



Trematode infection modulates cockles biochemical response to climate change

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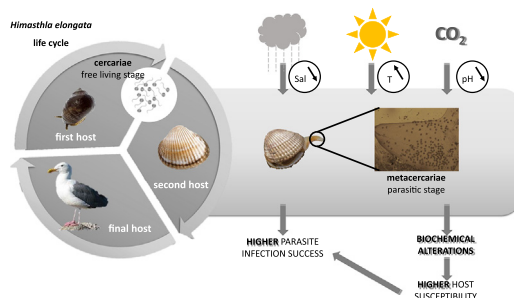
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HIGHLIGHTS

- Higher infection success with water salinity decrease, warming and acidification
- Under lower water salinity, parasite infection reduced cockle antioxidant defence.
- Under higher water temperature, parasite infection increased cockle cellular damage.
- Under higher $p\text{CO}_2$, parasite infection induced cockle metabolic depression.

GRAPHICAL ABSTRACT



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ABSTRACT

Resulting mainly from atmospheric carbon dioxide (CO_2) build-up, seawater temperature rise is among the most important climate change related factors affecting coastal marine ecosystems. Global warming will have implications on the water cycle, increasing the risk of heavy rainfalls and consequent freshwater input into the oceans but also increasing the frequency of extreme drought periods with consequent salinity increase. For Europe, by the end of the century, projections describe an increase of CO_2 concentration up to 1120 ppm (corresponding to 0.5 pH unit decrease), an increase in the water temperature up to 4 °C and a higher frequency of heavy precipitation. These changes are likely to impact many biotic interactions, including host–parasite relationships which are particularly dependent on abiotic conditions. In the present study, we tested the hypothesis that the edible cockle, *Cerastoderma edule*, exposed to different salinity, temperature and pH levels as proxy for climate change, modify the infection success of the trematode parasite *Himasthia elongata*, with consequences to cockles biochemical performance. The results showed that the cercariae infection success increased with acidification but higher biochemical alterations were observed in infected cockles exposed to all abiotic experimental stressful conditions tested. The present study suggested that changes forecasted by many models may promote the proliferation of the parasites infective stages in many ecosystems leading to enhanced transmission, especially on temperate regions, that will influence the geographical distribution of some diseases and, probably, the survival capacity of infected bivalves.

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1. Introduction

It is of prime relevance to understand the consequences imposed by occurring and predicted climate change (IPCC, 2014) on marine species interactions such as host–parasite systems. Climate-related changes,

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namely sea level rise, increasing storm frequency, temperature rise and ocean acidification are expected to have negative consequences particularly for the biota of intertidal and shallow marine areas (Ringwood and Keppler, 2002). These consequences include biodiversity and habitat reduction, shifts of species distributional patterns, and/or even ecosystem loss (Brierley and Kingsford, 2009; Cheung et al., 2009; Doney et al., 2012; Sarà et al., 2014). Effects on one species can drive changes up to the population or community levels. For example, effects at the individual reproduction level can drive changes on the population recruitment which in turn can influence the interactions among populations at the community level, such as predation and competition (Harley et al., 2006). Therefore, predicted changes are likely to impact many biotic interactions including host–parasite relationships which are particularly dependent on abiotic conditions (de Montaudouin et al., 2016). In fact, the negative effects of infectious diseases may become more severe in a global climate change scenario (Harvell et al., 2002).

Parasitic fauna represents 40% of total known eukaryotic species (Dobson et al., 2008) and can influence the composition and structure of natural animal communities being important elements of worldwide ecosystems (Poulin, 1999). However, studies converging parasitology and climate change are still scarce and focused mainly on cercariae emergence and survival (MacLeod, 2017). Increasing of river flows (Robins et al., 2016) and shifts on the rainfalls frequency (Feyen and Dankers, 2009; Robins et al., 2016) are among the environmental factors derived from climate change which can impact the aquatic organisms. These changes will have a significant impact on the salinity of the aquatic systems, especially noticed in lagoons and estuaries (Schmitt, 2008). Salinity plays an important role in defining structural and functional characteristics of aquatic biota (Telesh and Khlebovich, 2010; Fazio et al., 2013) and has been recognised as an important driver for parasitism and disease dynamics (Messick et al., 1999; Coffey et al., 2012).

According to recent studies (IPCC, 2014), climate change will also include the increase of earth surface temperature up to 4 °C by the end of the 21st century. Temperature is among the most pervasive and important physical factors in the environment of an organism and can have implications from molecular to biogeographical levels (Somero, 2011). Temperature effects on parasites are well described, demonstrating that an increase in temperature induces higher cercariae emergence until an optimum (Mouritsen, 2002; Thielges and Rick, 2006; Studer et al., 2010; Koprivnikar et al., 2014) and higher cercariae infectivity (Thielges and Rick, 2006; Studer et al., 2010) but lower cercariae survival (Mouritsen, 2002; Thielges and Rick, 2006; Studer et al., 2010).

Oceanic partial pressure of carbon dioxide ($p\text{CO}_2$) has been increasing. In 2011 ocean pH had already decreased by 0.1 pH unit since the beginning of the industrial era and is predicted to decrease further by 0.3 to 0.5 pH unit (Caldeira and Wickett, 2003). Beyond implications of low pH on shell production due to a decrease in calcium carbonate availability (Raven et al., 2005), the most important effect of acidification is on the increased organisms metabolic demand for the acid-base regulation which can reduce the amount of energy available for other activities such as respiration, growth and reproduction (Kroeker et al., 2010). The specific effects of ocean acidification on host–parasite interactions are almost unknown although some evidences suggest significantly higher infection success in the environment subjected to reduced pH levels (Koprivnikar et al., 2010; Harland et al., 2016).

Despite increasing efforts on parasitological studies over the last decades (Poulin et al., 2016), parasites still play a discrete role in marine ecosystems and little is known about how parasites are influenced by environmental changes (Koprivnikar et al., 2010; Studer and Poulin, 2013). Therefore, in the present study, we used the edible cockle, *Cerastoderma edule*, as a host model and the trematode parasite, *Himasthla elongata* as a parasite model, to test the hypothesis that host exposure to different salinity, temperature and pH levels, as proxy for climate change, can modify the infection success of the parasite. Besides, this work aimed to investigate the interactive effects of each abiotic

variable tested (salinity, temperature and pH) and trematode infection on the host biochemical performance. Accordingly, a series of laboratory experiments were conducted by exposing cockles as second intermediate host of *H. elongata* cercariae, to the three distinct experimental conditions.

2. Material and methods

2.1. Hosts and parasites

The parasite species used was *Himasthla elongata*, a marine trematode, i.e. the most dominant clade of macroparasites in coastal waters (Lauckner, 1983). This parasite has a complex life cycle with three host species: i) a water bird as definitive host, where the adult parasitic stage develops and sexually reproduces; ii) the gastropod *Littorina littorea* as first intermediate host, where the sporocyst parasitic stage matures and the cercariae are formed and released (asexual multiplication). Usually, cercariae display a short lifespan (<48 h) and their functional ability to infect has a duration of <12 h (de Montaudouin et al., 2016); iii) next, *H. elongata* cercariae penetrate a cockle as second intermediate host and settle as metacercariae.

Potential first intermediate host *L. littorea* infected with *H. elongata* were collected from NIOZ harbour, Texel, the Netherlands (53° 00' 32.1"N, 4° 47' 36.5"E) in September 2017. Returning from the field, snails were screened for infections by incubating them in wells (6-well plate) with ~16 mL seawater (salinity = 35 ± 1) at 25 °C under constant illumination for 4 h. After, each well of each plate was observed at the stereomicroscope to check for the presence or absence of emitted cercariae in the water where the snails were immersed. Non-infected snails were returned to their natural habitat, while infected snails, a stock composed by six individuals (shell height ranged between 14 and 18 mm), were transported to Portugal at room temperature and dark conditions. When in the laboratory, snails were kept in the dark, in a 70 L aquarium filled with artificial seawater (salinity = 35 ± 1) constantly refreshed by a chiller to maintain 14 ± 1 °C and fed with fresh sea lettuce (*Ulva* sp.) ad libitum.

Potential second intermediate host *Cerastoderma edule* (edible cockle) was collected from the Mira channel, Ria de Aveiro coastal lagoon, Portugal (40° 38' 31.7"N, 8° 44' 10.9"W) in September 2017. After collection, cockles were transferred to the laboratory and acclimated for two weeks prior to exposure. The cockles were kept randomly distributed in two aquaria with constant filtration under controlled (CTL) conditions: salinity = 30 ± 1 , temperature = 17 ± 0 °C, pH = 8.2 and photoperiod = 12:12 h (light/dark). Cockles were fed with a heterotrophic and phototrophic species mixture (Algamac Protein Plus®) at a concentration of 720 cells $\mu\text{L}^{-1} \text{day}^{-1}$ adapted from Pronker et al. (2015). Cockles shell length ranged between 13 and 17 mm, i.e. young individuals, in order to limit natural trematode former infection.

2.2. Experimental design

In order to stimulate cercariae emergence from the infected snails, these organisms were individually transferred to a plate well (6-well plate) with ~16 mL artificial seawater (salinity = 35 ± 1) and exposed to constant illumination and, consequently, higher temperature (~25 °C) during a period that ranged between 4 and 6 h. Emitted cercariae were then individually collected with a pipette and separated into groups of twenty five for immediate cockles infestation.

After cockles acclimation period (see Section 2.1), three different experiments were carried out with sixty cockles (thirty cockles per treatment from which fifteen were infected) and 750 cercariae (Fig. 1). Experiments lasted for 144 h (96 h + 48 h) and were performed in three interspersed weeks to allow snails and parasites recovery and consequent maintenance of the cercariae production.

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