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

Nazik Alfeddy[1,*], Hocein Bazairi[1,2], Mériame Gam[1,3], Xavier de Montaudouin[3]

[1] Mohammed V University in Rabat, Faculty of Sciences, Laboratory of Biodiversity, Ecology and Genome, 4 Avenue Ibn Battouta, B.P. 1014 RP, Rabat, Morocco
[2] Natural Sciences and Environment Research Hub, University of Gibraltar, Europa Point Campus, Gibraltar
[3] Université de Bordeaux, CNRS, EPOC, EPHE, UMR 5805, Station Marine, 2 rue du Pr Jolyet, 33120 Arcachon, France

* Correspondence: nazik_alfeddy@um5.ac.ma

Authors Orcid ID:
(NA) 0000-0003-2972-7652
(HB) 0000-0002-1788-0580

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

Declarations

Funding: This study was partly financed jointly by CNRS (France) and CNRST (Morocco). Gam M. was granted a CNRST-Morocco excellence scholarship.

Conflicts of interest: The authors declare that they have no conflict of interest.

Competing interests: The authors declare that they have no competing interests

Ethics approval: This article does not contain any studies with animals performed by any of the authors.

Consent to participate: Not applicable**.**

Consent for publication: Not applicable

Availability of data and material: Not Data sharing not applicable to this article as no datasets were generated or analyzed during the current study.

Code availability: Not applicable

Authors' Contributions: Nazik Alfeddy: Investigation, data curation, writing – original draft, visualization. **Hocein Bazairi:** Conceptualization, methodology, data curation, writing – original draft, review & editing, supervision. **Mériame Gam:** Investigation, data curation, review. **Xavier de Montaudouin:** Conceptualization, methodology, investigation, data curation, writing – original draft, review & editing, supervision.

Introduction

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

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

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

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

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

Materials and Methods

Study sites

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

Arcachon Bay is a macrotidal lagoon on the Atlantic coast of southwest France. The lagoon is characterized by semi-diurnal tides with amplitudes ranging from 0.9 to 4.9 meters, and significant water exchange with the ocean via its south-western inlet. Cockles were collected at Banc d'Arguin (44.60°N, 1.25°W), with an annual mean surface water 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 population settles on sands with a median grain size of 350 µm (de Montaudouin 1996).

The second station is located at Merja Zerga (34.87°N, 6.28°W), a shallow lagoon of 37 km², in Morocco. Salinity in this lagoon fluctuates between 8 and 36 (Labbardi et al. 2005), with mean water temperature varying between 14.6 and 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 the station is characterized by a median grain size of around 300 µm.

Finally, the third sampling station is located downstream of the Oualidia lagoon (32.74°N, 9.02°W), in Morocco. This macrotidal lagoon is 7 km long and 0.5 km wide, covering a total area of 3.5 km². Water is exchanged with the ocean via 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 (Hilmi et al. 2005). The average water temperature ranges from 16.1 to 21.1 °C, and the lagoon's salinity varies between 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 established on fine sands with a median grain size of 260 µm.

Sampling process and data collection

Host (cockles)

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

Parasites (trematodes)

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

Data analysis

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

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

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

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

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

with d = number of days after spring equinox;

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

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

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

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

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

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

Results

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

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

Phenology of *Himasthla quissetensis*

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. quissetensis* prevalent enough to study its phenology. In ARC-05, the abundance of *H. quissetensis* was low (median < 11 metacercariae per cockle) and was not correlated with temperature, darkness duration (i.e., seasons) and cockle individual biomass (i.e., cockle size) **(Table 2)**. The first and only significant peak of infection occurred in August (20 °C), when the length of the cockle shell reached 11 mm. This was followed by a decrease in infection in October and a low-noise variation over the remainder of the cohort's lifespan.

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

Phenology of *Himasthla interrupta*

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

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

Phenology of *Curtuteria arguinae*

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

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

Phenology of *Gymnophallus minutus*

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

Discussion

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

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

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

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

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

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

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

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

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

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

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

Acknowledgements.

The authors are very thankful to the Editor and to an anonymous reviewer for their helpful comments. This study was partly financed jointly by CNRS (France) and CNRST (Morocco). We thank Dr Meriem Chahbi for reading and correcting the manuscript. Sampling in Arcachon Bay was performed thanks to Planula 4 vessels (CNRS-INSU, Flotte Océanographique Française) and its staff. We also thank the staff of SEPANSO in charge of the management of Banc d'Arguin's National Natural Reserve. Authors are grateful to local fishers for their help in sampling at Merja Zerga and Oualidia lagoons. Ms. Gam M. was granted a CNRST-Morocco excellence scholarship.

References

André C, Jonsson PR, Lindegarth M (1993) Predation on settling bivalve larvae by benthic suspension feeders: the role of hydrodynamics and larval behaviour. Mar Ecol Prog Ser 97:183-192

Auby I, Trut G, D'Amico F, Beliaeff B (1999) Réseau hydrologique du Bassin d'Arcachon-Synthèse des résultats 1988-1997, IFREMER, Arcachon.

Bommarito C, Thieltges DW, Pansch C, Barboza FR, Pranovi F, Wahl M (2021) Effects of first intermediate host density, host size and salinity on trematode infections in mussels of the south-western Baltic Sea. Parasitology 148(4):486-494. https://doi.org/10.1017/S0031182020002188

Bush AO, Lafferty KD, Lotz JM, Shostak AW (1997) Parasitology meets ecology on its own terms: Margolis et al. revisited. J Parasitol 575-583

Coen LD, Bishop MJ (2015) The ecology, evolution, impacts and management of host–parasite interactions of marine molluscs. J Invertebr Pathol 131:177-211. https://doi.org/10.1016/j.jip.2015.08.005

Craig TM (1975) The prevalence of bovine parasites in various environments within the lowland tropical country of Guyana. Dissertation, Texas A & M University

de Montaudouin X, Grimault S, Grandpierre M, Garenne A (2021) Juvenile growth deficit as an early alert of cockle *Cerastoderma edule* mortality. Mar Ecol Prog Ser 679:85-99. https://doi.org/10.3354/meps13892

de Montaudouin X, Blanchet H, Desclaux-Marchand C, Lavesque N, Bachelet G (2016b) Cockle infection by *Himasthla quissetensis* - I. From cercariae emergence to metacercariae infection. J Sea Res 113:99-107. https://doi.org/10.1016/j.seares.2015.02.008

de Montaudouin X, Blanchet H, Desclaux-Marchand C, Bazairi H, Alfeddy N, Bachelet G (2016a) Cockle infection by *Himasthla quissetensis* - II. The theoretical effects of climate change. J Sea Res 113:108-114. http://dx.doi.org/10.1016/j.seares.2014.12.007

de Montaudouin X, Binias C, Lassalle G (2012) Assessing parasite community structure in cockles *Cerastoderma edule* at various spatio-temporal scales. Estuar Coast Shelf Sci 110:54-60. http://dx.doi.org/10.1016/j.ecss.2012.02.005

de Montaudouin X, Jensen KT, Desclaux C, Wegeberg AM, Sajus MC (2005) Effect of intermediate host size (*Cerastoderma edule*) on infectivity of cercariae of *Himasthla quissetensis* (Echinostomatidae: Trematoda). J Mar Biol Assoc UK 85(4):809-812. https://doi.org/10.1017/S0025315405011744

de Montaudouin X, Wegeberg AM, Jensen KT, Sauriau PG (1998) Infection characteristics of *Himasthla elongata* cercariae in cockles as a function of water current. Dis Aquat Org 34(1):63-70.

de Montaudouin X (1996) Factors involved in growth plasticity of cockles *Cerastoderma edule* (L.) identified by field survey and transplant experiments. J Sea Res 36: 251-265. https://doi.org/10.1016/S1385-1101(96)90794-7

Desclaux C, de Montaudouin X, Bachelet G (2004) Cockle *Cerastoderma edule* population mortality: role of the digenean parasite *Himasthla quissetensis*. Mar Ecol Prog Ser 279:141-150. https://doi.org/10.3354/meps279141

Desclaux C, Russell-Pinto F, de Montaudouin X, Bachelet G (2006) First record and description of metacercariae of *Curtuteria arguinae* n. sp. (Digenea: Echinostomatidae), parasite of cockles *Cerastoderma edule* (Mollusca: Bivalvia) in Arcachon Bay, France. J Parasitol 92(3):578-587. https://doi.org/10.1016/j.ecss.2012.02.005

Díaz-Morales DM, Bommarito C, Vajedsamiei J, Grabner DS, Rilov G, Wahl M, Sures B (2022) Heat sensitivity of first host and cercariae may restrict parasite transmission in a warming sea. Sci Rep 12:1174. https://doi.org/10.1038/s41598-022-05139-5

Esposito G, Pastorino P, Prearo M (2022) Environmental stressors and pathology of marine molluscs. J Mar Sci Eng 10 :313. https://doi.org/10.3390/jmse10030313

Evans NA (1985) The influence of environmental temperature upon transmission of the cercariae of *Echinostoma liei* (Digenea: Echinostomatidae). Parasitology 90(2):269-275. https://doi.org/10.1017/S0031182000050976

Fingerut JT, Zimmer CA, Zimmer RK (2003) Patterns and processes of larval emergence in an estuarine parasite system. Biol Bull 205(2): https://doi.org/110-120. 10.2307/1543232

Fortunato H (2015) Mollusks: Tools in environmental and climate research. Am Malacol Bull 33(2):1–15. https://doi.org/10.4003/006.033.0208

Fredensborg BL, Mouritsen KN, Poulin R (2004) Intensity-dependent mortality of *Paracalliope novizealandiae* (Amphipoda: Crustacea) infected by a trematode: experimental infections and field observations. J Exp Mar Biol Ecol 311(2):253-265. https://doi.org/10.1016/j.jembe.2004.05.011

Fredensborg BL, Mouritsen KN, Poulin R (2006) Relating bird host distribution and spatial heterogeneity in trematode infections in an intertidal snail—from small to large scale. Mar Biol 149:275-283. https://doi.org/10.1007/s00227-005-0184-1

Gam M (2008) Dynamique des systèmes parasites-hote, entre trématodes digènes et coque *Cerastoderma edule*: Comparaison de la lagune de Merja Zerga avec le bassin d'Arcachon. Dissertation, Univ Bordeaux 1

Gam M, De Montaudouin X, Bazairi H (2009) Do trematode parasites affect cockle (*Cerastoderma edule*) secondary production and elimination? J Mar Biol Assoc UK 89(7):1395-1402. https://doi.org/10.1017/S0025315409000599

Gayanilo FC, Sparre P (2005) FAO-ICLARM stock assessment tools II: User's guide. Food & Agriculture Org. Roma.

Hilmi K, Orbi A, Lakhdar Idrissi J (2009) Hydrodynamisme de la lagune de Oualidia (Maroc) durant l'été et l'automne 2005. Bull Inst Sci Rabat Sect Sci Terre 31:29-34

Holmstrup M, Bindesbøl A-M, Oostingh GJ, Duschl A, Scheil V, Köhler H-R, Loureiro S, Soares A, Ferreira A, Kienle C, et al. (2010) Interactions between effects of environmental chemicals and natural stressors: A review. Sci Total Environ 408:3746–3762. https://doi.org/10.1016/j.scitotenv.2009.10.067

Kennedy CR (1984) The use of frequency distributions in an attempt to detect host mortality induced by infections of diplostomatid metacercariae. Parasitology 89(2):209-220. https://doi.org/10.1017/S0031182000001244

Koprivnikar J, Poulin R (2009b) Interspecific and intraspecific variation in cercariae release. J Parasitol 95(1):14-19. https://doi.org/10.1645/GE-1582.1

Koprivnikar J, Thieltges DW, Johnson PTJ (2023) Consumption of trematode parasite infectious stages: from conceptual synthesis to future research agenda. J Helminthol 97:e33. https://doi.org/10.1017/S0022149X23000111

Koprivnikar J, Poulin R (2009a) Effects of temperature, salinity, and water level on the emergence of marine cercariae. Parasitol Res 105:957-965. https://doi.org/10.1007/s00436-009-1477-y

Kube J, Kube S, Dierschke V (2002) Spatial and temporal variations in the trematode component community of the mudsnail *Hydrobia ventrosa* in relation to the occurrence of waterfowl as definitive hosts. J Parasitol 88(6):1075-1086. https://doi.org/10.1645/0022-3395(2002)088[1075:SATVIT]2.0.CO;2

Labbardi H, Ettahiri O, Lazar S, Massik Z, El Antri S (2005) Etude de la variation spatio-temporelle des paramètres physico-chimiques caractérisant la qualité des eaux d'une lagune côtière et ses zonations écologiques: cas de Moulay Bousselham, Maroc. C R Geoscience 337:504-514.

Lauckner G (1983) Diseases of mollusca: bivalvia. In: Kinne O. (Ed) Diseases of Marine Animals, Vol. 2. John Wiley & Sons, Chichester NeweYorj Brisbane Toronto.

Levin LA, Boesch DF, Covich A, Dahm C, Erseus C, Ewel KC, Kneib RT, Moldenke A, Palmer MA, Snelgrove P, Strayer D, Weslawski JM (2001) The function of marine critical transition zones and the importance of sediment biodiversity. Ecosystems 4(5):430–451. https://doi.org/10.1007/s10021-001-0021-4

Lo CT, Lee KM (1996) *Cercaria kuntzi* n. sp. (Trematoda) from *Oncomelania hupensis formosana*, its Metacercariae and chromosomes. Zool Stud-Taipei 35:255-260.

MacKenzie K, Williams HH, Williams B, McVicar AH, Siddall R (1995) Parasites as indicators of water quality and the potential use of helminth transmission in marine pollution studies. Adv Parasitol 35:85-144. https://doi.org/10.1016/s0065-308x(08)60070-6

Magalhães L, Freitas R, Dairain A, De Montaudouin X (2017) Can host density attenuate parasitism? J Mar Biol Assoc UK 97(3):497-505. https://doi.org/10.1017/S0025315416001107

Makaoui A, Idrissi M, Agouzouk A, Larissi J, Baibai T, El Ouehabi Z, Ait Laamel M, Bessa I, Ettahiri O, Hilmi K (2018) Etat océanographique de la lagune de Oualidia, Maroc (2011-2012). Eur Sci J 14(18) :93. https://doi.org/10.19044/esj.2018.v14n18p93

Malham SK, Hutchinson TH, Longshaw M (2012) A review of the biology of European cockles (*Cerastoderma* spp.). J Mar Biol Assoc UK 92(7):1563-1577. https://doi.org/10.1017/S0025315412000355

Marcogliese DJ (2008) The impact of climate change on the parasites and infectious diseases of aquatic animals. Rev Sci Tech 27(2):467-484

Marcogliese DJ (2001) Implications of climate change for parasitism of animals in the aquatic environment. Can J Zool 79(8):1331-1352. https://doi.org/10.1139/z01-067

Mas-Coma S, Valero MA, Bargues MD (2009) Climate change effects on trematodiases, with emphasis on zoonotic fascioliasis and schistosomiasis. Vet Parasitol 163(4):264-80. https://doi.org/10.1016/j.vetpar.2009.03.024.

Moore ME, Alston MA, Kingsolver JG (2023) Behavioral thermoregulation of caterpillars is altered by temperature, but not parasitism: An empirical field study. Ecosphere 14(6):e4578. https://doi.org/10.1002/ecs2.4578

Morley NJ, Lewis JW (2013) Thermodynamics of cercarial development and emergence in trematodes. Parasitology 140(10):1211-1224. https://doi.org/10.1017/S0031182012001783

Morley NJ, Irwin SWB, Lewis JW (2003) Pollution toxicity to the transmission of larval digeneans through their molluscan hosts. Parasitology 126(7):S5-S26. https://doi.org/10.1017/S0031182003003755

Mouritsen KN, McKechnie S, Meenken E, Toynbee JL, Poulin R (2003) Spatial heterogeneity in parasite loads in the New Zealand cockle: the importance of host condition and density. J Mar Biol Assoc UK 83(2):307-310. https://doi.org/10.1017/S0025315403007124h

Mouritsen KN, Poulin R (2002) Parasitism, community structure and biodiversity in intertidal ecosystems. Parasitology 124(7):101-117. https://doi.org/10.1017/S0031182002001476

Mouritsen KN, Jensen KT (1997) Parasite transmission between soft-bottom invertebrates: temperature mediated infection rates and mortality in *Corophium volutator*. Mar Ecol Prog Ser 151:123-134.

Mouritsen KN, Jensen KT (1994) The enigma of gigantism: effect of larval trematodes on growth, fecundity, egestion and locomotion in *Hydrobia ulvae* (Pennant) (Gastropoda: Prosobranchia). J Exp Mar Biol Ecol 181(1):53-66. https://doi.org/10.1016/0022-0981(94)90103-1

Nikolaev KE, Levakin IA, Galaktionov KV (2021) A month for the mission: using a sentinel approach to determine the transmission window of digenean cercariae in the subarctic White Sea. J Helminthol 95:e50. https://doi.org/10.1017/S0022149X21000456

Paterson RA, Poulin R, Selbach C (2023) Global analysis of seasonal changes in trematode infection levels reveals weak and variable link to temperature. Oecologia 204:373-378. https://doi.org/10.1007/s00442-023-05408-8

Pechenik JA, Fried B (1995) Effect of temperature on survival and infectivity of *Echinostoma trivolvis* cercariae: a test of the energy limitation hypothesis. Parasitology 111(3):373-378. https://doi.org/10.1017/S0031182000081920

Poulin R (2006) Global warming and temperature-mediated increases in cercarial emergence in trematode parasites. Parasitology 132(1):143-151. https://doi.org/10.1017/S0031182005008693

Riisgård HU (2001) On measurement of filtration rates in bivalves—the stony road to reliable data: review and interpretation. Mar Ecol Prog Ser 211:275-291. https://doi.org/10.3354/meps211275

Richard A, Maire O, Daffe G, Magalhães L, de Montaudouin X (2022) *Himasthla* spp.(Trematoda) in the edible cockle *Cerastoderma edule*: review, long-term monitoring and new molecular insights. Parasitology 149(7):878-892. https://doi.org/10.1017/S0031182022000373

Rousset F, Thomas F, De Meeus T, Renaud F (1996) Inference of parasite-induced host mortality from distributions of parasite loads. Ecology 77(7):2203-2211. https://doi.org/10.2307/2265713

Selbach C, Poulin R (2020) Some like it hotter: trematode transmission under changing temperature conditions. Oecologia 194(4):745-755. https://doi.org/10.1007/s00442-020-04800-y

Shostak AW, Esch GW (1990) Temperature effects on survival and excystment of cercariae of *Halipegus occidualis* (Trematoda). Int J Parasitol 20(1):95-99

Stout L, Garenne A, de Montaudouin X (2022) Marine trematode parasites as indicators of environmental changes. Ecol Indic 141:109089. https://doi.org/10.1016/j.ecolind.2022.109089

Studer A, Poulin R (2014) Analysis of trait mean and variability versus temperature in trematode cercariae: is there scope for adaptation to global warming? Int J Parasitol 44(6):403-413. https://doi.org/10.1016/j.ijpara.2014.02.006

Studer A, Widmann M, Poulin R, Krkošek M (2013) Large scale patterns of trematode parasitism in a bivalve host: no evidence for a latitudinal gradient in infection levels. Mar Ecol Prog Ser 491:125-135. https://doi.org/10.3354/meps10483

Thieltges DW, Engelsma MY, Wendling CC, Wegner KM (2013) Parasites in the Wadden Sea food web. J Sea Res 82:122-133. https://doi.org/10.1016/j.seares.2012.06.002

Thieltges DW, Bordalo MD, Hernández AC, Prinz K, Jensen KT (2008) Ambient fauna impairs parasite transmission in a marine parasite-host system. Parasitology 135(9):1111-1116. https://doi.org/10.1017/S0031182008004526

Thieltges DW, Reise K (2007) Spatial heterogeneity in parasite infections at different spatial scales in an intertidal bivalve. Oecologia 150:569-581. https://doi.org/10.1007/s00442-006-0557-2

Thieltges DW, Reise K (2006) Metazoan parasites in intertidal cockles *Cerastoderma edule* from the northern Wadden Sea. J Sea Res 56(4):284-293. https://doi.org/10.1016/j.seares.2006.06.002

Thieltges DW, Rick J (2006) Effect of temperature on emergence, survival and infectivity of cercariae of the marine trematode *Renicola roscovita* (Digenea: Renicolidae). Dis Aquat Org 73(1):63-68.

Turner HM (1985) Parasites of eastern oysters from subtidal reefs in a Louisiana estuary with a note on their use as indicators of water quality. Estuaries 8:323-325.

Verdelhos T, Marques JC, Anastácio P (2015) Behavioral and mortality responses of the bivalves *Scrobicularia plana* and *Cerastoderma edule* to temperature, as indicator of climate change's potential impacts. Ecol Indic 58:95-103. https://doi.org/10.1016/j.ecolind.2015.05.042

Vielma S, Lagrue C, Poulin R, Selbach C (2019) Non-host organisms impact transmission at two different life stages in a marine parasite. Parasitol Res 118:111-117. https://doi.org/10.1007/s00436-018-6121-2

Figures caption

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

Figure 2. Growth curve (shell length = f(date)) of the different cohorts in the different sites (ARC = Arcachon, MZ = Merja Zerga, OUA = Oualidia).

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

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

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

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

Figure 1

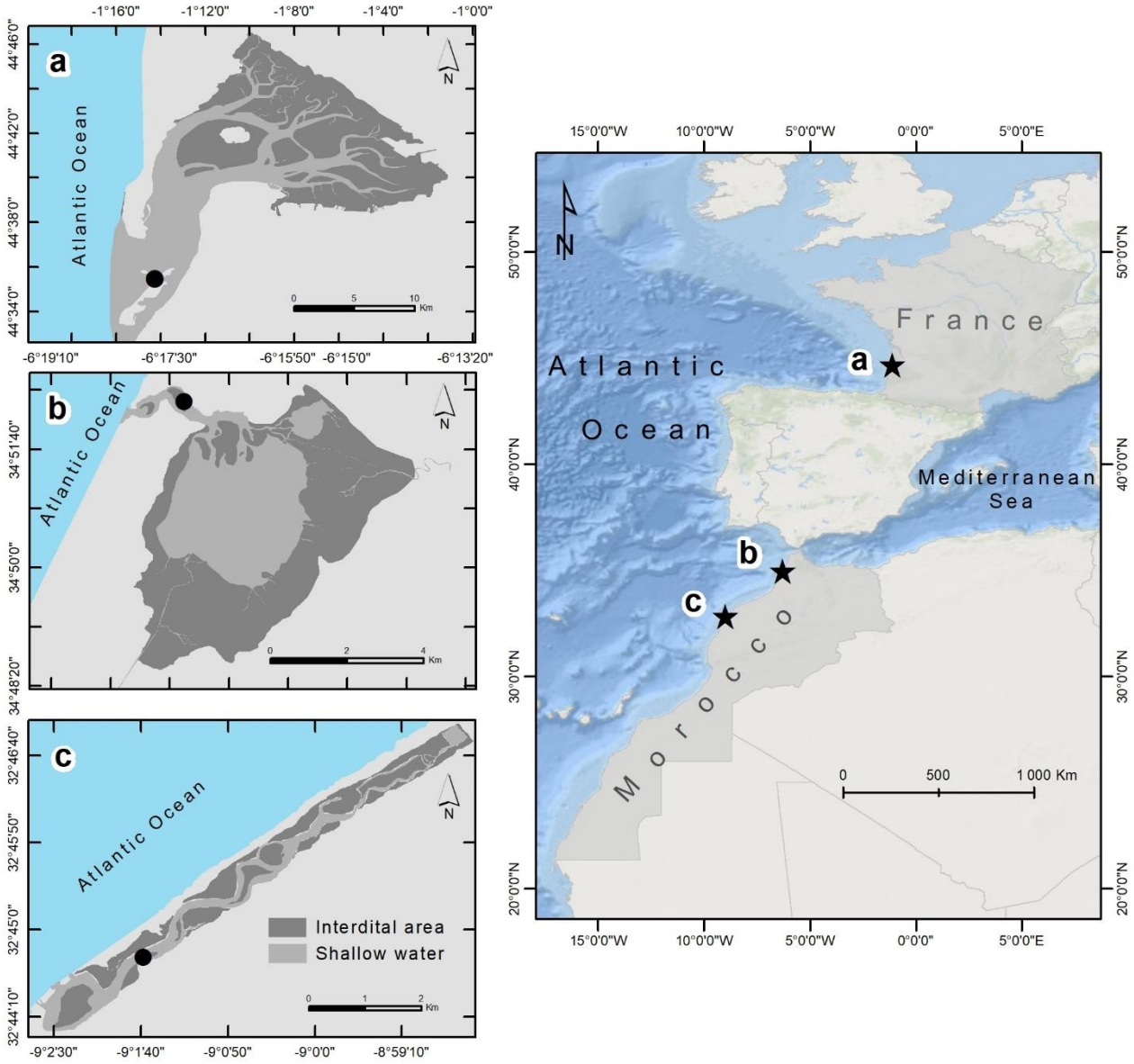

a
Atlantic Ocean
-1°16'0"
-1°12'0"
-1°8'0"
-1°4'0"
-1°0'0"
44°46'0"
44°42'0"
44°38'0"
44°34'0"
0 5 10 Km
b
Atlantic Ocean
-6°19'10"
-6°17'30"
-6°15'50"
-6°15'0"
-6°13'20"
34°51'40"
34°50'0"
34°48'20"
0 2 4 Km
c
Atlantic Ocean
32°46'40"
32°45'50"
32°45'0"
32°44'10"
Interdital area
Shallow water
0 1 2 Km
-9°2'30"
-9°1'40"
-9°0'50"
-9°0'0"
-8°59'10"
N
15°0'0"W
10°0'0"W
5°0'0"W
0°0'0"
5°0'0"E
50°0'0"N
40°0'0"N
30°0'0"N
20°0'0"N
France
Atlantic
Ocean
Mediterranean
Sea
Morocco
0 500 1 000 Km

Figure 2.

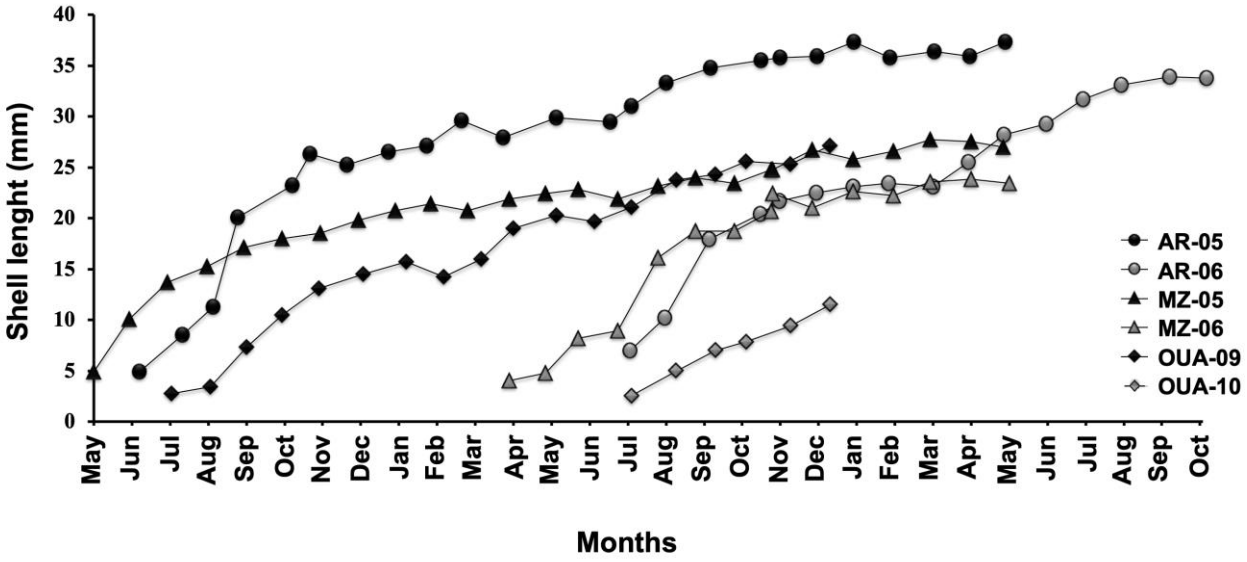

Shell lenght (mm)
0
5
10
15
20
25
30
35
40
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Months
AR-05
AR-06
MZ-05
MZ-06
OUA-09
OUA-10

Figure 3.

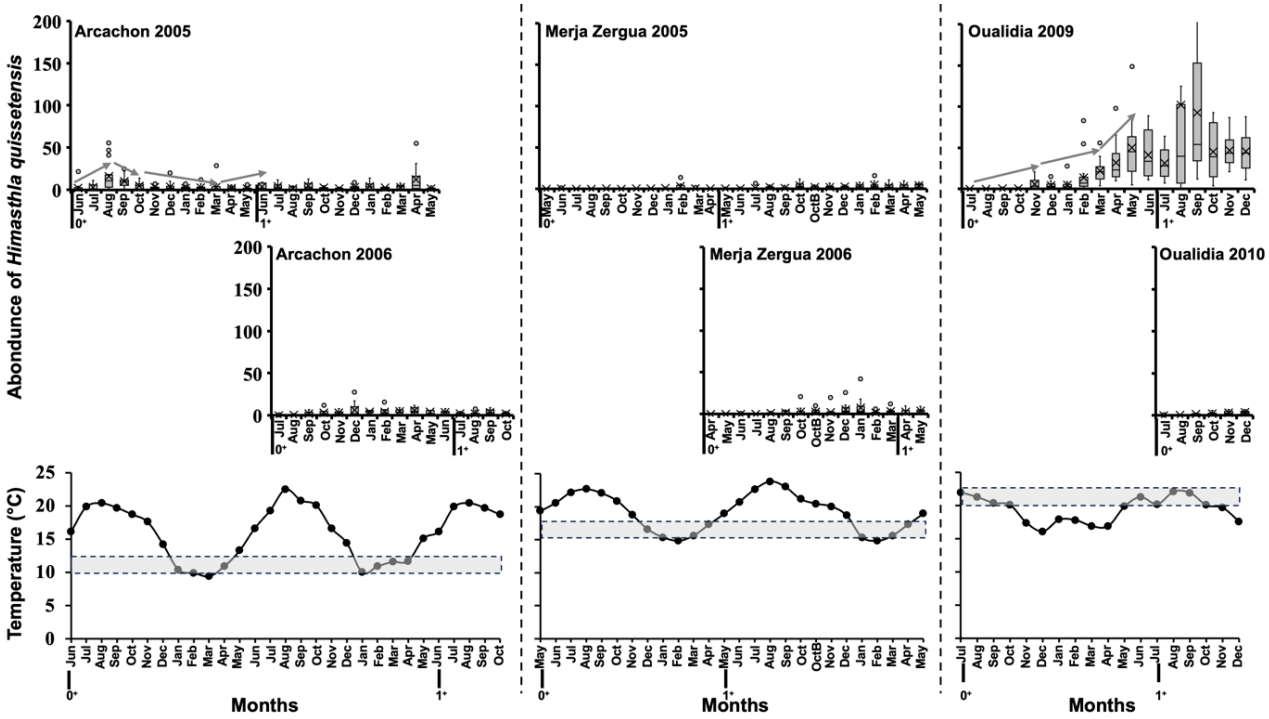

Arcachon 2005
Merja Zergua 2005
Oualidia 2009
Arcachon 2006
Merja Zergua 2006
Oualidia 2010
Abondance of Himasthla quissetensis
Temperature (°C)
Months
0+
1+

Figure 4.

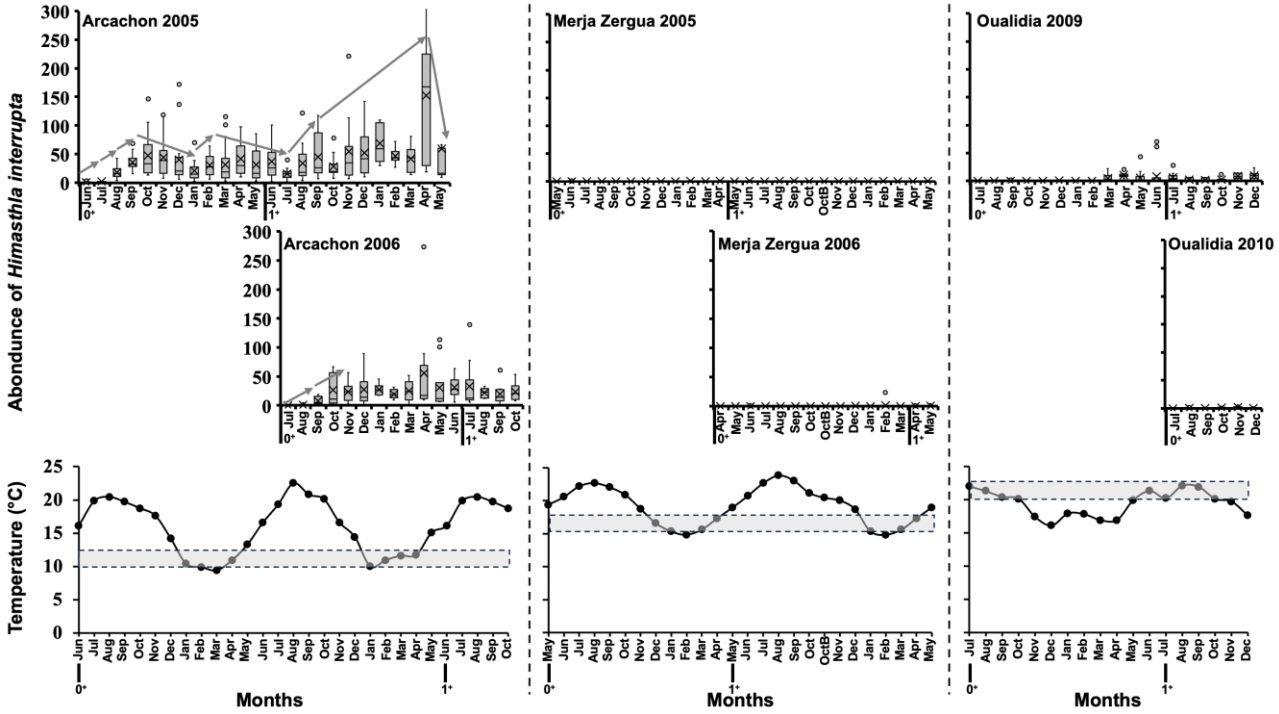

Arcachon 2005
Merja Zergua 2005
Oualidia 2009
Arcachon 2006
Merja Zergua 2006
Oualidia 2010
Abondunce of Himasthla interrupta
Temperature (°C)
Months
0+
1+

Figure 5.

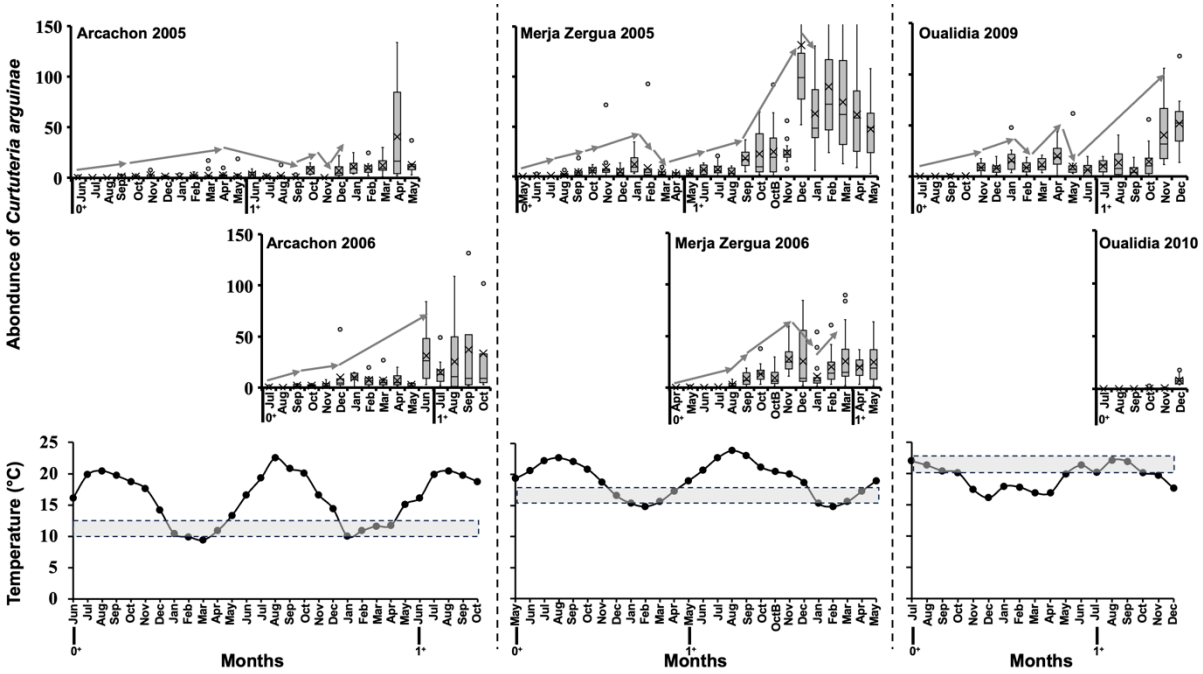
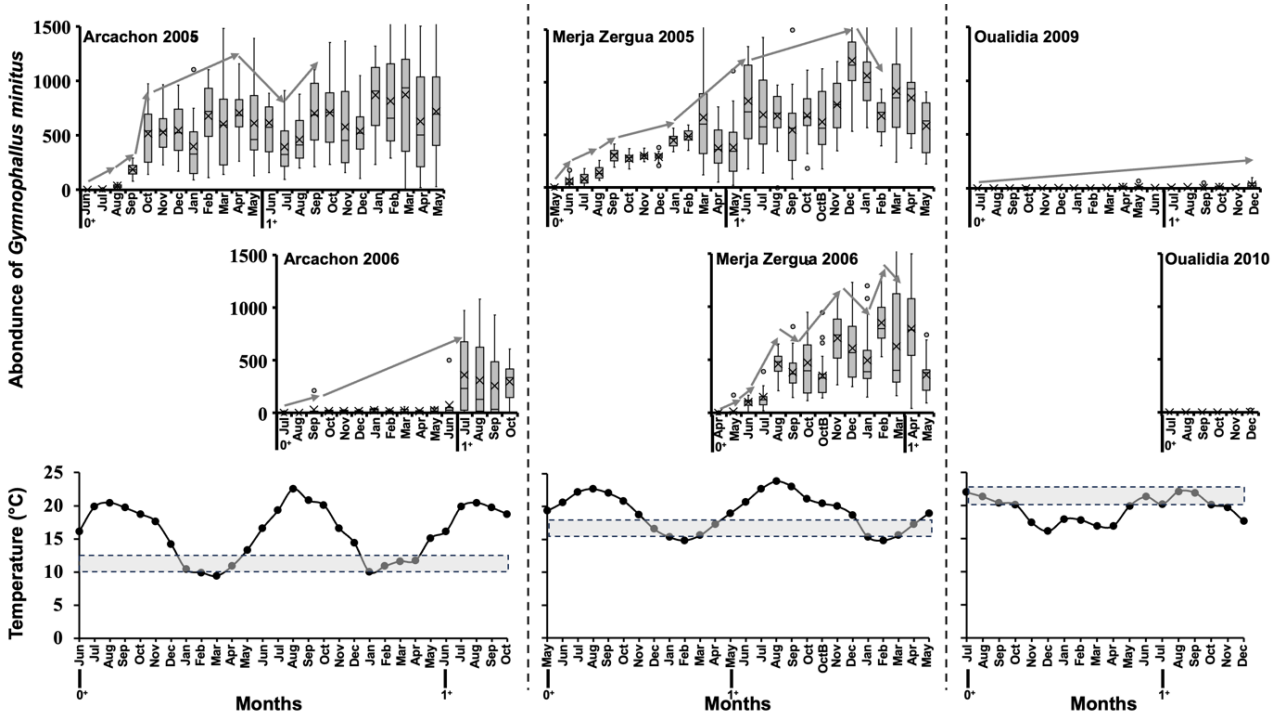

Arcachon 2005
Merja Zergua 2005
Oualidia 2009
Arcachon 2006
Merja Zergua 2006
Oualidia 2010
Abondunce of Curtuteria arguinae
Temperature (°C)
Months
0+
1+

Figure 6.


Arcachon 2005
Merja Zergua 2005
Oualidia 2009
Arcachon 2006
Merja Zergua 2006
Oualidia 2010
Abondunce of Gymnophallus minitus
Temperature (°C)
Months
0+
1+

Tables Caption

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

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

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

Table 1.

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

ARC = Arcachon, OUA = Oualidia, MZ = Merja Zerga

Table 2.

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

ARC = Arcachon, OUA = Oualidia, MZ = Merja Zerga, cohorts 2005, 2006 and 2009 according to sites. *p*-value is compared to 0.050/14 (Bonferroni correction). Significant results ($p < 0.0036$) are in bold.

Table 3.

	Survey	N	R	*p*
Ca	**ARC/MZ**	**25**	**0.58**	**0.0022**
	ARC/OUA	19	0.31	0.1987
	MZ/OUA	**19**	**0.64**	**0.0031**
Gm	**ARC/MZ**	**25**	**0.56**	**0.0038**
	ARC/OUA	19	0.03	0.8969
	MZ/OUA	19	0.00	1.0000
Ca vs. Gm	**ARC-05**	**22**	**0.74**	**0.0014**
	ARC-06	14	0.70	0.0057
	MZ-05	**24**	**0.78**	**<0.0001**
	MZ-06	**14**	**0.75**	**0.0020**
	OUA-09	15	0.37	0.1779

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