

Impact of climate change on population dynamics and temporal patterns of benthic assemblages of rivers

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EXTENDED ABSTRACT

Seasonal cycles of temperature, water regime and day length act as “Zeitgeber” (timer) triggering stage transitions in the life cycle of organisms provoking temporal patterns of communities at different levels of organization. Climate change is both affecting temperature forcings and water regime. Mathematical models are set up to investigate the mechanisms for the change of temporal patterns in aquatic invertebrates as brought about by climate change.

Based on temperature data from rivers in Northern Germany a stochastic time series model was set up. This model combines a deterministic seasonal trend, a long term linear trend and an ARMA model for the stochastic component. The model is used to generate input temperature data for population dynamic models. Based on the scenarios for climate change of the IPCC, both an elevation of temperature and alterations of parameters of the stochastic process were taken into account.

Biological populations are structured by age, size and stage. Two mathematical approaches were employed. For the simulation of long term time patterns in dragonfly populations, a projection matrix model is devised, i.e. the life cycle graph is mapped into a population matrix. The model yields emergence curves of larvae and adults. Figure 1 shows a simulation example of the projection matrix model. For the simulation of the time course of length density distributions of *Gammarus pulex*, a partial differential equation was employed. Transition probabilities and growth rates were devised as a function of temperature. The models are applied to the population dynamics of two common lotic invertebrates, a dragonfly (*Gomphus vulgatissimus*) and an amphipod (*Gammarus pulex*).

Most global change scenarios predict temperature rises especially in higher latitudes affecting the north-south temperature gradient. The model predicts that indications of global change should imply both a shift of geographical extension of *G. vulgatissimus* and a shift to longer cycle lengths to higher latitudes.

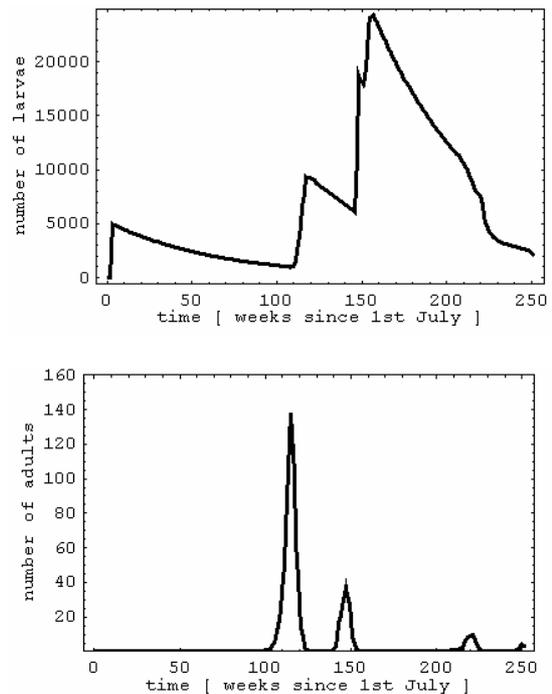


Figure 1. Simulated emergence pattern of a structured population with stages eggs, larvae and adults. Shown are only the last two stages.

The emergence of temporal patterns and the synchronizing effect of temperature forcing are studied in a model system comprising a predator and a prey population which are under the control of different timers. If the development of the prey is controlled by day length and temperature and the development of the predator only by temperature a desynchronisation occurs.

1. INTRODUCTION

Based on scenarios for climate change the IPCC (2001) stated that all model simulations show a warming in the future across the whole of Europe and in all seasons. The frequency of winters classified as cold will decrease, whereas hot summers will become much more frequent. It is the objective of the model developments presented here, to study the effect of a temperature rise on the population dynamics in an aquatic community. The first model focuses on the time patterns of a stage structured species and is applied to a dragonfly species with egg, larval and adult stage. The second model describes the dynamics of an age structured species with length as age parameter including the dynamics of the prey. The questions addressed to these models

- i) In which way are life cycle periods affected by a temperature rise?
- ii) What are the effects on the geographical distribution?
- iii) Can temperature elevation cause a mismatch of time patterns between predator and prey?

Two invertebrate species common in northern central European river systems were selected as key organisms. *Gammarus pulex* (Crustacea: Amphipoda) is detritivorous, feeding mainly on leaves. Its life cycle is fully aquatic, with life spans of about one year (up to 700 days). From birth to death it conformed to a logistic growth curve, with optimal growth at 20°C for juveniles and 15°C for adults (Sutcliffe et al. 1981). By contrast, the dragonfly *Gomphus vulgatissimus* (Insecta: Odonata) is an obligate predator throughout its semiaquatic life cycle, with the eggs and larvae being aquatic. Development varies between two years in large, warmer rivers and up to four years in small and cold streams, with three years being the ‘normal’ duration. Emergence usually occurs highly synchronized, starting between end of April and mid of May, depending on the temperature conditions (Suhling and Müller 1996, Müller et al. 2000). Growth rates are estimated to be at optimum above 25°C.

2. TEMPERATURE SCENARIOS

To construct realistic temperature scenarios daily temperature data of several rivers and streams in Northern Germany collected up to 20 years were analyzed. To these data a model combining a deterministic seasonal trend, a long term linear trend and an ARMA (autoregressive moving average) model for the stochastic component was fitted (Box & Jenkins, 1976). The seasonal and

long term linear trend is described via the following function:

$$Temp(t) = m_0 + \alpha t + m_1 \sin\left(\frac{2\pi(t-p)}{365}\right) + \varepsilon_t \quad (1)$$

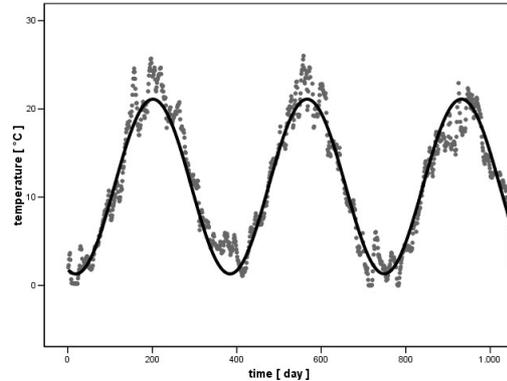


Figure 2. Temperatures measured at gauge “Schnackenburg” at the Elbe River (grey points) and fitted sine curve (black line). Fitted parameters are $m_0 = 11.2 \pm 0.0446$, $A = 2.2E-05 \pm 9.1E-06$, $m_1 = 9.9 \pm 0.031$, $p = 109.9 \pm 0.185$ ($R^2 = 0.9260$).

The involved parameters can be taken as: mean temperature m_0 , temperature amplitude m_1 , slope α of temperature increase and displacement p of the phase of the sine curve (because the coldest day in Mid Europe is approximately at the end of January). Figure 2 shows as an example the first three years measured at the gauge “Schnackenburg” at the Elbe River together with the fitted sine curve.

In a further step the residuals of the regression model were tested for temporal correlations. For this reason an ARMA(p,q)-model with white noise δ_t was fitted to the residuals:

$$\varepsilon_t = CONST + AR_1 \varepsilon_{t-1} + \dots + AR_p \varepsilon_{t-p} + \delta_t + MA_1 \delta_{t-1} + \dots + MA_q \delta_{t-q} \quad (2)$$

The orders p and q of this model were determined by inspecting the autocorrelation and the partial autocorrelation function, respectively. Figure 3 shows as an example a realistic temperature scenario based on the fitted sine curve and an ARMA(3,2)-model for the “Schnackenburg” data.

3. PROJECTION MATRIX MODELS

Like in all invertebrates the populations of both study organisms are structured by age, size and stage (cf. Figure 4). Their population dynamic theory is based either on partial differential equations or on time discrete multivariate iterations, the so-called matrix models.

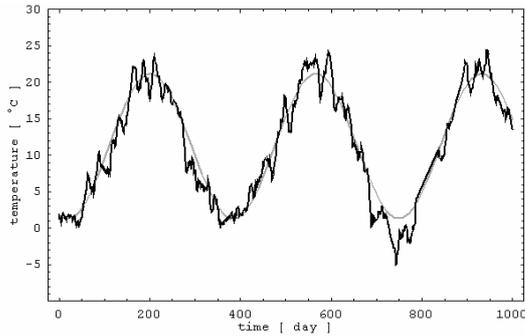


Figure 3. A realistic temperature scenario (black) based on the fitted sine curve (grey) with an ARMA(3,2)-model overlaid.

In the original Leslie matrix model (Leslie, 1945) the population vector \vec{x} consists of individuals divided in classes according to their age. Based on an initial age distribution and a projection matrix M , comprising the age-dependent survival and fertility rates of the population, one is able to evaluate the population vector at any future time point:

$$\vec{x}(t+1) = M \vec{x}(t) \quad (3)$$

The extended Leslie matrix model (Söndgerath & Richter, 1990) formulates such kind of Leslie process for each stage of the life cycle (Figure 4). The single stages are linked via transition probabilities which depend on environmental factors, e.g. temperature.

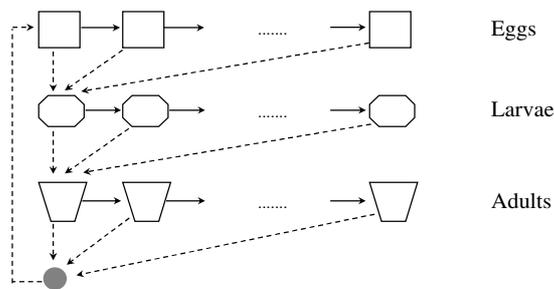


Figure 4. Life cycle graph of an age and stage and stage structured population (→ survival probabilities, ----> transition probabilities)

4. INFLUENCE OF TEMPERATURE AND DAY LENGTH

The life cycle of an age and stage structured population depends on two types of parameters: fertility rates and probabilities for transition from one stage to the next. The appropriate random variables are development times or life times respectively.

Thus, the temporal pattern of the life cycle is determined by the distribution functions of these random variables, which depend on the time course of environmental covariates. This dependency is modeled by the accelerated life model (Cox and Oakes 1984). Let $F_0(t)$ denote the distribution function of the random variable T_d “development time” under reference condition, e.g. a constant temperature T_0 . In the accelerated life model, the distribution under at $T=T_i$ is given by the transformation

$$F_1(t) = F_0(\phi t) \quad (4)$$

Via the density function $f_1(t) = \phi f_0(\phi t)$ the following relations between the expectations and the variances are derived as

$$E_1[T_d] = \frac{E_0[T_d]}{\phi} \quad \text{and} \quad \text{Var}_1[T_d] = \frac{\text{Var}_0[T_d]}{\phi^2}.$$

If $\phi > 1$ both the expectation and variance of the development time are decreased with respect to standard conditions, hence the name accelerated life model. The factor ϕ is formulated as a function of temperature by a O’Neill temperature response function (Spain, 1982).

$$\phi(T) = k_{\max} \left[\frac{T_{\max} - T}{T_{\max} - T_{opt}} \right]^X \text{Exp} \left[X \frac{T_{\max} - T}{T_{\max} - T_{opt}} \right] \quad (5)$$

For time dependent environmental variables, the argument t denoting the physical time is replaced by the integral (τ denotes the integration variable)

$$\Phi(t) = \int_0^t \phi(T(\tau)) d\tau \quad (6)$$

which is referred to as “biological time”. The function $E(t) = 1 - F(t)$ has the meaning of an emergence function. Figure 5 shows emergence curves of one odonate species in rivers with different temperature regimens. In many Odonata species in Europe the onset of development stages is triggered by day length d .

A day length response- function of the form

$$f(d(t)) = 1 - \exp[-(d(t)/d_{crit})^\alpha] \quad (7)$$

is used, which controls physiological activity. Day length $d(t)$ is computed by a standard astronomical expression as a function of Julian date and geographical latitude.

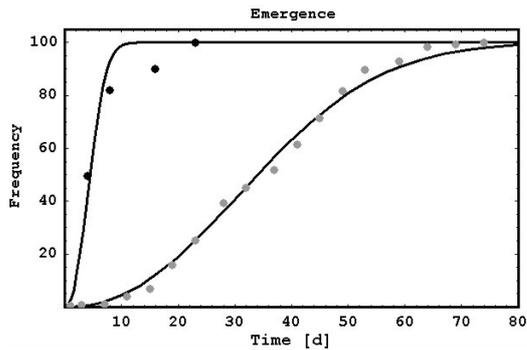


Figure 5. Emergence curves of the dragonfly *Onychogomphus uncatius* under different temperature regimes in two canals of the Crau region in southern France. (Black: Canal Centre Crau, temperature maximum of 33.0 °C, Grey: Canal de Vergière, temperature maximum of 23.5 °C, data from Suhling 1996).

5. TIME PATTERNS OF SINGLE POPULATIONS

The model constructed for *Gomphus vulgatissimus* includes the three stadia, namely eggs, larvae and adults. The time step was one week as a compromise between the short egg and adult development (not exceeding 5 or 6 weeks) and the long larval development (up to three years). This results in 5, 156 and 6 age classes for the three stadia, respectively.

Temperature time series were generated according to the method described above. The simulation starts in July with eggs. The biological age was evaluated based on O'Neill functions (Spain, 1982) multiplied with a factor depending on day-length in form of the Weibull distribution (eq. 7). Figure 6 shows the time courses of adult density under the following climate change scenarios: mean temperature m_0 as fitted, $m_0 + 1^\circ\text{C}$, $m_0 + 2^\circ\text{C}$, $m_0 + 3^\circ\text{C}$. The simulations show a pronounced effect of temperature rise on life cycle periods. They change from a 3-year cycle over mixtures of 3- and 2-year cycles to a 2-year-cycle. This corresponds to observations done by Müller et al. (2000). The basic time patterns are found regardless of the special realisation of the stochastic part of the time series.

6. EFFECT ON GEOGRAPHICAL DISTRIBUTION PATTERNS

The global change scenarios predict temperature rises especially in higher latitudes affecting the north-south temperature gradient. Therefore, indications of global change should imply both a shift of geographical extension of *G. vulgatissimus* and a shift to longer cycle lengths to higher latitudes.

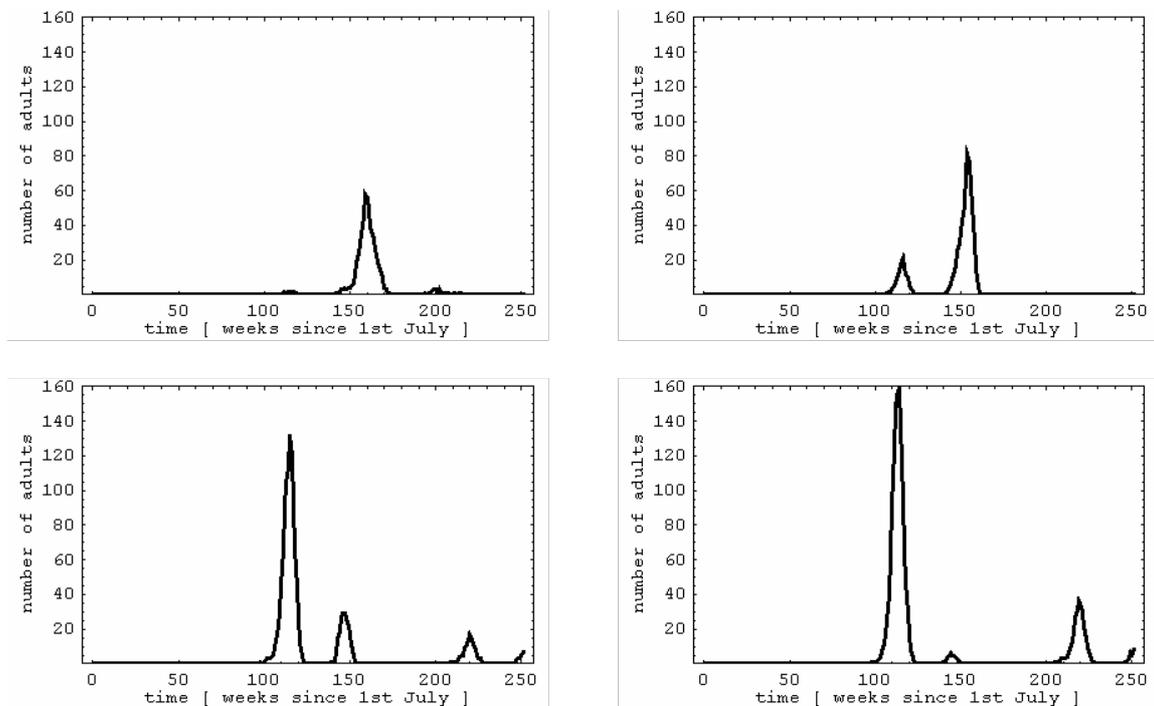


Figure 6. Simulated time series of adult densities of *Gomphus vulgatissimus* under four different temperature regimes: mean temperature as fitted (upper left), mean temperature + 1°C (upper right), mean temperature + 2°C (lower left), mean temperature + 3°C (lower right). This general time pattern is insensitive to the stochastic component of the underlying temperature time series.

A simulation applying a temperature and day-length gradient to the population dynamic model was performed. The gradient reaches from about the southernmost (Toulouse, France, 43.5° N) to the northernmost geographical extension of *G. vulgatissimus*. (Halmstad, Sweden, 56.5° N). Mean air temperatures were correlated with latitude and served as input for the respective temperature scenario. Simulations were done in 0.25° - latitude steps. Changes in day length d were also implemented in the model. Figure 7

indicates that in southern France most *G. vulgatissimus* populations have a two year life cycle. With a northward shift of the gradient the life cycle turns into a 3-year cycle with few individuals being able to complete the larval stage in 2 years. This effect is known as cohort splitting. In higher latitudes the number of adults decreases and a part of the population needs 4 years for development. The 4-year peak in the south results from a 2nd 2-year generation.

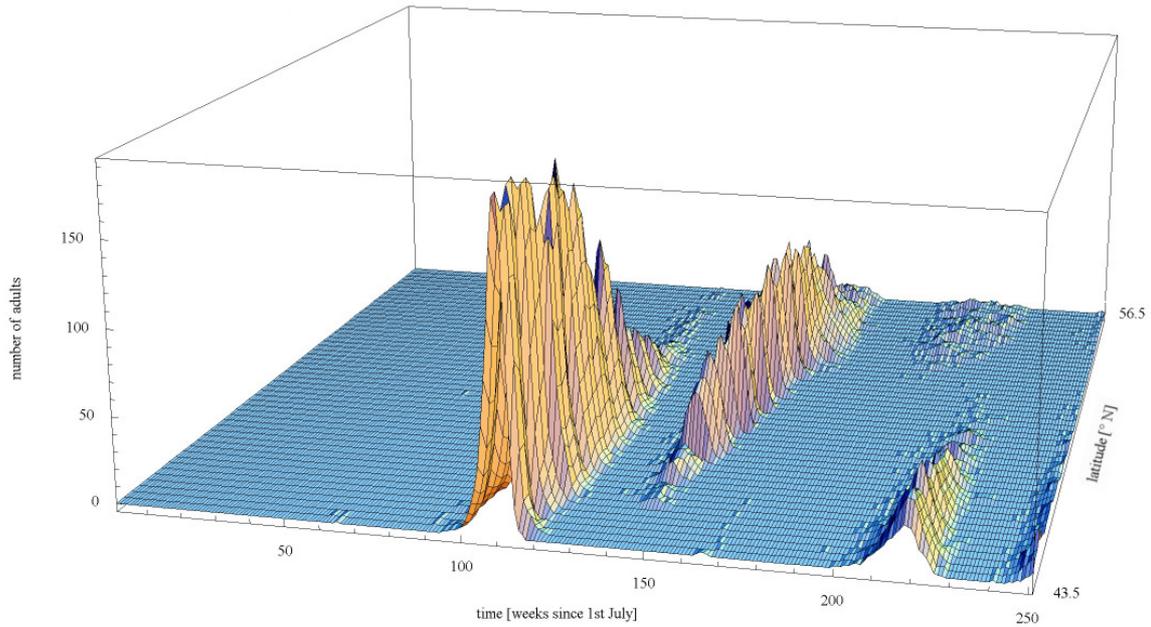


Figure 7. Simulation of the adult densities of *Gomphus vulgatissimus* along a temperature- and day length-gradient from southern France to Sweden.

7. CONTINUOUS MODELS

Notations:

- l : length
- F : prey density
- F_h : saturation constant
- I_{\max} : maximal consumption rate per predator
- $g(l, F)$: growth function dependent on length l and prey density F
- $\mu(l, t)$: mortality rate
- $b(l, F)$: fertility rate
- l_{\max}, l_{\min} : maximum, minimum length
- γ : maximum growth rate of *G. pulex*
- K : environmental capacity of algal population
- r : maximum algal growth rate

For the population dynamics of *G. pulex* the model of Metz and Diekmann (1986) for an age structured *Daphnia* (Crustacea: Cladocera) population was modified by temperature response

functions for growth and mortality rates $\Phi_1(T)$ and $\Phi_2(T)$ for the predator and by a temperature response function $\Psi(T)$ for the growth of the prey. The model describes the development in time of the length density function of a *G. pulex* population, $n(l, t)$, by the partial differential equation

$$\frac{\partial n(l, t)}{\partial t} + \frac{\partial \Phi_1(T(t)) g(l, F) n(l, t)}{\partial l} = -\Phi_2(T(t)) \mu(l, t) n(l, t) \quad (8)$$

Individual growth follows the equation

$$g(F, l) = \gamma \left(\frac{a_{\max} F}{F + F_h} - l \right) \quad (9)$$

The equation is completed by the renewal boundary condition

$$g(F, l_{\min}) n(0, t) = \int_{l_{\min}}^{l_{\max}} b(F, l) n(l, t) dl \quad (10)$$

with fertility rate

$$b(F, l) = \frac{r_{\max} F}{F + F_h} l^2 \quad (11)$$

The dynamics of the prey population (detritus) is coupled to the *Gammarus* population via

$$\frac{dF}{dt} = r \Psi(T(t)) F \left(1 - \frac{F}{K}\right) - \frac{I_{\max} F}{F + F_h} \int_{l_b}^{l_{\max}} l^2 n(l, t) dl \quad (12)$$

The above equation system was numerically solved by the “Escalator Boxcar Train method” (de Roos & Metz 1991). Figure 8 shows the simulated length density functions of an age structured population as described by the preceding equations at different temperature regimes. Growth is accelerated with increasing temperature and reproduction begins earlier. In these computer experiments, food density F was kept constant near saturation levels. Note that maximum population density is lowest at the highest temperature.

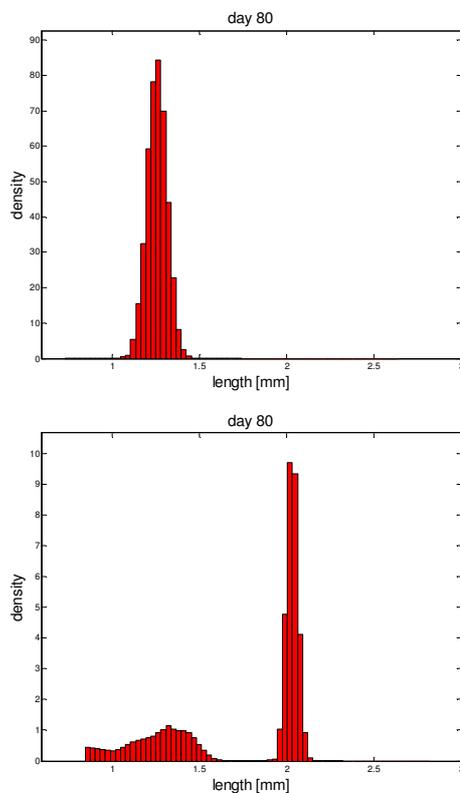


Figure 8. Simulated length density functions of an age structured population at different temperature regimens. Food density F was kept constant near saturation levels. Note the different axes for the densities.

8. TEMPORAL MISMATCH

A situation was considered, where predator and prey development are triggered by different “timers”. It was assumed that prey (e.g. algae) growth is dependent on day length and temperature and predator growth is triggered by temperature alone. Increasing temperatures therefore may cause desynchronisation between prey and predator development. This situation was simulated by means of the above model. The temperature response function of the prey in equation (12) was multiplied by the day-length response function (eq. 7), whereas predator development was kept only temperature dependent. Figure 9 shows the development of predator densities at standard temperature levels and at elevated (+4°C) temperature levels.

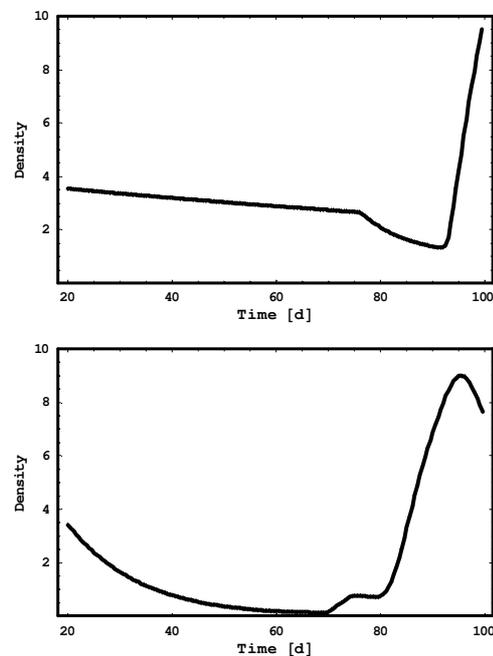


Figure 9. Effect of a temperature rise on predator densities. Under the standard temperature scenario (upper figure) mortality is low during the winter months. If temperatures are increased, the need of the organism for nutrition cannot be met and mortality rates are high.

In the high temperature scenario, the metabolism of the predator is activated early in the year. Because the onset of prey growth is controlled by the photoperiod, a temporal mismatch occurs between the need of the predator for food and the renewal rate of the prey. This mismatch causes an increase of mortality of the prey population. This simple model only serves to illustrate possible effects of a temperature increase. In nature, no such simple systems occur and one has to take into account community networks and their interactions.

9. CONCLUSIONS

What do we have to expect if temperatures are increasing? In the case of the Odonata the model has shown, that emergence patterns will be changed, i.e. the number of life cycles will increase and cohort splitting will occur. Therefore, field biologists have to investigate parameters of the life cycle patterns, which are sensitive indicators for temperature changes. In case of the fast growing amphipod, all life processes are accelerated. Egg deposition and larval development and mortality rates are accelerated, hence population densities are lower at elevated temperatures. In a predator-prey system a temporal mismatch occurs if prey and predator development is controlled by differing timers.

However, it might be argued that a change of environmental conditions is a major driving force of evolution. The basic question to be answered is: can the rate of environmental change be matched by the rate of evolutionary change? The models presented here are based on constant parameter values. In order to simulate evolutionary response to global change statistical distributions of model parameters have to be introduced giving rise to different fitness (Jacob 1997). An ensemble of populations each with different parameters has to be studied, combining deterministic population dynamic models with stochastic models of random genetic drift. Conclusions can be drawn only from a large number of random experiments.

10. ACKNOWLEDGEMENT

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