GLOBAL CHANGE ECOLOGY

Kim N. Mouritsen · Daniel M. Tompkins · Robert Poulin

Climate warming may cause a parasite-induced collapse in coastal amphipod populations

Abstract Besides the direct impact on the general performance of individual organisms, the ecological consequences of climate change in terrestrial and marine ecosystems are expected to be determined by complex cascading effects arising from modified trophic interactions and competitive relationships. Recently, the synergistic effect of parasitism and climate change has been emphasised as potentially important to host population dynamics and community structure, but robust empirical evidence is generally lacking. The amphipod *Corophium volutator* is an ecologically important species in coastal soft-bottom habitats of the temperate North Atlantic, and commonly serves as host to microphallid trematodes that cause intensity-dependent and temperature-dependent mortality in the amphipod population. Using a simulation model parameterised with experimental and field data, we demonstrate that a 3.8°C increase in ambient temperature will likely result in a parasite-induced collapse of the amphipod population. This temperature increase is well within the range predicted to prevail by the year 2075 in the International Wadden Sea region from where the model data are obtained. Due to the amphipods' ecological importance, their population decline may impact the coastal ecosystem as a whole.

K. N. Mouritsen (✉)
Department of Marine Ecology, Institute of Biological Sciences, University of Aarhus, Finlandsgade 14, 8200 Aarhus N, Denmark
E-mail: kim.mouritsen@biology.au.dk
Tel.: +45-89424386
Fax: +45-89424380

D. M. Tompkins
Manaaki Whenua, Landcare Research,
Private Bag 11 052, Palmerston North, New Zealand

R. Poulin
Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand

Introduction

Climate changes have significant ecological consequences in both terrestrial and marine environments as is evident from the literature (Holmgren et al. 2001; Mysterud et al. 2001; Ottersen et al. 2001; Stenseth et al. 2002; Walther et al. 2002). Although climatic conditions influence the general performance of organisms directly, it is increasingly apparent that the impact recorded from populations to communities may be the result of complex cascading effects initiated by modified trophic interactions and competitive relationships (Ottersen et al. 2001; Stenseth et al. 2002; Walther et al. 2002). Moreover, two recent reviews have emphasised the potential importance of parasites and pathogens as mediators of host population dynamics under changing climatic conditions in general and global warming in particular (Harvell et al. 2002; Mouritsen and Poulin 2002a). The development and transmission rates of parasitic organisms are particularly sensitive to weather conditions (Harvell et al. 2002; Mouritsen and Poulin 2002a), and since parasites can regulate the abundance of their host population as well as influence the composition and structure of natural communities (Minchella and Scott 1991; Hudson et al. 1998; Tompkins et al. 2000, 2003; Mouritsen and Poulin 2002b, 2005), any influence of climate on parasitism is therefore important for natural communities and ecosystems. However, due to the lack of suitable host–parasite time-series, the impact of climatic changes on host–parasite systems and its ramifications to higher levels of organisation, have received only limited empirical attention.

In the absence of adequate time-series data, the combined effect of climate change and parasitism on host population dynamics may alternatively be elucidated in well-studied host–parasite systems using

simulation models to predict the outcome of forecasted climate change. Here, we have adopted this approach, focusing on the commonly studied coastal mud-shrimp *Corophium volutator* (Amphipoda) and its detrimental microphallid trematode parasites.

Corophium volutator is widespread in coastal soft-bottom habitats on both sides of the North Atlantic, with densities often approaching 100,000 individuals m^{-2} (Matthews et al. 1992; Gerdol and Hughes 1994; Mouritsen et al. 1997). As an important secondary producer, the amphipod serves as prey for a wide range of benthic invertebrates and demersal fishes as well as for the millions of migratory shorebirds that, twice a year, move along the west and east Atlantic migration corridors (Matthews et al. 1992; Mouritsen 1994; Wilson and Parker 1996). Due to its abundance and burying activity, the amphipod significantly alters the stability of coastal sediments, influencing benthic community structure and even coastal zone management (Jensen and Mouritsen 1992; Daborn et al. 1993; Gerdol and Hughes 1994; Mouritsen et al. 1998). The amphipod acts as second intermediate host for a guild of microphallid trematodes that in European waters use the mud-snail *Hydrobia ulvae* as first intermediate host, and shorebirds as definitive hosts (Mouritsen et al. 1997). These parasites are extremely common along European coastlines and the host–parasite system has been the subject of intensive studies in the International Wadden Sea during the last two decades. The system appears very sensitive to climatic fluctuations, because the transmission rates of larval parasites from snails to amphipods and the rate of parasite-induced amphipod mortality are strong positive functions of temperature (Jensen and Mouritsen 1992; Mouritsen and Jensen 1997; Mouritsen 2002). Hence, under a climate warming scenario the population of *C. volutator* is likely to decline. Such a simple prediction should not be made based solely on a couple of parameters, however, but needs to be validated by a complete analysis of the whole host–parasite system. In addition, the question is not simply whether climate warming would cause a parasite-mediated decline in the amphipod population, but whether it would be a partial decline or a total collapse, and what sort of temperature increase would be necessary for this to occur.

To explore these possibilities, we developed a simulation model, accounting for the entire life cycle of the parasite *Maritrema subdolum*, and the population of its intermediate hosts. The model was parameterised by experimental and observational data mainly from the Danish Wadden Sea region, where *M. subdolum* is the most common and ecologically well-known species of microphallid infecting *C. volutator*. Simulations were subsequently carried out using progressive temperature increases, up to the level predicted for the year 2075 in the Wadden Sea region by the high-resolution regional climate model (HIRHAM4) developed by the Danish Meteorological Institute, Copenhagen, in collaboration with the Max-Planck Institute for Meteorology,

Hamburg (Christensen et al. 1998, 2001, see coloured contour maps on http://www.dmi.dk/dmi/index/viden/drivhuseffekten.htm#drivhuseffekten-konsekvenser-anchor).

Materials and methods

Model formulation

The life cycle of *M subdolum* was modelled using a linked set of equations, simulating (on a daily basis, scaled to 1 m^2 of sediment surface) the accumulation of metacercaria (M) within amphipods (A), the population of flukes (H) in the definitive host, and the number of infected snails (I) present in the system. Although simulated in discrete time-steps, the model is presented here as rate equations for clarity:

$$\frac{dM}{dt} = I\lambda_I\beta_{IM} - \alpha_A M - \mu M/A \tag{1}$$

$$\frac{dA}{dt} = A\left(S\lambda_A e^{-\sigma A} - \alpha_A\right) - \mu \tag{2}$$

$$\frac{dH}{dt} = e^{-aH}\mu/A - \alpha_H H \tag{3}$$

$$\frac{dI}{dt} = \beta_{HI}\gamma_I H\lambda_H - \alpha_I I \tag{4}$$

In Eq. 1, λ_I is the number of cercariae produced per infected snail per day, and β_{IM} is the proportion of cercariae shed by infected snails that successfully transmit to amphipods, assuming that those failing to infect on the day that they are produced are lost from the system (Mouritsen 2002). In Eqs. 1 and 2, α_A is the daily mortality rate of amphipods, and μ is the number of amphipods ingested per day by definitive hosts. In Eq. 2, S is a logic switch used to toggle amphipod reproduction on (1) and off (0), λ_A is the rate of amphipod fecundity per individual per day during the breeding season, and σ denotes a density-dependent reduction in amphipod recruitment with increasing amphipod population size. In Eq. 3, α_H is the daily mortality rate of flukes in the definitive host, while a denotes a density-dependent reduction in the proportion of ingested parasites which successfully establishes in the definitive host with increasing fluke population size. Finally, in Eq. 4, β_{HI} is the proportion of parasite eggs excreted by birds that are ingested by the snail population at 15°C (see below), γ_I is a temperature-dependent modifier of the rate at which snails encounter parasite eggs (calibrated to 1 at 15°C), λ_H is the rate of fluke fecundity per parasite per day, and α_I is the daily mortality rate of infected snails.

Note that out of the hosts, only the amphipod population was dynamically modelled. Preliminary simulations indicated that the number of metacercariae (and hence the parasite impact on the amphipod population) is far more sensitive to changes in model parameters

than the number of either flukes or infected snails, with parasite impacts on the definitive host and snail populations being relatively benign in comparison. Parasite density-dependent constraints were only placed on the population of flukes in the definitive host, since there is no evidence that either the number of susceptible snails available for infection or the capacity of the amphipod population as hosts for metacercariae is limiting.

Model parameterisation

The model was parameterised, where possible, from sources in the literature and unpublished data. Both 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}) vary with temperature (T) in a non-linear fashion, based on experimental data corrected to field-relevant rates (Mouritsen and Jensen 1997; Meissner and Bick 1999a; Mouritsen 2002). The two relationships are best fitted ($r^2 > 0.99$) by the breakpoint regressions:

$$\lambda_I = 0 \qquad (T<13.4°C)$$
$$\lambda_I = 32.1T - 485.5 \quad (13.4°C<T<20.4°C)$$
$$\lambda_I = 23.9T - 320.6 \quad (T > 20.4°C)$$

and

$$\beta_{IM} = 0 \qquad (T<15°C)$$
$$\beta_{IM} = 0.0046T - 0.069 \quad (15°C<T<22.2°C)$$
$$\beta_{IM} = 0.025T - 0.51 \quad (T > 22.2°C)$$

Cercarial survival is likely to decrease with increasing temperatures. However, in species studied previously, slight decreases in cercarial survival at higher temperatures are generally offset by higher infectivity, such that transmission efficiency remains roughly constant within the temperature range used in our study (see Evans 1985; McCarthy 1999). In any event, cercarial survival is a component of the transmission efficiency parameter (β_{IM}) above, and is thus included in the model.

The daily mortality rate of infected snails (α_I) was set at 0.0022, based on a mean longevity of uninfected snails of 2 years and an infected mortality rate of 1.61 times the uninfected rate (Mouritsen et al. 1997, 1999).

The amphipod breeding season (toggled in Eq. 2 by S), was set from April through September (Wilson and Parker 1996), during which new individuals were produced at a daily rate (λ_A) of 0.52 per amphipod. This was based on a maximum of four broods in an amphipods lifetime and an average brood size of 36, assuming a sex ratio of 65% females (Fish and Mills 1979; Peer et al. 1986; Jensen and Kristensen 1990; Schneider et al. 1994). The daily mortality rate of amphipods (α_A) was a combination of both natural mortality, based on a maximum life span of 1 year (Hughes 1988), and parasite-induced mortality (Mouritsen and Jensen 1997), such that

$$\alpha_A = 0.0027 - 7.89 \times 10^{-6}M/A + 8.36 \times 10^{-5}(M/A)^2$$
$$(r^2 > 0.99)$$

The number of amphipods ingested per day by definitive hosts (μ) was set at 84 during April through May and August through October (migration periods), and 8.4 at all other times. This is based on observations by Mouritsen (1994) that the mean density of feeding Dunlins *Calidris alpina* on Danish Wadden Sea amphipod beds is 0.00713 m^{-2} during periods of peak migration, data indicating that density is only one-tenth of this at other times of the year (Laursen and Frikke 1984), and observations that Dunlins on amphipod beds feed on an average of 8.2 amphipods per minute (Gratto et al. 1984; Matthews et al. 1992; Mouritsen 1994; K. N. Mouritsen unpublished data). The Dunlin is by far the most abundant species of shorebird in the Wadden Sea region (Laursen and Frikke 1984).

The daily mortality rate of flukes in the definitive host (α_H) was estimated as 0.1, based on a 10-day life span (Ginetsinskaya 1988), while the rate of fluke fecundity per parasite per day (λ_H) was set at 40, based on studies of the related *Microphallus papillorobustus* (Wang and Thomas 2002). As with λ_I and β_{IM}, the rate at which uninfected snails encounter the parasite eggs produced and excreted from the definitive host onto the amphipod bed (β_{HI}) is also modified by temperature, due to changes in snail feeding activity (Hylleberg 1975). This is included in the model through the use of a modifier term (γ_I), calibrated to equal 1 at 15°C ($r^2 > 0.99$):

$$\gamma_I = 0 \qquad (T<10°C)$$
$$\gamma_I = 0.19T - 1.85 \quad (10°C<T<20.3°C)$$
$$\gamma_I = 0.237T - 2.785 \quad (T > 20.3°C)$$

Model simulation

Model properties were explored by numerical simulation. Data was not available to allow direct estimation of either the strengths of density dependence in amphipod (σ) and fluke (a) populations, or the proportion of parasite eggs excreted by birds that are ingested by the snail population at 15°C (β_{HI}). Hence, model behaviour was analysed in two steps to determine the parameter combination in which the model output conformed to observed characteristics of the system under consideration in the Danish Wadden Sea. First, the level of density-dependent reduction in amphipod recruitment with increasing amphipod population size (σ) which resulted in a maximum population size of 100,000 m^{-2} for uninfected amphipods at equilibrium dynamics was determined, corresponding to observed late summer peaks in density (Mouritsen 1994; Mouritsen et al. 1997). Second, the a/β_{HI} parameter region in which the population of infected snails peaked at 2750 m^{-2} at equilibrium dynamics, and fluke population size peaked at 1 m^{-2}, was then determined. This density of infected

snails again corresponds to field observations (Jensen and Mouritsen 1992; Mouritsen et al. 1997). Little is known about the intensity of *M subdolum* infections in Dunlins, although each square metre of amphipod bed supporting a single fluke in the definitive host seems reasonable since this translates to a maximum infection per bird of approximately 200 parasites. This magnitude of infection is realistic, given the recorded levels of infection for other microphallid species in other water-birds (Bishop and Threlfall 1974; Bush and Forrester 1976; Stock and Holmes 1987; Thul et al. 1985; Fredensborg et al. 2004), and the high prevalence of metacercariae in the amphipod population which the birds are feeding on (usually exceeding 50% and often approaching 100%; Meissner and Bick 1997; Mouritsen et al. 1997). Only one combination of a and β_{HI} satisfied these requirements (see Results) and were thus the parameter estimates used in subsequent simulations.

Daily temperatures used in all simulations were taken from a full year series of surface sediment temperatures obtained from the Dutch part of the International Wadden Sea, using the mean of daily maximum and minimum recordings (de Wilde and Berghuis 1978). The effect that an overall increase in temperature (i.e. climate change) has on the model output was explored by increasing the daily mean values year round by 1–6°C, in intervals of 0.1°C, and determining the new equilibrium dynamics. This is the range of values by which the average near-ground air-temperature in the International Wadden Sea region is expected to rise during the next 70 years under an A2 emission scenario (Christensen et al. 1998, 2001, IPCC 2000, see also http://www.dmi.dk/dmi/index/viden/drivhuseffekten.htm#driv huseffekten-konsekvenser-anchor). Since there are many sources of variability and possible errors in the model, sensitivity analyses were conducted in which all model parameters were varied singly ±50% around their estimated value.

Results

Parameter estimation

The level of density-dependent reduction in amphipod recruitment with increasing amphipod population size (σ), which resulted in a maximum population size of 100,000 m^{-2} for uninfected amphipods, was 5.0×10^{-5}. At this level, the minimum amphipod population size reached was 58,455 m^{-2}. When parasites were included in the simulation, the combination of a (fluke density dependence) and β_{HI} (the proportion of parasite eggs excreted by birds that are ingested by the snail population at 15°C) that gave the desired output (infected snails and flukes peaking at 2750 and 1 m^{-2}, respectively) was 12 and 0.30, respectively. At these parameter estimates a 5.6% depression in peak amphipod population size, and a 59% reduction in minimum population size, was observed (Fig. 1a), due to the additional mortality

caused by a mean intensity of infection in amphipods of 1.4–7.6 metacercariae over the yearly cycle (Fig. 1b).

Climate change

Increasing the year round mean daily temperatures rapidly reached the point where the amphipod population (and the parasite it supports) was lost from the model system (Fig. 2). At an increase of 3.8°C, the modelled amphipod population was barely avoiding extinction (declining each year from peaks of 87,587 individuals m^{-2} to just 191 individuals m^{-2}), while the mean intensity of metacercariae infection in amphipods was predicted to fluctuate more widely (0–37). At this level, the number of flukes and infected snails supported per square metre of sediment was predicted to fluctuate between 0.18–1.27 and 3503–5092, respectively. At increases above 3.8°C in the model, the higher maximum burden of metacercariae infection was predicted to drive the amphipod population to extinction.

The sensitivity analyses conducted indicated that this prediction of amphipod extinction is robust in the face
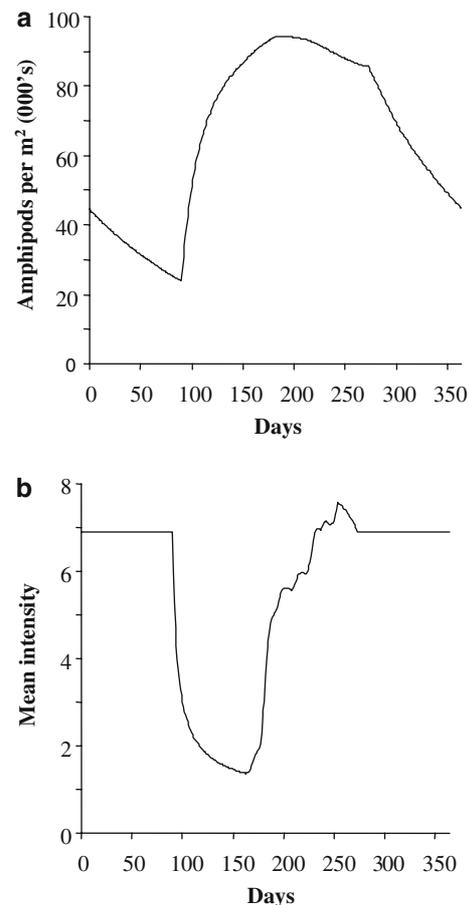

Fig. 1 a Yearly population trajectory of amphipods, at equilibrium model dynamics with parasites present. **b** Yearly fluctuations in the mean intensity of metacercariae infection in the amphipod populations. *Day 1* denotes January first
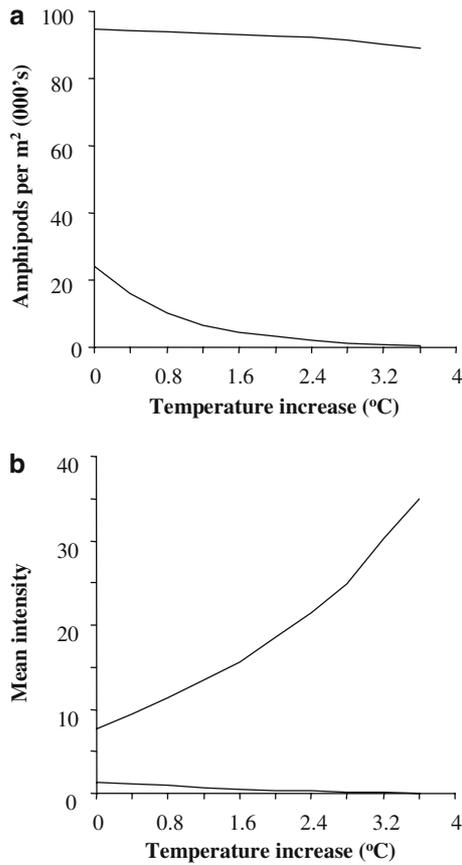
Fig. 2 Simulating the effect of climate change on the parasite/host system modelled. Estimated minimum and maximum levels predicted to occur over the course of the yearly cycle for both, **a** amphipod population sizes, and **b** mean intensity of metacercariae infection, are plotted in relation to the increase in mean temperature modelled

of variation in all model parameters (Table 1). Furthermore, for all levels of variation investigated in all parameters bar one, amphipod extinction was still predicted to occur within the range of temperature increases likely to be experienced in the International Wadden Sea region over the next 70 years. For amphipod mortality (α_A), the 8.0°C rise predicted to be required for amphipod extinction if α_A is only half its estimated value is

outside of this range. However, this parameter is a combination of both parasite-induced mortality and natural mortality. Since we are confident about our estimate of natural amphipod mortality (maximum lifespan of 1 year; Hughes 1988), a more appropriate sensitivity analysis would be one that only varies the parasite-induced mortality component. When this was conducted, a 50% drop in the rate of parasite-induced mortality only pushed the predicted temperature increase required for amphipod extinction out to 4.4°C.

Since increasing temperatures may affect amphipod reproduction (not included in the model developed here, due to lack of data), the temperature rise required to cause the amphipod population to be excluded from the model was explored in relation to even higher levels of λ_A (amphipod fecundity). However, even when λ_A was doubled, any increase in mean daily temperature over 4.5°C was still predicted to be sufficient to cause amphipod extinction (Fig. 3a); at a 4.5°C increase, the number of flukes and infected snails supported per square metre of sediment was predicted to fluctuate between 0.14–1.28 and 3880–5547, respectively, while the mean intensity of metacercariae infection in amphipods was predicted to fluctuate between 0 and 43.

If the effect of temperature on amphipod reproduction was assumed to be a lengthening of the breeding season from 6 to 8 months (March–October, instead of April–September), rather than an increase in λ_A, viable amphipod populations were maintained up to a temperature increase of 5.1°C (Fig. 3b). At this point, the number of flukes and infected snails supported per square metre of sediment was predicted to fluctuate between 0.49–1.36 and 4514–6285, respectively, while the mean intensity of metacercariae infection in amphipods was predicted to fluctuate between 2 and 80. The dynamics observed in these simulations were markedly different from those observed previously: rather than a gradual decrease in minimum amphipod population size leading to a point where the population was no longer viable (see Figs. 2, 3a), the amphipod population abruptly crashed, dynamics caused by the non-linearities in the model structure. In simulations in which both λ_A was doubled and the breeding season was extended, the

Table 1 Sensitivity analysis on all model parameters

Symbol	Parameter	−50%	−25%	±0%	+25%	+50%
λ_I	Cercariae production	5.0	4.3	3.8	3.4	3.1
β_{IM}	Cercariae transmission	5.0	4.3	3.8	3.4	3.1
α_A	Amphipod mortality	8.0	6.2	3.8	0.3	0.0
μ	Amphipod predation by birds	5.1	4.4	3.8	3.3	2.9
λ_A	Amphipod fecundity	2.8	3.4	3.8	4.0	4.2
σ	Amphipod density dependence	5.4	4.5	3.8	3.2	2.8
α_H	Fluke mortality	3.7	3.7	3.8	3.8	3.9
λ_H	Fluke fecundity	4.6	4.3	3.8	3.4	3.1
a	Fluke density dependence	2.8	3.4	3.8	4.2	4.4
β_{HI}	Egg ingestion by snails	4.6	4.3	3.8	3.5	3.3
α_I	Infected snail mortality	2.8	3.4	3.8	4.1	4.2

The temperature increase above which amphipod extinction is predicted by the model is presented for all parameters varied singly ± 50% around their estimated value. See methods for parameter descriptions
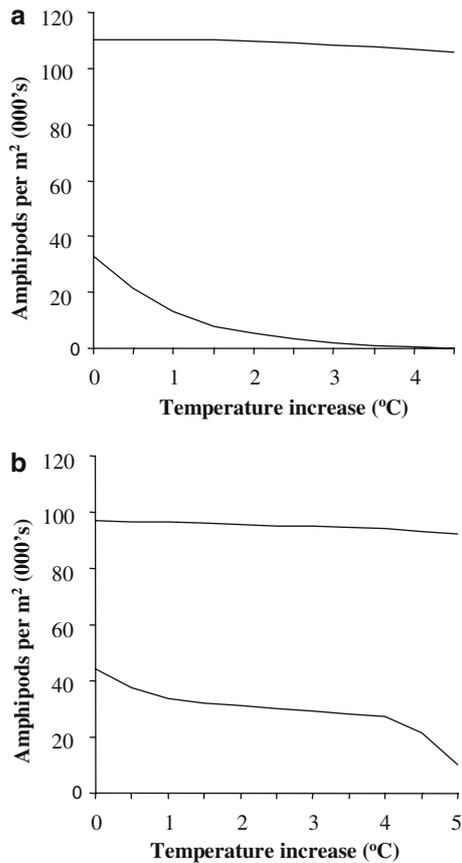
Fig. 3 Maximum and minimum amphipod population sizes (predicted to occur over the course of the yearly cycle) in relation to simulated temperature increases, when either, **a** the rate of amphipod fecundity per individual per day is doubled to 1.04, or **b** the amphipod breeding season is extended from 6 to 8 months

population remained viable up to an increase of 7.0°C, beyond the temperature rise predicted to occur over the next 70 years.

Discussion

Our models and their predictions do not take into account two general phenomena that may occur with climate warming: other ecological changes in the coastal ecosystem that may indirectly affect either the amphipods or their parasites, and rapid evolutionary changes in either hosts or parasites in response to increasing temperatures. There are no data available to allow one to evaluate the likelihood of these phenomena, and thus no way of including their effects in our models. These effects may influence our predictions, but are unlikely to alter them completely. Having said that, the most realistic model we can construct using the best available data predicts that it is not a matter of whether dense populations of *C. volutator* will crash due to parasite effects, in the face of increasing temperatures, but when. This prediction is unlikely to be due to errors in model construction or parameterization since it is highly robust in the face of

variation in model parameters (Table 1). Furthermore, in addition to the selection criteria for the parameter estimation procedure, four key characteristics of the model output lend weight to both its biological realism, and the validity of its predictions. First, Fish and Mills (1979) recorded, for the amphipod *C. volutator*, a percentage survival to reproduction of 10.5% at the point of peak-release of juveniles. In our infected model with no adjustments to daily temperature, this rate is reached at an amphipod population size of approximately 45,000 m^{-2}, as occurs during the first half of the breeding season (Fig. 1a). Second, in the same model, the mean intensity of metacercariae infection in amphipods is predicted to fluctuate over the course of each year between 1.4 and 7.6 (Fig. 1b). This closely agrees with the range of 2–8 observed at the modelled locality (Mouritsen et al. 1997). Third, also in the same model, the minimum amphipod population sizes reached is a realistic simulation of the spring densities observed (Mouritsen et al. 1997, 1998). Finally, the level of metacercariae infection in amphipods reached at the 3.8 temperature increase (just prior to the population crash in the model with normal amphipod reproduction; Fig. 2a) agrees with predictions of the average infection level at which infection would be lethal to the population (Mouritsen et al. 1997; Meissner and Bick 1999b).

The relatively minor changes in fluke and infected snail numbers (even an increase up to 6285 infected snails m^{-2} is still only approximately 30% of the snail population) prior to amphipod population crash confirm the preliminary observation that both fluke and infected snail numbers are far less sensitive to changes in model parameters than the number of metacercariae and hence the parasite impact on the amphipod population, justifying the decision not to model them explicitly. Also, the decision to parameterise the model to a fluke intensity of one individual supported per square metre of amphipod bed has little effect on the model output generated. Model exploration revealed how parameterising the model to different fluke intensities simply changes the estimated value of the parameter β_{HI} (the proportion of parasite eggs excreted by birds that are ingested by the snail population), with very little influence on the dynamics of infection in either snails or amphipods.

Both increasing amphipod fecundity and extending the amphipod breeding season, as possible additional effects of climate warming, raised the critical temperature necessary for a parasite-induced collapse of the *Corophium* population. However, a 3.8°C increase in ambient temperature will double the period of the breeding season (from 9 to 18 weeks) during which temperatures are substantially above the amphipod's preferred temperature of about 18°C (as determined through choice experiments; Meadows and Ruagh 1981; de Wilde and Berghuis 1978). Hence, since this may negatively affect reproduction, increasing temperatures will not necessarily increase fecundity. Furthermore, in addition to causing increased mortality, microphallid

infection may also reduce amphipod fecundity (although the evidence for this is inconclusive; Bick 1994; T. Jensen unpublished data). The overall reproductive output of the amphipod populations may thus actually decrease rather than increase under a climate warming scenario, lending less support to the alternative simulations shown in Fig. 3. The occurrence and behaviour of definitive hosts may also change as a response to climate warming. For instance, birds may arrive earlier in the spring and have longer residence times in the Wadden Sea during the autumn migration (e.g. Cotton 2003; Rehfisch et al. 2004, and references therein). This will extend the season during which the parasite life cycle can be completed, in turn elevating the density of infected first intermediate snail hosts, and thus working to lower the critical temperature for the amphipod die-off. Because of pelagic development and a broad latitudinal distribution from the White Sea to West Africa, the population of mud snails can in contrast be envisaged to be relatively stable under rising temperatures. In conclusion, we find the temperature increase of 3.8°C as the critical value for a collapse in the amphipod populations to be the most parsimonious result of ones generated in our simulations. This value is clearly within the range of temperature increases expected to prevail by year 2075 in the northern part of the International Wadden Sea, and is likely to be a conservative estimate, since our model does not include the increased variability predicted to accompany climate change.

In the absence of an adequate host–parasite time-series that might be used to substantiate a general relationship between large-scale climate fluctuations and fluke-mediated population dynamics of *C. volutator*, the occurrence of a population crash due to microphallid trematodes in the Danish Wadden Sea in spring 1990 may serve to emphasise the realism of our predictions (Jensen and Mouritsen 1992). At that time, a 80 ha *Corophium* bed vanished entirely over a mere 5 weeks in combination with ambient temperature 3–5°C above normal during the preceding couple of months. The amphipods did not return to the former bed area until the following year.

The present model was parameterised mainly by data from dense populations of *C. volutator*. Although such amphipod beds can occupy a substantial part of the intertidal zone of the Wadden Sea, there will be areas where the amphipods occur in low numbers, where the definitive hosts rarely feed, and where the prevalence of trematode infections in the sympatric snail population is subsequently low. Hence, *C. volutator* is unlikely to disappear entirely from the Wadden Sea region. Rather, dense assemblages of the amphipods may tend to disappear along with a general population decline as temperatures are rising. This scenario may have important ecological ramifications due not only to the amphipod's importance as prey for benthic invertebrates, fish and birds, but also to their stabilising effect on non-cohesive sediments. The disappearance of such amphipod beds will result in significant sea-bed erosion and, in turn, structural changes to the benthic animal and microflora community (Jensen and Mouritsen 1992; Mouritsen et al. 1998). In light of the expected sea-level rise (also as a consequence of global climate warming), and its predicted negative impact on salt marshes and anthropogenic coastal constructions, reduced sea-bed stability due to the absence of dense assemblages of amphipods will only serve to exacerbate problems.

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