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# Dynamics of “trematode – edible cockle (*Cerastoderma edule*)” parasite-host systems in three coastal ecosystems along a North-Eastern Atlantic gradient

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## Abstract:

This study explores the dynamics of trematode infections in the edible cockle, *Cerastoderma edule*, across three diverse coastal ecosystems in the Northeast Atlantic: the Arcachon Bay in France, and the Merja Zerga and Oualidia lagoons in Morocco. Over a period of two years, the research focused on the infection patterns of four dominant trematode species: *Himasthla quissetensis*, *H. interrupta*, *Curtuteria arguinae*, and *Gymnophallus minutus*. The correlation between parasite abundance and three key parameters was evaluated: mean sea temperature, seasonal variations, and individual cockle biomass. The findings reveal distinct infection patterns for the four trematode parasites across the coastal ecosystems, with significant infection variations typically occurring between 17 and 22°C. In nearly all cases, infection was correlated with the individual biomass of the host, *i.e.* its age. The results indicate clear seasonal infection patterns influenced by mean sea temperature, highlighting its critical but insufficient role in explaining infection patterns. The study suggests that temperature acts as an "on/off" factor in infection, with infection intensity depending on other habitat-specific factors. Additionally, it uncovers a nuanced interplay between various environmental parameters, demonstrating that no single factor can predict the parasitic dynamics in these marine organisms conclusively.

**Keywords:** Host–parasite interactions, Phenology, Environmental drivers, Temperature, Latitude

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## 1 Introduction

2 Molluscs are a diverse and abundant animal group in coastal and marine habitats, where they provide a variety of  
3 ecological and economic functions (Esposito et al. 2022). They are essential ecosystem engineers in addition to  
4 supporting valuable aquaculture and wild-harvest enterprises. They influence the composition of benthic ecosystems,  
5 offer habitat, aid in nutrient cycling, serve as a key food source for higher trophic levels, and, in some situations, help to  
6 shoreline stabilization and water quality preservation (Coen and Bishop 2015; Fortunato 2015).

7 In natural environments, molluscs are often affected by various physical and biological factors, whose synergistic  
8 interaction with anthropogenic stressors (e.g., chemicals) can amplify their effects (Holmstrup et al. 2009). Among these  
9 factors, parasitism can play a dominant role in controlling their population dynamics (Coen and Bishop 2015). Parasites  
10 have various effects at the host individual, host population, and ecosystem scales in which they are found (Thieltges et al.  
11 2013).

12 In coastal ecosystems, trematodes are the most common and abundant macroparasites (Lauckner 1983; Mouritsen and  
13 Poulin 2002). They have a complicated life cycle that includes three different host species. The parasite reproduces  
14 within a vertebrate host (i.e., the final host), such as fish or birds. The eggs are subsequently discharged into the  
15 environment; once mature free-living miracidia larvae hatch from the egg and infect a mollusc as the first intermediate  
16 host. The miracidia develop into inter-molluscan stages (sporocysts, redia) within the mollusc's gonads and/or digestive  
17 system where cercarial stages are eventually created by asexual reproduction before being released into the sea. These  
18 cercariae have a brief free-living stage, usually a few hours, before infecting a second intermediate host and developing  
19 into metacercariae. This second intermediate host could be from any taxonomic group, including molluscs. This life  
20 cycle is completed when the second intermediate host is predated by the final host. The success of this cycle is dependent  
21 on various abiotic and biotic factors, including host species diversity (Thieltges and Reise 2007), hydrodynamics (de  
22 Montaudouin et al. 1998), light/dark rhythm (de Montaudouin et al. 2016), target host density (Magalhes et al. 2017), and  
23 temperature, which is a major factor that can control cercariae survival and infecting efficiency (Evans 1985; Mouritsen  
24 and Jensen 1994; Pechenik and Fried 1995; Lo and Lee 1996; Thieltges and Rick 2006).

25 Monitoring the evolution of parasite communities in coastal ecosystems is especially relevant in the current context of  
26 global change, including global warming. Indeed, parasites are frequently sensitive markers of environmental change  
27 (Stout et al. 2022; Moore et al. 2023), and their abundance and variety can represent the health of coastal ecosystems  
28 (Turner 1985; MacKenzie et al. 1995). Thus, understanding molluscan host-parasite dynamics is becoming increasingly  
29 important in the context of various challenges, including (1) expanding aquaculture; (2) current and future climate  
30 change; (3) non-native species movement; and (4) coastal development (Coen and Bishop 2015). The current study aims  
31 to investigate and compare the dynamics of "trematode - edible cockle (*Cerastoderma edule*)" host-parasites system in  
32 three coastal ecosystems: the Oualidia and Merja Zerga lagoons in Morocco, and Arcachon Bay in France, which is also  
33 a lagoon (France). These coastal habitats differ in climatic variables, particularly temperature regimes, along a latitudinal  
34 gradient in the northeastern Atlantic. However, these three ecosystems share the same trematode host species, which  
35 include cockles *Cerastoderma edule* (Linnaeus, 1758) as first and/or second intermediate hosts. The cockle and its  
36 trematode parasites are a great model for understanding the complicated host/parasite dynamics in coastal ecosystems.  
37 The cockle is one of the most common and numerous bivalves in soft bottom shallow environments around the northeast  
38 Atlantic (Malham et al. 2012), and it serves as a host for a wide range of parasites, including sixteen known trematode  
39 species (de Montaudouin et al. 2009; 2021). A comparison of *C. edule* / trematode dynamics at various latitudes could  
40 provide insight into the possible influence of global warming on such interactions (Mas-Coma et al. 2009).

41 The dynamics of parasite abundance for each cockle cohort in each site was compared to three shared parameters: 1) The  
42 mean sea temperature. Temperature is a key factor in cercariae infection processes (Mouritsen and Jensen 1997; Poulin  
43 2006; Selbach and Poulin 2020; Dias-Morales et al. 2022; de Montaudouin et al. 2016), and it is expected to be the most  
44 important driver in comparing infection amongst the three sites. However, as recently reported (Paterson et al. 2023), an  
45 increase in temperature (e.g., between spring and summer) can either stimulate or inhibit infection. 2) As a result, the  
46 seasonal influence was also explored by comparing parasite infection dynamics and night duration. Temperatures in  
47 spring and fall may be similar, but with different nyctemeral rhythms. Light is an important driver of cercarial emission  
48 (Shostak et al. 1990; de Montaudouin et al. 2016) and may also affect cockle/parasite interactions indirectly via other  
49 factors such as phytoplankton availability, salinity, and so on; 3) Finally, individual biomass was tested to measure  
50 parasite accumulation according to host growth (and age), independent of environmental factors. Although there are  
51 exceptions, such a positive correlation has already been reported (Mouritsen et al. 2003; Thieltges and Reise 2006; de  
52 Montaudouin et al. 2012).

## 1 **Materials and Methods**

### 2 **Study sites**

3 Our sampling stations are located in three semi-enclosed coastal ecosystems in the north-east Atlantic: Arcachon Bay  
4 (ARC) in France, and the lagoons of Merja Zerga (MZ) and Oualidia (OUA) in Morocco (**Fig. 1**).

5 Arcachon Bay is a macrotidal lagoon on the Atlantic coast of southwest France. The lagoon is characterized by semi-  
6 diurnal tides with amplitudes ranging from 0.9 to 4.9 meters, and significant water exchange with the ocean via its south-  
7 western inlet. Cockles were collected at Banc d'Arguin (44.60°N, 1.25°W), with an annual mean surface water  
8 temperature ranging from 6.5 °C to 21.5 °C, and a relatively high salinity of 32 to 35 (Auby et al., 1999). The cockle  
9 population settles on sands with a median grain size of 350 µm (de Montaudouin 1996).

10 The second station is located at Merja Zerga (34.87°N, 6.28°W), a shallow lagoon of 37 km<sup>2</sup>, in Morocco. Salinity in this  
11 lagoon fluctuates between 8 and 36 (Labbaridi et al. 2005), with mean water temperature varying between 14.6 and  
12 24.15 °C. Tides are semi-diurnal, with an average amplitude of 0.15 to 1.50 meters (Gam et al. 2008). The sediment at  
13 the station is characterized by a median grain size of around 300 µm.

14 Finally, the third sampling station is located downstream of the Oualidia lagoon (32.74°N, 9.02°W), in Morocco. This  
15 macrotidal lagoon is 7 km long and 0.5 km wide, covering a total area of 3.5 km<sup>2</sup>. Water is exchanged with the ocean via  
16 a major inlet some 150 m wide and 2 m deep. Tides are semi-diurnal, with amplitudes ranging from 0.8 to 3.6 meters  
17 (Hilmi et al. 2005). The average water temperature ranges from 16.1 to 21.1 °C, and the lagoon's salinity varies between  
18 20 and 35 at low tide, while at high tide it can reach 30 to 36 throughout the year (Makaoui et al. 2018). Cockles are  
19 established on fine sands with a median grain size of 260 µm.

### 20 **Sampling process and data collection**

#### 21 *Host (cockles)*

22 Cockles were sampled monthly at the three sites over a two-years period, between May 2005 and April 2007 for ARC  
23 and MZ, and between January 2009 and December 2010 for OUA. At each occasion, six quadrats of 0.25 m<sup>2</sup> and 10 cm  
24 depth were sampled and sieved through a 1-mm mesh. Shell length was measured with a Vernier Calliper at the least  
25 mm. Cohorts (*i.e.*, age class) of cockles were determined on FISAT software using a modal progression analysis  
26 (Bhattacharya's method (1967)) subroutine (Gayaniilo et al. 2005). Each representative component, with a separation  
27 index greater than 2, was assumed to be a single cohort.

#### 28 *Parasites (trematodes)*

29 Twenty cockles per cohort were dissected and squeezed between two large glass slides for trematode parasites  
30 observation under a stereomicroscope. All trematode species were identified based on morphological criteria (de  
31 Montaudouin et al. 2009). The present study focused on the four dominant species utilizing the cockle as second  
32 intermediate host, *Himasthla quissetensis* (Miller & Northup, 1926) Stunkard, 1934, *H. interrupta* Loos-Frank, 1967,  
33 *Curtuteria arguinae* Desclaux, Russell-Pinto, de Montaudouin & Bachelet, 2006 and *Gymnophallus minutus* (Cobbold,  
34 1859) (**Table 1**). The parasite abundance of each trematode species was defined as the median number of parasite  
35 individuals per cockle (Bush et al. 1997).

### 36 **Data analysis**

37 Temporal dynamics, or phenology, of infection of each parasite was investigated using its abundance (Ab) in the host.  
38 The non-parametric Mann and Whitney test was used to compare the abundance of each trematode species for each  
39 month compared to the following month, until a significant difference ( $p < 0.05$ ) was observed. A significant increase  
40 was considered as an infection period and a significant decrease as a parasite dependent mortality period (Desclaux et al.  
41 2004; Gam et al. 2009).

42 For each parasite species in each cohort and in each site, Ab was correlated (Spearman test) with:

43 1. the mean sea temperature (°C) between the sampling date and the previous one;

1 2. the darkness duration per day (h) as a proxy of seasons. Day duration D is given by the following equation as a  
2 function of the number d of days after spring equinox and the latitude  $\beta$  (in decimal degrees):

$$3 \quad D = -2/15 \times \text{Arccos}(\tan\beta \times \tan(\text{Arcsin}(\sin(23.44) \times \sin((d \times 360)/365)))) + 24 \quad (1)$$

4 with d = number of days after spring equinox;

5 3. the individual cockle biomass (W, g dry weight). This biomass was deduced from the shell length (L, mm) by using  
6 the following relationships:

$$7 \quad \text{Oualidia (unpubl. data): } \log_{10}W = 2.9084 \times \log_{10}(L) - 4.9564 \quad (r^2 = 0.63)$$

$$8 \quad \text{Merja Zerga (Gam 2008): } \log_{10}W = 2.55 \times \log_{10}(L) - 4.53 \quad (r^2 = 0.86)$$

$$9 \quad \text{Arcachon (de Montaudouin 1995): } \log_{10}W = 3.37 \times \log_{10}(L) - 5.5362 \quad (r^2 = 0.89)$$

10 Statistics were performed only when median parasite abundance was >10 metacercariae per cockle, at least once during  
11 the cohort monitoring.

12 *Curtuteria arguinae* and *G. minutus* were the only species to be present (with more than 10 metacercariae per cockle) in  
13 the five selected surveys (ARC-05, ARC-06, MZ-05, MZ-06, and OUA-09). To determine which trematode species or  
14 site is most important in driving infection, Spearman correlation tests were performed. These tests aimed first to compare  
15 species infection per site and cohort, and second, to compare the infection of each species across the three sites using the  
16 longest survey, i.e., ARC-05, MZ-05, and OUA-09 (at comparable months). Due to multiple comparisons, a Bonferroni  
17 correction was applied to establish the significance threshold.

## 18 **Results**

19 Growth curves revealed contrasting patterns between sites (**Fig. 2**). Arcachon cockles had the fastest growth rate and the  
20 longest asymptotic length (approximately 37 mm). Young cockles from Merja Zerga grew faster than those from  
21 Oualidia, but the curves of both groups gradually converged after one year, attaining a common maximum shell length  
22 (approximately 25 mm). Cockle recruitment occurred in all sites during the spring.

23 Six trematode species were observed using the cockle as their second intermediate host at Arcachon, Merja Zerga and  
24 Oualidia (**Table 2**). The current study concentrated on four prominent species: *Himasthla quissetensis*, *H. interrupta*,  
25 *Curtuteria arguinae*, and *Gymnophallus minutus*. These species accounted for 98-99 percent of the overall number of  
26 metacercariae with important inter-site differences (**Table 1**).

### 27 **Phenology of *Himasthla quissetensis***

28 Infection began in August or September of the first cockle year at all sites (**Fig. 3**). Only in ARC-05 and OUA-09 was *H.*  
29 *quissetensis* prevalent enough to study its phenology. In ARC-05, the abundance of *H. quissetensis* was low (median <  
30 11 metacercariae per cockle) and was not correlated with temperature, darkness duration (i.e., seasons) and cockle  
31 individual biomass (i.e., cockle size) (**Table 2**). The first and only significant peak of infection occurred in August  
32 (20 °C), when the length of the cockle shell reached 11 mm. This was followed by a decrease in infection in October and  
33 a low-noise variation over the remainder of the cohort's lifespan.

34 In contrast, after a low infection process during their first summer, OUA-09 cockles waited until the following spring to  
35 reach a peak of infection, corresponding to temperatures between 17 and 18 °C and shell length between 14 and 20 mm.  
36 The abundance of *H. quissetensis* in these cockles was quite considerable (median up to 46 metacercariae per cockle).  
37 Independent of temperature and season, there was a definite consistent increase in parasites with cockle individual  
38 biomass. The sea temperature in the OUA was quite high (always greater than 16 °C) with a modest annual variability  
39 (6 °C). In this environment, infection seemed to be possible at any time, but was inhibited when T° exceeded 20 °C  
40 (**Fig. 3**).

### 41 **Phenology of *Himasthla interrupta***

1 Infection began in August/September of the first cockle year in ARC, the only site where *H. interrupta* was significantly  
2 present (**Fig. 4**). Only in ARC-05 and ARC-06 was *H. interrupta* abundant enough to study its phenology (median up to  
3 60 metacercariae per cockle, and 168 at one occasion).

4 The parasite abundance fluctuated along time, resulting in no correlation with cockle size. The infection peaks were  
5 temperature and season independent, however with a preference for warmer waters: peaks of infection in ARC occurred  
6 at the end of summer, when temperatures were 20-22 °C, but also, to a lesser extent, in winter and spring, when  
7 temperatures were 10-12 °C (**Fig. 4**).

#### 8 **Phenology of *Curtuteria arguinae***

9 *Curtuteria arguinae* was present in three locations in moderate abundance (100 metacercariae per cockle) (**Fig. 5**).  
10 Except in MZ-05, where there was a positive correlation between abundance and darkness, there was a clear regular  
11 increase in parasites with cockle individual biomass in all sites, regardless of temperature or season. Peaks of infection  
12 occurred in the latter case during the winter, when the darkness period was the longest (and temperatures ranged between  
13 15 and 18 °C).

14 Peaks of infection in ARC occurred in cold waters in December-06 (T=14-15 °C) (**Fig. 5**). Infection peaks were also  
15 observed in OUA-09 during the coldest months (January, April, and November), but the sea temperature at this site was  
16 always above 17 °C. When the phenological patterns of the three sites were compared, a similarity was found between  
17 ARC, OUA, and MZ, despite the fact that OUA and ARC displayed a different infection scheme (**Table 3**). Furthermore,  
18 phenological patterns in ARC (at least for the longer survey, ARC-05) and MZ (MZ-05) were similar to those observed  
19 for *G. minutus* (**Table 3**).

#### 20 **Phenology of *Gymnophallus minutus***

21 *Gymnophallus minutus* was found in all three locations, with the highest abundance in ARC and MZ (up to 800  
22 metacercariae per cockle) and the lowest abundance in OUA (25 metacercariae per cockle) (**Fig. 6**). Except for OUA-09,  
23 where individual biomass was not correlated with parasite abundance, there was a clear regular increase in parasites with  
24 cockle individual biomass, independent of temperature or season (**Table 2**). In the latter case, there was a significant  
25 anticorrelation with temperature, due mainly to the occurrence of an infection peak in December 2010 during a period  
26 when sea temperature was low (**Fig. 6**). Infection began in all sites during the first summer. Following that, new  
27 infections could occur at any time of year. When the phenological patterns of the three sites were compared, ARC and  
28 MZ showed similarities, whereas OUA displayed a different infection scheme (**Table 3**).

#### 29 **Discussion**

30 The different sea temperatures measured at the various sites correspond to favorable conditions for cockles  
31 *Cerastoderma edule* (Verdelhos et al. 2015). Although some periodic and extreme temperatures may have bypassed our  
32 detection, we believe that sea temperature alone had no effect on cockles in the ARC, MZ, and OUA. The abundance of  
33 parasites increased with cockle age for all species and in all sites, as expected. The older the cockles, the more likely they  
34 are to encounter a parasite (Thieltges and Reise 2006; Richard et al. 2022); and the larger the cockles, the more intense  
35 their filtration rate is (route of infection by cercariae) (André et al. 1993; Riisgrd 2001). However, there was no clear and  
36 similar pattern of infection for 1) a given trematode species in different sites, and 2) a given site for the different  
37 trematode species at a lower temporal scale (season) and/or in different temperature conditions.

38 *Himashtla quissetensis* was found in only two sites, ARC and OUA. In both sites, infection occurred when the sea  
39 temperature ranged between 17 °C and 20 °C. This temperature range, on the other hand, did not always stimulate cockle  
40 infection, explaining the lack of correlation between parasite abundance and temperature. The phenology in ARC was  
41 consistent with previous studies that identified summer as the infection period, with maximum cercarial emission by the  
42 first intermediate host coinciding with maximum sea temperatures (*Tritia reticulata* (Linnaeus, 1758)). If summer  
43 appears to be the most favorable season, the corresponding temperature may differ depending on region, for example,  
44 20 °C in Arcachon (France) and 25 °C in South Carolina (USA) (Craig 1975; de Montaudouin et al. 2016b).  
45 Furthermore, it has been found that summer infection was followed by a decrease in metacercariae abundance in cockles,  
46 which can be interpreted as a parasite-dependent mortality event (Desclaux et al. 2004; Gam et al. 2009). However, the  
47 recorded abundance was always lower than what was commonly observed in this area (de Montaudouin et al. 2021). Sea  
48 temperatures in OUA were always within this theoretical thermal window of *H. quissetensis* infection. However,  
49 infection was not observed at this site all year, demonstrating that temperature alone is insufficient to interpret *H.*

1 *quissetensis*/cockle phenology (de Montaudouin et al. 2016a). Temperature may interact with cockle growth, which is  
2 dependent on many environmental factors. Indeed, in OUA, the first significant peak of infection occurred 7 months later  
3 than in ARC. This could be due to slower cockle growth in OUA, which prevented an early infection (de Montaudouin et  
4 al. 2005).

5 In addition, *H. interrupta* showed distinct infection patterns in the two sites where it was found, ARC and OUA. If  
6 infection was common in both sites during summer/autumn (thermal window:  $18\text{ }^{\circ}\text{C} < T < 20\text{ }^{\circ}\text{C}$ ), it was much less  
7 common in ARC during winter/spring ( $10\text{ }^{\circ}\text{C} < T < 12\text{ }^{\circ}\text{C}$ ). This result is not entirely consistent with a recent review in this  
8 area, which found that infection was possible until December ( $15\text{ }^{\circ}\text{C}$ ), but it is consistent with the fact that parasite  
9 abundance decreased after this month (Richard et al. 2022). Indeed, this decrease was observed in the current survey in  
10 both ARC and OUA, indicating parasite-dependent mortality. This review, however, revealed significant interannual  
11 variability in infection processes.

12 *Curtuteria arguinae* was found in all three locations studied. The main infection window in ARC occurred between  
13 December 06 and January 07, when sea temperatures ranged between 12 and 16 °C. These findings contradict previous  
14 ones obtained at the same site between 1998 and 2003. (Desclaux et al. 2006). In this survey, authors showed that  
15 infection occurred between July and October ( $18\text{--}20\text{ }^{\circ}\text{C}$ ). They did, however, notice two minor peaks of *C. arguinae* in  
16 January 2000 and 2003. As a result, while infection could theoretically occur at any time in OUA and MZ where sea  
17 temperatures are always above 14 °C, infection was only observed between July and April.

18 Finally, *G. minutus* was found in all three sites, with periods of infection similar to MZ and ARC and completely  
19 different from OUA, but covering the entire year when all sites were considered.

20 These results, combined with previous research, show that there is a thermal window for cercariae infection (de  
21 Montaudouin et al. 2016b), with the characteristics of this window varying depending on the site, species, and period. A  
22 global study of 99 articles found a weak and variable relationship between temperature and trematode infection levels at  
23 all stages of the trematode life cycle (Paterson et al. 2023). Consequently, the impact of seasons on the variation of  
24 prevalence or parasite abundance is minimal. Temperature appears as a necessary, but not a sufficient factor, to structure  
25 trematode/host phenology. Within a potential thermal window (which could differ in width in nature than experimentally  
26 assessed), a variety of factors (and their interactions) may play a role, owing to the high complexity of the trematode life  
27 cycle (Marcogliese 2001, 2008). In the case of the second intermediate host, the abundance of metacercariae also  
28 depends on: i) the dynamics of other hosts in the trematode cycle, particularly the upstream first intermediate host  
29 (Bommarito et al. 2021), and it is noteworthy that the dynamics of the first intermediate host are related to the final host  
30 populations through parasite or predation interactions (Kube et al. 2002; Fredensborg et al. 2006); ii) the survival of  
31 cercariae, which can be affected by pollution (Morley et al. 2003), predation (Vielma et al. 2019; Koprivnikar et al.  
32 2023), host biomass (de Montaudouin and Stout 2023), host density (Thieltges et al. 2008; Magalhães et al. 2017), and  
33 host fitness (de Montaudouin et al. 1998).

34 Besides, mean increase of the number of metacercariae per cockle can be hidden by the disappearance of the most  
35 infected cockles, related to cockle parasite-induced mortality (Kennedy 1984; Rousset et al. 1996; Desclaux et al. 2004;  
36 Fredensborg et al. 2004). This decrease in periodic infection was observed for all parasites in all sites.

37 Different species exhibited distinct phenologies in a given site. Some intra-site patterns, however, were discovered. There  
38 was no significant infection by any of the four parasites in OUA between May and September, when temperatures ranged  
39 from 20 to 24 °C, the highest of the year. When the infection patterns of the various trematode species were combined, a  
40 clear seasonal pattern emerged. Between February and April in MZ, no infection was observed for any of the parasite  
41 species, corresponding to temperatures ranging between 15 and 17 °C, the lowest of the year. Similarly, except for rare  
42 and low infection events, there was no infection in Arcachon between January and May, corresponding to temperatures  
43 ranging from 10 to 13 °C, the lowest of the year. *Curtuteria arguinae* and *G. minutus* had comparable phenological  
44 patterns in ARC and MZ. Temperature has been shown to precisely modulate certain mechanisms in the trematode life  
45 cycle, including sporocyst maturation ("minimum development temperature threshold" (Morley and Lewis 2013)),  
46 cercariae emergence (Koprivnikar and Poulin 2009b; de Montaudouin et al. 2016b), cercariae infectivity (Pechenik and  
47 Fried 1995), and so on. Under natural conditions, however, the effect of temperature can be hidden by a plethora of other  
48 factors (Paterson et al. 2023). Temperature tends to play a more "on/off" role in the field, with the intensity of the  
49 infection depending on other habitat-specific factors.

50 In this context, it becomes very challenging to disentangle the various factors involved in the phenological patterns of  
51 trematode/host systems (Selbach and Poulin 2020). As a result, predicting "what could happen" at higher latitudes based

1 on observations at lower latitudes is difficult when comparing the dynamics of these systems across different latitudinal  
2 scales. This problem persists even when multiple host and parasite species are present, because other habitat  
3 characteristics will always vary (Studer et al. 2013). However, most studies suggest that the optimal thermal infection  
4 window for many trematode cercariae in temperate and cold climates is between 15 and 25 °C (Fingerut et al. 2003;  
5 Koprivnikar and Poulin 2009a; de Montaudouin et al. 2016b), even at the most northern latitudes (Nikolaev et al. 2021).  
6 At the scale of our study, our findings show that at lower latitudes (OUA), warmer temperatures inhibited species, with  
7 no inhibition at the lower temperature range, whereas at higher latitudes (MZ and ARC), colder temperatures inhibited  
8 species with no inhibition at the higher temperature range. Further to that, our understanding of parasite adaptation to  
9 global change is still limited (Studer and Poulin 2014; de Montaudouin et al. 2016a). Given the complexity of trematode  
10 life cycles, the ecosystem scale appears to be the best scale for analyzing their phenological patterns at this point, with  
11 different trematode species exhibiting varying phenologies in the studied ecosystems. Comparisons between ecosystems,  
12 however, seem to be useful for understanding the plasticity of these parasites when adapted to contrasting environmental  
13 conditions.

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#### 22 **References**

- 23 André C, Jonsson PR, Lindegarth M (1993) Predation on settling bivalve larvae by benthic suspension feeders: the role  
24 of hydrodynamics and larval behaviour. *Mar Ecol Prog Ser* 97:183-192
- 25 Auby I, Trut G, D'Amico F, Beliaeff B (1999) Réseau hydrologique du Bassin d'Arcachon-Synthèse des résultats 1988-  
26 1997, IFREMER, Arcachon.
- 27 Bommarito C, Thieltges DW, Pansch C, Barboza FR, Pranovi F, Wahl M (2021) Effects of first intermediate host  
28 density, host size and salinity on trematode infections in mussels of the south-western Baltic Sea. *Parasitology*  
29 148(4):486-494. <https://doi.org/10.1017/S0031182020002188>
- 30 Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al.  
31 revisited. *J Parasitol* 575-583
- 32 Coen LD, Bishop MJ (2015) The ecology, evolution, impacts and management of host-parasite interactions of marine  
33 molluscs. *J Invertebr Pathol* 131:177-211. <https://doi.org/10.1016/j.jip.2015.08.005>
- 34 Craig TM (1975) The prevalence of bovine parasites in various environments within the lowland tropical country of  
35 Guyana. Dissertation, Texas A & M University
- 36 de Montaudouin X, Grimault S, Grandpierre M, Garenne A (2021) Juvenile growth deficit as an early alert of cockle  
37 *Cerastoderma edule* mortality. *Mar Ecol Prog Ser* 679:85-99. <https://doi.org/10.3354/meps13892>
- 38 de Montaudouin X, Blanchet H, Desclaux-Marchand C, Lavesque N, Bachelet G (2016b) Cockle infection by *Himasthla*  
39 *quissetensis* - I. From cercariae emergence to metacercariae infection. *J Sea Res* 113:99-107.  
40 <https://doi.org/10.1016/j.seares.2015.02.008>
- 41 de Montaudouin X, Blanchet H, Desclaux-Marchand C, Bazairi H, Alfeddy N, Bachelet G (2016a) Cockle infection by  
42 *Himasthla quissetensis* - II. The theoretical effects of climate change. *J Sea Res* 113:108-114.  
43 <http://dx.doi.org/10.1016/j.seares.2014.12.007>



- 1 de Montaudouin X, Biniac C, Lassalle G (2012) Assessing parasite community structure in cockles *Cerastoderma edule*  
2 at various spatio-temporal scales. Estuar Coast Shelf Sci 110:54-60.  
3 <http://dx.doi.org/10.1016/j.ecss.2012.02.005>
- 4 de Montaudouin X, Jensen KT, Desclaux C, Wegeberg AM, Sajus MC (2005) Effect of intermediate host size  
5 (*Cerastoderma edule*) on infectivity of cercariae of *Himasthla quissetensis* (Echinostomatidae: Trematoda). J  
6 Mar Biol Assoc UK 85(4):809-812. <https://doi.org/10.1017/S0025315405011744>
- 7 de Montaudouin X, Wegeberg AM, Jensen KT, Sauriau PG (1998) Infection characteristics of *Himasthla elongata*  
8 cercariae in cockles as a function of water current. Dis Aquat Org 34(1):63-70.
- 9 de Montaudouin X (1996) Factors involved in growth plasticity of cockles *Cerastoderma edule* (L.) identified by field  
10 survey and transplant experiments. J Sea Res 36: 251-265. [https://doi.org/10.1016/S1385-1101\(96\)90794-7](https://doi.org/10.1016/S1385-1101(96)90794-7)
- 11 Desclaux C, de Montaudouin X, Bachelet G (2004) Cockle *Cerastoderma edule* population mortality: role of the  
12 digenean parasite *Himasthla quissetensis*. Mar Ecol Prog Ser 279:141-150.  
13 <https://doi.org/10.3354/meps279141>
- 14 Desclaux C, Russell-Pinto F, de Montaudouin X, Bachelet G (2006) First record and description of metacercariae of  
15 *Curtuteria arguinae* n. sp. (Digenea: Echinostomatidae), parasite of cockles *Cerastoderma edule* (Mollusca:  
16 Bivalvia) in Arcachon Bay, France. J Parasitol 92(3):578-587. <https://doi.org/10.1016/j.ecss.2012.02.005>
- 17 Díaz-Morales DM, Bommarito C, Vajedsamiei J, Grabner DS, Rilov G, Wahl M, Sures B (2022) Heat sensitivity of first  
18 host and cercariae may restrict parasite transmission in a warming sea. Sci Rep 12:1174.  
19 <https://doi.org/10.1038/s41598-022-05139-5>
- 20 Esposito G, Pastorino P, Prearo M (2022) Environmental stressors and pathology of marine molluscs. J Mar Sci Eng  
21 10 :313. <https://doi.org/10.3390/jmse10030313>
- 22 Evans NA (1985) The influence of environmental temperature upon transmission of the cercariae of *Echinostoma liei*  
23 (Digenea: Echinostomatidae). Parasitology 90(2):269-275. <https://doi.org/10.1017/S0031182000050976>
- 24 Fingerut JT, Zimmer CA, Zimmer RK (2003) Patterns and processes of larval emergence in an estuarine parasite system.  
25 Biol Bull 205(2): <https://doi.org/110-120.10.2307/1543232>
- 26 Fortunato H (2015) Mollusks: Tools in environmental and climate research. Am Malacol Bull 33(2):1–15.  
27 <https://doi.org/10.4003/006.033.0208>
- 28 Fredensborg BL, Mouritsen KN, Poulin R (2004) Intensity-dependent mortality of *Paracalliope novizealandiae*  
29 (Amphipoda: Crustacea) infected by a trematode: experimental infections and field observations. J Exp Mar  
30 Biol Ecol 311(2):253-265. <https://doi.org/10.1016/j.jembe.2004.05.011>
- 31 Fredensborg BL, Mouritsen KN, Poulin R (2006) Relating bird host distribution and spatial heterogeneity in trematode  
32 infections in an intertidal snail—from small to large scale. Mar Biol 149:275-283.  
33 <https://doi.org/10.1007/s00227-005-0184-1>
- 34 Gam M (2008) Dynamique des systèmes parasites-hôte, entre trématodes digènes et coque *Cerastoderma edule*:  
35 Comparaison de la lagune de Merja Zerga avec le bassin d'Arcachon. Dissertation, Univ Bordeaux 1
- 36 Gam M, De Montaudouin X, Bazairi H (2009) Do trematode parasites affect cockle (*Cerastoderma edule*) secondary  
37 production and elimination? J Mar Biol Assoc UK 89(7):1395-1402.  
38 <https://doi.org/10.1017/S0025315409000599>
- 39 Gayanilo FC, Sparre P (2005) FAO-ICLARM stock assessment tools II: User's guide. Food & Agriculture Org. Roma.
- 40 Hilmi K, Orbi A, Lakhdar Idrissi J (2009) Hydrodynamisme de la lagune de Oualidia (Maroc) durant l'été et l'automne  
41 2005. Bull Inst Sci Rabat Sect Sci Terre 31:29-34

- 1 Holmstrup M, Bindsbøl A-M, Oostingh GJ, Duschl A, Scheil V, Köhler H-R, Loureiro S, Soares A, Ferreira A, Kienle  
2 C, et al. (2010) Interactions between effects of environmental chemicals and natural stressors: A review. *Sci*  
3 *Total Environ* 408:3746–3762. <https://doi.org/10.1016/j.scitotenv.2009.10.067>
- 4 Kennedy CR (1984) The use of frequency distributions in an attempt to detect host mortality induced by infections of  
5 diplostomatid metacercariae. *Parasitology* 89(2):209-220. <https://doi.org/10.1017/S003118200001244>
- 6 Koprivnikar J, Poulin R (2009b) Interspecific and intraspecific variation in cercariae release. *J Parasitol* 95(1):14-19.  
7 <https://doi.org/10.1645/GE-1582.1>
- 8 Koprivnikar J, Thieltges DW, Johnson PTJ (2023) Consumption of trematode parasite infectious stages: from conceptual  
9 synthesis to future research agenda. *J Helminthol* 97:e33. <https://doi.org/10.1017/S0022149X23000111>
- 10 Koprivnikar J, Poulin R (2009a) Effects of temperature, salinity, and water level on the emergence of marine cercariae.  
11 *Parasitol Res* 105:957-965. <https://doi.org/10.1007/s00436-009-1477-y>
- 12 Kube J, Kube S, Dierschke V (2002) Spatial and temporal variations in the trematode component community of the  
13 mudsnail *Hydrobia ventrosa* in relation to the occurrence of waterfowl as definitive hosts. *J Parasitol*  
14 88(6):1075-1086. [https://doi.org/10.1645/0022-3395\(2002\)088\[1075:SATVIT\]2.0.CO;2](https://doi.org/10.1645/0022-3395(2002)088[1075:SATVIT]2.0.CO;2)
- 15 Labbardi H, Ettahiri O, Lazar S, Massik Z, El Antri S (2005) Etude de la variation spatio-temporelle des paramètres  
16 physico-chimiques caractérisant la qualité des eaux d'une lagune côtière et ses zonations écologiques: cas de  
17 Moulay Bousselham, Maroc. *C R Geoscience* 337:504-514.
- 18 Lauckner G (1983) Diseases of mollusca: bivalvia. In: Kinne O. (Ed) *Diseases of Marine Animals*, Vol. 2. John Wiley &  
19 Sons, Chichester New York Brisbane Toronto.
- 20 Levin LA, Boesch DF, Covich A, Dahm C, Erseus C, Ewel KC, Kneib RT, Moldenke A, Palmer MA, Snelgrove P,  
21 Strayer D, Weslawski JM (2001) The function of marine critical transition zones and the importance of  
22 sediment biodiversity. *Ecosystems* 4(5):430–451. <https://doi.org/10.1007/s10021-001-0021-4>
- 23 Lo CT, Lee KM (1996) *Cercaria kuntzi* n. sp. (Trematoda) from *Oncomelania hupensis formosana*, its Metacercariae and  
24 chromosomes. *Zool Stud-Taipei* 35:255-260.
- 25 MacKenzie K, Williams HH, Williams B, McVicar AH, Siddall R (1995) Parasites as indicators of water quality and the  
26 potential use of helminth transmission in marine pollution studies. *Adv Parasitol* 35:85-144.  
27 [https://doi.org/10.1016/s0065-308x\(08\)60070-6](https://doi.org/10.1016/s0065-308x(08)60070-6)
- 28 Magalhães L, Freitas R, Dairain A, De Montaudouin X (2017) Can host density attenuate parasitism? *J Mar Biol Assoc*  
29 *UK* 97(3):497-505. <https://doi.org/10.1017/S0025315416001107>
- 30 Makaoui A, Idrissi M, Agouzouk A, Larissi J, Baibai T, El Ouehabi Z, Ait Laamel M, Bessa I, Ettahiri O, Hilmi K  
31 (2018) Etat océanographique de la lagune de Oualidia, Maroc (2011-2012). *Eur Sci J* 14(18) :93.  
32 <https://doi.org/10.19044/esj.2018.v14n18p93>
- 33 Malham SK, Hutchinson TH, Longshaw M (2012) A review of the biology of European cockles (*Cerastoderma* spp.). *J*  
34 *Mar Biol Assoc UK* 92(7):1563-1577. <https://doi.org/10.1017/S0025315412000355>
- 35 Marcogliese DJ (2008) The impact of climate change on the parasites and infectious diseases of aquatic animals. *Rev Sci*  
36 *Tech* 27(2):467-484
- 37 Marcogliese DJ (2001) Implications of climate change for parasitism of animals in the aquatic environment. *Can J Zool*  
38 79(8):1331-1352. <https://doi.org/10.1139/z01-067>
- 39 Mas-Coma S, Valero MA, Bargues MD (2009) Climate change effects on trematodiasis, with emphasis on zoonotic  
40 fascioliasis and schistosomiasis. *Vet Parasitol* 163(4):264-80. <https://doi.org/10.1016/j.vetpar.2009.03.024>

- 1 Moore ME, Alston MA, Kingsolver JG (2023) Behavioral thermoregulation of caterpillars is altered by temperature, but  
2 not parasitism: An empirical field study. *Ecosphere* 14(6):e4578. <https://doi.org/10.1002/ecs2.4578>
- 3 Morley NJ, Lewis JW (2013) Thermodynamics of cercarial development and emergence in trematodes. *Parasitology*  
4 140(10):1211-1224. <https://doi.org/10.1017/S0031182012001783>
- 5 Morley NJ, Irwin SWB, Lewis JW (2003) Pollution toxicity to the transmission of larval digeneans through their  
6 molluscan hosts. *Parasitology* 126(7):S5-S26. <https://doi.org/10.1017/S0031182003003755>
- 7 Mouritsen KN, McKechnie S, Meenken E, Toynbee JL, Poulin R (2003) Spatial heterogeneity in parasite loads in the  
8 New Zealand cockle: the importance of host condition and density. *J Mar Biol Assoc UK* 83(2):307-310.  
9 <https://doi.org/10.1017/S0025315403007124h>
- 10 Mouritsen KN, Poulin R (2002) Parasitism, community structure and biodiversity in intertidal ecosystems. *Parasitology*  
11 124(7):101-117. <https://doi.org/10.1017/S0031182002001476>
- 12 Mouritsen KN, Jensen KT (1997) Parasite transmission between soft-bottom invertebrates: temperature mediated  
13 infection rates and mortality in *Corophium volutator*. *Mar Ecol Prog Ser* 151:123-134.
- 14 Mouritsen KN, Jensen KT (1994) The enigma of gigantism: effect of larval trematodes on growth, fecundity, egestion  
15 and locomotion in *Hydrobia ulvae* (Pennant) (Gastropoda: Prosobranchia). *J Exp Mar Biol Ecol* 181(1):53-66.  
16 [https://doi.org/10.1016/0022-0981\(94\)90103-1](https://doi.org/10.1016/0022-0981(94)90103-1)
- 17 Nikolaev KE, Levakin IA, Galaktionov KV (2021) A month for the mission: using a sentinel approach to determine the  
18 transmission window of digenean cercariae in the subarctic White Sea. *J Helminthol* 95:e50.  
19 <https://doi.org/10.1017/S0022149X21000456>
- 20 Paterson RA, Poulin R, Selbach C (2023) Global analysis of seasonal changes in trematode infection levels reveals weak  
21 and variable link to temperature. *Oecologia* 204:373-378. <https://doi.org/10.1007/s00442-023-05408-8>
- 22 Pechenik JA, Fried B (1995) Effect of temperature on survival and infectivity of *Echinostoma trivolvis* cercariae: a test of  
23 the energy limitation hypothesis. *Parasitology* 111(3):373-378. <https://doi.org/10.1017/S0031182000081920>
- 24 Poulin R (2006) Global warming and temperature-mediated increases in cercarial emergence in trematode parasites.  
25 *Parasitology* 132(1):143-151. <https://doi.org/10.1017/S0031182005008693>
- 26 Riisgård HU (2001) On measurement of filtration rates in bivalves—the stony road to reliable data: review and  
27 interpretation. *Mar Ecol Prog Ser* 211:275-291. <https://doi.org/10.3354/meps211275>
- 28 Richard A, Maire O, Daffe G, Magalhães L, de Montaudouin X (2022) *Himasthla* spp.(Trematoda) in the edible cockle  
29 *Cerastoderma edule*: review, long-term monitoring and new molecular insights. *Parasitology* 149(7):878-892.  
30 <https://doi.org/10.1017/S0031182022000373>
- 31 Rousset F, Thomas F, De Meeus T, Renaud F (1996) Inference of parasite-induced host mortality from distributions of  
32 parasite loads. *Ecology* 77(7):2203-2211. <https://doi.org/10.2307/2265713>
- 33 Selbach C, Poulin R (2020) Some like it hotter: trematode transmission under changing temperature conditions.  
34 *Oecologia* 194(4):745-755. <https://doi.org/10.1007/s00442-020-04800-y>
- 35 Shostak AW, Esch GW (1990) Temperature effects on survival and excystment of cercariae of *Halipegus occidualis*  
36 (Trematoda). *Int J Parasitol* 20(1):95-99
- 37 Stout L, Garenne A, de Montaudouin X (2022) Marine trematode parasites as indicators of environmental changes. *Ecol*  
38 *Indic* 141:109089. <https://doi.org/10.1016/j.ecolind.2022.109089>
- 39 Studer A, Poulin R (2014) Analysis of trait mean and variability versus temperature in trematode cercariae: is there scope  
40 for adaptation to global warming? *Int J Parasitol* 44(6):403-413. <https://doi.org/10.1016/j.ijpara.2014.02.006>

- 1 Studer A, Widmann M, Poulin R, Krkošek M (2013) Large scale patterns of trematode parasitism in a bivalve host: no  
2 evidence for a latitudinal gradient in infection levels. *Mar Ecol Prog Ser* 491:125-135.  
3 <https://doi.org/10.3354/meps10483>
- 4 Thieltges DW, Engelsma MY, Wendling CC, Wegner KM (2013) Parasites in the Wadden Sea food web. *J Sea Res*  
5 82:122-133. <https://doi.org/10.1016/j.seares.2012.06.002>
- 6 Thieltges DW, Bordalo MD, Hernández AC, Prinz K, Jensen KT (2008) Ambient fauna impairs parasite transmission in  
7 a marine parasite-host system. *Parasitology* 135(9):1111-1116. <https://doi.org/10.1017/S0031182008004526>
- 8 Thieltges DW, Reise K (2007) Spatial heterogeneity in parasite infections at different spatial scales in an intertidal  
9 bivalve. *Oecologia* 150:569-581. <https://doi.org/10.1007/s00442-006-0557-2>
- 10 Thieltges DW, Reise K (2006) Metazoan parasites in intertidal cockles *Cerastoderma edule* from the northern Wadden  
11 Sea. *J Sea Res* 56(4):284-293. <https://doi.org/10.1016/j.seares.2006.06.002>
- 12 Thieltges DW, Rick J (2006) Effect of temperature on emergence, survival and infectivity of cercariae of the marine  
13 trematode *Renicola roscovita* (Digenea: Rencolidae). *Dis Aquat Org* 73(1):63-68.
- 14 Turner HM (1985) Parasites of eastern oysters from subtidal reefs in a Louisiana estuary with a note on their use as  
15 indicators of water quality. *Estuaries* 8:323-325.
- 16 Verdelhos T, Marques JC, Anastácio P (2015) Behavioral and mortality responses of the bivalves *Scrobicularia plana*  
17 and *Cerastoderma edule* to temperature, as indicator of climate change's potential impacts. *Ecol Indic* 58:95-  
18 103. <https://doi.org/10.1016/j.ecolind.2015.05.042>
- 19 Vielma S, Lagrue C, Poulin R, Selbach C (2019) Non-host organisms impact transmission at two different life stages in a  
20 marine parasite. *Parasitol Res* 118:111-117. <https://doi.org/10.1007/s00436-018-6121-2>
- 21

1 **Figures caption**

2  
3 **Figure 1.** Geographical distribution of the three sampling stations at Arcachon bay (a) (France), Merja Zerga (b)  
4 (Morocco) and Oualidia (c) lagoons (Morocco).

5  
6 **Figure 2.** Growth curve (shell length =  $f(\text{date})$ ) of the different cohorts in the different sites (ARC = Arcachon, MZ =  
7 Merja Zerga, OUA = Oualidia).

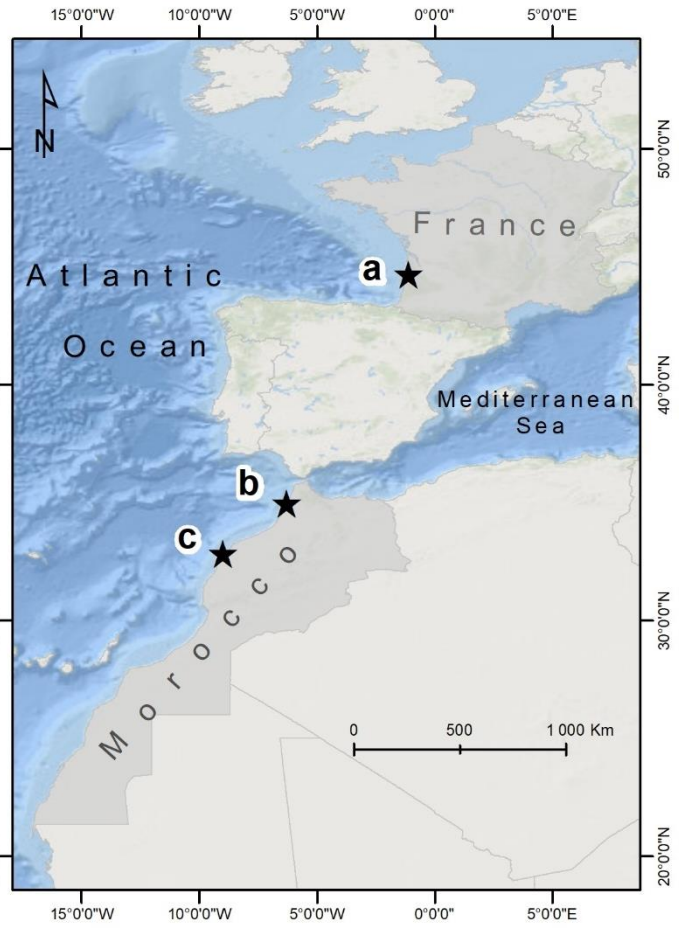
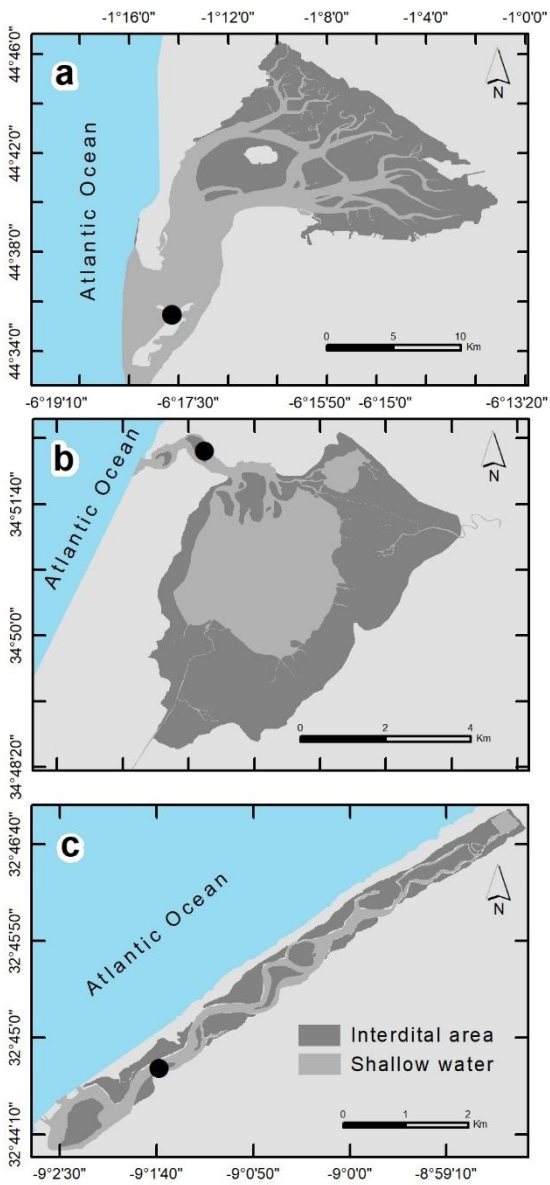
8  
9 **Figure 3. (a)** Boxplots of *H. quissetensis* abundance per cockle per month, for each site and each cohort. The box (25–  
10 75% of the data) contains a black line (median). Whiskers represent the lower and upper values in the range of  $\pm 1.5$   
11 interquartile range, with outliers as black circles. Arrows indicate significant variation between successive months  
12 (Mann-Whitney U test,  $p < 0.05$ , performed when the infection was sufficient (see material and methods). **(b)** Monthly  
13 mean temperature for each site, the dashed lines delimiting a non-infection period for all parasite species.

14  
15 **Figure 4. (a)** Boxplots of *H. interrupta* abundance per cockle per month, for each site and each cohort. The box (25–75%  
16 of the data) contains a black line (median). Whiskers represent the lower and upper values in the range of  $\pm 1.5$   
17 interquartile range, with outliers as black circles. Arrows indicate significant variation between successive months  
18 (Mann-Whitney U test,  $p < 0.05$ , performed when the infection was sufficient (see material and methods). **(b)** Monthly  
19 mean temperature for each site, the dashed lines delimiting a non-infection period for all parasite species.

20  
21 **Figure 5. (a)** Boxplots of *C. arguinae* abundance per cockle per month, for each site and each cohort. The box (25–75%  
22 of the data) contains a black line (median). Whiskers represent the lower and upper values in the range of  $\pm 1.5$   
23 interquartile range, with outliers as black circles. Arrows indicate significant variation between successive months  
24 (Mann-Whitney U test,  $p < 0.05$ , performed when the infection was sufficient (see material and methods). **(b)** Monthly  
25 mean temperature for each site, the dashed lines delimiting a non-infection period for all parasite species.

26  
27 **Figure 6. (a)** Boxplots of *G. minutus* abundance per cockle per month, for each site and each cohort. The box (25–75%  
28 of the data) contains a black line (median). Whiskers represent the lower and upper values in the range of  $\pm 1.5$   
29 interquartile range, with outliers as black circles. Arrows indicate significant variation between successive months  
30 (Mann-Whitney U test,  $p < 0.05$ , performed when the infection was sufficient (see material and methods). **(b)** Monthly  
31 mean temperature for each site, the dashed lines delimiting a non-infection period for all parasite species.

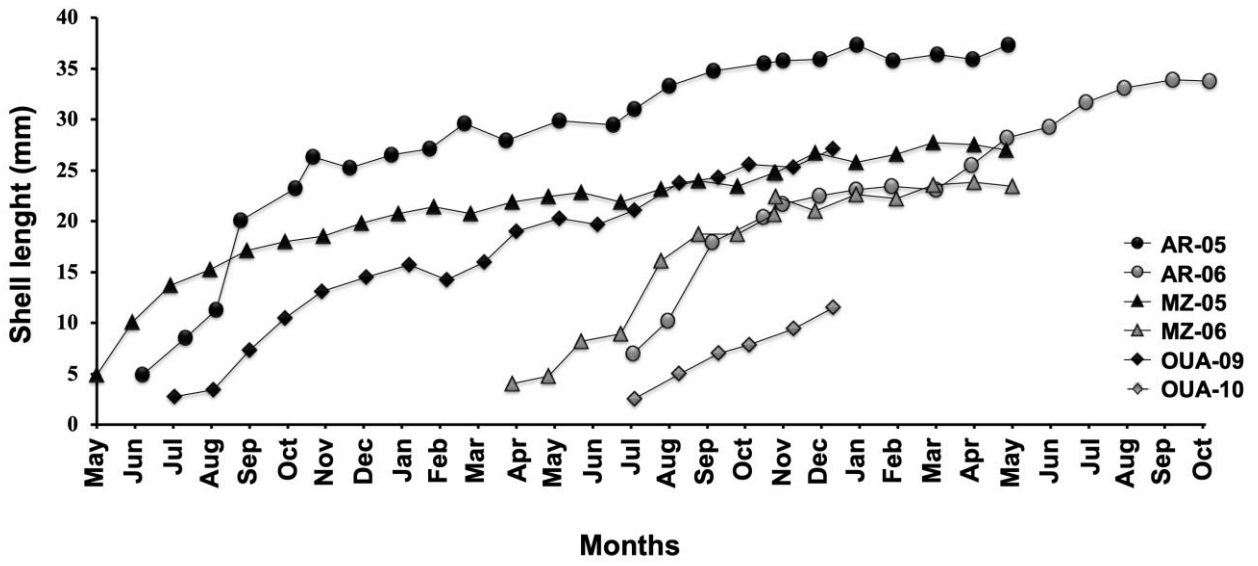
1 **Figure 1**  
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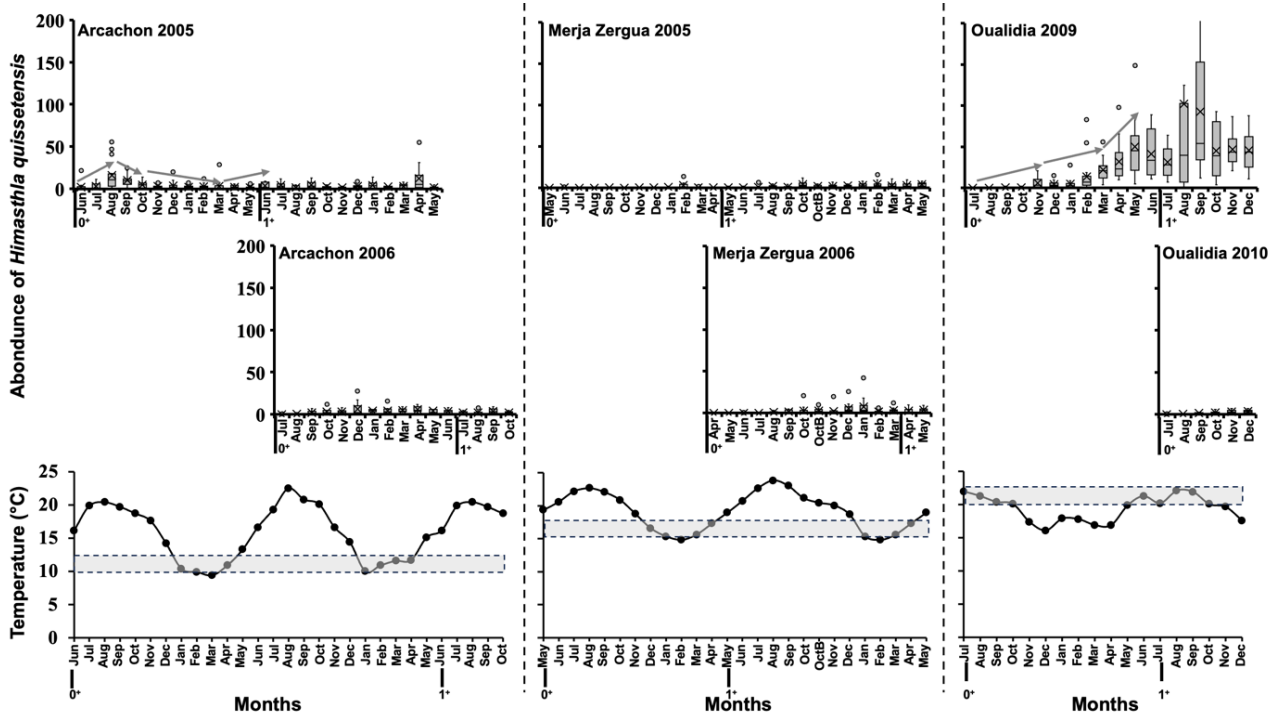
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Figure 3.

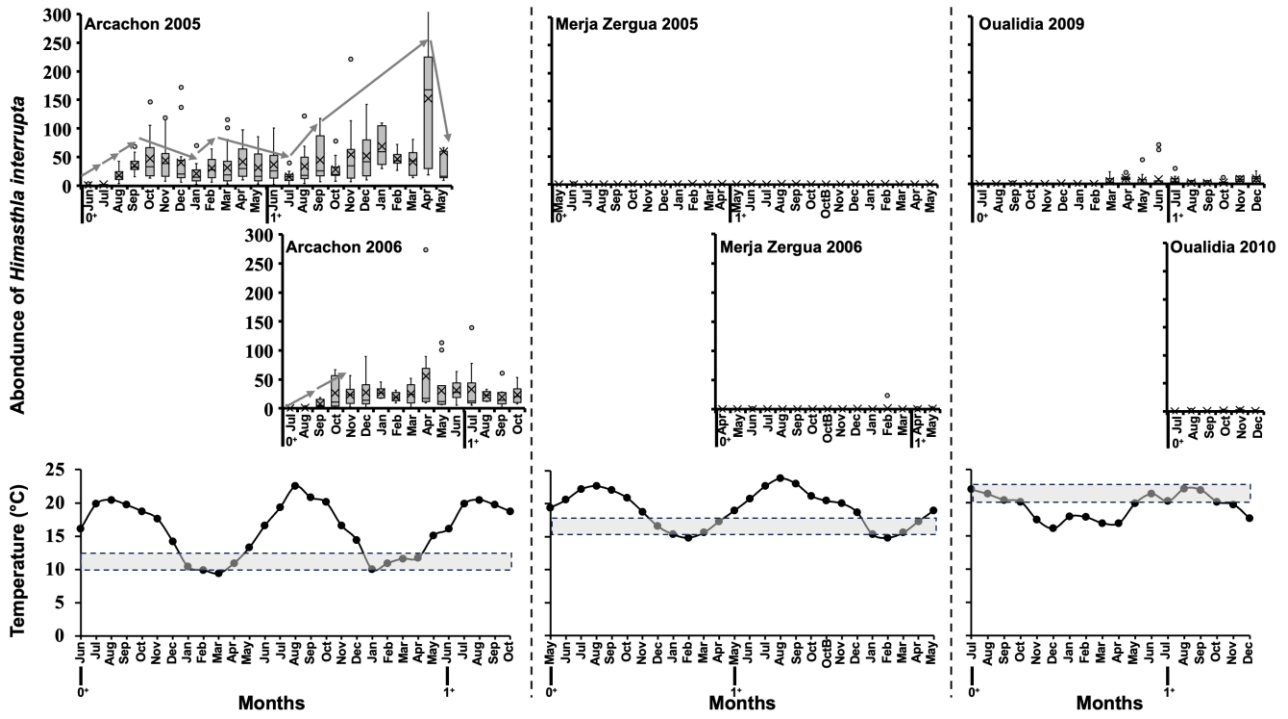


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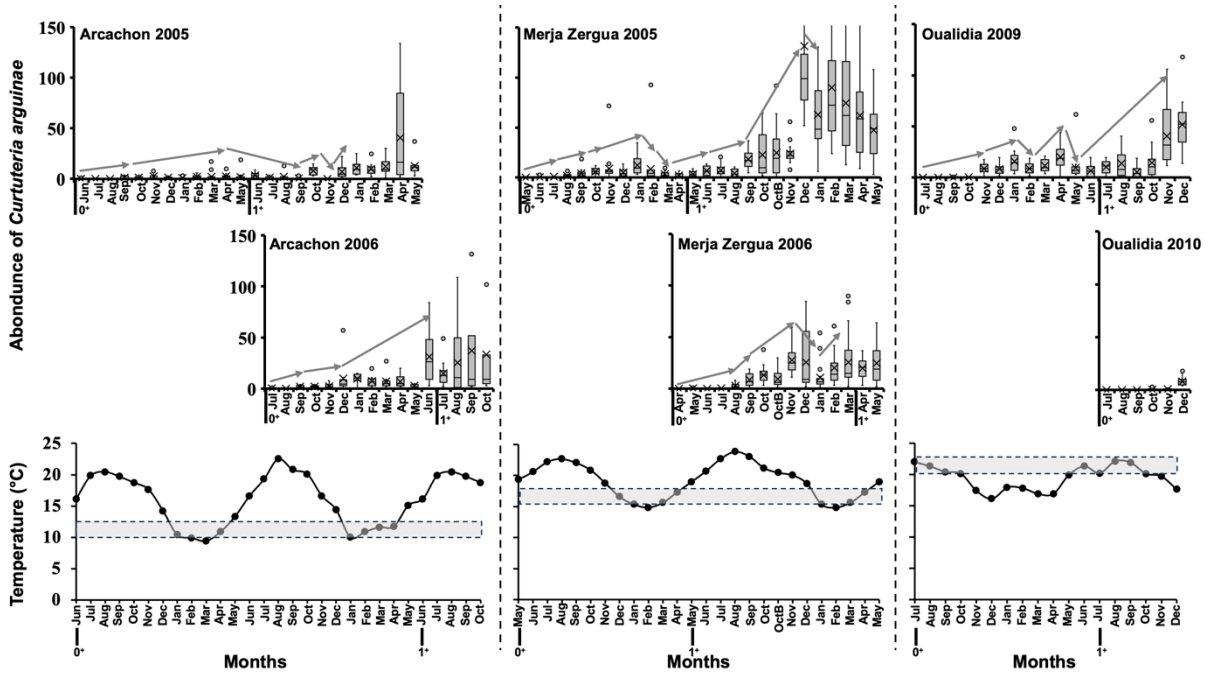
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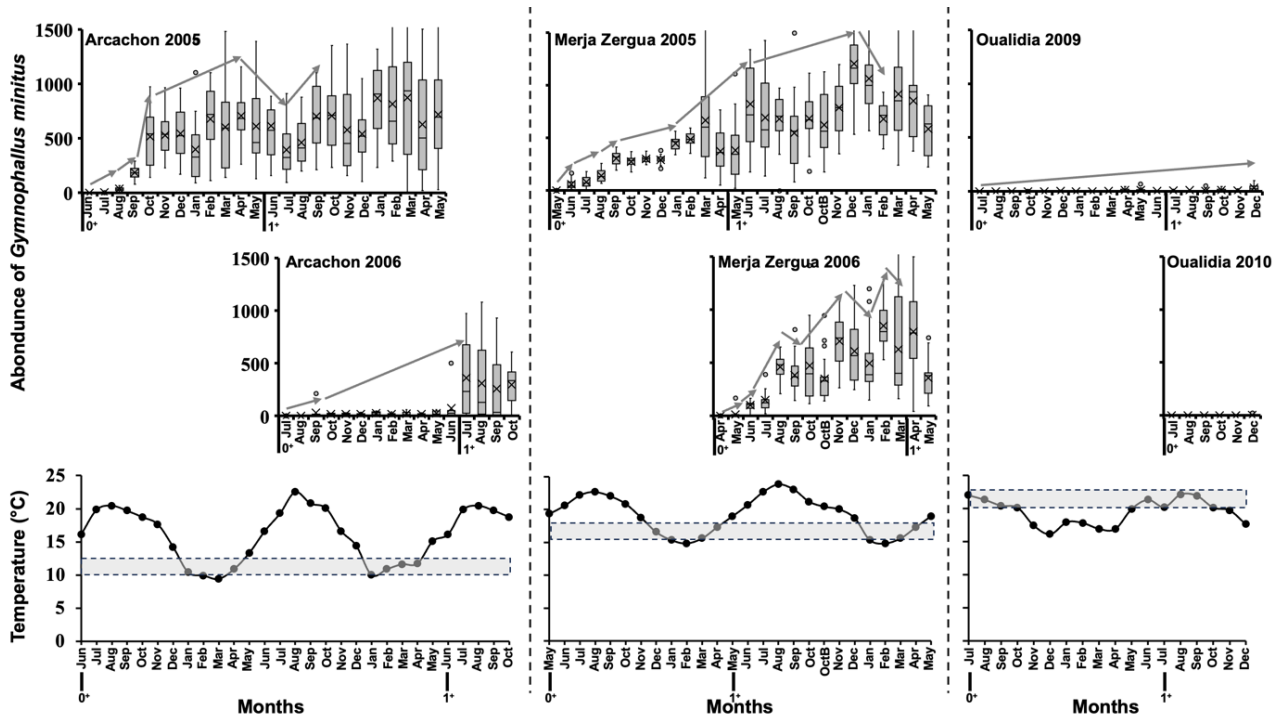
Figure 5.



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Figure 6.



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1 **Tables Caption**

2

3 **Table 1.** Trematode species which appeared in this study, their life-cycle and the percentage of metacercariae in  
4 *Cerastoderma edule* in each cohort and study site. ARC = Arcachon, OUA = Oualidia, MZ = Merja Zerga.

5

6 **Table 2.** Spearman coefficient (R) of the correlation between metacercariae median abundance for the different  
7 trematode species in cockles and three variables, sea temperature, percentage of darkness per day and individual cockle  
8 biomass (ARC = Arcachon, OUA = Oualidia, MZ = Merja Zerga, cohorts 2005, 2006 and 2009 according to sites). *p*-  
9 value is compared to 0.050/14 (Bonferroni correction). Significant results ( $p < 0.0036$ ) are in bold.

10

11 **Table 3.** Spearman coefficient (R) of the correlation 1) between *Curtuteria arguinae* (Ca) and *Gymnophallus minutus*  
12 (Gm) metacercariae median abundance in each cockle cohort, in each site and 2) between each site (using the longest  
13 cockle cohort in terms of monitoring, i.e. ARC-05, MZ-05 and OUA-09) for the two same trematode species (Ca and  
14 Gm) (ARC = Arcachon, OUA = Oualidia, MZ = Merja Zerga, cohorts 2005, 2006 and 2009 according to sites). *p*-value  
15 is compared to 0.050/11 (Bonferroni correction). Significant results ( $p$ -value  $< 0.0045$ ) are in bold.

1 **Table 1.**  
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		<i>% percentage of metacercariae</i>						
	<b>1st int. host</b>	<b>Final host</b>	<b>AR-05</b>	<b>AR-06</b>	<b>MZ-05</b>	<b>MZ-06</b>	<b>OUA-09</b>	<b>OUA-10</b>
<i>Himasthla quissetensis</i>	<i>Littorina littorea</i>	Birds	0,8	2,5	0,3	0,5	54,5	38,0
<i>Himasthla interrupta</i>	<i>Hydrobia ulvae</i>	Birds	6,8	17,5	0,0	0,1	7,1	17,9
<i>Curtuteria arguinae</i>	?	Birds	0,7	8,9	4,3	2,8	24,8	31,4
<i>Gymnophallus minutus</i>	<i>Scrobularia plana</i>	Birds	91,1	68,9	95,1	96,4	12,2	12,2
<i>Psilostomum brevicolle</i>	<i>Hydrobia ulvae</i>	Birds	0,5	1,2	0,0	0,0	0,3	0,2
<i>Diptherostomum brusinae</i>	<i>Nassarius reticulatus</i>	Fish	0,2	1,1	0,2	0,1	1,1	0,3

3 ARC = Arcachon, OUA = Oualidia, MZ = Merja Zerga  
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1 **Table 2.**  
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<b>Species</b>	<b>Site/cohort</b>	<b>N</b>	<b>Variable</b>	<b>R</b>	<b>p</b>	
<i>H. quissetensis</i>	<b>ARC-05</b>	24	Temperature	0.12	0.5911	
			Darkness	0.23	0.2767	
			Biomass	0.06	0.7714	
	<b>OUA-09</b>	18	Temperature	-0.00	0.9934	
			Darkness	-0.04	0.8896	
			<b>Biomass</b>	<b>0.92</b>	<b>&lt;0.0001</b>	
<i>H. interrupta</i>	<b>ARC-05</b>	24	Temperature	-0.24	0.2670	
			Darkness	0.53	0.0082	
			Biomass	0.51	0.0100	
	<b>ARC-06</b>	16	Temperature	-0.46	0.0723	
			Darkness	0.23	0.3823	
			Biomass	0.48	0.0578	
	<i>C. arguinae</i>	<b>ARC-05</b>	24	Temperature	-0.51	0.0105
				Darkness	0.24	0.2560
				<b>Biomass</b>	<b>0.69</b>	<b>0.0002</b>
<b>ARC-06</b>		16	Temperature	-0.07	0.8066	
			Darkness	-0.17	0.5251	
			<b>Biomass</b>	<b>0.81</b>	<b>0.0002</b>	
<b>MZ-05</b>		25	Temperature	-0.32	0.1214	
			<b>Darkness</b>	<b>0.58</b>	<b>0.0022</b>	
			<b>Biomass</b>	<b>0.86</b>	<b>&lt;0.0001</b>	
<b>MZ-06</b>		15	Temperature	-0.35	0.1950	
			Darkness	0.48	0.0707	
			<b>Biomass</b>	<b>0.86</b>	<b>&lt;0.0001</b>	
<b>OUA-09</b>		18	Temperature	-0.54	0.0199	
			Darkness	0.36	0.1381	
			<b>Biomass</b>	<b>0.65</b>	<b>0.0037</b>	
<i>G. minutus</i>	<b>ARC-05</b>	24	Temperature	-0.40	0.0522	
			Darkness	0.36	0.0847	
			<b>Biomass</b>	<b>0.59</b>	<b>0.0022</b>	
	<b>ARC-06</b>	16	Temperature	0.19	0.4876	
			Darkness	-0.11	0.6914	
			<b>Biomass</b>	<b>0.83</b>	<b>&lt;0.0001</b>	
	<b>MZ-05</b>	25	Temperature	-0.29	0.1553	
			Darkness	0.34	0.0940	
			<b>Biomass</b>	<b>0.93</b>	<b>&lt;0.0001</b>	
	<b>MZ-06</b>	15	Temperature	-0.32	0.2451	
			Darkness	0.58	0.0235	
			<b>Biomass</b>	<b>0.74</b>	<b>0.0016</b>	
	<b>OUA-09</b>	18	<b>Temperature</b>	<b>-0.66</b>	<b>0.0029</b>	
			Darkness	0.21	0.4046	
			Biomass	0.18	0.4775	

3 ARC = Arcachon, OUA = Oualidia, MZ = Merja Zerga, cohorts 2005, 2006 and 2009 according to sites. *p*-value is  
4 compared to 0.050/14 (Bonferroni correction). Significant results (*p* < 0.0036) are in bold.  
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1 **Table 3.**  
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	<b>Survey</b>	<b>N</b>	<b>R</b>	<b><i>p</i></b>
<i>Ca</i>	<b>ARC/MZ</b>	<b>25</b>	<b>0.58</b>	<b>0.0022</b>
	ARC/OUA	19	0.31	0.1987
	<b>MZ/OUA</b>	<b>19</b>	<b>0.64</b>	<b>0.0031</b>
<i>Gm</i>	<b>ARC/MZ</b>	<b>25</b>	<b>0.56</b>	<b>0.0038</b>
	ARC/OUA	19	0.03	0.8969
	MZ/OUA	19	0.00	1.0000
<i>Ca vs. Gm</i>	<b>ARC-05</b>	<b>22</b>	<b>0.74</b>	<b>0.0014</b>
	ARC-06	14	0.70	0.0057
	<b>MZ-05</b>	<b>24</b>	<b>0.78</b>	<b>&lt;0.0001</b>
	<b>MZ-06</b>	<b>14</b>	<b>0.75</b>	<b>0.0020</b>
	OUA-09	15	0.37	0.1779

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4 ARC = Arcachon, OUA = Oualidia, MZ = Merja Zerga, cohorts 2005, 2006 and 2009 according to sites). *p*-value is  
5 compared to 0.050/11 (Bonferroni correction). Significant results (*p*-value < 0.0045) are in bold.  
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