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GLOBAL CHANGE ECOLOGY - ORIGINAL RESEARCH

Local effects of a global problem: modelling the risk of parasite-induced mortality in an intertidal trematode–amphipod system

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Abstract The interactive effects of climate change and parasitism are of concern because of potentially important consequences for host populations, communities and entire ecosystems. In marine environments, the absence of historic baseline data on parasitism and disease limits our ability to make realistic predictions about these consequences. Here, we adapt a simulation model developed for a Northern Hemisphere intertidal host–parasite system to a comparable system in the Southern Hemisphere. The entire life cycle of the intertidal trematode parasite *Maritrema novaezealandensis* was modelled in order to investigate the interactive effects of parasitic infections and increasing temperatures on the population dynamics of the amphipod host *Paracalliope novizealandiae*. Despite uncertainties associated with the model and its parameterisation, most temperature increases that were predicted to cause the collapse of the modelled amphipod population in the long term lay within the range of predicted warming for the study area. The high vulnerability of the amphipods in the modelled system illustrates a potentially important ecological mechanism by which consequences of a global problem might manifest on the local scale.

Keywords Parasite transmission · Population dynamics · Climate change · Temperature dependence · Mortality risk

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Introduction

Ecological processes are highly influenced by climatic conditions (Mysterud et al. 2001; Ottersen et al. 2001; Stenseth et al. 2002). As a consequence, anthropogenically induced global changes have been linked to significant alterations in these processes (Parmesan 2006; Parmesan and Yohe 2003; Root et al. 2003; Walther 2010; Walther et al. 2002). Besides direct effects of environmental conditions on individual organisms or species, it is becoming increasingly acknowledged that these effects also extend to biotic interactions due to differential impacts on, or responsiveness by, individual ecological components (Gilman et al. 2010; Walther 2010). This can lead to altered interaction strengths and may have cascading effects through ecological networks such as food webs (Ottersen et al. 2001; Stenseth et al. 2002; Walther 2010). Not only trophic relationships or competitive interactions are affected, but also interactions between parasites and their hosts (Mouritsen and Poulin 2002a).

The importance of parasites and pathogens in relation to climate change, especially global warming, has been of major concern in many systems (Dobson et al. 2003; Harvell et al. 2002; Kutz et al. 2005; Poulin and Mouritsen 2006; Rohr et al. 2011). In marine environments, there has also been considerable concern about increasing diseases and parasitism coinciding with ongoing climate change (Harvell et al. 2004; Ward and Lafferty 2004). However, in the absence of historic baseline data and due to the lack of long-term monitoring programmes that include parasites, our ability to assess the influence of climate change on parasitism and diseases is limited. Looking back, determinations of whether diseases have been increasing in the ocean can only be attempted indirectly (Ward and Lafferty 2004). Looking ahead, simulation models can be used to forecast how predicted climate change—especially global warming—and parasitism may impact on marine host populations (Mouritsen et al. 2005).

Parasites are integral components of marine ecosystems (Mouritsen and Poulin 2002b; Sousa 1991). Moreover, parasites play crucial ecological roles, for example by regulating host population dynamics or influencing community structure and food webs (Tompkins and Begon 1999; Tompkins et al. 2011). By definition, parasites depend on one or more hosts to complete their life cycle; each component of a life cycle is likely to be differentially affected by environmental parameters, and thus the effects of climate change on these systems are likely to be complex as well as species and context dependent (Marcogliese 2001, 2008). Climatic or environmental conditions modulate the extent and intensity of parasitism in hosts (Cattadori et al. 2005; Hudson et al. 2006; Kutz et al. 2005; Mouritsen and Poulin 2002a; Poulin and Mouritsen 2006) through effects on the parasite itself, on its hosts (e.g. host condition and hence susceptibility), and/or on the interaction between hosts and parasites (Harvell et al. 2009; Lafferty 2009; Rohr et al. 2011). As a consequence, changes in climate or in the local environment are bound to affect levels of parasitism, with potentially important repercussions not only for host individuals, populations, communities and ecosystems but ultimately also for the parasite's ability to complete its life cycle (Dobson et al. 2008; Rohr et al. 2011).

Parasites with complex life cycles and/or those with ectothermic hosts should be disproportionally affected by climate changes such as global warming (Harvell et al. 2002; Marcogliese 2008). For example, trematode parasites have complex life cycles and usually depend on three hosts to complete their life cycle. Within the first intermediate mollusc host, trematodes asexually produce large numbers of their free-living transmission stage (cercariae). The fact that the production of these cercariae is highly temperature dependent has led to the prediction that trematodes may find suitable conditions for transmission more often in a warming world (Poulin 2006). The larger numbers of trematode transmission stages potentially present in a system raises the risk of parasite-induced mortality of second intermediate hosts (Poulin and Mouritsen 2006). The impact of a parasite on second intermediate hosts will depend not only on temperature but also on pre-existing local conditions. For instance, there can be considerable differences between the proportions of infected first intermediate hosts, even between populations in close proximity (e.g. Fredensborg and Poulin 2006). Hence, we would only expect second intermediate hosts to be at risk of parasite-induced mortality with increasing temperatures in areas where prevalence in first intermediate snail hosts is high. However, increasing temperatures may also positively influence the reproduction of hosts, which may counterbalance, to some extent, an increased pressure of parasitism (Neuparth et al. 2002). Thus, predicting the outcome of such interactions is a complex task, and requires an objective framework such as modelling can provide.

Maritrema novaezealandensis is an intertidal microphallid trematode that uses birds attracted to New Zealand mudflats, such as red-billed gulls (*Chroicocephalus scopulinus*), as definitive hosts in which adult worms live in the intestine and reproduce sexually (Martorelli et al. 2004). *M. novaezealandensis* eggs pass out with the bird's faeces and may get ingested by first intermediate hosts, mudsnails (*Zeacumantus subcarinatus*), foraging on soft-sediment intertidal mudflats. Within a snail host, the parasite replaces the snail's gonads, thus castrating it, and begins the asexual production of large numbers of its transmission stages (cercariae). Cercariae emerge from infected snails into the environment in order to infect second intermediate crustacean hosts. A range of crustaceans are suitable second intermediate hosts for *M. novaezealandensis* (Koehler and Poulin 2010), with the amphipod *Paracalliope novizealandiae* (an important component of intertidal food webs; Fredensborg et al. 2004b; Thompson et al. 2005) being the dominant such species on many mudflats where *M. novazealandensis* is also the only metazoan parasite found to infect it. Within a crustacean host, the parasite matures into a cyst stage (metacercaria) and awaits trophic transmission to a final bird host. *Paracalliope novizealandiae* has not only been shown to be highly infected during warm summer months in the field (Studer and Poulin 2012), but also to be affected by parasite-induced mortality (Bates et al. 2010; Fredensborg et al. 2004b) and to be highly susceptible to high temperatures (Studer et al. 2010).

The aim of the present study was to model the dynamics of the entire life cycle of *M. novaezealandensis*, and in particular the amphipod host population, on a mudflat where prevalence in first intermediate snail hosts is high (Lower Portobello Bay, Otago Harbour; Fredensborg and Poulin 2006). How global warming may influence this system was then explored. Three questions were addressed. (1) At what temperature increase is the modelled amphipod population of Lower Portobello Bay no longer sustainable? (2) How do changes in amphipod reproduction affect this critical temperature threshold? (3) What short-term extreme event (heat wave) would be necessary to cause an immediate (i.e. within a year) population collapse?

Materials and methods

Model formulation

The study and the model of Mouritsen et al. (2005) of a similar system in the Northern Hemisphere provided the basis for the current assessment of *M. novaezealandensis* and *P. novizealandiae* amphipods. The model links equations simulating the flow of the parasite through its complex life cycle: the dynamics of metacercariae (*M*) within adult amphipods (*A*), the population of adult worms (*H*) in the definitive bird hosts, and the number of infected snails (*I*) present in a system (see Table 1):

$$\frac{dM}{dt} = I \times \lambda_I \times \beta_{IM} \times \gamma_{adjust} - \alpha_A \times M - \alpha_{AT} \times M - \mu \times M/A$$

$$\frac{dA}{dt} = \lambda_{JA} \times J - \alpha_A \times A - \alpha_{AT} \times A - \mu$$

$$\frac{dH}{dt} = e^{-a \times H} \times \mu \times M/A - \alpha_H \times H$$

$$\frac{dI}{dt} = \beta_{HI} \times \gamma_I \times H \times \lambda_H - \alpha_I \times I.$$

As in Mouritsen et al. (2005), the amphipod population was the only host component dynamically modelled. In the present study, we distinguished juvenile (*J*) from adult amphipods:

$$\frac{dJ}{dt} = A \times \delta \times \lambda_A \times e^{-\sigma A} - \alpha_{AT} \times J - \lambda_{JA} \times J.$$

Model parameterisation

Data from the field (Studer and Poulin 2012), experiments (Fredensborg et al. 2004b; Studer et al. 2010) and the literature (especially Mouritsen et al. 2005 and references therein) were used to parameterise the model. Parameter estimates were scaled to 1 m^2 of the sediment surface and expressed in units of per day. The number of cercariae produced per infected snail per day (λ_I) and the proportion of those cercariae that successfully transmit to amphipods (β_{IM}) are, amongst other factors, temperature (*T*) dependent (Studer et al. 2010). Although cercarial survival is also temperature dependent (Studer et al. 2010), the decrease in survival with increasing temperature is generally compensated for by higher infectivity up to an optimum temperature (approx. 25 °C), such that transmission efficiency is relatively constant up to that temperature level (McCarthy 1999; Poulin 2006), after which there is a net negative effect on cercariae (Studer et al. 2010). Hence, cercarial survival was not explicitly included in the model, but is incorporated as a component of the overall transmission efficiency (β_{IM}) (see also Mouritsen et al. 2005). Both the output rate and transmission efficiency of *M. novaezealandensis* cercariae increase up to 25 °C, after which they drop off (Studer et al. 2010). These patterns were described by fitting linear regressions to the means from 16 to 25 °C and from 25 to 30 °C, respectively ($r^2 \geq 0.99$). Cercarial output (λ_I) per infected snail per day was described as:

$$\begin{array}{ll} \lambda_I = 0 & T < 16\,°C \\ \lambda_I = 13.68\,T - 215.89 & 16\,°C < T < 25\,°C \\ \lambda_I = -17.67\,T + 571.55 & T > 25\,°C \end{array}$$

and the transmission success rate of cercariae as:

$$\begin{array}{ll} \beta_{IM} = 0 & T < 16\,°C \\ \beta_{IM} = 0.062T - 0.24 & 16\,°C < T < 25\,°C \\ \beta_{IM} = -0.039T + 1.39 & T > 25\,°C. \end{array}$$

Trematode transmission can be affected by a range of biotic and abiotic environmental factors (see Thieltges et al. 2008), as well as by parasite- and/or host-related

Table 1 Symbol specifications for each parameter used in the model equations

Model parameters	
λ_I	Number of cercariae produced per infected snail per day
β_{IM}	Proportion of cercariae shed by infected snails that successfully transmit to amphipods and thus remain in the system
γ_{adjust}	Adjustment term for laboratory-based estimates of cercarial production and transmission
λ_{JA}	Maturation rate of juvenile amphipods into adults
α_A	Daily mortality rate of amphipods based on a maximum life span
α_{AT}	Daily temperature-dependent mortality rate of amphipods
μ	Number of amphipods ingested per day by definitive hosts
δ	Amphipod breeding activity
λ_A	Rate of amphipod fecundity per individual per day
σ	Density-dependent reduction in amphipod recruitment with increasing population size
α_H	Daily mortality rate of adult worms in the definitive host
a	Density-dependent reduction in the proportion of ingested parasites which successfully establish in the definitive host with increasing worm population size
β_{HI}	Proportion of parasite eggs excreted by birds that are ingested by the snail population at 15 °C
γ_I	Temperature-dependent modifier of the rate at which snails encounter parasite eggs (calibrated to 1 at 15 °C)
λ_H	Fecundity of adult worms per parasite per day
α_I	Daily mortality of infected snails

factors (e.g. McCarthy et al. 2002), which could not be directly accounted for here. However, an adjustment term (γ_{adjust}) was included to convert from laboratory-derived cercarial output and transmission estimates to field-relevant rates. Nonetheless, results still need to be interpreted in an "all else being equal" framework.

Adult amphipod breeding activity was based on data from the seasonal sampling at Lower Portobello Bay (Studer and Poulin 2012). Females with eggs can be found all year round but at different proportions (24, 43, 31 and 9 % in spring, summer, fall and winter, respectively; overall 53 % females, of which 66 % were gravid). The daily rate at which new amphipods are produced (λ_A) was based on a maximum number of four broods per female amphipod lifetime (Mouritsen et al. 2005) and an average brood size of 7.7 eggs (Studer and Poulin 2012). For an assumed nine-month amphipod life span (i.e. 270 days, based on Fredensborg et al. 2004b; Studer and Poulin 2012), the daily rate of offspring production per gravid female thus equalled 0.1141. Juvenile amphipods produced at this rate were assumed to mature into adults (i.e. size $\geq$2.5 mm) within three months, so their daily rate of maturation was set to 0.01. Juveniles were included in the model separately, being affected by natural mortality only, since they are rarely found to be infected, even during summer (and then only with very few parasites; A. Studer, personal observation). While this observation is possibly due to rapid parasite-induced mortality and fast loss of infected juveniles from the system, it may also be due to the small size of juveniles, as infection levels in amphipods tend to increase with increasing size (Fredensborg et al. 2004b; Studer and Poulin 2012). The daily mortality rate of adult amphipods (α_A) was a combination of natural mortality (assumed maximum life span of nine months) and parasite-induced mortality dependent on intensity of infection (estimated from Fredensborg et al. 2004b) such that ($r^2 > 0.95$)

$$\alpha_A = 0.0037 + 0.005\,(M/A)$$

Mortality of both juvenile and adult amphipods in the model (α_{AT}) was temperature dependent. Studer et al. (2010) documented 100 % mortality in the laboratory within 2 h at 34 °C, and within 2 days at 30 °C. At temperatures between 20 and 30 °C, 50 % mortality occurred within about 10–12 days. Below 20 °C, there was almost no mortality during the experiment, so a default mortality rate based on a nine-month life span was used. As with other parameters in this model, the survival of amphipods in nature is affected by a range of environmental factors which could not be accounted for here, such as (potentially temperature-mediated) predation by other organisms. Hence, again, the proviso of "all else being equal" needs to be made in the interpretation of results. Also, laboratory-derived mortality rates generally do not equate to natural conditions. Hence, all survival-related parameters and equations were corrected based on an observed eightfold difference between uninfected rates from the laboratory and the estimated nine-month survival of amphipods in the field (Studer et al. 2010).

The number of adult amphipods ingested by definitive hosts per day (μ) was set to 6.42 during the main bird visitation season from October to January, and to 1.28 for the rest of the time. This estimate was based on seasonal differences in bird abundance on the high prevalence mudflat of Lower Portobello Bay (abundance on an area of approx. 3.6 ha was 156.53 (mostly gulls) for October to January, and 31.28 for the rest of the year; Studer and Poulin 2012) and an estimated feeding rate of individual birds visiting mudflats adapted from the literature, since no data are available for the study system used here. The estimate (ingestion of 4.1 amphipods per minute per bird during one 6 h low tide per day, i.e. half that used in Mouritsen et al. 2005) was based on a relatively low predation pressure by birds on amphipods (McClatchie et al. 1989; Wootton 1997). While a number of birds (e.g. ducks and waders) that feed on amphipods are present year-round in the study system, their numbers are low relative to gulls (Fredensborg et al. 2006; Studer and Poulin 2012). Overall, amphipod depredation by birds is probably minor relative to the total population size, and gulls are the only proven final hosts of *M. novaezealandensis* (Fredensborg et al. 2004a; Martorelli et al. 2004). The chosen value therefore reflects the average of the ingestion rates of ducks and waders (i.e. the value used in Mouritsen et al. 2005) and the low ingestion rate of gulls.

The daily mortality of adult worms in the definitive bird host (α_H) was set at 0.1, based on a ten-day life span (Fredensborg and Poulin 2005; Ginetsinskaya 1988; Mouritsen et al. 2005). The rate of adult worm fecundity per parasite per day (λ_H) was set at 55 eggs. This was based on an in vitro study by Koehler et al. (2012), and may be a rather conservative estimate. However, the means by which adult worm density dependence was adjusted in the model fitting process (see below) means that such an error will not influence our model dynamics. These parasite eggs are excreted onto the mudflat by the definitive bird hosts, where they are encountered by uninfected snails at a baseline rate (β_{HI}) of 0.299 (based on the value estimated in Mouritsen et al. 2005). Temperature effects on the feeding activity of snails (Hylleberg 1975) were simulated using a modifier term (γ_I) calibrated to equal 1 at 15 °C ($r^2 > 0.99$), such that

$$\begin{array}{ll} \gamma_I = 0 & T < 10\,^\circ\text{C} \\ \gamma_I = 0.19\,T - 1.85 & 10\,^\circ\text{C} < T < 20.3\,^\circ\text{C}\,. \\ \gamma_I = 0.237\,T - 2.785 & T > 20.3\,^\circ\text{C} \end{array}$$

The daily mortality of infected snails ($\alpha_I = 0.00106$) was based on a mean life span of uninfected snails of five years and an estimated mortality rate of infected snails of 1.93 times that of uninfected snails (Fredensborg et al. 2005).

Model simulation

Numerical simulations with a daily time step were conducted in the software package Modelmaker 4.0 (Cherwell 2000) to explore model properties. Since no data were available to estimate density dependence in the amphipods (σ) and the adult worm population (a), as well as the appropriate value for the adjustment term (γ_{adjust}), the model was analysed to determine which parameter combination yielded the model output that best fitted the available field data (Studer and Poulin 2012). The parameters were simultaneously estimated so that the total amphipod population peaked at 1,500 amphipods m^{-2}, the maximum number of infected snails was approx. 210 m^{-2} and the maximum mean infection intensity in amphipods was 12 metacercariae per amphipod.

The temperature data used in the present model (mean daily temperatures) were collected during a one-year temperature recording period on the Lower Portobello Bay mudflat (Studer and Poulin 2012). The effect of an overall increase in temperature was assessed by increasing the daily mean temperatures year-round in intervals of 0.1 °C, to determine the new equilibrium dynamics or to identify an amphipod population crash. The climate change predictions for the study area (Otago, New Zealand) are, for the full range of scenarios, an increase of 0.6–1.3 °C until 2040 and 1.3–2.8 °C until 2090, respectively (http://www.niwa.co.nz/our-science/climate/information-and-resources/clivar/scenarios). The model was run for 80 years in each instance, except for the heat wave assessment.

Because all of the abovementioned processes and parameters are taking place within a complex natural setting, there is likely variation and unknown factors that our model does not account for. Therefore, sensitivity analyses were performed; all model parameters were varied individually by ±25 and ±50 % around their estimated values, and the change in the respective critical temperature increase at which the amphipod population is predicted to crash was determined.

Results

Parameter estimation

The optimised parameter values were 0.0017 for the density-dependent reduction in amphipod recruitment with increasing population size (σ), 337.52 for the density-dependent reduction in adult worms (a), and 0.04 for the adjustment term (γ_{adjust}). The adjustment term most likely reflects scale effects of cercarial output and transmission in an open water column in the natural situation, as opposed to a closed system in the laboratory (in which context parameters were estimated). Using these values, the total amphipod populations at equilibrium dynamics fluctuated yearly between 1,052 and 1,495 amphipods m^{-2} (Fig. 1), the number of infected snails fluctuated between 176 and 210 m^{-2}, and the mean infection intensity of amphipods fluctuated between less than one and twelve metacercariae per amphipod (Fig. 2a).

Effects of global warming

An increase in the mean daily temperature of 0.7 °C was sufficient to drive the modelled amphipod population of Lower Portobello Bay to extinction in the long term (Fig. 1). At an increase of 0.6 °C, the amphipod population still maintained itself, fluctuating between 888 and 1,173 amphipods m^{-2} (Fig. 1), while the number of infected snails peaked at 257 m^{-2} and the maximum infection intensity of amphipods increased to 29 metacercariae per amphipod (Fig. 2b). With an increase of 0.7 °C, a threshold was exceeded which caused a sharp increase in the parasite-related parameters, leading to a spike in the number of metacercariae that caused the amphipod population to collapse. This is likely due to nonlinearities in the model structure (Mouritsen et al. 2005).

The prediction of the Lower Portobello Bay amphipod population collapse was consistent in all sensitivity analyses conducted, with a collapse simulated to occur in the

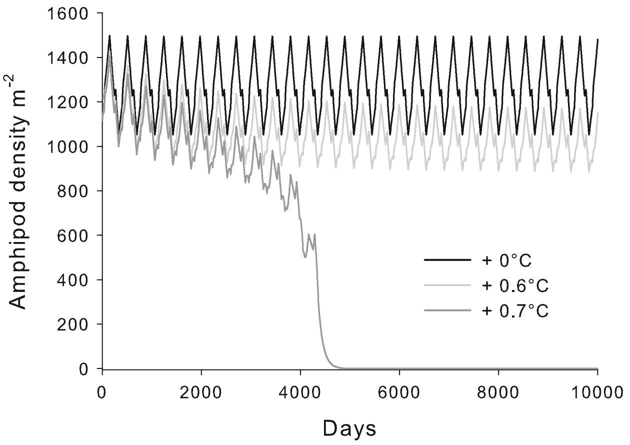

Fig. 1 Yearly population fluctuations of amphipods per m^2 under different climate warming scenarios. Predicted population trajectory from the default model under current conditions (+0 °C, *black line*), with an increase in the mean daily temperature of 0.6 °C (*light grey line*) and with an increase of 0.7 °C (*dark grey line*). Day 0 denotes January 1st (austral summer). For each temperature level, the model was run over 80 years; only trajectories over the first 10,000 days (i.e. approx. 27 years) are shown

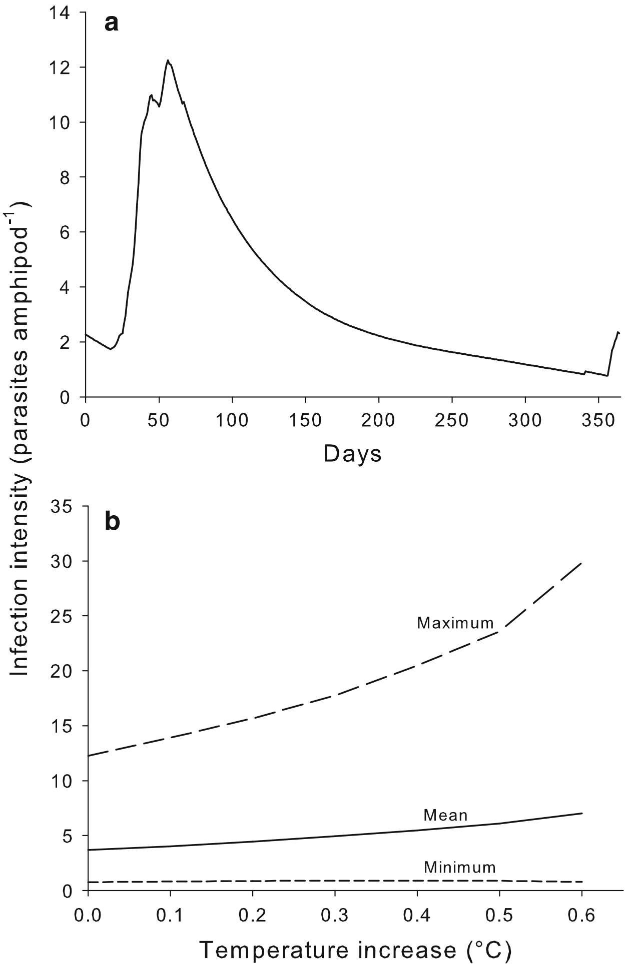

Fig. 2 Infection intensity (mean number of parasites per infected amphipod) at equilibrium amphipod population dynamics **a** over the course of a year under current climatic conditions (day 0 denotes January 1st, i.e. austral summer) and **b** with increasing mean daily temperatures. **b** Minimum (*short dashed line*), mean (*solid line*), and maximum (*long dashed line*) number of parasites per amphipod predicted under global warming scenarios

long term at temperature rises of between 0 and +3.2 °C (Table 2) (removing the parasite from the model increased the rise in temperature required for collapse to 5.1 °C). The most influential parameters were all related to the amphipods: the proportion of amphipods breeding, the fecundity of amphipods, the density dependence of the amphipod population, and the predation of amphipods by birds (Table 2).

Considering the temperature sensitivity of amphipod reproduction and the influence of these parameters on the predicted increase necessary to drive the amphipod population to extinction, the model was also used to assess the temperature increase that would be needed for the amphipod population to collapse (1) when the proportion of amphipods breeding during winter was set equal to the proportion breeding in spring, and (2) when the proportion of breeding amphipods in all seasons, the fecundity of amphipods and the maturation rate of juvenile amphipods were simultaneously increased by 50 % each. Increasing winter temperatures have been identified as a main consequence of global warming (IPCC 2007), and sea surface temperatures in the study area during winter months have indeed been increasing in recent decades (unpublished data). Assuming that, as a consequence, amphipod breeding would be similar in winter and spring, the temperature increase necessary to drive the amphipod population to extinction under such conditions was predicted by the model to be 1.9 °C. When simultaneously raising the amphipod reproduction parameters, the amphipod population remained viable up to an increase of 4.9 °C.

Another prediction regarding global warming is increased frequency and severity of extreme events, such as heat waves (IPCC 2007). Hence, the model was also explored to assess the temperature increase necessary to drive the amphipod population to an immediate collapse within a year (model started on January 1st, i.e. austral summer; temperature increase ongoing). Model outputs indicated that the increase would have to be on the order of about 14 °C to cause an immediate crash in the modelled population (Fig. 3), but the population was pushed to very low levels at substantially lower temperature increases; levels at which extinction due to stochastic effects may readily occur.

Discussion

The most striking finding of this study is the sensitivity of the modelled *Paracalliope novizealandiae* amphipod population to the trematode parasite *Maritrema novaezealandensis* and the effects of increasing temperature on this relationship. Even increases at the lower end of the expected range for the study area are therefore predicted to affect the amphipod population of the Lower Portobello Bay mudflat. Moreover, even when varying parameters to account for variation and errors in the model, most temperature increases at which the modelled amphipod population collapsed were still within the predicted range likely to occur in the next 80 years. The predictions regarding the potential collapse of this amphipod population are therefore relatively robust.

The model developed for a European *Corophium volutator* amphipod population served as a basis for the present model (Mouritsen et al. 2005). There are a number of similarities as well as differences between these two systems. Both systems are known to be highly influenced by environmental factors (e.g. Meissner and Bick 1999; Mouritsen 2002; Studer et al. 2010), with increasing temperatures in particular expected to increase parasite

Table 2 Results from the sensitivity analyses of all model parameters, indicating the temperature increase (in °C) at which the long-term amphipod population collapse is predicted. All model parameters were varied individually by ±25 and ±50 % around their estimated value

	Parameter	−50 %	−25 %	±0 %	+25 %	+50 %
λ_I	Production of cercariae	1.4	0.9	0.7	0.4	0.2
β_{IM}	Transmission of cercariae	1.4	0.9	0.7	0.4	0.2
γ_{adjust}	Adjustment term	2.2	1.3	0.7	0.2	0
α_A	Natural amphipod mortality	1.5	1.1	0.7	0.1	0
α_A	Parasite-induced amphipod mortality	1.3	0.9	0.7	0.4	0.3
α_{AT}	Temperature induced amphipod mortality	0.7	0.7	0.7	0.6	0.6
μ	Amphipod predation by birds	2.4	1.7	0.7	0	0
λ_A	Amphipod fecundity	0	0	0.7	2.3	3.2
δ	Proportion of breeding amphipods	0	0	0.7	2.3	3.2
λ_{JA}	Maturation rate of juvenile amphipods	0.4	0.7	0.7	0.6	0.6
σ	Density dependence of amphipods	3.0	2.0	0.7	0	0
a	Density dependence of adult worms	0	0.4	0.7	0.8	1.0
λ_H	Adult worm fecundity	1.4	0.9	0.7	0.4	0.2
α_H	Adult worm mortality	0.6	0.6	0.7	0.7	0.7
β_{HI}	Parasite egg ingestion by snails	1.4	0.9	0.7	0.4	0.2
α_I	Mortality of infected snails	0	0.4	0.7	0.8	1.1

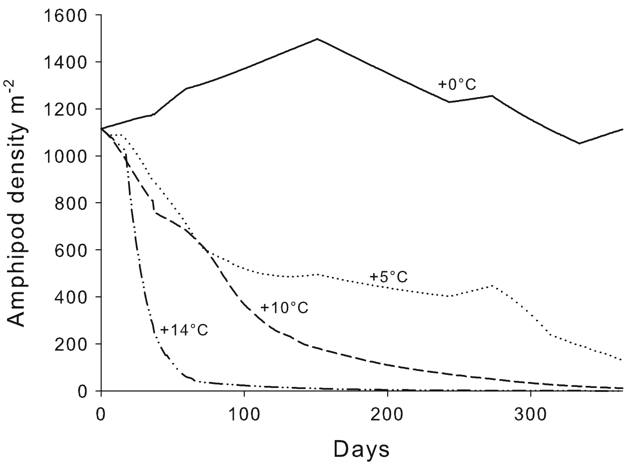

Fig. 3 Amphipod population fluctuation (density per m^2) over a yearly cycle under current conditions (*solid line*) and predicted trajectories of the amphipod population for an increase of +5 °C (*dotted line*), +10 °C (*dashed line*), or +14 °C (*dash-dotted line*) under heat wave scenarios

transmission as well as parasite-induced mortality (Bates et al. 2010; Fredensborg et al. 2004b; Jensen and Mouritsen 1992; Mouritsen and Jensen 1997; Studer et al. 2010). However, *C. volutator* amphipods can reach densities up to 100,000 m^{-2}, while *P. novizealandiae* occur in the study area at much lower densities. The higher density of *C. volutator* is likely to buffer the population up to higher temperatures, even though the density of infected snails and predation by birds during migration periods are also higher than in the *P. novizealandiae* system. Indeed, the high density of *C. volutator* is probably responsible for the “decline” of the population predicted in Mouritsen et al. (2005), rather than the long-term collapse predicted in the present study. However, even the *C. volutator* system was predicted to collapse when amphipod reproduction parameters were altered, and this system is also known for already having suffered from a natural mortality event (Mouritsen et al. 2005). The temperature increases necessary to cause the collapse or decline in both amphipod populations were therefore consistent, and were mostly within the ranges predicted to occur in each part of the world over the coming decades.

The model presented here was the most realistic we were able to construct based on current knowledge. It is, however, limited by several issues and is clearly an oversimplification of the natural situation. Such exercises do not take into account any other changes that may occur with ongoing and predicted climate change, which may directly or indirectly affect the hosts, the parasite and/or the interaction between them. For instance, rising sea levels are expected to cause the loss of intertidal habitats, especially in areas where inland movement is restricted. This may fundamentally alter ecological processes occurring in intertidal systems. It is also not possible to account for the possible adaptive or evolutionary potential of the components involved, and it remains unknown how this may affect our study system, the parameters included or the predictions made. It is also not possible to account for many other ecological processes that may affect the parameters and processes investigated. For example, the dispersal and migration dynamics of amphipods at the meta-population level could be important for re-colonisation and/or the continuous supply of immigrants from nearby areas that are less affected by the parasite.

There are also uncertainties associated with some of the model parameters due to a lack of appropriate data for aspects of the study system. For example, the definitive bird hosts are one of the least investigated components of the life cycle of *M. novaezealandensis*. Moreover, multiple effects of global changes on the occurrence and behaviour of birds are possible. The number of birds and the time they spend in the area may increase due to an increased abundance of food (Mouritsen et al. 2005 and references therein). This may prolong the period in which the entire life cycle of *M. novaezealandensis* can take place, and thus may increase the impact of the parasite on the studied amphipod population. It is also possible that fewer birds visit the area due to shifts in the feeding grounds or migration routes elsewhere or the loss of suitable feeding grounds with the rising sea level (e.g. Galbraith et al. 2002). This may reduce opportunities for parasite life cycle completion.

The consequences of global warming for the reproduction of amphipods are likely to be a key factor in this and comparable systems. According to sensitivity analyses and other model simulations (see "Results"), increasing amphipod reproduction parameters substantially prolonged the viability of the amphipod population. Increasing winter temperatures are particularly likely to benefit the amphipods' reproductive output and may therefore be an important mechanism for prolonged sustainability of the affected population. However, amphipods may only be positively influenced by increasing temperatures up to an optimum (Neuparth et al. 2002), and many intertidal organisms are thought to already live close to their thermal tolerance levels (e.g. Hofmann and Todgham 2010; Stillman and Somero 2000). With increasing temperatures, especially during warmer months, periods when temperatures may exceed the optimal temperature range are thus likely to become more frequent, with negative rather than positive consequences for the amphipods' reproductive output (Mouritsen et al. 2005; Wiklund and Sundelin 2001). However, little information is available on the thermal biology of *P. novizealandiae* amphipods, and thus the critical temperature threshold at which a positive effect on reproduction may become negative remains unclear at this stage. Based on Studer et al. (2010) and Studer and Poulin (2012), stressful temperature levels for amphipods are likely to be reached even under current conditions during warm periods in summer. Such periods may negatively affect not only their reproduction but also their immune system (Le Moullac and Haffner 2000; Roth et al. 2010), and thus enhance the impact of parasitism. Moreover, during an extreme event, in particular a heat wave, the combined effect of the parasite and the high temperatures would be expected to have an immediate and strongly negative effect, which may override any positive effect on amphipod reproduction that a gradual increase in mean temperatures may have.

Another limitation of the model was that mean daily temperatures across an entire year were used, ignoring daily temperature fluctuations in the microhabitat where parasite transmission takes place. However, the use of maximum daily temperatures would have exacerbated the high vulnerability of the amphipod population to temperature increases, and thus was not additionally explored. Instead, the effect of a large, short-term temperature increase (a heat wave event) was assessed. For this, the temperature increase at which the modelled amphipod population is predicted to collapse within a year was estimated (see "Results"). The increase of 14 °C found to be necessary to cause a collapse of the modelled population lies about 4 °C above current maximum temperatures occurring in the field (Studer and Poulin 2012). Due to the high temperature fluctuations in intertidal systems, such extreme values may eventually be reached, even if the mean temperature increase is only moderate. However, it remains unclear if such extremes would be sustained for long enough under natural conditions to have immediate drastic consequences (but see Jensen and Mouritsen 1992; Mouritsen et al. 1998).

Snail first intermediate hosts are a crucial component of the life cycle of *M. novaezealandensis*, as infection levels in snails determine the degree of parasite transmission pressure on second intermediate hosts. When compared to amphipod hosts, the snail population is expected to be relatively stable. However, the consequences of climate warming for the snails are uncertain, even though they may have important repercussions for the study system or the predictions made by the model. A moderate increase in temperature may increase the reproduction and development of snails, hence increasing the number of susceptible snail hosts present on a mudflat. Snail activity, parasite egg encounters and thus parasite recruitment into a snail population may also be increased. Moreover, parasite development within snails could also be accelerated, therefore enhancing the impact of the parasite on second intermediate crustacean hosts. In contrast, infected snails have a higher mortality than uninfected snails under prolonged exposure to high temperatures (Fredensborg et al. 2005). Under relatively high temperatures and especially during heat waves, mortality may occur, which may lower the density of infected snails in a high-prevalence area and thus reduce the impact of the parasite on second intermediate host populations. This range of possibilities of how each component of the model system may be affected, coupled with the complex framework in which the system is embedded, present major challenges when attempting to predict what might happen in reality on the Lower Portobello Bay mudflat.

In conclusion, the modelled amphipod population was found to be highly vulnerable to temperature increases, with most of the increases that are predicted to cause a population collapse lying within the range of temperatures expected for the study area over the coming decades. Although the exact temperature at which the amphipod population on Lower Portobello Bay collapses may differ from what is predicted by the current model, it seems likely that the collapse of this amphipod population is—consistent with Mouritsen et al. (2005)—not a question of if but rather when. Simulation models, despite being oversimplifications of what is happening in nature, provide a powerful tool to explore the possible impacts of climate change on ecological systems and to formulate predictions. However, long-term monitoring efforts are necessary to verify and detect the actual consequences for species, species interactions and entire ecosystems in nature.

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