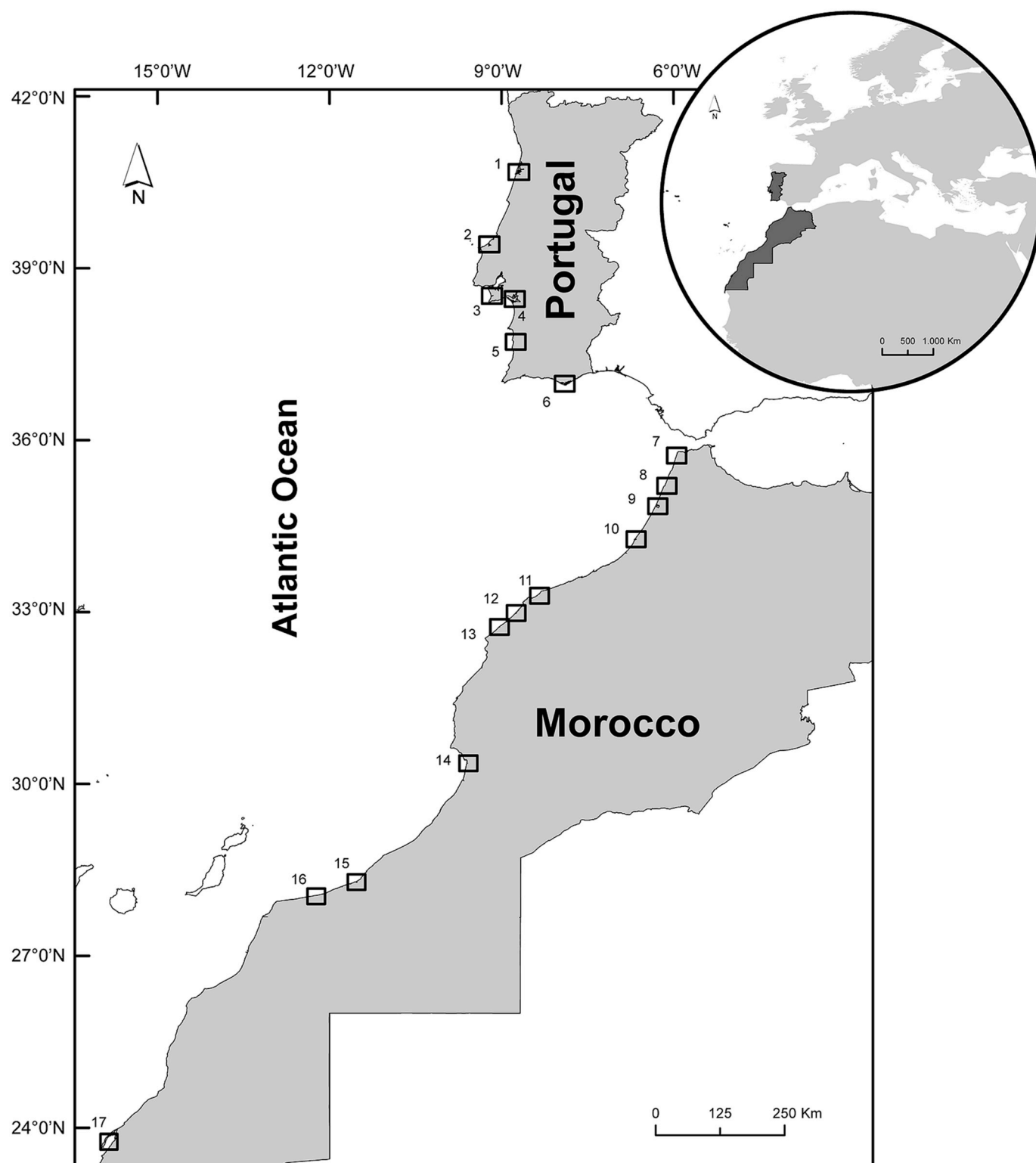


Fig. 1. Study area. Geographical location of the 17 aquatic systems distributed along the Portuguese and Moroccan coastlines. Sampling sites: 1 - Ria de Aveiro; 2 - Óbidos lagoon; 3 - Albufeira lagoon; 4 - Sado estuary; 5 - Mira estuary; 6 - Ria Formosa; 7 - Tahaddart estuary; 8 - Loukkos estuary; 9 - 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.

form that will reproduce sexually and produce eggs (Bartoli and Gibson, 2007; Esch, 2002; Roberts et al., 2009).

The complex life cycle described here, shows not only how important host diversity is in the distribution of trematode parasites, but also highlights that environmental parameters must have a key role in the modulation of parasite population dynamics, especially by their impact on infective free-living larvae transmission and infection success (Anderson and Sukhdeo, 2010; de Montaudouin et al., 2016a, 2016b; Koprivnikar and Poulin, 2009; Studer and Poulin, 2013). Indeed, a greater host diversity is usually reflected in a greater diversity of parasites, particularly for those with complex life cycles (Sukhdeo and Sukhdeo, 2004) and in the same sense, higher abundance of suitable hosts increases the abundance and prevalence of parasites in the ecosystem (Combes, 2001). As an example, Hechinger and Lafferty (2005) found a positive correlation between bird communities composition (the final hosts of several trematode species) and trematode communities composition in a snail host. Similarly, Thieltges and Reise (2007) demonstrated higher metacercariae abundance (the trematode parasitic stage occurring in the second intermediate host) positively correlated to an increase in abundance and diversity of higher trophic level host communities. On the other hand, higher host density can also promote a dilution effect and therefore decrease the parasite burden in a specific host (Buck et al., 2017; Magalhães et al., 2016; Mouritsen et al., 2003). Concerning the abiotic environmental factors, different conditions of temperature (Achiorno and Martorelli, 2016; de Montaudouin et al., 2016a), salinity and pH (Koprivnikar et al., 2010, 2014; Mouritsen, 2002; Studer and Poulin, 2013), among others, can also have an influence on trematode dynamics (Wilson et al., 2002). As an example, higher cercariae emission from the first intermediate host is related to an increase on the water temperature (de Montaudouin et al., 2016a) and consequently a higher trematode infectivity (Thieltges and Rick, 2006). Favourable salinity conditions have been reported to benefit, as well, trematode emergence from the first intermediate host (Koprivnikar et al., 2014; Lei and Poulin, 2011).

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

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

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

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

2. Material and methods

2.1. Study area

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

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

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

2.2. Field sampling and parasite identification

At each sampling area, sediment samples were collected to perform grain size analysis following the method described by Quintino et al. (1989). Silt and clay fraction (fine particles with diameter below 63 µm) were assessed by wet sieving and the remaining fractions (sand and gravel) were determined by sieving through a column of five sieves with decreasing mesh sizes (2.00, 1.00, 0.50, 0.250 and 0.125 mm).

Cockles were collected in the intertidal zone (with exception of Óbidos lagoon) using six quadrats (0.25 m² each) randomly placed along a 100 m parallel to the water transect and by sieving the sediment through a 1-mm mesh. The number of cockles per square meter (density) was then estimated. In the Óbidos lagoon, a subtidal area where the quadrat method was impossible to perform, samples were collected with a hand dredge and cockle density (d) was calculated following the equation:

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 (km²), 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 ²)	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)
Óbidos	1	39°24'	9°12'	7.0	22.0	10.0	37.0	26.0	0.392	Lillebø et al. (2015)
Albufeira	1	38°30'	9°10'	1.3	22.5	11.0	36.0	31.0	0.404	Malhadas et al. (2009)
Sado	2	38°28'	8°50'	240.0	21.9	13.8	36.0	10.9	0.304	Oliveira et al. (2006)
Mira	2	37°43'	8°46'	16.0	22.5	12.0	35.0	27.0	0.353	Fortunato et al. (2014)
Ria Formosa	1	36°58'	7°52'	170.0	26.0	12.0	36.5	13.0	0.326	Bao et al. (1999)
Tahaddart	2	35°46'	5°42'	10.0	26.0	13.0	41.0	21.0	0.194	Martins et al. (2001)
Loukkos	2	35°07'	06°00'	72.0	27.0	15.0	34.0	22.0	0.203	Silva et al. (2006)
Merja Zerga	1	34°51'	06°16'	27.0	28.0	11.0	35.0	27.0	0.272	Gamito and Erzini (2005)
Sebou	2	34°16'	06°39'	17.5	30.0	16.0	35.0	12.0	0.219	Achab (2011)
Oum Er Rbia	2	33°28'	08°34'	1.5	25.0	15.0	35.0	30.0	0.146	Geawhari et al. (2014)
Sidi Moussa	1	32°54'	08°49'	4.2	27.0	15.0	33.0	22.0	0.273	Gam et al. (2010)
Qualidia	1	32°45'	08°30'	3.0	21.0	16.0	36.0	28.0	0.181	Haddout et al., 2016
Souss	2	30°21'	09°35'	16.0	25.0	19.0	39.0	35.0	0.202	Khalki and Moncef (2007)
Chbika	2	28°14'	11°42'	0.2	ND	ND	ND	ND	0.184	Maanan et al. (2004)
Khniass	1	28°03'	12°15'	65.0	22.0	16.0	38.0	34.0	0.150	Hilmi et al. (2005)
Dakhla	3	23°45'	15°50'	400.0	26.0	14.0	39.5	37.0	0.120	Anajjar et al., 2008
										Semlali et al. (2012)
										Zidane et al. (2017)

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

where “n” corresponds to the total number of cockles collected; “a” to the hand dredge area (m²); “t” to the mean number of trawls (mean number of times the dredge was dragged in the sediment per launch); and “l” to the total number of launches.

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

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

2.3. Data analysis

To test the influence of latitude (independent variable) on the variation of Trematode Species Richness (TSR), Trematode Total Prevalence (TTP) and Trematode Mean Abundance (TMA) (dependent variables), individual regression analyses were performed using the SPSS v.25 software.

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

The data matrix with the abundance of trematode per site [abundance per trematode species metacercariae x sampling site] was square root transformed and the Bray-Curtis (Legendre and Legendre, 1998) similarity calculated between sites. To identify the biological affinity groups, the resemblance matrix was then analysed using a hierarchical clustering analysis tool. The affinity groups were characterized according to environmental and biological features by calculating the mean value of annual maximum and minimum water temperature, annual maximum and minimum water salinity, median grain-size, cockle density at sampling time and the rarefaction index, i.e. an estimation of the trematode species diversity through standardization of the number of samples (Gotelli and Colwell, 2001). Differences in terms of trematode metacercariae

abundance were then tested among affinity groups, type of aquatic system (lagoons vs. estuaries) and geographical position (north vs. south of strait of Gibraltar). Differences were tested using permutational multivariate analysis of variance (Anderson et al., 2008) following unrestricted permutation of the raw data (9999 permutations) and the calculation of type III sums of squares. Similarity Percentages (SIMPER) were used to characterize the type of aquatic system and the geographical position by the species that most contributed to the dissimilarity between groups. Affinity groups differences were visualized through Principal Coordinates Ordination analysis (PCO) after a distance among centroids resemblance (Clarke and Warwick, 2001). The abiotic variables that were highly correlated (Spearman $\rho > |0.7|$) to samples ordination were represented as superimposed vectors in the PCO graph.

To model the relationship and provide quantitative measures of abiotic and biotic data (annual maximum and minimum water temperature, annual maximum and minimum water salinity and median grain-size and cockle density) on metacercariae community of each aquatic system, a Distance-based linear model (DistLM) was performed (Anderson et al., 2008). The results were obtained using appropriate permutation (9999 permutations) and following the step-wise method and Akaike information criterion (AICc). This criterion balances between data fitness and the most parsimonious model (the model with lower power loss). Thus, it is considered the best model, among the possible ones, the one showing the lowest AIC (Symonds and Moussalli, 2011). Distances among aquatic systems were visualized through a dbRDA plot.

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

3. Results

3.1. Trematode species richness, prevalence and abundance

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

P. minutum was the most prevalent and abundant trematode species,

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	1st intermediate host	2nd 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

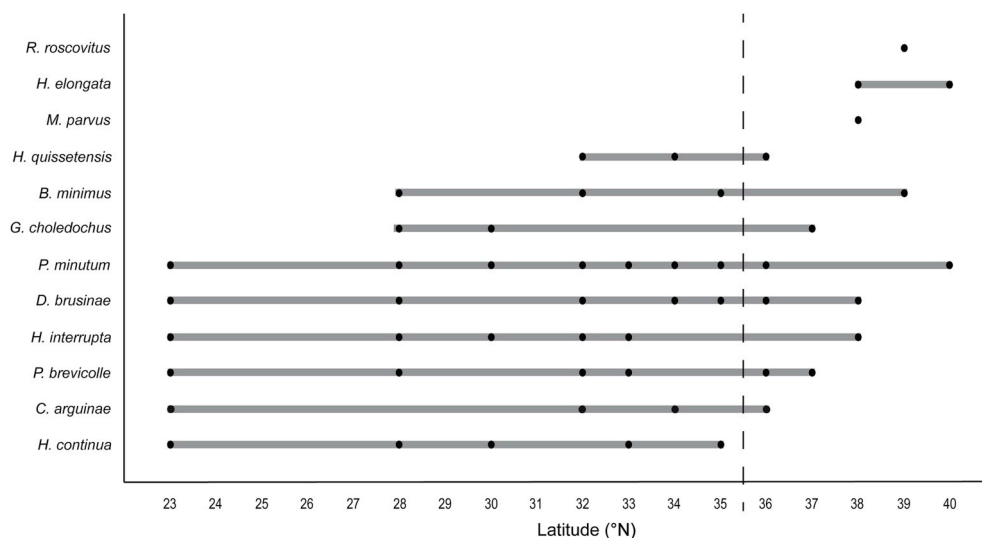


Fig. 2. Latitudinal distribution of the 12 trematode species found in *Cerastoderma edule*. Black point: occurrence data. Dashed line: Strait of Gibraltar. Grey bar: Presumable distributional range.

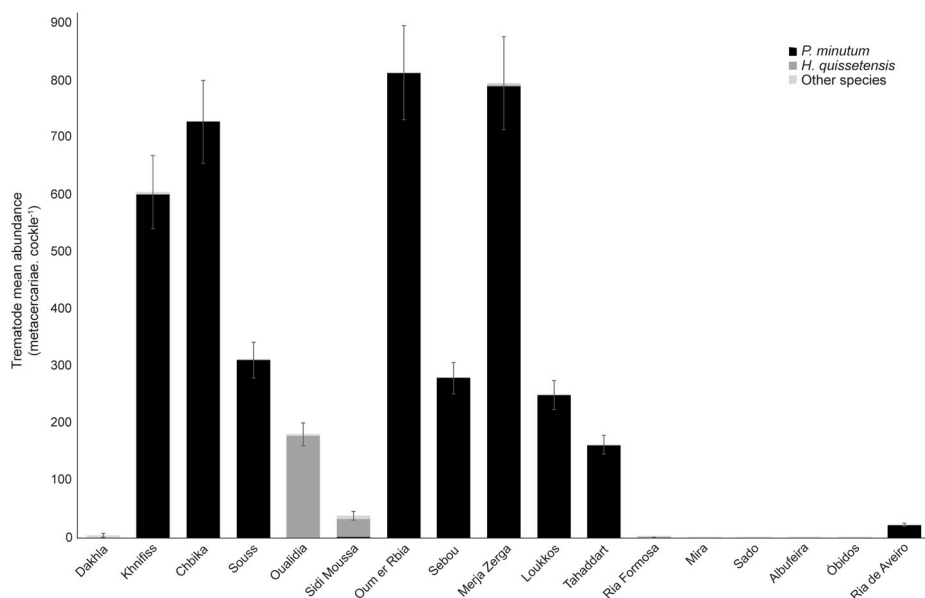


Fig. 3. Trematode mean abundance per aquatic system for the two most representative species, *Parvatrema minutum* (black bar) and *Himasthla quissetensis* (dark grey bar), and for the other cercariae (light grey bar).

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 ²
TSR	Constant	11.265	3.272	0.004	0.217
	Latitude	-0.225	0.096	0.034	
	Model	1.164	0.034	0.001	
(w/o Se & Ch)	Constant	14.501	2.344	<0.001	0.608
	Latitude	-0.307	0.068	0.001	
	Model	1.164	0.001	0.001	
TTP	Constant	-4.158	1.454	0.013	0.821
	Latitude	0.371	0.091	0.001	
	Latitude ²	-0.007	0.001	<0.001	
	Model	0.136	<0.001	<0.001	

representing approximately 90% of total metacercariae abundance. This species was found in twelve out of the seventeen sampled systems and therefore throughout the whole sampled latitudinal gradient. *H. elongata* was exclusively found in three aquatic systems located north of 38 °N (northern Portuguese aquatic systems) whereas *H. continua* was only present in five aquatic systems located south of 35 °N. *R. roscovitus* was the rarest and the least abundant species, represented by 1 metacercariae identified in the Óbidos lagoon. *C. arguinae*, *H. quissetensis* (representing 5% of total trematode abundance) and *P. brevicolle* were common in several aquatic systems south of 37 °N, found in the two aquatic systems nearest to the north Atlantic Ocean – Mediterranean transition (strait of Gibraltar, 36 °N) and in several aquatic systems south of this biogeographical barrier (Fig. 2). *G. choledochus*, *D. brusinae* and *H. interrupta*, the remaining species infecting cockles as second intermediate host, showed low abundance, each representing less than 1.5% of total abundance (Fig. 3).

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

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

Trematode Mean Abundance (TMA, considering trematode species infecting cockles as second intermediate host) did not follow significantly any model. Nonetheless, higher TMA was observed in the central zone of the total extent of the sampled area in comparison to the aquatic systems located at the northern and southern edges of the total area sampled in this study. The Óbidos lagoon (39 °N, Portugal) presented the lowest TMA (0.03 ± 0.17 metacercariae. cockle⁻¹) whereas, Oum Er Rbia (33 °N, Morocco) presented the highest TMA (820 ± 595 metacercariae. cockle⁻¹).

3.2. Multivariate analysis

Cluster analysis, at a similarity distance of 70%, allowed to assemble the different areas in three affinity groups (Fig. 4A): group A, subdivided into A1 composed by Tahaddart, Loukkos, Sebou and Souss estuaries and A2 composed by Merja Zerga lagoon, Oum Er Rbia estuary and Khnifiss lagoon; group B, divided in B1 composed by Sidi Moussa and Oualidia lagoons and group B2, splitted into B2.1 composed by Dakhla bay and B2.2 composed by all Portuguese systems (Ria de Aveiro lagoon, Óbidos lagoon, Albufeira lagoon, Sado estuary, Mira estuary and Ria Formosa lagoon). Cockle density showed to be significantly higher in

group B1 and lower in group B2.1. Sediment median grain-size was significantly higher in group B2.2 and lower in group B2.1 (Table 5). Concerning water physico-chemical characterization, all descriptors showed no significant differences among the affinity groups. Nevertheless, group A1 displayed the highest values of maximum and minimum water temperature while, group B2.2 registered the lowest values for the same variables. Maximum and minimum water salinity presented the highest values for group B2.1 and the lowest for groups B1 and B2.2, respectively (Table 5).

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

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

4. Discussion

Trematode parasites can have a significant impact on population dynamics of their hosts, implying modification on host growth (Wegeberg and Jensen, 1999) or inducing higher mortality rates (Desclaux et al., 2004), which highlights the importance to study host-parasite interactions. This study is among the few reports on large-scale trematode communities infecting cockles (e.g. de Montaudouin et al., 2009; Magalhães et al., 2015) and represents the first large-scale assessment of latitudinal gradient (and abiotic related factors) as a driver of trematode communities composition in *Cerastoderma edule* as a host model. In addition, this is the first exhaustive study on trematode species composition in Moroccan cockles.

There are sixteen trematode species infecting *Cerastoderma edule* in its distributional range that use this bivalve as first and/or second intermediate host (de Montaudouin et al., 2009). In the present study, a total of 12 species were identified along the whole sampled latitudinal gradient. Nine (*Bucephalus minimus*, *Curtuteria arguinae*, *Diptherostomum brusinae*, *Gymnophallus choledochus*, *Himasthla continua*, *H. interrupta*, *H. quissetensis*, *Psilostomum brevicolle* and *Parvatrematode minutum*) showed a great dispersal ability, since they were present in a wide range, i.e. along the sampled latitudes, possibly related to migration of birds and fish which are trematode final hosts (Feis et al., 2015). For a trematode species, to complete its life cycle, the three intermediate/final host

Table 4
Prevalence of trematode parasites infecting cockle populations in the aquatic systems of Portugal and Morocco. 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. n = number of dissected cockles.

	<i>B. minutus</i>	<i>M. parvus</i>	<i>G. choleadochus</i>	<i>D. brusinae</i>	<i>H. continua</i>	<i>H. elongata</i>	<i>H. interrupta</i>	<i>H. quissetensis</i>	<i>C. argutinae</i>	<i>P. brevicolle</i>	<i>P. minutum</i>	<i>R. roscoffius</i>	Total parasite prevalence
Portugal													
1 (n = 65)	-	-	-	-	-	11	-	-	-	-	26	-	35
2 (n = 35)	3	-	-	-	-	-	-	-	-	-	-	3	6
3 (n = 20)	-	40	-	20	-	10	-	-	-	-	-	-	55
4 (n = 21)	-	-	-	-	-	48	5	-	-	-	-	-	52
5 (n = 20)	-	-	50	-	-	-	-	-	5	-	-	-	55
6 (n = 25)	-	-	-	4	-	-	-	-	-	4	8	-	48
7 (n = 13)	8	-	-	15	54	-	-	36	20	-	100	-	100
8 (n = 20)	10	-	-	10	-	-	-	-	-	-	90	-	90
9 (n = 20)	-	-	-	30	-	-	-	70	100	-	100	-	100
10 (n = 17)	-	-	-	-	-	-	-	-	-	-	100	-	100
11 (n = 20)	-	-	-	-	80	-	65	-	-	45	95	-	100
12 (n = 15)	7	-	-	47	-	-	100	100	100	13	67	-	100
13 (n = 20)	5	-	-	30	-	-	75	100	100	20	-	-	100
14 (n = 20)	-	-	5	-	10	-	60	-	-	-	95	-	100
15 (n = 11)	-	-	-	-	-	-	-	-	-	-	100	-	100
16 (n = 20)	10	-	5	85	100	-	60	-	-	45	100	-	100
17 (n = 36)	-	-	-	92	47	-	39	75	-	25	11	-	100
Morocco													

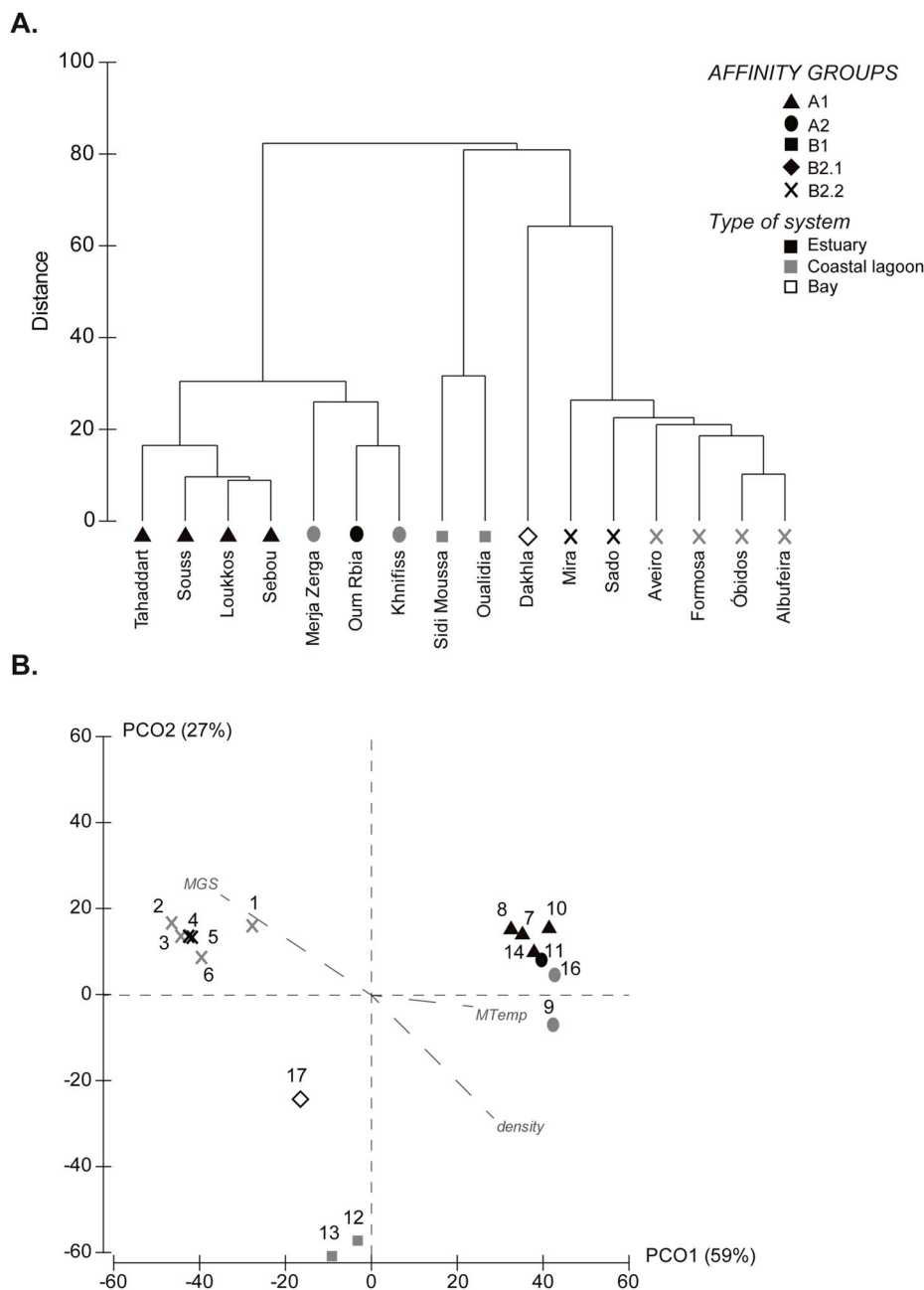


Fig. 4. Cluster analysis based on trematode parasites communities in seventeen aquatic systems from Portugal and Morocco (A) and Principal coordinates ordination (PCO) showing the variables that better explained samples distribution (B). MGS: Sediment median grain-size; M Temp: Maximum annual water temperature; 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.

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⁻²) 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: 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; 16 - Khnifiss lagoon and 17 - Dakhla bay.

Affinity groups	Sampling sites	M Temp	m Temp	M Sal	m Sal	MGS	Cockle density	ES (10)
A1	7, 8, 10, 14	27.0 ± 2.2	15.8 ± 2.5	37.3 ± 3.3	22.5 ± 9.5	0.2 ± 0.0 ^a	404 ± 457 ^a	1.0
A2	9, 11, 16	25.0 ± 3.0	14.0 ± 2.6	36.0 ± 1.7	30.3 ± 3.5	0.2 ± 0.1 ^{a,b}	1643 ± 2267 ^{a,b}	1.3
B1	12, 13	24.0 ± 4.2	15.5 ± 0.7	34.5 ± 2.1	25.0 ± 4.2	0.2 ± 0.1 ^{a,b}	6092 ± 1114 ^b	2.4
B2.1	17	26.0	14.0	39.5	37.0	0.1 ^b	15 ^c	2.4
B2.2	1, 2, 3, 4, 5, 6	22.8 ± 1.6	12.3 ± 1.8	34.8 ± 3.4	20.0 ± 9.0	0.3 ± 0.0 ^c	135 ± 304 ^a	1.0

species should be present in the same aquatic system (Bustnes and Galaktionov, 1999). Nonetheless, biogeographical barriers, such as oceans in the case of continental species, are among the most important

factors contributing to isolation and prevention of species exchange among regions (Cox and Moore, 1980; Ricklefs and Schluter, 1993).

In the present study, the strait of Gibraltar (36 °N), a known

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.

	Species	Average abundance group 1	Average abundance group 2	Dissimilarity Contribution (%)
Coastal lagoons (1) vs. estuaries (2)	<i>P. minutum</i>	5.42	12.22	69.28
	<i>H. quissetensis</i>	1.70	0.00	8.76
	<i>H. interrupta</i>	0.66	0.29	4.64
	<i>C. arguinae</i>	0.91	0.00	3.83
	<i>H. elongata</i>	0.05	0.13	3.74
Northern systems (1) vs. southern systems (2)	<i>P. minutum</i>	0.84	13.15	58.62
	<i>H. quissetensis</i>	0.06	1.81	10.26
	<i>D. brusinae</i>	0.04	1.04	9.12
	<i>C. arguinae</i>	0.00	1.30	8.48
	<i>H. interrupta</i>	0.01	0.99	6.02

geographical barrier, showed some influence on trematode communities, dividing the observed trematode species in three different categories. The first category gathered seven trematode species (*Monorchis parvus*, *B. minimus*, *P. brevicolle*, *G. choledochus*, *P. minutum*, *C. arguinae* and *H. interrupta*) for which there was no influence of the biogeographical barrier (i.e. Gibraltar) and which occurrence was possibly mediated by the predominant presence of the intermediate hosts in the sampled area (*Peringia ulvae*, *Scrobicularia plana*, *Gobius* spp., among others (cf. Table 2)). In this study *H. continua* was only found south of Gibraltar (36 °N), however, its published distribution (de Montaudouin et al., 2009) places this species in this ubiquitous group of parasites. The life cycle of *C. arguinae* is unknown (Desclaux et al., 2006), preventing any hypothesis concerning the link with first intermediate and final hosts distribution. *M. parvus* was only observed at the Portuguese coast, still this isolated occurrence is more likely related to the fact that trematodes infecting first intermediate host usually display very low prevalence (Granovitch and Johannesson, 2000; Islam et al., 2012; Tigga et al., 2014). Indeed, *M. parvus* has been previously recorded along the whole studied latitudinal gradient (de Montaudouin et al., 2009). The second category, contrastingly, gathered two trematode species with a southern distribution, *D. brusinae* and *H. quissetensis*, possibly mediated by the biogeographical barrier and first intermediate host,

Tritia reticulata, an abundant gastropod in southern areas, from France to Morocco (but its actual northern latitude corresponds to Baltic Sea (Pizzolla, 2005)). Thirdly, *H. elongata* and *Renicola roscovitus* displayed a northern distribution likewise their first intermediate host *Littorina littorea*, a marine gastropod that inhabits the intertidal zone from the White Sea to Gibraltar, on the Atlantic east coast (Johannesson, 1988). Thus, this study confirms that at this latitudinal scale, the distribution of the trematode species is mainly driven by the occurrence of the first intermediate host (de Montaudouin and Lanceleur, 2011; Thieltges, 2007; Thieltges et al., 2009), considering that final hosts have generally a wider distribution area (Magalhães et al., 2015).

Trematode Species Richness (TSR) and Trematode Total Prevalence (TTP) increased towards south (from 40 °N to 23 °N). This latitudinal dependent pattern of TSR follows the same trend described for benthic macrofaunal diversity which show higher values with decreasing latitudes (Macpherson, 2002; Martins et al., 2013; Roy et al., 2004). However, this pattern was not observed in the case of Chbika and Sebou estuaries, located at 28 °N and 34 °N, respectively, that presented the lowest TSR.

Chbika is not a permanent estuary ('Oued'), which might induce lower macrofaunal and parasite diversity. Conversely, the Sebou river is one of the biggest north African rivers, crossing several riverside

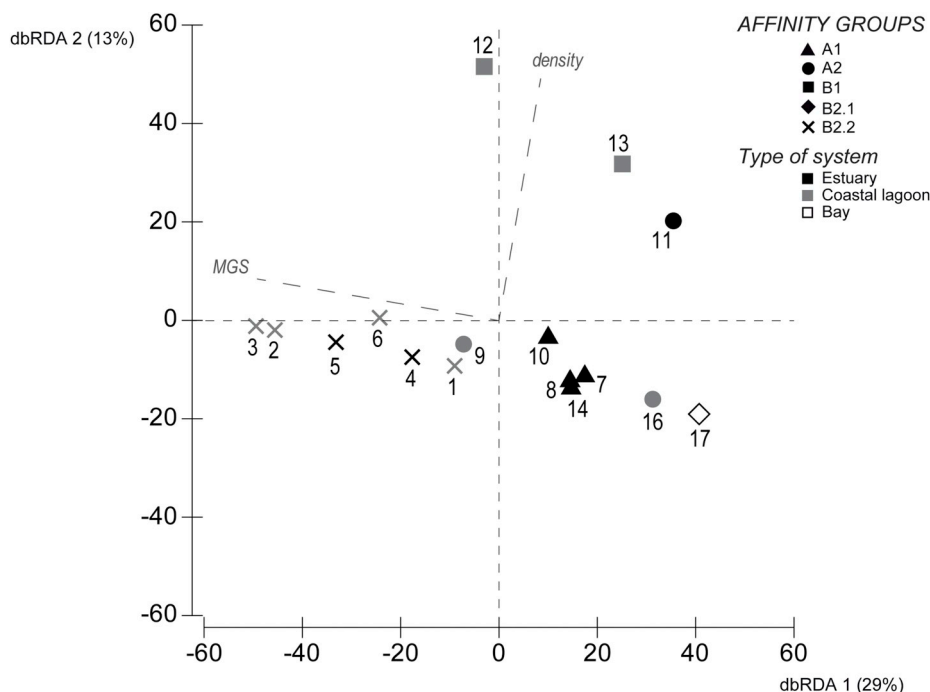


Fig. 5. Distance-based redundancy analysis plot and the correlated variables that explained aquatic systems distribution based on trematode abundance. Sampling sites: 1 - Ria de Aveiro; 2 - Óbidos lagoon; 3 - Albufeira lagoon; 4 - Sado estuary; 5 - Mira estuary; 6 - Ria Formosa; 7 - Tahaddart estuary;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

populations and then impacted by several anthropogenic activities, including agricultural activities (Perrin et al., 2014). The constant use of pesticides and fertilizers by the agricultural activities, plus the connection with untreated sewage from peripheral cities, result in high pollutant loads that contaminate the river to its estuary (Perrin et al., 2014). This presumable poor health and ecological status of this ecosystem might be inducing a low trematode parasites diversity, opposing to the latitudinal trend. Indeed, trematodes, especially free-living stages, are sensitive to water disturbance, reducing their survival, preventing transmission between hosts (Pietroock and Marcoligiese, 2003; Koprivnikar et al., 2007) and can be used as indicators of retrograde condition (MacKenzie, 1999). Therefore, our results showed that such as free-living species, parasitic fauna seems to follow a latitudinal gradient of decreasing species richness from tropical to extra-tropical areas, one of the oldest recognized ecological patterns (Wright et al., 1993; Willig et al., 2003). This latitudinal pattern is usually not clear for communities of parasites with complex life cycles (Poulin and Leung, 2011; Studer et al., 2013) due to the complexity of host/parasite interactions, but also because these cycles (and in particular infection success stage) depend on several abiotic factors, including anthropogenic stressors (Rohr et al., 2008; Altman and Byers, 2014).

Among abiotic factors, temperature is one of the strongest drivers of trematode activity (propagule dispersal, survival, infection (Thieltges and Rick, 2006)) as well as of host infection levels (higher values observed during the warmer seasons (Goater, 1993; Desclaux et al., 2004)). As an example, in Arcachon bay, a synchrony was observed between parasites emergence from the first intermediate host and the infection in the second intermediate host when water temperature was above 15 °C (de Montaudouin et al., 2016a). In the case of the present study, the minimum water temperature of the aquatic systems south of 36 °N was around 15 °C, 3 °C above north of 36 °N. This temperature difference can explain why Morocco displays higher TTP and TMA than Portugal. In fact, this study showed that abundance and prevalence of trematode communities presented higher values in ecosystems characterized by higher maximum water temperature (affinity group A). In contrast, all the northern sampled areas (Portuguese aquatic systems located north of the strait of Gibraltar) were all gathered in the same affinity group (group B2.2) characterized by the lowest TMA and TTP. The Portuguese coast proximity to an upwelling front and consequent occurrence of cold vertical currents (Queiroz et al., 2012) may operate as a shield against trematode infection.

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

The type of aquatic system (estuaries, lagoons or bays) showed also to be determinant for the trematode community composition. There was a clear separation between three particular areas south of 36 °N, that presented higher trematode biodiversity: Oualidia and Sidi Moussa lagoon, and Dakhla bay corresponding to group B1 and B2.1, respectively. These areas are classified as coastal lagoons (group B1) or bays (group B2.1) and therefore characterized by higher oceanic influence and hydrodynamics (Kjerfve and Magill, 1989) and lower water temperature variations, especially Dakhla bay which is located in the interaction between the Canary stream and the subtropical ridge currents (Orbi et al., 1999). Leung et al. (2009) and Mouritsen and Poulin (2005) referred that these combinations of characteristics are usually

related to higher trematode diversity and abundance, which was confirmed by our results (the highest rarefaction indices were found in affinity groups B1 and B2.1). Additionally, coastal lagoons tend to be shallower compared to estuaries (Kjerfve, 1986). This enables light to penetrate up to the bottom, allowing benthic plants to thrive (higher productivity) (Kennish and Paerl, 2010) which could lead to an increase of benthic communities (first hosts of trematode species) diversity and abundance. As previously discussed, higher hosts diversity and abundance is usually correlated to higher trematode diversity (Hechinger and Lafferty, 2005).

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

The temporal gap and the seasonal differences among some of the samples could of course bias our spatial analysis. However, at these scales, we assume that spatial effects (17° in latitude corresponding to approx. 3000 km) are stronger than temporal effects (8 years), once trematode composition at a given site is often stable at multiannual scale. As an illustration, de Montaudouin et al. (2012) showed that trematode communities of Arcachon bay, France, were the same after 8 years, the same temporal gap as in this study, due to environmental stability along time. In the same direction, in the Ria de Aveiro coastal lagoon, one of the sampled systems, diversity of trematode was equivalent after 6 years (Freitas et al., 2014; Russell-Pinto et al., 2006). On the other hand, concerning seasonal differences, actually, trematode abundance (infecting cockles as second host) follows a seasonal pattern, increasing their infections during the warmer seasons, contrary to what is observed in the colder seasons (Desclaux et al., 2004; Goater, 1993). This could mean a positive influence of the results (in terms of infection intensity) in the Portuguese aquatic systems (systems sampled during summer). However, due to the low trematode abundance on the Portuguese systems, seasonal effects are not so evident (Magalhães et al., 2018). Moreover, the present study findings demonstrated a higher trematode abundance on Moroccan aquatic systems (winter samples), which means that seasonal effects were not exacerbated. Finally, we believe that the present findings are of high impact because of the interest in trematode communities knowledge improvement in each sampled area and each country.

5. Conclusion

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

Furthermore, the obtained results highlighted the ubiquity of trematode parasites in the different aquatic systems and alert to a possible change on the trematode fauna composition and abundance in cockle populations driven by thermal modification mediated by oceanographic global circulation. Besides global temperature monitoring, it is then

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

Declaration of competing interest

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

CRediT authorship contribution 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. **Hocein Bazairi:** Conceptualization, Methodology, Investigation, Resources. **Meriam Gam:** Investigation. **Xavier de Montaudouin:** Conceptualization, Methodology, Formal analysis, Investigation, Resources, Writing - review & editing, Supervision.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecss.2019.106546>.

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