Journal of Sea Research xxx (2015) xxx–xxx

Contents lists available at ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares

Cockle infection by *Himasthla quissetensis* — II. The theoretical effects of climate change

Xavier de Montaudouin [a,]*, Hugues Blanchet [a], Céline Desclaux-Marchand [a], Hocein Bazairi [b], Nazik Alfeddy [b], Guy Bachelet [a]

[a] *UMR EPOC 5805, Université de Bordeaux-CNRS, Station Marine d'Arcachon, 2 rue du Professeur Jolyet, 33120 Arcachon, France*
[b] *University Mohammed V-Agdal, Faculty of Sciences, 4 Av. Ibn Battota, Rabat, Morocco*

ARTICLE INFO

Article history:
Received 29 September 2014
Received in revised form 19 December 2014
Accepted 22 December 2014
Available online xxxx

Keywords:
Parasitism
Trematodes
Cockles
Climate change
Temperature

ABSTRACT

Numerous marine populations experience parasite pressure. This is the case of the cockles *Cerastoderma edule* which are often highly infected by trematode macroparasites. These parasites display a complex life cycle, with a succession of free-living and parasitic stages. Climate, and in particular temperature, is an important modulator of the transmission dynamics of parasites. Consequently, global change is thought to have implications for the epidemiology of infectious diseases. Using *Himasthla quissetensis*, a dominant parasite of cockles as 2nd intermediate host in Arcachon Bay (France), we used mathematical models of parasite emergence (cercariae) and parasite infection (metacercariae) in cockles as a function of water temperature, in order to study different scenarios of temperature increases. Globally, with a +0.5 °C to +6.0 °C simulation, cumulated emergence of cercariae and accumulation of metacercariae tended to decrease or stagnate, respectively. This is the consequence of a trade-off between sooner (spring) and later (autumn) cercariae emergence/infestation on one hand, and a longer inhibition period of cercariae emergence/infestation during the hottest days in summer. Using sea water temperature in Oualidia (Morocco) where mean annual sea temperature is 3 °C higher than in Arcachon Bay, our model predicted infestation all year long (no seasonality). The model gave a correct estimation of the total number of parasites that was expected in cockles. Conversely, observed infestation in Oualidia followed a seasonal pattern like in Arcachon Bay. These results suggest that, if temperature is a strong driver of parasite transmission, extrapolation in the framework of climate change should be performed with caution.

1. Introduction

Many marine invertebrate populations experience a parasite pressure that may, in some circumstances, play a major role in their dynamics. Under extreme conditions, parasite-related population collapse has been observed which had a strong impact on the local economy (Bushek et al., 2012). Molluscs, in particular, commonly host trematodes (Lauckner, 1980, 1983). These macroparasites have a complex life cycle with a succession of hosts and free-living stages. There is today a general consensus to admit that a large part of these trematode life-cycles is strongly dependent on temperature, even though there is also a large interspecific variability among trematode species (Poulin, 2006). Besides, the relation between parasite processes (sporocyst/rediae maturation, cercariae emergence, metacercariae infection) and temperature can display different forms (linear, dome-shaped, logistic). Morley and Lewis (2013), in their meta-analysis on thermodynamics of cercarial development in freshwater systems, showed that temperature does not exert only substantial disproportionate effect, but that many trematode species can demonstrate zone of thermostability over optimal temperature of cercariae emergence. Beyond the fact that temperature affects directly the distribution of potential hosts and consequently the occurrence of related trematode species (Harvell et al., 1999), it is one of the important factors driving the phenology of parasites themselves. The most studied stage is certainly the one between the first and the second intermediate host. In the first intermediate host (always a Mollusc), the parasite is asexually multiplying and developing cercariae larvae, without obvious effect of temperature, at least in freshwater systems (Morley and Lewis, 2013). However, cercariae emergence is related to the development rates within the molluscan host which depends on the temperature that should rise above a minimum value ("minimum development temperature threshold" (Morley and Lewis, 2013)). Conversely, emergence of cercariae follows a seasonal pattern (de Montaudouin et al., submitted for publication; Meißner, 2001) and is dependent on temperature (Mouritsen and Jensen, 1997; Poulin, 2006) but also on other abiotic factors such as salinity or light (Koprivnikar and Poulin, 2009; Koprivnikar et al., 2014; Morley et al., 2010; Shostak and Esch, 1990). Cercariae lifespan in the water is short (a few hours), and cercariae survival as well as infection efficiency (in the second intermediate host) decrease with temperature increase (Evans, 1985; Fried and Ponder, 2003; Lo

---

* Corresponding author. Tel.: +33 5 56 22 39 04; fax: +33 5 56 83 86 51.
E-mail address: x.de-montaudouin@epoc.u-bordeaux1.fr (X. de Montaudouin).

http://dx.doi.org/10.1016/j.seares.2014.12.007
1385-1101/© 2015 Elsevier B.V. All rights reserved.

Please cite this article as: de Montaudouin, X., et al., Cockle infection by *Himasthla quissetensis* — II. The theoretical effects of climate change, J. Sea Res. (2015), http://dx.doi.org/10.1016/j.seares.2014.12.007

and Lee, 1996; Mouritsen, 2002; Pechenik and Fried, 1995), with however some intraspecific (Berkhout et al., 2014) and interspecific variability (Evans, 1985; Meißner and Bick, 1999; Mouritsen and Jensen, 1997; Pechenik and Fried, 1995). For a given trematode species, however, the different effects of a given temperature on the various infectious stages (cercariae emergence, survival and infectivity) make the final result tricky to estimate (Studer et al., 2010).

Stating that climate, and in particular temperature, is a salient modulator of the transmission dynamics of parasites, suggests that as a consequence, global climate change will have implications for the epidemiology of infectious diseases, acting on pathogen development and survival rates, disease transmission and host susceptibility (Harvell et al., 2002; Marcogliese, 2001). Temperature effect on an amphipod/trematode system has been modelled. In a first attempt, the inhibiting impact of a too high temperature was not considered (Mouritsen et al., 2005). The model was revisited in the southern hemisphere with a correction concerning high temperatures (Studer et al., 2013b). In both cases, the collapse of amphipod populations was predicted, with a delay of several years when temperature increase was ca. +1 °C but within a year if the increase was ca. +4–5 °C. Modifying the average temperature in a model has an impact on the period of infection if one considers that parasite transmission success follows a dome-shaped relation with temperature (i.e. there is an optimal temperature but both too low and too high temperatures have inhibiting effect). It has also possible outputs if light is another driver of infestation, even assuming that light levels will remain unaffected by global change. Shortened winter periods might increase the growth potential of many parasite populations with the occurrence of more generations within a year or longer parasite release during the favourable season (Hakalahti et al., 2006). However, a modification of the "infestation window" may also decrease the overlap of presence between parasites and their host and result in less infection and less host mortality (Paull and Johnson, 2014). Finally, another important process can also perturb any prediction: the potential adaptation of parasites and host to increasing temperature, from phenotypic plasticity to evolutionary genotypic adaptation. The variability of results obtained when challenging cercariae emergence, survival and infectivity (i.e. variance compared to the mean) suggests that parasites can adapt through adaptative evolution (Studer and Poulin, 2014). Another argument in favour of parasite/host adaptation capacity consists in comparing similar parasite/host systems at different latitudes and/or in observing the similarity of infection loads between sites with contrasted average temperatures (Studer et al., 2013c).

In a previous study, we evaluated the effect of temperature on emergence of *Himasthla quissetensis* (Miller & Northup, 1926) Stunkard, 1938, cercariae from dog whelks *Nassarius reticulatus* (Linnaeus) (first intermediate host) and monitored the infection of the second intermediate host, the cockle *Cerastoderma edule* (Linnaeus) in a semi-sheltered sandflat of Arcachon Bay (France) (de Montaudouin et al., submitted for publication). In the present paper, our aim was to consider the cercariae emergence model (de Montaudouin et al., submitted for publication), to perform a similar type of model for cockle infection and to explore different scenarios of temperature increase on both cercariae emergence and metacercariae accumulation rates. Then, the obtained result will be compared to a site in Morocco (Oualidia), where dog whelks, cockles and *H. quissetensis* are present and where annual temperature is currently higher than in Arcachon Bay.

2. Materials and methods

2.1. Study site

The study was conducted in Arcachon Bay (44°40′N, 1°10′W), a 180-km^2 macrotidal lagoon on the south-western Atlantic coast of France. The monitoring site was a sheltered sandflat in the inner part of the bay (La Canelette), where salinity range was 22–32. Water temperature was precisely measured with a Prosensor thermic probe (frequency 15 min, precision 0.4 °C), implanted in the water immediately near the study area. Sediment was a medium sand (median grain size = 225 μm).

2.2. H. quissetensis model of emergence

H. quissetensis cercariae emergence (C) per hour by the dog whelk *N. reticulatus* in relation with water temperature (T) has been recently modelled (de Montaudouin et al., submitted for publication) through a set of experimental data. The function was:

$$C = A \times e^{\left(-\frac{1}{2}\times\frac{(T-M)^2}{s^2}\right)} \qquad (1)$$

where A is the maximal number of cercariae emerging per hour and per dog whelk ($A = 220$ at night and 41 at light), M is the optimal temperature for emergence ($M = 20.8$ at night and 20.3 at light), and s is the standard deviation of the optimal temperature ($s = 1.74$ at night and 2.71 at light).

These parameters were obtained by non-linear fitting procedure (Bates and Watts, 1988) which was performed using function nls() in R platform (R, 2014).

From this function and the water temperature values at La Canelette during 5 years, it was possible to simulate the emergence of cercariae (de Montaudouin et al., submitted for publication). In the present work, we performed additional simulations corresponding to an increase of temperature with different scenarios (i.e. different levels of temperature increase).

These additional simulations were performed to evaluate the possible consequences of temperature increase on the seasonal pattern of emergence and on the intensity of cercariae emergence by one first intermediate host during one year. The tested range of water temperature increase was between +0.5 and +6 °C, in accordance with the different scenarios proposed by the last Intergovernmental Panel on Climate Change report (IPCC, 2013).

2.3. Model of H. quissetensis infection in cockles

Five one-year cockle transplant experiments were performed in Arcachon Bay from 1998 to 2002, from a site where cockles were free of *H. quissetensis* ("Arguin") to a site where infection was reported ("La Canelette"). The number of *H. quissetensis* metacercariae per cockle was determined each month (de Montaudouin et al., submitted for publication). The 5-years survey of both temperature and metacercariae accumulation was used to fit a mathematical model simulating the number of metacercariae infecting an average cockle as a function of water temperature.

This model allowed us to simulate the effect of a water temperature increase (climate change) on cockle infection. The range of tested temperature was similar to the one previously mentioned for cercariae emergence (+0.5 to +6 °C). The simulation was based on an average water temperature profile corresponding to the mean of the five water temperature profiles measured during the five consecutive years of survey.

A similar non linear curve fitting method was used than those described in § 2.2 (Eq. (1)) to fit a Lorentz function to these experimental data.

While this equation only considers cercariae emergence according to water temperature, the sister paper also considers cercariae longevity and infectivity (de Montaudouin et al., submitted for publication).

2.4. Cockle infection in warmer waters: the case of Oualidia (Morocco)

Oualidia is an Atlantic lagoon (32°44′N, 9°01′W) which also harbours cockles (*C. edule*), dog whelks (*N. reticulatus*) and the trematode

Please cite this article as: de Montaudouin, X., et al., Cockle infection by *Himasthla quissetensis* — II. The theoretical effects of climate change, J. Sea Res. (2015), http://dx.doi.org/10.1016/j.seares.2014.12.007