

Consequences of altered temperature and food conditions for individuals and populations: a Dynamic Energy Budget analysis for *Corbicula fluminea* in the Rhine

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SUMMARY

1. On the basis of simulations at two levels of organisation (individuals and populations), we analysed the impact of altered food and temperature conditions on the Asian clam *Corbicula fluminea*. In particular, we addressed the role of food and temperature in explaining occasional mass mortalities.
2. A Dynamic Energy Budget Model (DEBM) was used for simulations at the individual level. We calibrated the DEBM successfully using experimental data on growth in length and mass of *C. fluminea* under four combinations of temperature and food.
3. The calibrated DEBM was used to simulate the annual growth in length and mass and the reproductive success under different environmental scenarios. In general, an increase in temperature and food concentration resulted in larger and heavier clams and a higher *per capita* rate of reproduction. However, phytoplankton densities in rivers often fluctuate strongly and densities are high only briefly. Under such conditions, our simulations suggest that the temporal interactions of temperature and food concentration are particularly important and can decisively influence annual growth.
4. With regard to occasional mass mortalities, it has been hypothesised that increased temperature might induce an unmet metabolic demand and hence starvation. To test this, we simulated the conditions observed in the Rhine in 2003, when there was a severe heat wave and a mass mortality. For this purpose, we used the calibrated DEBM and, in addition, integrated it into a Physiologically Structured Population Model (PSPM) to account for processes at the population level.
5. Based on these simulations, it seems unlikely that starvation was the main cause of the mass mortality, although not all mechanisms affecting the energy budget are fully understood. However, a prolonged negative energy budget during heat waves can increase the vulnerability of clams to direct effects of high temperatures or additional stressors and might thus be regarded as an important factor indirectly increasing mortality rates.

Keywords: Dynamic Energy Budget, environmental change, mass mortality, Physiologically Structured Population Model, phytoplankton

Introduction

After its first appearance in Europe in the early 1980s, the Asian clam *Corbicula fluminea* has invaded many freshwater ecosystems and was first detected in the study area, the Rhine, in 1988 (Mouthon, 1981; Bij de Vaate & Greijdanus-Klaas, 1990). Its rapid maturation, high

fecundity and tolerance of a wide range of environmental conditions are often assumed to be the principal reasons for its success (McMahon, 1999; Rajagopal, Van der Velde & Bij de Vaate, 2000). It is considered a benthic keystone species in many freshwater ecosystems, due to its high population density and ecological effects (Meister, 1997). *Corbicula fluminea* removes nano- and micro-sized

particles from the water column by filter feeding and deposits them as faeces and pseudofaeces in the benthos (Atkinson *et al.*, 2011). As a result, it can reduce phytoplankton density, increase water clarity and modify nutrient cycling (Lauritsen & Mozley, 1989; Hakenkamp & Palmer, 1999; Hakenkamp *et al.*, 2001; Strayer, 2010; Hwang *et al.*, 2011).

Despite its adaptability, mass mortalities have frequently been observed, for instance in the Rhine in 2003 (Westermann & Wendling, 2003) and in the Minho Estuary in 2005 and 2009 (Ilarri *et al.*, 2011). These events occur during summer droughts, with high temperature and associated low flow (Schönwiese, Staeger & Trömel, 2004; Zwolsman & van Bokhoven, 2007; Ilarri *et al.*, 2011). Extreme summer droughts commonly induce additional changes in factors, such as the concentrations of dissolved oxygen, nutrients and heavy metals, and in phytoplankton abundance (Zwolsman & van Bokhoven, 2007; Whitehead, Wade & Butterfield, 2009). However, the causes of mass mortalities are still controversial. It has been hypothesised that energetic constraints during hot weather may result in starvation (Westermann & Wendling, 2003; McCue, 2010). The clams might not be able to compensate for increased metabolic costs at high temperature, while food may be limited. In mesocosm experiments by Weitere *et al.* (2009) and Vohmann *et al.* (2010), strong indications of prolonged starvation, due to low phytoplankton abundance in the Rhine enhanced by high temperature and corresponding increasing energetic demand, were found, and thus, this hypothesis appears to be a likely option.

Our main objective in this study was to test the hypothesis that starvation was a main cause of the mass mortality of *C. fluminea* in the Rhine in 2003 using a modelling approach. Because temperature and food intake directly influence the metabolism of poikilotherms (Gillooly *et al.*, 2001; Enquist *et al.*, 2003), we applied a Dynamic Energy Budget Model (DEBM). DEBMs provide a detailed description of metabolic processes and allow for the integration of seasonal fluctuations in temperature and food availability, as have been observed in the Rhine (Friedrich & Pohlmann, 2009; Kooijman, 2009; Nisbet, McCauley & Johnson, 2010). In addition, to consider population-level effects, we integrated the DEBM into a Physiologically Structured Population Model (PSPM; Metz & Diekmann, 1986; De Roos, 1997).

An additional objective was to analyse how altered temperature and food conditions affect growth in length and mass of *C. fluminea* in general. According to the IPCC (2007), an increase in mean temperature, as well as seasonal changes (e.g. an increased frequency of summer

heat waves), can be expected in the near future. In contrast, phytoplankton concentration in the Rhine has declined over recent years, which is expected to continue, partly caused by the high filtration rates of *C. fluminea* itself and other filter feeders (Weitere & Arndt, 2002; Friedrich & Pohlmann, 2009). We analysed the effects of expected changes in temperature and food conditions, alongside varying internal initial conditions of mass and shell length, in scenario simulations.

Methods

Models

We employed a Dynamic Energy Budget Model (DEBM; Kooijman, 2009) to simulate the development of *C. fluminea* at the individual level and a Physiologically Structured Population Model (PSPM; Metz & Diekmann, 1986; De Roos, 1997) to simulate population dynamics. In the following, we provide the essential ideas and model descriptions (see Table 1 for equations (E), hereafter referred to as E1–E30; Table 2 for DEBM parameters; Table 3 for other parameters). More details are provided in Tables S1–S3 (Supporting Information).

Individual level: Dynamic Energy Budget Model. DEBMs have been applied to several bivalve species so far (Bacher & Gangnery, 2006; Van der Veer, Cardoso & Van der Meer, 2006; Rosland *et al.*, 2009). They describe the energy flow through an organism, that is, energy uptake, consumption and storage, as a function of environmental conditions (here, food F [μg chlorophyll- a L^{-1}] and temperature T [$^{\circ}\text{C}$]) and the state of the organism (Fig. 1; E1–E9; Kooijman, 2009). The latter is defined by the structural volume V [mm^3], the amount of non-allocated energy in the reserve E [J] and the amount of energy allocated for reproduction R [J]. The entire assimilated energy is distributed among these state variables; the structural volume V comprises all structural materials (e.g. muscles, organs) that require maintenance costs, the energy reserve E comprises all materials used as energy storage (e.g. polymeric carbohydrates, lipids), and the 'reproduction buffer' R comprises all reproductive tissues (e.g. gonads, larvae). We assumed that the structural volume increases in proportion to shell length, as proposed by Kooijman (2009) for isomorphic organisms (E24). The commonly measured parameters shell length l [mm], ash-free dry mass of the soft body W_D [mg] and reproductive success N_L [-] are directly linked to the state variables and *vice versa* (E26–E30; see Appendix S1 for details).

Table 1 Equations of the Dynamic Energy Budget Model (1–9) and the Physiologically Structured Population Model (10–17), as well as additional important equations (18–30). A complete list of all equations used in this study is given in Table S3

Explanation	Unit	Equation	Number
<i>Dynamic Energy Budget Model (DEBM)</i>			
Assimilation rate	J d ⁻¹	$p_A = \Phi(T) \cdot f(F) \cdot \{p_{Am}\} \cdot (\delta \cdot l)^2$	(1)
Ingestion rate	J d ⁻¹	$p_X = \Phi(T) \cdot f(F) \cdot \{p_{Xm}\} \cdot (\delta \cdot l)^2$	(2)
Maintenance rate	J d ⁻¹	$p_M = \Phi(T) \cdot [p_M] \cdot (\delta \cdot l)^3$	(3)
Maturity maintenance rate	J d ⁻¹	$p_J = \Phi(T) \cdot [p_M] \cdot \min((\delta \cdot l)^3, (\delta \cdot l_p)^3) \cdot \frac{1-\kappa}{\kappa}$	(4)
Mobilisation rate	J d ⁻¹	$p_C = \Phi(T) \cdot \frac{[E]}{[E_G] + \kappa \cdot [E]} \cdot \left(\frac{[E_G] \cdot \{p_{Am}\} \cdot (\delta \cdot l)^2}{[E_M]} + [p_M] \cdot (\delta \cdot l)^3 \right)$	(5)
Reserve dynamics	J d ⁻¹	$\frac{dE}{dt} = p_A - p_C$	(6)
Reproduction buffer dynamics	J d ⁻¹	$\frac{dR}{dt} = (1 - \kappa) \cdot p_C - p_J$	(7)
Structural volume dynamics	mm ³ d ⁻¹	$\frac{dV}{dt} = \frac{\kappa \cdot p_C - p_M}{[E_G]}$	(8)
Length growth dynamics	mm d ⁻¹	$\frac{dl}{dt} = \frac{\kappa \cdot p_C - p_M}{[E_G]} \cdot \frac{1}{3 \cdot \delta \cdot l^2}$	(9)
<i>Physiologically Structured Population Model (PSPM)</i>			
Population dynamics	m ⁻² mm ⁻¹ d ⁻¹	$\frac{\partial n}{\partial t} = - \left(\frac{\partial dl}{\partial t} \cdot n \right) + \vartheta_O \cdot G(l) - \mu_E \cdot n$	(10)
Energy density dynamics	J mm ⁻³ d ⁻¹	$\frac{d[E]}{dt} = \frac{p_A - p_C}{V} - [E] \cdot \frac{1}{V} \cdot \left(\frac{\kappa \cdot p_C - p_M}{[E_G]} \right)$	(11)
Reproductive energy density dynamics	J mm ⁻³ d ⁻¹	$\frac{d[R]}{dt} = \frac{(1 - \kappa) \cdot p_C - p_J}{V} - [R] \cdot \frac{1}{V} \cdot \left(\frac{\kappa \cdot p_C - p_M}{[E_G]} \right)$	(12)
Recruitment rate	m ⁻² d ⁻¹	$\vartheta_O = \frac{\tau(T)}{\Delta_R} \cdot \left(K - \int_{l_0}^{l_{max}} n \, dl \right) \cdot \left(\frac{N_{LP}}{N_{LP} + N_H} \right)$	(13)
Potential reproductive success (population)	m ⁻²	$N_{LP} = \frac{1}{\omega_{LS}} \cdot \int_{l_p}^{l_{max}} (R - E_H) \cdot n \, dl$	(14)
Mortality rate	d ⁻¹	$\mu_E = \left(e^{-[E]} \right)^4$	(15)
Food accessibility factor	–	$r_F = e^{-\left(\frac{\int n \cdot V \cdot dl}{O_v} \right)^{20}}$	(16)
Population food response function	–	$f_P(F) = \frac{r_F \cdot F}{r_F \cdot F + F_H}$	(17)
<i>Additional equations</i>			
Food response function	–	$f(F) = \frac{F}{F + F_H}$	(18)
Temperature response function	–	$\Phi(T) = \begin{cases} \left(\frac{T_{max} - T}{T_{max} - T_{opt}} \right)^k \cdot e^{-k \cdot \left(\frac{T - T_{opt}}{T_{max} - T_{opt}} \right)} & \text{if } T_{min} < T < T_{max} \\ 0 & \text{otherwise} \end{cases}$	(19)
–	–	$k = \frac{1}{400} \cdot W^2 \cdot \left(1 + \sqrt{1 + \frac{40}{W}} \right)^2$	(20)
–	–	$W = (Q_{10} - 1) \cdot (T_{max} - T_{opt})$	(21)
Objective function (per treatment)	–	$S_Q = \frac{1}{n_l} \sum_{l=1}^{n_l} \left(\frac{I_S(t) - I_O(t)}{I_O(t)} \right)^2 + \frac{1}{n_W} \sum_{l=1}^{n_W} \left(\frac{W_{DS}(t) - W_{DO}(t)}{W_{DO}(t)} \right)^2$	(22)
Objective function (all treatments)	–	$S_{QT} = S_{Q\Delta 0AF} + S_{Q\Delta 0SF} + S_{Q\Delta 3AF} + S_{Q\Delta 3SF}$	(23)
Structural volume	mm ³	$V = (\delta \cdot l)^3$	(24)
Surface area	mm ²	$A = (\delta \cdot l)^2$	(25)
Shell length	mm	$l = \frac{V^{\frac{1}{3}}}{\delta}$	(26)
Dry mass of reserve	mg	$W_{DE} = \frac{E}{\omega_E}$	(27)
Dry mass of structural volume	mg	$W_{DV} = V \cdot \rho_V$	(28)
Dry weight of soft body	mg	$W_D = W_{DV} + W_{DE}$	(29)
Reproductive success	–	$N_L = \frac{R - E_H}{\omega_{LS}}$	(30)

Table 2 DEBM parameters. Parameter values of the first six parameters are based on literature or unpublished data. For the consecutive six parameters, parameter ranges were derived from literature or unpublished data and used in parameter estimation process. Parameter estimates are shown in column 'Value'. More details are provided in Appendix S1

Parameter	Unit	Value	Range	Explanation	Reference
$[E_G]$	$J\ mm^{-3}$	58		Volume-specific costs of structure	Van der Veer <i>et al.</i> , 2006; Aldridge & McMahon, 1978; Drack, 2002;
$\{p_{X_m}\}$	$J\ mm^{-2}\ d^{-1}$	26.6		Surface-area-specific maximum ingestion rate	Rosland <i>et al.</i> , 2009; Viergutz, unpublished data
T_{max}	$^{\circ}C$	37		Maximum temperature	Aldridge & McMahon, 1978; Cherry <i>et al.</i> , 1980;
T_{min}	$^{\circ}C$	2		Minimum temperature	Mattice & Dye, 1976; French & Schloesser, 1996;
δ	–	0.158		Shape parameter	Weitere <i>et al.</i> , 2009;
κ	–	0.85		Fraction of mobilised energy spent on maintenance and growth	Aldridge & McMahon, 1978; Van der Veer <i>et al.</i> , 2006;
$[E_M]$	$J\ mm^{-3}$	212.5	100–400	Maximum energy density	Weitere <i>et al.</i> , 2009;
F_H	$\mu g\ L^{-1}$	10	10–30	Half-saturation coefficient for food	Foe & Knight, 1986;
$\{p_{A_m}\}$	$J\ mm^{-2}\ d^{-1}$	20	10–30	Surface-area-specific maximum assimilation rate	Rosland <i>et al.</i> , 2009; Viergutz, unpublished data; Van der Veer <i>et al.</i> , 2006;
$[p_M]$	$J\ mm^{-3}\ d^{-1}$	1.5	0.5–5	Volume-specific maintenance rate	Gnaiger & Forstner, 1983; Linn, unpublished data
Q_{10}	$^{\circ}C^{-1}$	2.4	2–3	Temperature coefficient	Schulz, unpublished data
T_{opt}	$^{\circ}C$	22	17–26	Optimum temperature	Viergutz <i>et al.</i> , 2007

A Holling type II functional food response $f(F)$ [-] (Holling, 1959; E18) and the O'Neill temperature response $\Phi(T)$ [-] (O'Neill *et al.*, 1972; E19–E21) were used to link physiological processes and environmental conditions (E1–E5). Although originally developed for mammals, the principles giving rise to the hyperbolic Holling type II functional response are similar for filter feeders, and this response function has widely been applied for clams (see Kooijman (2009) for a detailed discussion). The O'Neill temperature response was applied rather than the similar van't Hoff-Arrhenius response suggested by Kooijman (2009) because its parameters T_{min} , T_{max} , T_{opt} and Q_{10} are biologically meaningful and easy to interpret.

The quantity of food was characterised by chlorophyll-*a* concentration. Friedrich and Pohlmann (2009) have shown that, for the Rhine, phytoplankton biovolume and chlorophyll-*a* concentration are highly correlated. Boltovskoy, Izaguirre and Correa (1995) have demonstrated the absence of feeding selectivity of *C. fluminea* within the typical size range of phytoplankton, that is, no specific taxa or size classes are ingested preferentially. Hence, we assumed that chlorophyll-*a* concentration is a suitable approximation of food quantity.

If an organism is starving, its physiology is evidently affected (Kooijman, 2009). In such cases, the basic DEBM equations need to be adapted. Thus, in accordance with the suggestions of Kooijman (2009), we applied the following modifications. If the maintenance costs exceed the amount of energy mobilised, the allocation of energy to reproduction is stopped and missing energy is mobi-

lised from the reserve E (see Table S3 for modified equations, and Appendix S2 for details). In this way, structural volume is maintained until E is completely depleted, such that non-sensical modelling of shrinking shells (through shrinkage of the structural volume) is avoided.

Population level: Physiologically Structured Population Model. Straightforward integration of the DEBM into a PSPM would yield a complex model in which population density depends on four independent variables (the three state variables E , l , R , and time t [d]). We simplified the model and assumed the population density n [$m^{-2}\ mm^{-1}$] to be structured exclusively by length l (E10), while the remaining two state variables, both unambiguously dependent on l , were simulated concurrently. (To be precise, energy density $[E] = E/V$ [$J\ mm^{-3}$] and reproductive energy density $[R] = R/V$ [$J\ mm^{-3}$] were used as state variables at the population level (E11–E12). These state variables can best be interpreted as stored energy in relation to size; if energy to satisfy the metabolic costs is no longer available, the energy density equals zero and the organism dies). By this simplification, one complex constitutive equation was replaced by three less complex equations. The suitability of this approach is justified as follows. Length–mass regressions (e.g. Brown *et al.*, 2007; Cooper, 2007; Vohmann, 2008; Weitere *et al.*, 2009) have demonstrated that, within a given area and timespan, clams of equal shell length do not vary substantially in mass. Therefore, we assumed that neglecting variations was not an oversimplification.

Table 3 PSPM parameters and key variables. Where no reference is given, parameter values are based on own estimates. A complete list of all parameters and variables used in this study is given in Table S1–S2

	Unit	Value	Explanation	Reference
<i>Parameter</i>				
K	m^{-2}	1000	Carrying capacity	This study
l_0	mm	2	Length at which recruits enter population	Hall, 1984;
l_p	mm	10	Length at which maturity is attained	Aldridge & McMahon, 1978; Meister, 1997;
N_H	m^{-2}	10000	Half-saturation coefficient for reproduction (establishment)	This study
O_V	$\text{mm}^3 \text{m}^{-2}$	5400	Population threshold at which food accessibility is reduced	This study
A_R	d	45	Length of reproductive period	Meister, 1997;
ρ_V	mg mm^{-3}	1	Density of structural volume	Kooijman, 2009;
ω_E	J mg^{-1}	23	Energy content of reserve	Bagatini, Benedito-Cecilio & Higuiri, 2007;
ω_{LC}	J	0.093	Calculated energy demand to produce one larvae	Aldridge & McMahon, 1978
ω_{LS}	J	0.05	Simulated energy demand to produce one larvae	This study (parameter estimation)
<i>Variable</i>				
E	J	–	Non-allocated energy in reserve	
$[E]$	J mm^{-3}	–	Energy density	
E_H	J	–	Maturation threshold for reproduction	
F	$\mu\text{g L}^{-1}$	–	Food (chlorophyll- <i>a</i> concentration)	
$G(l)$	mm^{-1}	–	Gaussian distribution	
l	mm	–	Shell length	
l_{\max}	mm	–	Maximum shell length	
l_O	mm	–	Observed shell length	
l_S	mm	–	Simulated shell length	
n	$\text{m}^{-2} \text{mm}^{-1}$	–	Population density	
n_l	–	–	Number of length observations	
n_W	–	–	Number of mass observations	
N_L	–	–	Reproductive success (individual)	
N_{LP}	m^{-2}	–	Potential reproductive success (pop.)	
R	J	–	Energy allocated for reproduction	
$[R]$	J mm^{-3}	–	Reproductive energy density	
R_M	J	–	Energy invested into maturation	
t	d	–	Time (day of the year)	
T	$^{\circ}\text{C}$	–	Temperature	
V	mm^3	–	Structural volume	
W_D	mg	–	Ash-free dry mass of soft body	
W_{DO}	mg	–	Observed ash-free dry mass	
W_{DS}	mg	–	Simulated ash-free dry mass	
$\tau(T)$	–	–	Boolean variable indicating reproductive period	

The balance equation for population dynamics consists of three terms (E10). The first term describes growth according to the DEBM. The second and third terms describe recruitment and mortality, respectively. The length-structured population density is simulated per square metre of substratum. Recruitment in clam populations occurs when juveniles attach to the substratum, typically when they are 1.5 to 2 mm long (Hall, 1984). Based on this, we assumed that new recruits enter the population with a Gaussian distribution ($\mu = 2$ mm, $\sigma = 0.6$ mm). Two reproductive periods, most likely controlled by temperature, are usually recorded in the Rhine (Meister, 1997). Apart from temperature, we assumed that the recruitment rate ϑ_0 [d^{-1}] (E13) depends on the actual population density, the carrying capacity K [$\text{m}^{-2} \text{mm}^{-1}$] and the potential reproductive success N_{LP} [-] (see

Appendix S3). Regarding the mortality term, we integrated an energy density-dependent mortality rate μ_E [d^{-1}] (E15). Instead of an artificial switch with a mortality rate of one if energy density is zero, the mortality rate was significantly increased at values close to zero (E15).

Parameter estimation

Individual level: Dynamic Energy Budget Model. We parameterised the DEBM using data collected by Weitere *et al.* (2009). In two independent experiments in summer 2007 (ES) and winter 2007/2008 (EW), clams (*C. fluminea*) were kept in a river bypass system at the Ecological Rhine Station of the University of Cologne (Germany) and their development was monitored. The conditions in the bypass corresponded to natural conditions in the

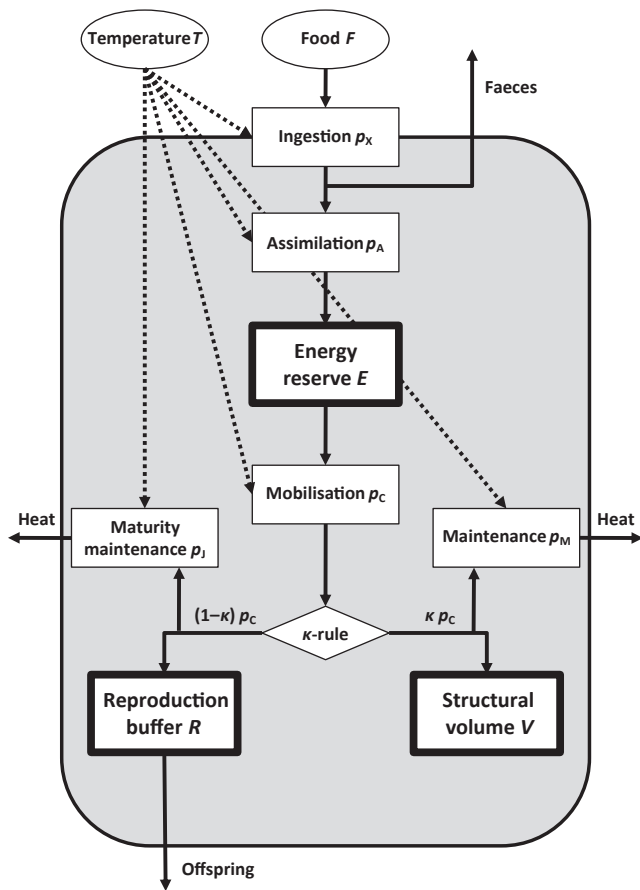


Fig. 1 Schematic representation of energy flow through an organism according to DEB theory (after Kooijman, 2009). Grey box: organism; bold rectangles: state variables; non-bold rectangles: physiological processes; ovals: environmental conditions; solid arrows: flow of energy; dotted arrows: temperature dependency. The κ -rule states that, in the standard DEBM, a constant fraction of mobilised energy is allocated to growth (plus maintenance) and reproduction (plus maturity maintenance).

Rhine with respect to water chemistry, plankton composition and temperature. Both temperature and food level were additionally manipulated in a two-factorial design by partially adding phytoplankton to the bypass system (treatments ambient food AF versus supplementary food SF), and by partially increasing the temperature by 3 °C above the natural background (treatments $\Delta 0$ versus $\Delta 3$), resulting in four treatment combinations ($\Delta 0$ AF, $\Delta 3$ AF, $\Delta 0$ SF, $\Delta 3$ SF). The experiments revealed a significant impact of temperature and food on the development of length, dry mass and reproductive success (Weitere *et al.*, 2009). Curiously, during the first period of the summer experiments, growth in the AF treatments exceeded that in the SF treatments. Weitere *et al.* (2009) suggested negative effects of supplementary food due to algal deposition. To take this effect into account, we

slightly modified the food response function for the SF treatment in ES (see Table S1).

In total, the DEBM included 12 free parameters (Table 2). Six parameter values were taken from literature or deduced from experiments (Table 2, first six parameters). For the remaining six parameters, we estimated reasonable ranges from ambiguous literature or experimental data (Table 2, see Appendix S1 for details). We then applied a grid-search procedure over the parameter space spanned by these estimated ranges, whereby 10 values were chosen to test for each of the six parameters, which resulted in approximately 1×10^6 simulation runs each for ES and EW. Deviations between the data and our simulated results were assessed with the objective function S_{QT} (E23), which is the sum of the weighted squares S_Q (E22) of all treatment combinations ($\Delta 0$ AF, $\Delta 3$ AF, $\Delta 0$ SF, $\Delta 3$ SF) and periods (EW, ES). S_Q considers deviations in length and mass development and their unequal number of observations (n_l , n_w). The parameter combination resulting in the lowest S_{QT} was selected as best fit and is referred to hereafter as the parameterised DEBM. In addition, to analyse the long-term suitability of the parameterised DEBM, simulations over the course of five years were conducted.

We excluded reproductive success from the parameter estimation procedure at the individual level due to difficulties in comparing experiments and simulations. In the experiments, offspring were counted, whereas in the DEBM, reproduction buffer R is expressed as energy. Thus, the amount of energy required to produce one offspring ω_L [J] would need to be known, which is not the case. However, because ω_L is an important parameter at the population level, we fitted R to the experimental data by applying different values of ω_L . Subsequently, the parameter value of the best fit (ω_{LS}) was compared to a theoretical value of the amount of energy needed to produce one offspring ω_{LC} , which was calculated on the basis of mass estimations of Aldridge and McMahon (1978; Appendix S1).

In all DEBM simulations, temperatures measured at the Ecological Rhine Station of the University of Cologne (Weitere *et al.*, 2009) and chlorophyll-*a* concentrations measured in Bad Honnef (Friedrich & Pohlmann, 2009) were used as environmental background data (Fig. 2). The initial conditions of l and E are based on Weitere *et al.* (2009), and the reproduction buffer R was set to be initially empty (Table S3). Because in the DEBM, no distinction is made between energy invested in maturation and energy invested in reproduction, an empty R of mature clams corresponds to $R_M = (1-\kappa)/\kappa (\delta l_p)^3 [E_G]$.

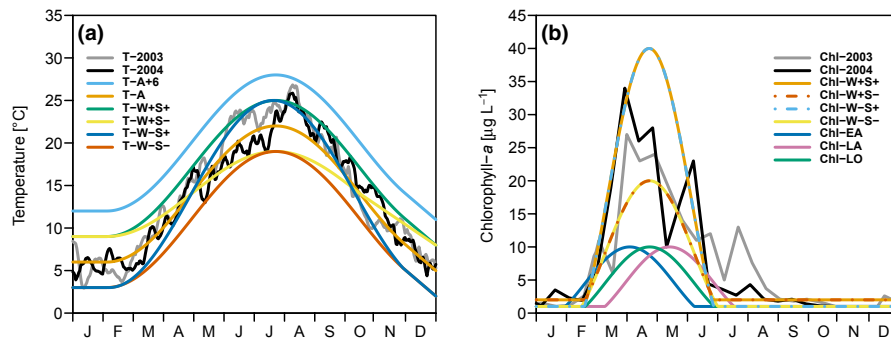


Fig. 2 Temperature (a) and chlorophyll-*a* concentration (b) applied in the systems analysis in comparison with data measured in the Rhine in 2003 and 2004. Based on the measured data, an average temperature scenario (T-A) and additional scenarios deviating from this in winter (W) and summer (S) temperature, as well as an extreme scenario (average temperature +6 °C: T-A+6), were generated (a). Likewise, scenarios differing in chlorophyll-*a* concentration during the spring peak (S) and the 'winter' period (W) characterised by generally low concentration were generated, and in addition, three scenarios with low spring concentration which differed in timing of the spring peak (Chl-LO, Chl-LA, Chl-EA) (b). Temperature was measured daily, chlorophyll-*a* at intervals of approximately 2 weeks (values between measurements were linearly interpolated). Letters on *x*-axis indicate month.

Simulations at the individual level were carried out using Mathematica 6.0 (Wolfram Research, Inc., Champaign, Illinois, USA).

Population level: Physiologically Structured Population Model. Controlled experiments on long-term population dynamics of *C. fluminea* are lacking. To estimate PSPM parameters and validate model suitability, we used field data from Meister (1997). A comprehensive review on the parameter estimation process is available in Appendix S4, and the estimated parameter values are listed in Table 3. Simulations at the population level were carried out using COMSOL Multiphysics 3.5 (COMSOL AB, Stockholm, Sweden) in combination with MATLAB R2009A (The MathWorks, Inc., Natick, MA, USA). Scripts are available on request.

Systems analysis

Scenarios. According to the DEBM, the development of *C. fluminea* is controlled mainly by the external factors temperature and food and the internal state variables length and energy reserve. To analyse the effect of changes in these four factors, we applied the parameterised DEBM to a range of possible scenarios. In temperature and food scenarios, the development of a virtual clam with an initial length of 10 mm was simulated over the period of one calendar year.

The annual water temperature profile in the Rhine shows a characteristic pattern with minimum winter temperatures usually above 2 °C and summer temperatures rarely exceeding 25 °C (Fig. 2a). We approximated average conditions by a sinusoidal curve (T-A; Fig. 2a),

and on this basis, we then either uniformly increased (T-A+6: +6 °C; T-W+S+: +3 °C) or decreased the temperature (T-W-S-: -3 °C). In addition, we created scenarios with low winter and high summer temperatures (T-W+S+) and *vice versa* (T-W+S-). In each scenario, the Chl-W+S- scenario (see next paragraph) was used as food background data.

The chlorophyll-*a* concentration in the Rhine has a pronounced spring peak and low values during autumn and winter (Fig. 2b). On this basis, seven food scenarios were created: four scenarios combining high or low winter concentrations with high or low spring concentrations (Chl-W+S+, Chl-W+S-, Chl-W-S+, Chl-W-S-; Fig 2b), and three scenarios with very low spring peaks (Chl-LO), which were additionally postponed (Chl-LA, Chl-EA). In all scenarios, average temperature conditions (T-A) were applied.

In the Rhine, clams released during the first annual reproductive period grew to a length of 8–10 mm by the end of the year (Meister, 1997). At this length, they commonly reach maturity. Thus, the previously described scenarios with an initial length of 10 mm correspond to typical second-year adult development. To examine the influence of length on further development, initial length was modified in additional scenarios, up to the natural maximum of 30 mm in the Rhine (Ini-L Scenarios).

Difference in mass of equal-sized clams (i.e., difference in energy density) may also affect development. In all previous scenarios, we assigned an initial energy density corresponding to the data from Weitere *et al.* (2009). In addition, we tested the effect of differences in energy density at the beginning of the year (Ini-E

Scenarios). In all Ini-scenarios, T-A and Chl-W+S+ conditions were applied.

Mass mortality. To test the hypothesis that the mass mortality in the Rhine in 2003 was caused mainly by starvation, we adopted the following three approaches.

First, we applied the parameterised DEBM to the 2003 environmental conditions (Fig. 2). To take into account within-population variation, we used a range of initial length values according to the Ini-L scenarios.

Second, we applied the parameterised DEBM to the 2003 environmental conditions, but modified the temperature response. Kooijman (2009) suggested the application of a single temperature function to control all physiological rates. However, experiments on temperature dependence of filtration and maintenance rates of *C. fluminea* demonstrated process specificity in temperature response (Viergutz *et al.*, 2007; Vohmann, 2008). While the filtration rate peaked at around 23 °C, the maintenance rate continued to increase with increasing temperature. Following Bourlès *et al.* (2009), who detected a similar pattern for *Crassostrea gigas*, we used two different temperature functions. This means that the temperature responses of all metabolic rates corresponded at low temperatures (<23 °C). Beyond this threshold, the ingestion rate p_X (and associated assimilation rate p_A) decreased with increasing temperatures, while the maintenance rates p_M , p_J and p_C continued to increase up to the maximum observed temperature of 27 °C.

Finally, we applied the PSPM to the 2003 environmental conditions. Virtual clams simulated with the DEBM can only be representative for the entire population if feedback effects of the population on processes at the individual level can be excluded. In the case of high population density, food ingestion of individuals might be impeded by restricted access to upper substratum layers. Consequently, we added a 'food accessibility factor' r_F (E16) to the food response function $f_P(F)$ (E17). In this way, the accessible food is reduced when the total volume of the population exceeds a threshold O_V . Westermann and Wendling (2003) described the population density in 2003 as high; hence, we assumed that the initial population density was close to O_V . However, we note that this is a speculative approach, as no comprehensive knowledge of real population densities during 2003 exists and the influence of population size on ingestion has not been examined. As initial condition, we used a population consisting of two cohorts through the combination of two Gaussian distributions differing in their means

(Meister, 1997; Cooper, 2007; Elliot & zu Ermgassen, 2008).

Results

Parameter estimation

The parameter values of the parameterised DEBM are given in Table 2. Deviations between model and data were larger for EW than for ES ($S_{QT} = 0.461$, $S_{QT-ES} = 0.029$, $S_{QT-EW} = 0.432$; see Fig. 3). However, the general annual patterns were reproduced by the model: stagnation during the winter period (Fig. 3d,e), simultaneous increases in shell length and dry mass during spring (Fig. 3d,e), and diverging rates of growth in length and mass during summer/autumn (Fig. 3a,b). In all simulations, length and mass at the end of each period were greatest in the $\Delta 3SF$ -treatment combination, in accordance with experiments. In contrast, the simulated clams in the $\Delta 0AF$ -treatment combination consistently grew least, whereas in the experiments, sometimes only small differences were observed between the $\Delta 0AF$ and other treatment combinations (e.g. Fig. 3d). While there was great consistency between simulated and observed mass in ES (Fig. 3b), final length and mass were slightly underestimated by the model in EW. Nevertheless, long-term simulations supported model suitability. Under normal Rhine conditions, the simulated average shell length after the first four years (*c.* 10, 17, 21 and 23 mm; see Fig. 3c) and the maximum shell length agreed well with observations in the Rhine (Meister, 1997; Vohmann, 2008). In addition, the energy demand to produce one offspring ω_{LS} derived from simulations (see Fig. 3f for fitted results) was of the same order of magnitude as the calculated value ω_{LC} ($\omega_{LS} = 0.05$, $\omega_{LC} = 0.09$).

Scenarios

A uniform increase in temperature (T-W-S- \rightarrow T-A \rightarrow T-W+S+ \rightarrow T-A+6) had an unambiguously positive impact on shell length, dry mass and reproduction buffer (Fig. 4a-c). Under warmed conditions, growth processes after winter stagnancy were initiated earlier in the year, and clams stayed larger and heavier throughout the remaining year. Similarly, their reproduction buffer was enlarged. In contrast, in scenarios with seasonally varying temperature shifts (T-W+S- and T-W+S+, compared to T-A), differences from the T-A scenario in length, mass and reproduction buffer were almost negligible. Energy density during the first half of the year was positively influenced by increasing temperature

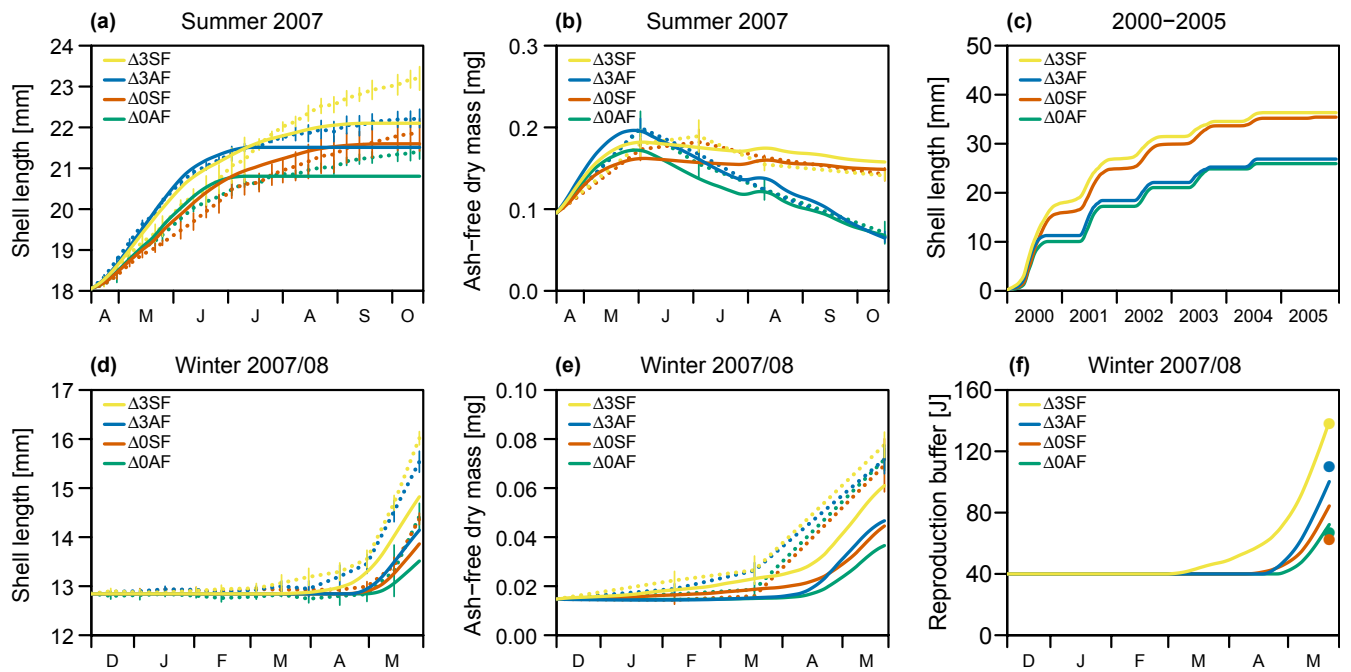


Fig. 3 Comparison between DEBM simulations (solid lines) and experiments (dotted lines). The DEBM was fitted to data of two independent mesocosm experiments conducted in river bypass systems fed with natural Rhine water in summer 2007 (a, b) and winter 2007/08 (d, e, f) (Weitere *et al.*, 2009). Vertical bars indicate standard deviation. The DEBM was additionally used for long-term growth simulations (c). Symbols indicate cross-manipulated environmental conditions, which were either kept at ambient temperature ($\Delta 0$) or ambient food level (AF), or altered by adding phytoplankton (SF, supplementary food) or increasing temperature by 3 °C above ambient conditions ($\Delta 3$), resulting in four treatment combinations ($\Delta 0AF$, $\Delta 3AF$, $\Delta 0SF$, $\Delta 3SF$). The filled circles in (f) indicate the reproductive success measured after the winter experiments when assuming an energy demand of 0.05 J to produce one offspring. Letters on x-axis indicate month.

(Fig. 4d). However, energy density during the second half was almost identical in all scenarios, except under extreme conditions (T-A+6).

In contrast to the temperature scenarios, different food scenarios did not affect the initiation of growth after winter dormancy (Fig. 4e–g). Subsequently, development was strongly influenced by the concentration of phytoplankton, but not all aspects of growth were affected in the same way. An increased amount of food during spring resulted in an overall increase in shell length and a greater reproduction buffer at the end of the year, whereas dry mass increased only until June. From July onwards, dry mass decreased and was more strongly affected by food availability at the time. In all scenarios with low winter food concentrations, the decrease in dry mass after spring was more pronounced (Fig. 4f), and ultimately the entire energy reserves were depleted (Fig. 4h). Thus, in our scenarios, low winter food concentrations led to death from starvation. However, the time of death depended on development during the summer. In addition, not only the total quantity of food, but also the period of time during which food was available (compare Chl-EA, Chl-LA and Chl-LO) had a decisive impact.

In the Ini-L scenarios, relative growth rate decreased with increased initial length (Fig. 4i), so that clams with a length of 30 mm virtually stopped growing in length. Nevertheless, they showed the same characteristic dynamics of dry mass, and the absolute mass increase in large clams during spring/summer exceeded that of smaller ones (Fig. 4j). Reproduction buffer showed a similar pattern – allocation of energy to reproduction increased with initial shell length (5–25 mm), with the exception of the largest clams (30 mm) (Fig. 4k). Energy density development was also size-dependent, with smaller clams starting to increase their energy density earlier, reaching a higher maximum in summer and maintaining a higher stable state in winter (Fig. 4l). Energy density of the largest clams decreased to zero in October.

In comparison with differences in initial shell length, differences in initial energy density were of minor importance for annual development (Fig. 4m–p). Clams replete with more energy initially started to grow earlier and reached a higher final length (Fig. 4m), but these differences were not pronounced. Variation resulting from differences in initial energy density reduced as time went on, and from June onwards, the growth

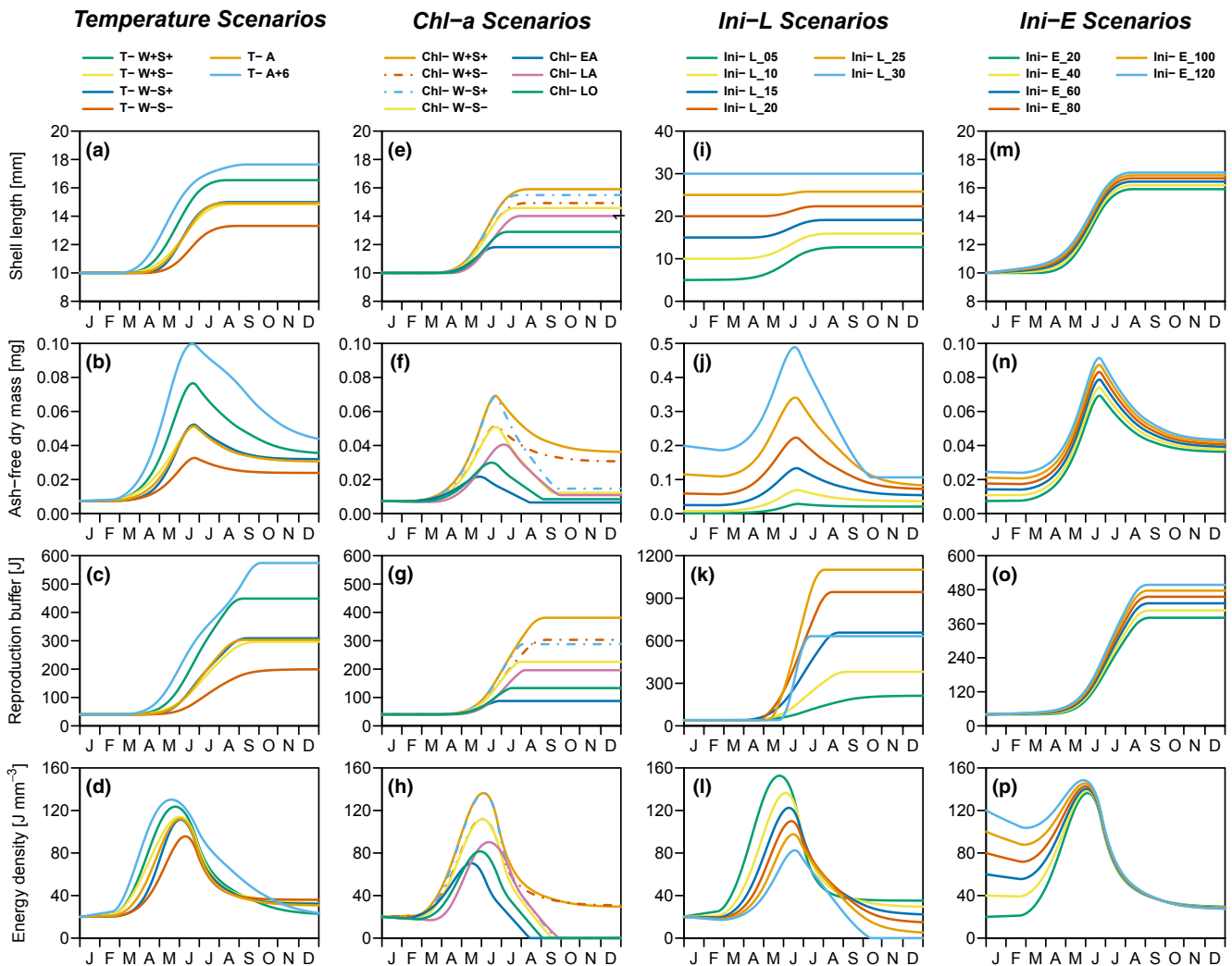


Fig. 4 DEBM simulations under different scenarios. The annual development of shell length, ash-free dry mass, reproduction buffer and energy density was simulated under different scenarios of temperature (a–d), chlorophyll-*a* (e–h), initial length (i–l) and initial energy density (m–p). The environmental conditions underlying the temperature and chlorophyll-*a* scenarios are shown in Fig. 2. In the initial length scenarios (Ini-L), clams with different initial shell lengths from 5 to 30 mm were simulated, while in the initial energy density scenarios (Ini-E), clams with an initial length of 10 mm differing in initial energy density were simulated. Letters on *x*-axis indicate month.

dynamics of clams with different initial energy densities were almost identical (Fig. 4p).

Mass mortality

Application of the 2003 environmental conditions using a single temperature function did not result in energy densities that would indicate death from starvation (Fig. 5a). Rather, the energy densities of both small and large simulated clams were relatively high throughout the year, particularly during the period in which the mass mortality was observed in the Rhine (end of June/beginning of July). In the approach where two temperature functions were applied, energy densities showed a

more pronounced decrease after the spring peak and, in the case of the largest individuals, even dropped to zero in September (Fig. 5b). However, during the mass mortality period, energy density remained high for all clams. In PSPM simulations, the length structure of the population showed the anticipated shift during the first 150 simulated days, that is, the clams of the initial population increased in length and new recruits entered the population during the first reproductive period (Fig. 5c). From day 150 to 195, which covers the mortality period, all clams smaller than 11 mm died. However, the survivors subsequently produced new offspring during the second reproductive period and losses could be compensated for quickly (Fig. 5c; $t = 250$).

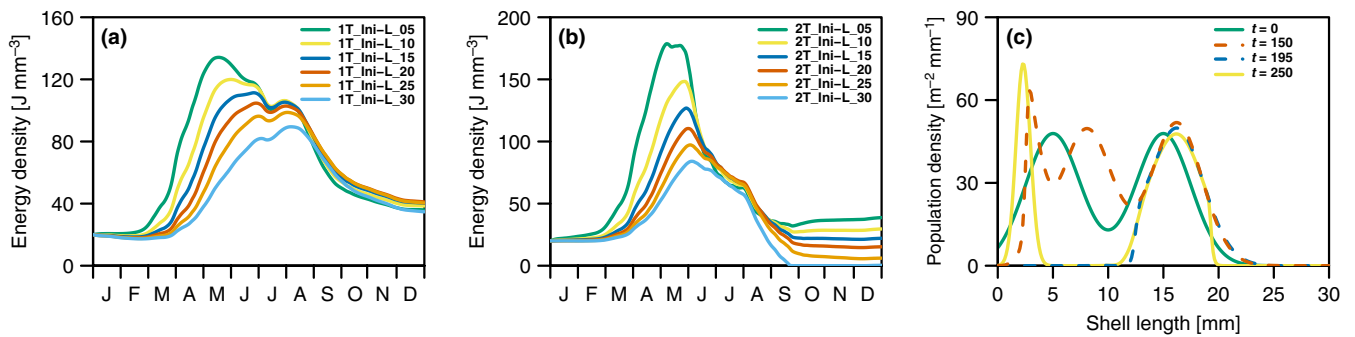


Fig. 5 DEBM and PSPM simulations under 2003 environmental conditions. The annual development of energy density as indicator of the nutritional status of clams differing in initial shell length (Ini-L) as simulated by the DEBM is shown in (a) and (b). Either one temperature response function (1T) for all metabolic processes (a) or two response functions (2T) differentially regulating filtration rate and maintenance rate (to account for their diverging development at high temperatures) were applied (b). Letters on x-axis indicate month (a, b). The length structured population density on selected days in 2003 (t : day of the year) as simulated by the PSPM is shown in (c). For comparison, the mass mortality in the Rhine in 2003 was observed between day 160 and 190.

Discussion

DEBM suitability

We assessed the suitability of the DEBM based on the fit between simulations and experiments by Weitere *et al.* (2009). Particular attention was paid to the observed annual dynamics, including (i) cessation of growth during winter, (ii) rapid increase in length and mass during spring and (iii) continued growth in length during late summer and simultaneous mass loss, as well as (iv) the distinct differences observed between different food and temperature treatments in experiments. By applying a Dynamic Energy Budget approach, we were able to reproduce these patterns with satisfactory accuracy. Especially with regard to the diverging development of length and dry mass, a pattern that has also been observed by other authors (Cooper, 2007; Vohmann, 2008), the energy budget-based description of the dynamics of energy reserve and structural volume proved to be useful. Furthermore, it was essential for the subsequent analysis of energy-based starvation. In addition, the long-term simulations under ambient conditions were in accordance with growth dynamics observed in the Rhine (Meister, 1997; Vohmann, 2008) and hence supported the suitability of the model.

Although the DEBM reproduced the general pattern well, there were deviations between the experimental data and simulations in some details. These deviations can have several explanations. (i) In summer experiments, clams taken from flow channels (average size 18 mm) were employed, whereas in winter experiments, clams taken directly from the Rhine (average size

13 mm) were used (Weitere *et al.*, 2009). Differences in stress or adaptation to environmental conditions between these sets of clams could result in different responses to environmental conditions. (ii) The temporal resolution of the food data was low: chlorophyll-*a* concentration was measured at irregular intervals of approximately two weeks. Particularly in spring, the phytoplankton concentration is highly dynamic (Friedrich & Pohlmann, 2009) and as a result, linear interpolation between these measurements might ignore significant additional variation. (iii) We modelled food ingestion solely as a function of chlorophyll-*a* concentration, assuming that clams obtain energy exclusively from filter feeding on phytoplankton. However, clams are also capable of pedal feeding on benthic organic matter, and this may be an important source of energy when phytoplankton is scarce, particularly during winter (Hakenkamp & Palmer, 1999). The fact that we did not integrate this alternative food supply may explain why clams in our simulations stopped growing earlier than those observed in the experiments. In addition, Ortmann and Grieshaber (2003) detected a circadian rhythm of valve movement during summer, whereas in winter an irregular pattern was observed. Valve movement, metabolic rate and filtration should be correlated for benthic filter feeders. In general, the adaptations of *C. fluminea* to variation in environmental conditions might be more diverse than the processes we included in the DEBM. However, the overall good agreement between model results and experimental data suggests that the processes we integrated into the model are dominant during the crucial period of development and that the DEBM is thus an acceptable simplification.

Scenarios

Simulations under the different scenarios revealed a substantial effect of temperature and food on the annual development of individual clams. Differences in the timing of initiation of development between scenarios with uniformly increased temperatures and scenarios in which only extreme summer or winter temperatures were altered indicate that a temperature threshold governs the initiation of development. These results agree with the observations of other authors (e.g. Joy, 1985). In contrast, cessation of development in our simulations was more influenced by food conditions over time. This is particularly obvious when comparing the Chl-EA, Chl-LA and Chl-LO scenarios: although the absolute quantity of food was equal, a shift of the chlorophyll-*a* peak to a later time resulted in extended growth. In general, the clams grew in length and mass and invested energy into reproduction only when suitable temperature and sufficient food were available simultaneously. In the Rhine, the period with these conditions is short; during cold periods (winter, early spring, late autumn), it is limited by low water temperatures and from late summer on it is limited by low phytoplankton concentrations. Thus, under natural Rhine conditions, a uniform increase in temperature extends the favourable period, as does a postponed or extended phytoplankton peak.

However, a correlation between environmental conditions and development could not explain all results. Although in all scenarios, the chlorophyll-*a* concentration was low after the spring peak, the clams continued to grow and invest energy into reproduction, a behaviour that is characteristic in the Rhine under natural conditions (Meister, 1997; Weitere *et al.*, 2009). The mechanisms that are described by the DEBM can help to explain this behaviour. According to DEB theory, food is initially assimilated into energy reserve (Fig. 1). The amount of assimilated energy in relation to size, that is, the energy density, then controls the growth rate (along with temperature), and growth is possible only when energy density exceeds a given threshold (see Appendix S5). Thus, the energy reserve can be regarded as a reservoir of energy that alleviates the dependence of the clam on the environment and enables it to grow in times of food shortage. However, the Ini-E scenarios also showed that differences in energy density between individual clams decreased rapidly over time (Fig. 4p) and that energy density converged to a steady state during winter unless the winter chlorophyll-*a* concentration was too low (Fig. 4h) or the clams were too long (Fig. 4l). This indicates that advantageous conditions in

spring allow clams to cope with food shortages in following weeks, but, on the whole, the effect of a filled energy reservoir does not persist.

Mass mortality

Natural mortality rates of *C. fluminea* are relatively high, causing large fluctuations in population density (McMahon, 1991; Meister, 1997; Cooper, 2007). In the Rhine, Meister (1997) observed an increased mortality rate, mainly of large individuals, from August to October, while during the rest of the year, the mortality rate was low. The results of our simulations agree with these observations. When the food was insufficient after the spring chlorophyll-*a* peak, stored energy was entirely consumed in the period from August to September (Fig. 4h), and larger clams were more likely to die in this period (Fig. 4l). Thus, natural mortality in Rhine might simply be a consequence of the energetic dynamics of individual clams and thus be well described by a DEBM.

In contrast, during the relevant period in 2003, in which a mass mortality was observed, critical energy levels indicating starvation were not simulated by the parameterised DEBM. The underlying mesocosm experiments used to parameterise this model covered the entire temperature range observed in 2003, and consequently, the DEBM should be suitable for projections. However, it is conceivable that, at high temperatures or under stress, mechanisms affecting the energy uptake or energy loss might be altered (Bayne *et al.*, 1977; Doherty & Cherry, 1988). One feasible deviation is contrasting changes in filtration and metabolic rate at high temperature, which intensifies the discrepancy between energy uptake and loss. This alternative mechanism was integrated via two separate temperature response functions. However, even under this scenario, critical energy densities were not simulated during the relevant period. The phytoplankton concentrations in 2003 were high compared with other years (Zwolsman & van Bokhoven, 2007), and under these circumstances, it appears unlikely that clams starved to death. In addition, our findings are supported by experimental studies by Ortmann and Grieshaber (2003) and Vohmann *et al.* (2010) who demonstrated the ability of *C. fluminea* to tolerate prolonged periods of insufficient energy supply. Ortmann and Grieshaber (2003) showed that *C. fluminea* can reduce its energy demand by 90% during valve closure, a possible mechanism for avoiding severe starvation, and Vohmann *et al.* (2010) demonstrated that *C. fluminea* can survive drastic mass reductions. Consequently,

when considering our simulation and the results of these aforementioned studies, it appears to be unlikely that non-stressed clams suffered from severe starvation during the heat wave in 2003.

However, high population densities are a conceivable source of stress. Food competition as one possible effect at high population densities was integrated into the PSPM; this resulted in the exclusive death of small clams. In general, it can be expected that, due to their different metabolic constraints, varying size classes would be affected differently by starvation-induced mortality. However, during the massive die-off in 2003, dead clams of all size classes were observed (A. Kureck, University of Cologne, personal communication). Of course, if a substantial part of the population dies, a negative feedback on the remaining part is imaginable. Cherry *et al.* (2005) tested such a scenario, although increased mortality rates were observed only when the water flow was stopped completely; a similar situation is unrealistic in the Rhine, even during hot periods. In addition, the associated changes in water quality (oxygen, ammonia) were not observed (Zwolsman & van Bokhoven, 2007). Overall, it seems unlikely that starvation was a main cause of the mass mortality in the Rhine in 2003.

Nevertheless, a prolonged negative energy budget, promoted by high temperature, is a source of stress that increases the vulnerability of individual clams (Kooijman, 2009; McCue, 2010). In combination with this increased vulnerability, additional abiotic or biotic factors, which are by themselves not critical, might intensify their negative effects (Doherty & Cherry, 1988). However, although the river discharge during the relevant period in June/July was extremely low and temperatures were the highest on record since 1761 (Schönwiese *et al.*, 2004), other prominent factors such as pH, conductivity, O₂, nitrogen and heavy metal concentrations were only slightly influenced and remained far below lethal limits (Doherty & Cherry, 1988; Zwolsman & van Bokhoven, 2007). Mortality imposed by such factors, even on weakened clams, is hard to imagine. We consider it more likely that a combination of direct and indirect effects, promoted by high temperature, was responsible. According to Mattice and Dye (1976), the incipient lethal temperature is 34 °C, but mortality was significantly increased at lower temperatures when clam had been acclimatised at low temperature. The rapid and intense increase in temperatures in early summer 2003 (Fig. 2a) might therefore have played an important role. Studies on other clams reported strong increases in stress proteins particularly when temperature was increased rapidly, and increased stress can have direct

and indirect impacts on mortality rates, for instance by damaging gill tissue (Chapple, Smerdon & Hawkins, 1997). In addition, increased vulnerability to stressors at high temperature, including pathogens and parasites, might also be relevant. However, these speculations need to be tested.

In conclusion, we demonstrated multiple effects of environmental conditions on the development of *C. fluminea* using a modelling approach. We showed that DEBMs and PSPMs are valuable tools to analyse species behaviour, especially under fluctuating environmental conditions. Our approach can serve as a starting point for studies on further dynamic interaction of environmental conditions. However, modelling approaches require well-designed experiments to incorporate mechanistic processes accurately. While field studies on *C. fluminea* are common, controlled experiments are still rare. We recommend a focus on micro- and mesocosm experiments aiming at identifying how changes in environmental conditions affect the performance of these bivalves. Even though we concluded that starvation-induced mortality is an unlikely cause of mass mortality, we cannot unequivocally reject this hypothesis, mainly because we lack detailed information on how effects of population size affect individual clams, particularly at high population density. Therefore, the inclusion of aspects of population density in experiments would appear promising, particularly because high density is a striking feature of most populations of *C. fluminea*.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Complete list of variables used in the DEBM or the PSPM.

Table S2. Complete list of parameters used in the DEBM or the PSPM.

Table S3. Complete list of equations.

Appendix S1. Derivation of DEBM parameters.

Appendix S2. DEBM adaptations in case of severe starvation.

Appendix S3. Motivation of recruitment representation in PSPM.

Appendix S4. Plausibility considerations for DEB structured population model.

Appendix S5. Critical energy density.

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