

Effects of increasing temperatures on population dynamics of the zebra mussel *Dreissena polymorpha*: implications from an individual-based model

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Abstract Zebra mussels (*Dreissena polymorpha*, Pallas, 1771) have had unprecedented success in colonizing European and North American waters under strongly differing temperature regimes. Thus, the mussel is an excellent model of a species which is able to cope with increasing water temperatures expected under global change. We study three principle scenarios for successful survival of the mussel under rising temperatures: (1) no adaptation to future thermal conditions is needed, existing performance is great enough; (2) a shift (adaptation) towards higher temperatures is required; or (3) a broadening of the range of tolerated temperatures (adaptation) is needed. We developed a stochastic individual-based model which describes the demographic growth of *D. polymorpha* to determine which of the alternative scenarios might enable future survival. It is a day-degree model which is determined by ambient water temperature. Daily temperatures are generated based on long-term data of the River Rhine. Predictions under temperature conditions as recently observed for this river that are made for the phenology of reproduction, the age distribution and the shell length distribution conform with field observations. Our simulations show that temporal patterns in the life cycle of the mussel will be altered under rising temperatures. In all scenarios spawning

started earlier in the year and the total reproductive output of a population was dominated by the events later in the spawning period. For maximum temperatures between 20 and 26°C no thermal adaptation of the mussel is required. No extinctions and stable age distributions over generations were observed in scenario 2 for all maximum temperatures studied. In contrast, no population with a fixed range of tolerated temperatures survived in scenario 3 with high maximum temperatures (28, 30, 32°C). Age distributions showed an excess of 0+ individuals which resulted in an extinction of the population for several thermal ranges investigated.

Keywords Global change · Thermal tolerance · Life history · Temperature-day-degree model · River Rhine

Introduction

Current models of global-scale environmental change predict an average surface temperature increase of 3–5°C for the period 2070–2100 (IPCC 2001). This rate of change is unprecedented, and thus the consequences for species or even ecosystems are largely unknown.

Evidence for effects of ongoing global change on biodiversity is accumulating. A multitude of poleward or altitudinal shifts of terrestrial plants (Grabherr 1994; Wand et al. 1999; White et al. 2000; Marco and Páez 2000; Keller et al. 2000) and animals (Pounds et al. 1999; Parmesan et al. 1999; Thomas and Lennon 1999) have been observed. Communities of birds, reptiles and amphibians have been altered due to crashes in population sizes (Wake 1991; Pounds et al. 1999;

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Houlahan et al. 2000). Individual life cycles of species, too, are already affected by global change (Sanz 2003) as well as temporal patterns of populations (Sparks and Carey 1995; Sparks and Yates 1997; Roy and Sparks 2000; Both and Visser 2001; Sanz 2002).

The responses of various aquatic ecosystems are similar. They include species replacements in zooplankton communities (Möllmann et al. 2000), shifts in the seasonal abundance of phyto- and zooplankton (Straile 2000; Edwards et al. 2002), and shifts in emergence and body size of fish (Elliott et al. 2000; North 2005).

Many models rating the effect of global change on species chose an ecological niche approach (Peterson 2002). Ecological niche models describe a set of ecological conditions within which a species is able to maintain stable populations. To derive the potential distribution of a species under global change scenarios, this multidimensional space is projected onto the future landscape. For poikilothermic species, many ecological niche models focus only on temperature conditions. The future distribution of a species is predicted from lower and upper temperature limits which are required to complete the life cycle of the species (e.g. Hill et al. 1999). Whereas the ecological niche of a species is a very abstract description, other models approach the impact of global warming by modelling populations (e.g. Pöckl et al. 2003) and thus take into consideration the effect temperature may have on the population dynamics.

The zebra mussel (*Dreissena polymorpha*, Pallas, 1771) is an exceptionally successful invader for which the ecological niche concept is used (Nalepa and Schloesser 1993; Ramcharan et al. 1997; Orlova 2002). Over the past 200 years it has spread across Europe (Minchin et al. 2002). In the mid 1980s, it was introduced to the North American Great Lakes, and now inhabits several major rivers and inland lakes in eastern North America (Hebert et al. 1989). Laboratory and field experiments have demonstrated that water temperature has a dominating influence on the life history, reproduction and growth of the mussel (Nalepa and Schloesser 1993; Orlova 2002). The broad geographic distribution of the species might suggest either that it is able to tolerate broad temperature conditions or that it has rapidly evolved locally adapted genotypes. Since mussel populations differ geographically in their thermal performance (Lewandowski and Ejsmont-Karabin 1983; Jenner and Jansen-Mommen 1993; Orlova 2002), rapid adaptation to local ambient temperature conditions seems to be more likely than a general tolerance of a broad range of temperature conditions. There is also genetic evidence that local

adaptation processes take place (Marsden et al. 1996; Müller et al. 2001).

In this paper we chose *D. polymorpha* as the model species. Since this mussel has successfully invaded warmer geographical regions it is expected to cope with rising water temperatures that are predicted under global change. We investigate three principle alternatives that may permit successful future persistence of this species under rising water temperatures:

1. The existing thermal performance of the mussel is sufficient to fit future temperature conditions, thus no further adaptation is required.
2. A shift of its ecological niche towards higher temperatures is required, thus adaptation to increased temperatures is necessary (strategy 1).
3. An increase in its thermal plasticity is required, thus adaptation towards increased thermal plasticity is necessary (strategy 2).

For this test we developed an individual-based simulation model (IBM). In this IBM population development follows a temperature-day-degree model. To construct realistic annual temperature conditions for the modelled population, we deducted a mathematical model for daily water temperatures from long-term data of the River Rhine. In a first simulation study, we aimed to test whether population development generated by the IBM is in agreement with field observations obtained for the River Rhine. In a second simulation study we analysed survival under alternatives 1–3 under different situations of increased water temperatures.

Materials and methods

Biology of the zebra mussel

The zebra mussel *D. polymorpha* is a bivalve native to lakes and slow-moving rivers of the Caspian and Black Sea region. It grows rapidly, matures quickly, and produces large numbers of well-dispersed offspring. This may have been advantageous for the mussel to expand its distribution within Europe and North America using available natural and man-mediated vectors. The mussel can live from shoreline to depths of tens of metres. Maximum abundance is found at 1–5 m depth (Liakhovich et al. 1994). The mussel is able to reach very high densities; for example up to 30,000–40,000 mussels m⁻² have been reported for the River Rhine (Neumann 1990).

The zebra mussel is bisexual with iteroparous reproduction (Meisenheimer 1901). It is a gamogenetic

species with equal occurrence of sexes in populations (Orlova 2002). The adults release their gametes freely into the surrounding water. The mussel develops several pelagic larval instars: preveliger, D-stage veliger, post-D-stage veliger, and plantigrade. The metabolism of larvae changes during their development. After a lecithotrophic phase that starts with the preveliger stage and ends normally with the D-stage veliger, larvae switch to planktotrophy (Sprung 1993). The free-living larval instars promote the rapid dispersal of the species. The metamorphosed veliger settles on hard substrates of both lakes and river-beds. Mortality during the free-living stages and metamorphosis is high. The longevity of the mussel has been estimated in the range of 3–5 years. Temperature and salinity are the most important environmental abiotic factors limiting the recruitment and development of *D. polymorpha* (Orlova 2002).

The individual-based model

We focus in this paper on European mussel populations that are considered to differ from North American populations in their physiological responses to temperature (McMahon 1996). We chose the River Rhine as model system to check which of the three alternatives for thermal performance may permit a successful survival of the mussel under increased temperature conditions expected from global change. Ample empirical data required for model development and validation are available for this river and its mussel populations.

The model presented in this paper utilizes individual-based modelling as an extension of classical modelling approaches. This enables us to include the complete life cycle of the mussel in our model and to allow for variability of individuals and their interaction with the environment (DeAngelis and Gross 1992; DeAngelis and Mooij 2005). This modelling technique is suitable for the study of the out-of-equilibrium dynamics of populations, which may occur in the situations where the thermal performance of mussels is insufficient. We will be able to analyse these situations at the level of different life stages and compare them to field data at the respective level. However, a new more stringent definition of individual-based models that was introduced by Railsback (2001) and recently elaborated in the book of Grimm and Railsback (2005) focuses on the capability of individuals to interact with each other and with their environment. Our study of scenarios of adaptation for successful survival of mussels under rising temperatures may call for this alternative modelling technique. Nevertheless, we decided

to construct our model according to the classical approach because empirical data on the process of adaptation of zebra mussels to changed thermal conditions are not available (e.g. trade-offs). In agreement with DeAngelis and Mooij (2005) who judge the alternative definition (Railsback 2001; Grimm and Railsback 2005) as a new philosophical paradigm that reflects only two opposite poles of thinking we believe that the conclusions drawn from our model are not affected by our decision.

The stochastic IBM presented in this paper consists of two submodels: one for the environment inhabited by the zebra mussel and a second that describes population development.

The submodel environment of the IBM

The closed population of *D. polymorpha* modelled inhabits a water cube where juvenile and adult mussels are attached on the ground. Parameter K designates the carrying capacity of this artificial habitat and limits the total number of mussels settled on the ground (adults + juveniles).

To construct realistic annual temperature conditions for the water cube we analysed mean daily temperature values of the River Rhine at Koblenz (Rhine-km 590, downstream from Constance, Germany) recorded between 1 January 1978 and 31 December 2004. The deterministic seasonal trend of data was sufficiently described by the fitted function:

$$T(t) = m \left(\sin \left(\frac{2\pi(t-p)}{365} \right) + 1 \right) + t_{\min} (R^2 = 0.921, \text{ } ^\circ\text{C}) \quad (1)$$

with a displacement of the sine curve p of 120.68 ± 0.18 (SE, in Julian days), a minimum water temperature t_{\min} of 5.58 ± 0.01 (in $^\circ\text{C}$), an amplitude of the sine curve $m = 8.33 \pm 0.02$ (in $^\circ\text{C}$) and a mean water temperature of $(m + t_{\min}) = 13.91$ (in $^\circ\text{C}$).

However, the introduction of a term for long-term linear change in water temperature in the regression function (αt) was significant ($\alpha = 0.0002 \pm 0.0000$). The explained variance ($R^2 = 0.926$) was slightly improved by this alternative model ($m = 8.33 \pm 0.02$; $p = 120.60 \pm 0.17$; $t_{\min} = 5.58 \pm 0.01$). This suggests that the mean water temperature of the River Rhine had increased about 1.90°C within the last 26 years most likely due to ongoing global change. Nevertheless, for our simulations we applied regression function 1 to implement the annual course of temperature in the artificial habitat. Increased mean annual temperatures are assumed in the simulation study.

The submodel population development of the IBM

The simulation of population development was performed in time steps of 1 day. The zebra mussel's population dynamics is implemented as a temperature-day-degree model (Kemp and Onsager 1986; Griebeler and Gottschalk 2000). The basic idea of this modelling approach is that individuals of a population accumulate temperature values during their development and pass to the next life stage when they have accumulated specific minimum temperature inputs. For simplicity, we distinguish only five instars of the zebra mussel in our model: eggs, lecithotrophic larvae, planktotrophic larvae, juvenile mussels and adult mussels. The sex of individuals is not distinguished, because the species is gamogenetic (Orlova 2002).

Development of eggs

Reproduction in zebra mussels is limited to water temperatures above 12°C (Borcherding 1991). Under these conditions, egg development lasts 1 day according to the laboratory measurements of Sprung (1987). This duration of the egg phase (A_{egg}) and this temperature threshold for reproduction ($T_{\text{reproduction}}$) are assumed in our model. Eggs die in our model with a mortality rate of 100% when the water temperature is below $T_{\text{reproduction}}$ because successful fertilisation of eggs is not possible below this threshold (Sprung 1987).

Development of lecithotrophic larvae

Sprung (1987) has shown that lecithotrophic larvae need 4 days at 12°C or 2.4 days at 20°C, respectively, to pass to the planktotrophic stage. These values lead to the minimum temperature sum (TS) input of 48°C days ($TS_{\text{lecithotrophic}}$), which we suppose in our model for the transition between the lecithotrophic and the subsequent planktotrophic phase.

Development of planktotrophic larvae

The planktotrophic stage takes between 2.5 and 4 weeks depending on temperature conditions (Sprung 1987). Within this time larvae have increased their size by about 0.13 mm (Borcherding and de Ruyter van Steveninck 1992). Borcherding and de Ruyter van Steveninck (1992) observed that larvae increased their length 0.0076 mm day⁻¹ at an average water temperature of 19.5°C during downstream transportation in the River Rhine. Thus, larvae need 17 days at 19.5°C to increase their length and complete the planktotrophic phase. Based on this field observation we assumed a

minimum TS input of 331.5°C days for planktotrophic larvae ($TS_{\text{planktotrophic}}$) before they metamorphose into juvenile mussels.

At the end of the planktotrophic phase we additionally considered a constant mortality rate (m_{larvae}) of 0.999913 which was observed by Sprung (1993) under the environmental conditions of the River Rhine. This rate determines the final transition of a planktotrophic larva if its TS input has exceeded the limit $TS_{\text{planktotrophic}}$. The settlement size of a young mussel [shell length (SL); $SL_{\text{settlement}}$] is assigned randomly with a value ranging from 0.2 up to 0.3 mm following the field observations of Borcherding and de Ruyter van Steveninck (1992).

Development of juvenile mussels

Juvenile mussels increase their shell length (SL) depending on the ambient water temperature (T). Larger mussels show larger temperature-dependent SL increments [$SLI(T, SL)$] than smaller ones. Smit et al. (1993) showed for mussels in the River Rhine and in some associated lakes that daily shell growth [$G(T)$ in mm] is temperature dependent according to function

$$G(T) = \begin{cases} 0.0063(T - 3)^2 & T > 3 \\ 0 & T \leq 3 \end{cases}, \quad (2)$$

with a minimum temperature of 3°C needed for SL to occur.

The influence of SL on growth is implemented as a negative exponential function which has been corroborated in several empirical studies on mussel populations in the River Rhine (Jantz and Neumann 1992; Smit et al. 1992; Jantz 1996). Assuming a maximum size for mussels of 35 mm found in this river (SL_{max} ; Neumann 1990) together with an arbitrary small shell growth increment of 10⁻⁶ mm day⁻¹ for such mussels this leads to the function:

$$SLI(T, SL) = G(T)e^{(-aSL)} \text{ with } a = \frac{-\ln\left(\frac{10^{-6}}{G(T)}\right)}{35}, \quad (3)$$

which describes the daily SL increment of mussels depending on shell size in millimetres and the ambient water temperature in °C in the IBM.

Juvenile mussels pass to the adult stage when they have reached the minimum SL of 8 mm (SL_{adult} ; Jantz and Neumann 1998). At this time each young mussel is assigned a random life span. Individual lifetime (L) of mussels is exponentially distributed with a mean of 2.5 years (L_{mean}). This L of mussels was found by Borcherding and de Ruyter van Steveninck (1992)

under the environmental conditions of the River Rhine.

Development of adult mussels

Shell growth of adults depends on both water temperature and SL and it follows also functions 2 and 3 in the IBM. In Europe, the zebra mussel is characterised by annual reproduction (except for the most northern population, Orlova 2002). Adults have two spawning periods as observed for the River Rhine: one from April to July and the second one in August. Thus, each adult individual has two randomly assigned but fixed spawning dates [first spawning date (S_1), and second S_2] in our model. These two dates correspond to two mature fractions of oocytes that Borcharding (1992) observed in the River Rhine within the year for the major fraction of females. Spawning requires water temperatures above 12°C (T_{spawning} , Borcharding 1991). This temperature threshold will lead to a delay of early individual first spawning events (S_1) until this minimum water temperature is reached. For late individual S_2 , however, water temperatures below this limit at S_2 can prevent the second spawning. The number of eggs that are produced per spawning event by an adult [Eggs(SL)] depends on the SL of the individual and follows a function derived from laboratory measurements by Sprung (1991):

$$\text{Eggs}(\text{SL}) = 10^6 \times 0.606\text{SL}^{4.42}. \quad (4)$$

Effect of temperature on life stages

The published maximum temperature values tolerated by European mussels vary, ranging from 100% mortality at 29°C (Lewandowski and Ejsmont-Karabin 1983) to 100% mortality at 34°C (Jenner and Jansen-Mommen 1993) with a mean of 31°C (Orlova 2002). The optimum temperature for mussels of different geographical regions ranges between 18 and 22°C (Schneider 1992; McMahon 1996). To implement the thermal plasticity of mussels we assumed a modified normal distribution for survival under different temperature conditions (Fig. 1, Schmidt-Nielsen 1997). The mean of the normal distribution corresponds to the optimal temperature (T_{opt}). Its SD (σ_T) is used to implement the strength of thermal stress caused by temperatures higher than the optimal ones. The function value at a given temperature $f(T)$ divided by the function value of the mean $f(T_{\text{opt}})$ determines the probability with that an individual survives. The division of function values $f(T)$ by $f(T_{\text{opt}})$ guarantees that

under T_{opt} conditions no mortality will occur. This model for temperature tolerance is applied at each simulated day when water temperature is higher than T_{opt} . We assumed this temperature-dependent survival probability of an individual for each of the five instars modelled. Mortalities of life stages caused by temperatures lower than T_{opt} are not explicitly addressed in our model. They are already implicitly included in the mortalities assumed for life stages and the L of mussels (Table 1) that were observed under present temperature conditions of the River Rhine.

Density regulation

K limits the number of settled juvenile and adult mussels. Competition for space has been shown to limit the population density of the zebra mussel (Borcharding and Sturm 2002; Lauer and Spacie 2004). We assumed a ceiling model for density regulation that is applied each simulated day. On each day attached mussels can die by chance because they exceed their individual L or die due to thermal stress. Thus, a young mussel that has completed the planktotrophic phase is only able to settle successfully if the actual total number of mussels attached is smaller than the K . Otherwise it dies in our IBM.

Simulation studies performed

We assumed in all simulations that the parameter combination ($T_{\text{opt}} = 20, \sigma_T = 5$) corresponds to the thermal tolerance of the mussels living currently in the River Rhine. In the following text we will refer to this

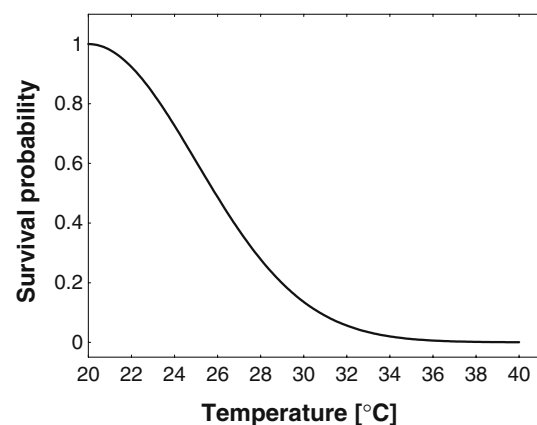


Fig. 1 Model for thermal performance. We assumed a modified normal distribution for the survival probability of an individual under a given temperature value above the optimal temperature (T_{opt}). Here, the survival function is shown for the standard thermal tolerance ($T_{\text{opt}} = 20 = \text{mean}$, $\sigma_T = 5 = \text{SD}$). Survival under temperatures below T_{opt} is 100%

Table 1 Model parameters assumed

| Parameter | Meaning | Value |
|------------------------------|--|---|
| t | Day of the year | (0, 1, ...) |
| $T(t)$ | Temperature value of day t | Function 1 |
| K | Carrying capacity | 10,000 attached mussels |
| $T_{\text{reproduction}}$ | Minimum temperature required for spawning and egg development | 12°C (Borcherding 1991) |
| A_{egg} | Duration of egg phase | 1 day (Sprung 1987) |
| $TS_{\text{lecithotrophic}}$ | Minimum temperature sum input needed to complete lecithotrophic phase | 48°C days (Sprung 1987) |
| $TS_{\text{planktotrophic}}$ | Minimum temperature sum input needed to complete planktotrophic phase | 331.5°C days (Borcherding and de Ruyter van Steveninck 1992) |
| m_{larvae} | Mortality rate of larvae, covers egg and larval development | 0.999913 (1 – 0.000087, Sprung 1993) |
| $SL_{\text{settlement}}$ | Settlement size of young mussels | ∈ (0.2; 0.3) mm; randomly assigned for each young mussel, uniformly distributed (Borcherding and de Ruyter van Steveninck 1992) |
| SL_{adult} | Minimum shell length of adults | 8 mm (Jantz and Neumann 1998) |
| SL_{max} | Maximal shell length of mussels | 35 mm (Neumann 1990) |
| $SLI(SL, T)$ | Shell length increment of mussels | Function 3 |
| L_{mean} | Mean lifetime of mussels | 2.5 years or 913 days (Borcherding and de Ruyter van Steveninck 1992) |
| L | Lifetime of a mussel | Randomly assigned, exponentially distributed with mean L_{mean} |
| (S_1, S_2) | Spawning dates of adults | (1 April–31 July); (1–31 August); randomly assigned, uniformly distributed (Borcherding 1992; Smit et al. 1993) |
| T_{spawning} | Minimum temperature required for spawning | 12°C (Borcherding 1991) |
| $\text{Eggs}(SL)$ | Number of eggs produced | Function 4 (Sprung 1991) |
| T_{opt} | Optimal temperature conditions | 20°C; for the standard thermal tolerance (Schneider 1992) |
| σ_T | Strength of thermal stress under temperatures higher than T_{opt} | 5; for the standard thermal tolerance, corresponds to ca. 100% mortality at 31°C (Jenner and Jansen-Mommen 1993) |

thermal performance as standard thermal tolerance. Schneider (1992) and McMahon (1996) have reported an average T_{opt} of 20°C for European zebra mussels. A thermal tolerance σ_T of 5 corresponds to ca. 100% mortality at 31°C reported by Orlova (2002) for European mussel populations.

We performed two simulation studies. In the first one we tested whether population dynamics generated by our model are in agreement with field observations obtained for the River Rhine. In the second we considered: (1) mussels with the standard thermal tolerance, and (2) mussels of the two strategies, in order to assess the impact of rising water temperatures on population survival. For strategy 1 we analysed zebra mussels that shift their T_{opt} towards higher values but retain a specific thermal tolerance (σ_T). For strategy 2 mussels keep an T_{opt} but increase the thermal tolerance (σ_T) to cope with the warmer temperature conditions.

We considered in all simulations a population inhabiting a water cube with a K of 10,000 mussels. Population development was always simulated over 100 years and repeated 10 times in order to obtain

estimates for population survival rates. All simulations were started with 10,000 adult mussels on 1 January. The initial population consisted of adult individuals of random age (in days, drawn from an exponential distribution with mean L_{mean}), a randomly chosen SL (out of 8–35 mm, drawn from a uniform distribution), two randomly assigned S s (1 March–31 July for S_1 and 1–31 August for S_2 , drawn from uniform distributions) and a random life time ($>$ age, in days, drawn from an exponential distribution with mean L_{mean}).

The number of individuals for each life stage was recorded daily in all simulations. In each October of a simulated year, we recorded the SL distribution of 0+, 1+, 2+ and $\geq 3+$ mussels.

Simulations for model validation

To validate our model, we assumed zebra mussels of standard thermal tolerance. The annual course of water temperature was generated based on function 1 and was chosen to be similar to that of the River Rhine with maximum temperatures ranging from 20 to 25°C

(Mehlig et al. 2004). These maxima correspond to values for parameter m ranging from 7.5 to 9.37 or mean water temperatures ($m + t_{\min}$) ranging from 13.08 to 14.95°C, respectively. To implement yearly differences in the annual course of the water temperature we chose a random value for m out of 7.5 to 9.37 at the beginning of each simulated year. Parameter values for the displacement of the sine curve p (120.68) and the minimum water temperature t_{\min} (5.58) were always kept constant.

Thermal performance of mussels under rising water temperatures

To test the three alternatives for thermal performance under rising water temperature, we considered seven amplitudes, m (function 1), determining the annual regime of water temperature. Values assumed for parameter m were 7.5, 8.25, 9.0, 9.75, 10.5, 11.25 and 12°C, which result from our temperature model (function 1) in maximum temperatures of 20, 22, 24, 26, 28, 30 and 32°C or mean water temperatures ($m + t_{\min}$) of 13.08, 13.83, 14.58, 15.33, 16.08, 16.83, 17.58, respectively. Maximum temperatures in the range of 20–25°C (Mehlig et al. 2004) are common in the River Rhine whereas 28°C is exceptional (e.g. summer 2003, Mehlig et al. 2004). Parameter values for p (120.68) and t_{\min} (5.58) were kept constant under all regimes of water temperature tested.

To check the existing thermal performance of the mussel under increasing temperature conditions we simulated populations of mussels with the standard thermal tolerance ($T_{\text{opt}} = 20^\circ\text{C}$, $\sigma_T = 5$) by considering these seven temperature regimes (alternative 1).

For strategy 1 where mussels adjust their T_{opt} , the latter was set to the respective maximum temperature in each of the seven temperature regimes examined. Each T_{opt} was studied for 3 SDs (σ_T : 1, 5, 20) implementing the strength of thermal stress caused by deviation from the T_{opt} . This resulted in 21 ($= 7 \times 3$) simulation scenarios.

For strategy 2 where mussels adjust their thermal tolerance the T_{opt} was set to 20°C in all seven temperature regimes considered. SDs σ_T assumed in each temperature regime tested for the thermal tolerance were 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 15 and 20. These tolerances correspond to about 100% mortality (survival probability $< 10^{-6}$) at 25, 27, 29, 30, 31, 32, 33, 34, 35, 36, 39 and 42°C. In total, we investigated for the second strategy 84 ($= 7 \times 12$) simulation scenarios. However, the range of thermal tolerances examined for strategy 2 includes also the standard thermal tolerance ($T_{\text{opt}} = 20$, $\sigma_T = 5$, alternative 1).

Results

Simulations for model validation

The populations never became extinct in the simulations where we assumed zebra mussels of standard thermal tolerance under temperature conditions similar to the River Rhine. The average number of sessile mussels (attached juveniles and adults) per day over 100 years was 9,456.9 mussels. The overall mean daily number of eggs produced per attached mussel was 45.7 eggs. Spawning started in the simulations on average on 12 April (earliest date 8 April, latest date 22 April) and ended on average on 22 October (earliest date 9 October, latest date 29 October). The phenology of larvae showed a clear first peak in the middle of May and a clear second peak in August (Fig. 2). The total reproductive output of the first spawning period was larger than in the second. Thus, the ratio of the total number of eggs produced in the first spawning phase and the total number produced in the second spawning phase was 1.53. The average SL of mussels in October was 19.56 mm for all mussels, 18.40 mm for 0+, 19.49 mm for 1+, 19.87 mm for 2+ and 20.96 mm for older individuals. The age distribution of the simulated mussel population and its SL distribution are shown in Fig. 3.

Thermal performance of mussels under rising water temperatures

Simulations with adjusted T_{opt} (strategy 1)

The populations never became extinct when the optimum temperature of mussels coincided with the maximum water temperature assumed. The mean number of sessile mussels per day increased hyperbolically with

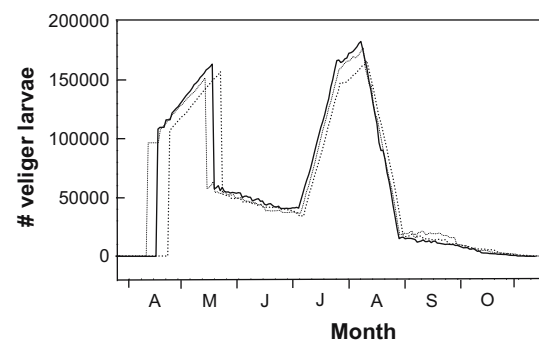


Fig. 2 Phenology of veliger larvae observed in the simulations for model validation. *Solid line* Average annual pattern, *dotted lines* extreme annual patterns. A M J J A S O April May June July August September October, #number of

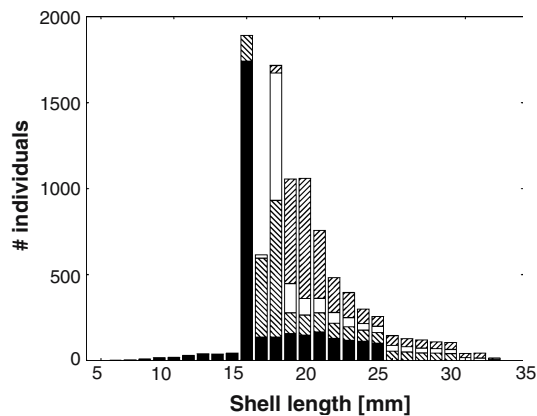


Fig. 3 SL distribution and age distribution of mussels in the simulations for model validation. *Filled bars* 0+ mussels, *right-hatched bars* 1+ mussels, *open bars* 2+ mussels, *left-hatched bars* 3+ and older mussels

increasing water temperatures for a fixed thermal tolerance [worst case $\sigma_T = 1$: $n = 7$ (number of temperatures regimes studied, #TR), $R = 0.904$, estimated limit of sessile mussels per day = 9,719.9]. The mean daily number of eggs laid per attached mussel increased exponentially with increasing mean water temperature for a fixed thermal tolerance [worst case $\sigma_T = 1$: $n = 7$ (#TR), $R = 0.999$]. Reproduction started earlier in the year when water temperatures increased (20°C, 27 April; 30°C, 18 March) and this increase was independent of the thermal tolerance value assumed. The shift towards the beginning of the year followed a linear model [$n = 7$ (#TR), $R = 0.993$, slope = -3.2 with $P < 10^{-6}$, axis intercept = 178.6 with $P < 10^{-6}$]. The end of the reproduction period was shifted towards the beginning of the year. This shift followed again a linear model [worst case $\sigma_T = 5$: $n = 7$ (#TR), $R = 0.979$, slope = -2.1 with $P < 0.0005$, axis intercept = 280.2 with $P < 10^{-6}$]. The length of the reproduction period increased hyperbolically with increasing water temperatures for a fixed thermal tolerance [(worst case $\sigma_T = 1$: $n = 7$ (#TR), $R = 0.828$, estimated limit of the period in days = 164.3]. The ratio defined as the total number of eggs produced in the first phase divided by the number generated in the second decreased linearly with increasing water temperatures for all thermal tolerance values assumed [worst case $\sigma_T = 5$: $n = 7$ (#TR), $R = 0.989$, slope = -0.1 with $P < 0.00005$, axis intercept = 3.0 with $P < 10^{-6}$]. However, the reproductive output in the first phase was always larger than in the second. The age distribution of the population observed in October was neither affected by the thermal tolerance considered nor by the water temperatures (overall χ^2 -test for homogeneity: $P = 0.984$). The mean SL of mussels, and lengths of 0+, 1+, 2+ and $\geq 3+$

mussels, however, all increased in a sigmoid manner with increasing water temperatures [worst case $\sigma_T = 5$, $\geq 3+$ mussels: $n = 7$ (#TR), $R = 0.987$, maximum mean length estimated = 21.34 mm].

Simulations with adjusted thermal tolerance σ_T (strategy 2)

The mussel populations never became extinct when the maximal water temperature was below 28°C ($m = 10.5$) for any of the thermal tolerance values studied (σ_T). In contrast, for maximal temperature values of 28, 30 and 32°C the populations were always extinct after 100 years for $\sigma_T = 1$. For $\sigma_T > 1$, populations with a broader thermal tolerance (σ_T) had a higher chance of becoming extinct than those with a smaller tolerance under these temperature conditions (Fig. 4). Populations of zebra mussels with the standard thermal tolerance ($\sigma_T = 5$, alternative 1) became extinct 7 times for a maximum temperature of 28°C but they always survived under all other temperature regimes studied.

The average daily number of mussels increased with increasing temperatures under temperature conditions with maximal temperatures smaller than 28°C. However, under warmer temperature conditions these numbers were inversely proportional to the extinction frequency. The average number of eggs produced per mussel per day increased exponentially with increasing water temperatures for $\sigma_T > 1$ [worst case $\sigma_T = 2$: $n = 7$ (#TR), $R = 0.992$]. In the case of $\sigma_T = 1$, however, the

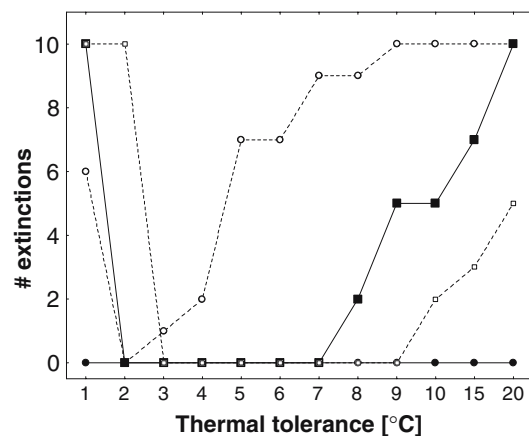


Fig. 4 Number of extinctions out of ten simulations observed depending on thermal tolerance (σ_T) and maximal water temperature. Simulation results for strategy 2 with $T_{opt} = 20$. *Filled circles* Maximal water temperatures ranging between 20 and 26°C, *open circles* maximal water temperatures to 28°C, *filled squares* maximal water temperatures to 30°C, *open squares* maximal water temperatures to 32°C

reproductive output only increased until a maximal temperature of 28°C was reached and then decreased monotonically when temperatures further increased. As in the simulations of the first strategy, spawning started in all simulations earlier in the year under increasing water temperatures (20°C, 27 April; 30°C, 18 March). This shift towards the beginning of the year followed a linear model [$n = 7$ (#TR), $R = 0.993$, slope = -3.2 with $P < 10^{-6}$, axis intercept = 178.5 with $P < 10^{-6}$]. In the simulations with maximum temperatures below 28°C, spawning ended on average at the end of August (22–31 August). The latest date observed was 20 September (for maximum temperature = 26°C, $\sigma_T = 2$). The ratio of the total number of eggs produced in the first spawning period to the number produced in the second differed highly between the scenarios (Fig. 5). It revealed a strong shift in spawning towards the first phase for $\sigma_T = 1$ and a shift towards the second phase for the larger thermal tolerances studied. An increase in water temperature affected the age structure of the populations in all simulations. The higher the water temperatures, the more 0+ mussels were found in October and the fewer old mussels were observed. Small thermal tolerances led to a rapid shift in the age distribution of the populations for increasing water temperatures (Fig. 6, $\sigma_T = 1$) whereas large tolerance values caused slower shifts (Fig. 6, $\sigma_T = 20$). The mean SL of mussels, and lengths of 0+, 1+, 2+ and $\geq 3+$ mussels, increased sigmoidally with increasing water temperatures [mean length: worst case $\sigma_T = 8$, all mussels: $n = 7$ (#TR), $R = 0.982$, maximum mean length estimated = 45.414 (mm)] in all simulations.

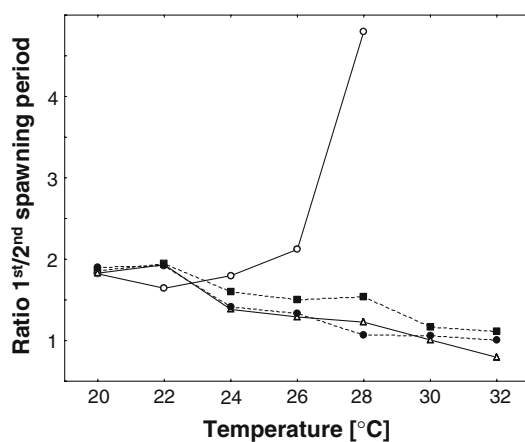


Fig. 5 Ratio of the total number of eggs produced in the first spawning period to that generated in the second for different thermal tolerances (σ_T) and maximal water temperatures. Simulation results for strategy 2 with $T_{opt} = 20$. Open circles $\sigma_T = 1$, filled squares $\sigma_T = 2$, open triangles $\sigma_T = 5$, filled circles $\sigma_T = 8$, filled squares $\sigma_T = 20$

Discussion

The objective of our simulation study was to derive which of three principle alternatives for thermal performance are more suitable for survival of the zebra mussel under rising temperatures expected from global change. However, whether a specific population will be able to switch to the most effective strategy depends finally on evolutionary constraints such as existing genetic variability or trade-offs limiting the adaptation required.

No extinctions and stable age distributions over all generations simulated were observed when mussels shifted their T_{opt} towards the higher maximum temperature (strategy 1). Although T_{opt} s of mussels from different geographical regions seem to show low variance (Schneider 1992; McMahon 1996) the feasibility of this strategy for the mussel may be supported by the predicted unimodal SL distributions that are frequently observed in nature under various temperature conditions (Table 2).

Our simulations show that mussels with an optimum temperatures of 20°C are able to survive under warming scenarios with maximum temperatures below 26°C. Survival requires neither a shift in the optimum temperature (strategy 1) nor an increase in the thermal tolerance (strategy 2). This may have aided the rapid spread of this invasive species all over Europe and corroborates that thermal performance is sufficient at least for such temperature conditions. For higher maximum temperatures, however, frequent extinctions occurred when the standard thermal tolerance (alternative 1) or strategy 2 was assumed. Consequently, neither the existing thermal performance is sufficient nor the strategy of solely increasing thermal tolerance seems to be suitable to cope with the high changes in temperature conditions predicted by IPCC (2001). Extinctions found in our simulations under warming scenarios with maximal temperatures higher than 26°C are supported by the mass mortality observed in the River Rhine during the exceptionally warm summer of 2003 with a maximum water temperature of 28°C (Mehlig et al. 2004). However, the dehydration of non-submerged mussels may have added to this remarkably high mortality.

Model validation

We assume that the prognoses of our IBM are reliable because they are in close agreement with field observations. The model predicts that under long-term annual temperature conditions, similar to those of the River Rhine, veliger larvae start to appear between 8

Fig. 6 Age groups of mussels observed depending on thermal tolerance (σ_T) and maximal water temperature. Simulation results for strategy 2 with $T_{opt} = 20$. Filled bars 0+ mussels, right-hatched bars 1+ mussels, open bars 2+ mussels, left-hatched bars 3+ and older mussels

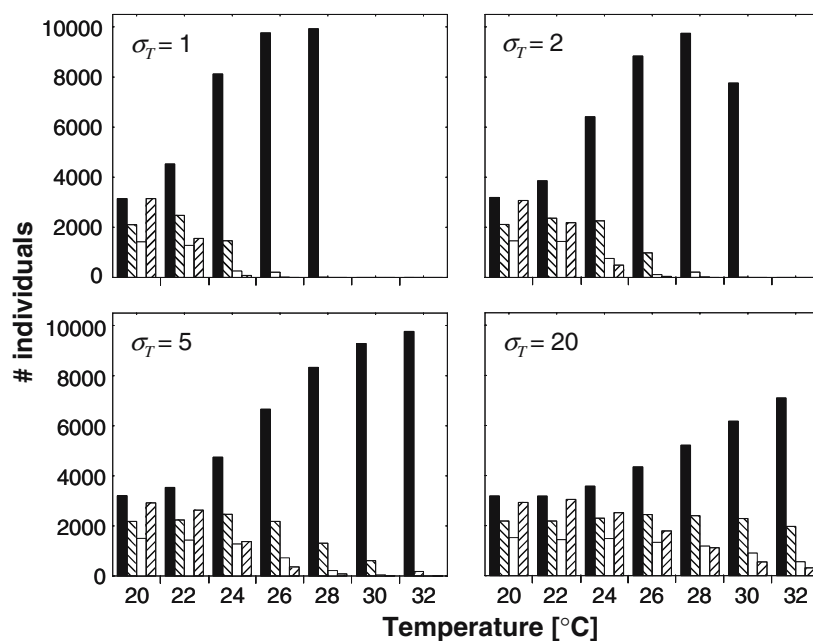


Table 2 SL distributions observed in the River Rhine

| Site | SLs (mm) | Distribution type | Source |
|----------------------------|----------|--------------------------------------|--------------------------|
| Dutch lower Rhine | 2–25 | Population: unimodal 0+: unimodal | Smit et al. (1993) |
| Grietherort (Rhine-km 845) | 2–30 | Population: unimodal 0+: unimodal | Jantz and Neumann (1992) |
| Helmlingen (Rhine-km 313) | 2–28 | Population: skewed | Jantz (1996) |
| Basel (Rhine-km 168–71) | 2–25 | Population: unimodal | Jantz (1996) |

and 22 April and are no longer present between 9 and 29 October depending on temperature conditions. The model, too, predicts a clear first peak of planktotrophic larvae in the middle of May and a clear second peak in August (Fig. 2).

Field data from the River Rhine conform well with these predictions (Table 3). Even the later spawning period (June up to and including October, Einsle 1973) in Lake Constance is consistent with the model’s predictions. The River Rhine flows into Lake Constance (the outlet of Lake Constance corresponds approximately to Rhine-km 0) and the lake has colder water temperature conditions. Reproduction started earlier in the year in all simulations when the mean water temperatures increased.

The overall SL distributions and those of the four age classes studied in the simulations with temperature conditions similar to the River Rhine were unimodal (Fig. 3) and correspond to those prevailing in this river (Table 2). Overall lengths predicted in these simulations ranged between 8 and 34 mm (mean = 19.56 mm). Means for 0+ mussels were 18.40 mm, 19.49 mm for 1+, 19.87 mm for 2+ and 20.96 mm for

older individuals. Overall SLs observed at different sites along the River Rhine coincide with the range predicted by our model (Table 3). The variance of SLs observed in simulations, however, is lower than those observed for natural populations. This, however, may be explained by the downstream drift of larvae. A population at a specific site consists of individuals that originate from different sites upstream with different temperature conditions that determine individual age and growth of larvae (Borcherding and de Ruyter van Steveninck 1992).

However, mean SLs seem to be wrongly estimated by our model for all age groups. Mean shell sizes recorded for 0+ individuals in the River Rhine range between 10.5 mm (Jantz and Neumann 1992) and 12 mm (Jantz and Neumann 1998) with a maximum size of 19 mm (Jantz and Neumann 1992). Whereas the SLs of young mussels are overestimated in our simulations, the size of older mussels is underestimated. Jantz and Neumann (1998) reported an average size of 2+ mussels of 24 mm which is clearly higher than the mean found in the simulations. This discrepancy in SL sizes may also be explained by downstream drift of

Table 3 Phenology of veliger larvae

| Site | Duration | First peak | Second peak | Source |
|------------------------------|--|---|--|---|
| Lobith (Rhine-km 863) | Middle of April–end of September 1987 End of April–middle of October 1988 End of April–middle of October 1989 | Beginning of July 1987 End of April 1988 Middle of May 1989 | End of August 1987 Beginning of August 1988 End of July 1989 | de Ruyter van Steveninck et al. (1990) |
| Bad Honnef (Rhine-km 642) | ?–Beginning of September 1992 April 20–end of August 1993 | | | Jantz and Neumann (1998) |
| Lake Constance ^a | June–October 1971 | | | Einsle (1973) |

^a Lake Constance is fed by the river Rhine. The outlet of Lake Constance corresponds approximately to Rhine-km 0

larvae combined with upstream decreasing water temperatures. For example, the mean annual water temperature was 11.96°C at Öhningen (Rhine-km 23), 12.84°C at Karlsruhe (Rhine-km 359) and 14.05°C at Koblenz (Rhine-km 590) between 1973 and 2003. Larvae that have settled at any site downstream of Constance (Rhine km 0) originate upstream and are born later due to the colder upstream temperature conditions (Borcherding and de Ruyter van Steveninck 1992). Thus, they will arrive later at the site under study and will have a shorter growth period when they have completed the 0+ age than predicted in simulations for a closed population with the favourable water temperature conditions at Koblenz. Larger mussels grow less than smaller ones according to our model for shell growth (function 3). This adds to the smaller increase in SL of older mussels observed in the model than found in field. Moreover, SLs predicted by our model are averaged over different temperature conditions (maximum temperature values range from 20 to 25°C). In contrast, the high average size of 2+ mussels (24 mm) was observed by Jantz and Neumann (1998) under extremely high water temperatures. The maximum temperature recorded during their study period was about 25°C. In the simulations with constant T_{opt} values 2+ mussels had an average SL of 23.86 mm for a maximum temperature of 24°C and had a size of 29.46 mm for 26°C. These sizes derived under warmer conditions conform much better to the field observations of Jantz and Neumann (1998).

Thermal adaptation under different water temperature regimes: population dynamics

Mussel populations of the standard thermal tolerance ($T_{opt} = 20^\circ\text{C}$, $\sigma_T = 5$) became extinct only when the maximum temperature was 28°C. However, there was no value within the interval (1, 20) of examined ther-

mal tolerances (σ_T) where the population employing strategy 2 survived under all maximum temperatures studied (Fig. 4). This suggests that for an T_{opt} of 20°C strategy 2 is insufficient to cope with steadily rising water temperatures resulting from global change. However, in the simulations for strategy 1 with a fixed thermal tolerance of $\sigma_T = 5$, the population never became extinct for all T_{opt} values studied. Consequently, determining whether the momentary thermal performance ($T_{opt} = 20^\circ\text{C}$, $\sigma_T = 5$) is sufficient depends eventually on the accuracy of the estimation of the thermal tolerance σ_T of the species.

Increasing ambient water temperatures had a significant effect on population dynamics. Whereas populations were rather stable under strategy 1, populations under strategy 2 were strongly affected. Under strategy 2 we had two situations: $\sigma_T = 1$ and $\sigma_T > 1$. For $\sigma_T = 1$, extinctions were frequent when maximum temperatures increased above 26°C (Fig. 4). The main reproductive output was shifted towards the beginning of the year (Fig. 5). This shift is the consequence of a steadily decreasing number of reproductive mussels caused by the high thermal mortality due to the small thermal tolerance. In contrast, for $\sigma_T > 1$, the main reproductive output was shifted towards August. This shift results from two factors: (1) the adult mortality generated by warmer temperatures is lower for $\sigma_T > 1$ than for $\sigma_T = 1$, and this results in an increasing probability for mussels to reach the second phase of reproduction with increasing thermal tolerances; (2) the months July and August show the highest temperatures throughout the year and thus have the best conditions for reproduction. Consequently, the ratio of the total number of eggs produced in the first spawning period to that generated in the second decreases with increasing water temperatures for a fixed thermal tolerance (Fig. 5). Decreasing thermal tolerances and increasing water temperatures increase

mortality among mussels attached and increase the probability of larvae settling successfully. The increased chance to settle leads to an increase in the number of 0+ mussels and a decrease in the number of older mussels observed for all thermal tolerances studied under increasing temperatures (Fig. 5). Since smaller 0+ mussels have a lower reproductive output than bigger older mussels (function 4) the total reproductive output of the population decreases from year to year and the chance of a population extinction increases. The fact that mussels that are born in August, are both smaller and have a lower reproductive output than those that are born during the first phase, adds to this reduction in the total reproductive output. In contrast, increasing water temperatures decelerate this reduction because they increase the number of eggs produced per mussel and spawning event (function 4) and thus increase again the number of 0+ mussels. As a consequence, the number of extinctions observed for a fixed thermal tolerance decreases with increasing water temperatures for $\sigma_T > 1$ (Fig. 4, 28, 30 and 30°C).

Populations that show age distributions with an excess of 0+ individuals have been found in the field (Smit et al. 1993; Jantz 1996). For the River Rhine, Jantz (1996) reported a skewed distribution at Helmlingen (Rhine-km 313) for which the conditions of strategy 2 may be fulfilled. Ambient water conditions at Helmlingen (Karlsruhe Rhine-km 359: mean = 12.84°C) are on average about 1°C higher than at Öhningen (Rhine-km 23: 11.96°C) where settled larvae may originate from.

Implications for survival under increasing water temperatures

Our simulations show that temporal patterns in the life cycle of the mussel will be altered under rising temperatures. Spawning started earlier in the year under all alternatives. Likewise, the second phase of spawning is expected to dominate the total reproductive output of the population (except for combination $T_{opt} = 20$, $\sigma_T = 1$ of strategy 2). An increase in the reproductive output during the second phase with increasing water temperatures was observed in nearly all simulations.

SL distributions predicted for rising temperatures, however, may possibly differ from those that will be found in nature. We assume in our model that food supply sufficient for growth is always available, but phytoplankton concentration will be also subject to environmental changes caused by global change (Straile 2000). Our assumption of an annual repro-

ductive cycle that is synchronized by the annual temperature cycle is based on Neumann et al. (1993). However, Bastviken et al. (1998) have shown that zebra mussels can cause most phytoplankton to decline. Garton and Johnson (2000), found a reduction in growth during the summer, associated with the water temperature approaching or exceeding 30°C. This reduction may have been caused by a mismatch in the food availability and the consumption of the mussel population. Further studies on the interaction between the mussel and phytoplankton are needed to improve our predictions of survival of the mussel under climate change scenarios as predicted by the IPCC (2001).

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