The Journal of Experimental Biology 214, 3678-3687
© 2011. Published by The Company of Biologists Ltd
doi:10.1242/jeb.061945

RESEARCH ARTICLE

From population-level effects to individual response: modelling temperature dependence in *Gammarus pulex*

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Accepted 16 July 2011

SUMMARY

Population-level effects of global warming result from concurrent direct and indirect processes. They are typically described by physiologically structured population models (PSPMs). Therefore, inverse modelling offers a tool to identify parameters of individual physiological processes through population-level data analysis, e.g. the temperature dependence of growth from size–frequency data of a field population. Here, we make use of experiments under laboratory conditions, in mesocosms and field monitoring to determine the temperature dependence of growth and mortality of *Gammarus pulex*. We found an optimum temperature for growth of approximately 17°C and a related temperature coefficient, Q_{10}, of 1.5°C^{-1}, irrespective of whether we classically fitted individual growth curves or applied inverse modelling based on PSPMs to laboratory data. From a comparison of underlying data sets we conclude that applying inverse modelling techniques to population-level data results in meaningful response parameters for physiological processes if additional temperature-driven effects, including within-population interaction, can be excluded or determined independently. If this is not the case, parameter estimates describe a cumulative response, e.g. comprising temperature-dependent resource dynamics. Finally, fluctuating temperatures in natural habitats increased the uncertainty in parameter values. Here, PSPM should be applied for virtual monitoring in order to determine a sampling scheme that comprises important dates to reduce parameter uncertainty.

Supplementary material available online at http://jeb.biologists.org/cgi/content/full/214/21/3678/DC1

Key words: temperature response, temperature coefficient, Q_{10}, optimum temperature, parameter estimation, inverse modelling.

INTRODUCTION

Physiologically structured population models (PSPMs) (De Roos, 1997; Caswell, 2001; Tuljapurkar and Caswell, 1997) are an expedient tool to analyse and project possible effects of global warming on population densities because they are able to take into account the concurrent direct and indirect effects. Considering poikilotherm aquatic species, rising water temperature may directly affect reproduction and mortality (Aktinson and Sibly, 1997; O'Connor, 2009; Hofmann and Todgham, 2010), but it also affects growth and, consequently, the size structure of the population (Sutcliffe et al., 1981). Through a shift in population size structure, a temperature change may additionally take indirect effects on reproduction and mortality because of the size dependence of these processes (e.g. Berrigan and Charnov, 1994). The advantage of joint accounting in PSPMs comes along with the disadvantage of needing a multitude of parameters. Would it be possible to make a virtue out of necessity and apply PSPM for parameter identification, i.e. determine parameters through inverse modelling based on PSPM? If this were sensible, length–frequency data of a population would suffice to determine not only the growth rate (e.g. Casale et al., 2011; Roa, 1993), but at the same time its temperature dependence.

We focus on temperature reactions in both growth and mortality, i.e. maximum rate constants and the specific temperature response. The latter will be described by two temperature response parameters: the temperature at which reactions are fastest, i.e. the optimum temperature (T_{opt}), and the increase of reaction with increasing temperature, often described by the temperature coefficient Q_{10} (Cossins and Bowler, 1987).

Our study species is the amphipod *Gammarus pulex* (Linnaeus 1758), which is one of the main shredders in running waters of temperate regions and, therefore, crucial for energy turnover in these ecosystems (Boyero et al., 2011). Experimental data that could serve for parameterisation generally embrace two extremes. The first extreme is laboratory experiments, where growth and survival of individuals are tracked under controlled conditions, as extensively carried out for *G. pulex* (Sutcliffe et al., 1981; Willoughby and Sutcliffe, 1976). Parameter identification is straightforward, but results may be biased by artificiality. For instance, laboratory experiments commonly utilise fixed temperatures, whereas in nature temperatures are variable, which may affect development and survival rates (Howe, 1967). The second extreme is field monitoring, where only changes in the size structure of populations can be tracked under fluctuating conditions (Gee, 1988; Goedmakers, 1981; Welton, 1979). Parameter identification is difficult because: (1) the environmental factor fluctuates naturally and not in the range and frequency that would guarantee the uniqueness of the parameters, (2) growth and survival must be parameterised simultaneously such that potential correlations increase uncertainty, and (3) additional

environmental factors might be ignored. Somewhere in between these extremes are mesocosm experiments, in which some environmental variables are under control whereas others, such as biotic interactions, might affect the life cycle parameters in unknown ways (Felten et al., 2008b; Moran et al., 2009; Sommer et al., 2007; Van Doorslaer et al., 2007).

This study focuses on the identifiability and transferability of temperature response parameters and reaction rates of *G. pulex* from different experimental setups. To this end we make use of an eclectic set of pre-existing experiments. These range from single-individual laboratory experiments to multi-individual mesocosm experiments to field monitoring. Supposing that laboratory experiments yield the most detailed and least biased database, we use these experiments to identify the targeted parameters, compare them with previous data (Sutcliffe et al., 1981) and analyse whether they are suitable for explaining population dynamics observed in mesocosm experiments and field monitoring. Then, we apply inverse modelling based on PSPM for parameter identification on all data sets and compare the results in order to determine the effects of population-level considerations. Here, we differentiate between the effects of database reduction (because we ignore the individual development) and the effects of probable biotic interaction. Summarising, the questions raised are: (1) what is the temperature response of *G. pulex* with respect to individual growth and mortality; (2) can temperature response parameters derived from laboratory experiments unambiguously be applied under natural conditions; (3) can we identify physiological parameters of growth at the population level; and (4) can we identify physiological parameters under natural conditions?

MATERIALS AND METHODS

Study species

In wide parts of Europe, *G. pulex* is common in most running waters, from headwaters to medium sized rivers. Although in Ireland *G. pulex* has been introduced and acts as an invasive species (Kelly et al., 2006), it became affected by other invading amphipods in central Europe (Felten et al., 2008b; MacNeil and Platvoet, 2005). In the running waters of Central Europe, *G. pulex* is the most frequent proxy of the aquatic functional feeding group of shredders, which feed mainly on leaf litter from the terrestrial system and on fungi and algae growing on detritus. They shred the material and, therefore, make it available for the decomposers and filterers in the stream system (Cummins and Klug, 1979). Thus, *G. pulex* accomplishes an important role by linking the energetic transport from the terrestrial to the aquatic system (Cummins and Klug, 1979; Graça et al., 2001; Felten et al., 2008a). At the same time, *G. pulex* may behave as a predator and as a cannibal (MacNeil et al., 1997; Kelly et al., 2002). It is a model organism for the study of several topics, for instance parasitology and sexual selection (Bollache and Cézilly, 2004; Dahl and Greenberg, 1996), understanding longitudinal drift (Elliott, 2002) and predation (Bakker et al., 1997).

The life span of *G. pulex* varies between 1 and 2 years (Sutcliffe et al., 1981). Growth rate varies with age, being highest shortly after birth; temperature optima for growth are at approximately 20°C for newborns and 15°C for small mature individuals (Sutcliffe et al., 1981). To our knowledge, data for temperature pessima are not available.

Experimental and field methods

In this study we made use of and compared a set of three experimental and field studies that were carried out with the same population of *G. pulex* from Schunter River and its tributary, Wabe River, in Braunschweig, Germany. Therefore, one important source of variation, differences between populations, was minimised. In contrast, the experiments were originally designed for various different purposes other than a comparison. For instance, different measurements were taken such as size or mass, which impeded a comparison. Other differences in design were intrinsic to the method, e.g. weekly size measurements are sensible in the laboratory, but in the field they are not.

Laboratory: monitoring growth at fixed temperature

Mature *G. pulex* (body length ≥6 mm) were individually placed into small containers (7×5.5 cm) and reared at five fixed temperatures: 8, 12, 16, 20 and 24°C. We simulated a circadian rhythm of 12 h (lights on from 08:00 to 20:00 h) with fluorescent lamps (all ca. 500 lx). Each container was provided *ad libitum* with elder leaves as food. Size measures were taken by photographing each individual and measuring body length using image analyser software (ImageJ, http://rsbweb.nih.gov/ij/) at the beginning of the experiment and thereafter every week for 5 weeks in total, so that six measurements were taken in total per individual. The number of replicates per temperature was 60 individuals. For considerations at the population level, individual lengths were classified to length–frequency data and a normal distribution was fitted for each temperature and measurement.

Mesocosm: monitoring growth in small populations with varying temperature regimes

We conducted mesocosm experiments in order to study the effect of rising temperatures on growth (here change in mass) and mortality under semi-natural conditions, i.e. varying, but precisely measured temperatures. We reared several individuals of *G. pulex* together in cages placed in artificial streams, allowing for intraspecific interactions. The water in the streams was circulated by water wheels generating a current of 0.2 m s^{-1}. The cages (30×20×15 cm), each stocked with 10 *G. pulex*, consisted of gauze with a mesh size of 0.5 mm. We placed the artificial streams in four large tanks, each containing approximately 15001 of water and with different temperature regimes. The tanks were situated outside, protected against precipitation by a transparent roof, thus prone to natural changes in temperature and light regimes. In one tank the water temperature was directly driven by the outside temperatures, except that we kept it to a minimum of 1°C so that it did not freeze. Compared with this ambient treatment, in the other tanks the water temperature was constantly increased by 2, 4 and 6°C using heaters. Thus, these tanks experienced identical temperature fluctuations as the ambient temperature tank but with increased mean temperature (see supplementary material Fig. S1). To keep the water temperature uniform within any one tank, pumps circulated the water. Water temperature in each tank was automatically recorded at 20 s intervals. To simulate natural food conditions, 10 leaves of *Acer pseudoplatanus* were introduced at the beginning of the experiment, mimicking the leaf fall. Thereafter, no external food was added, but algae, diatoms and other protozoans, which serve as food for *G. pulex*, were freely growing on the sandy-bottom sediment. The number of cages per treatment was 48. We measured wet mass of *G. pulex* at day 59 of 2004, the beginning of the experiment, and thereafter at days 81, 104 and 121. The low number of recordings was performed in order to keep disturbance of the population at a minimum. The amphipods were caught, counted and slightly dried on paper tissue before weighing. Because we were unable to track individuals, we jointly weighed all amphipods belonging to the same cage and calculated mean masses per cage, dividing the total mass of *G. pulex* per cage by the number of individuals per cage. For considerations at the

population level, mean masses were classified to mass–frequency data and a normal distribution was fitted for each tank and measurement.

Field: monitoring of size-structured populations under natural conditions

From 2006 to 2007, the population of *G. pulex* was also monitored *in situ* in both rivers. At both sample sites, five samples were taken randomly, using Surber-type square-samplers (0.011 m^2) (Suhling et al., 2000). In the laboratory, *G. pulex* were counted and photographed for subsequent size measurements using ImageJ. The size was determined as the length (mm), measured dorsally along the body from top of the head to the rump. All individuals were preserved in ethanol.

Size–frequency data of the population (intervals of Δ=0.25 mm) suggested the coexistence of several generations. As we focus on the development of a single generation here, we separated overlapping generations in the following way. We transformed size–frequency data (N_j, where N is the number of individuals in size interval j) into population density n (mm^{-1}) per sample and per body length l (mm) using the following equation:

$$N_j = \int_j n(l)\mathrm{d}l \approx n(l_j)\Delta . \quad (1)$$

We assumed that the entire population consists of M generations, each of which is normally distributed over body length l (mm) with mean length μ_i (mm), standard deviation σ_i (mm) and maximum density $u_{\max i}$ (mm^{-1}):

$$n(l) = \Sigma_M u_{\max i} e^{-1/2[(1-\mu_i)/\sigma_i]^2} . \quad (2)$$

Parameter fitting was performed with the subspace trust region optimisation algorithm implemented in MATLAB version 9b (www.mathworks.de). We concatenated individual generations of the different sampling data sets into the annual dynamics of one generation from June, July, August, October and April (see supplementary material Fig. S2 for exact dates for both sites) and checked it against previous descriptions of the life cycle of gammarids (e.g. Hynes, 1955; Iversen and Jessen, 1977; Pöckl et al., 2003).

Water temperature was measured daily. For a 2 month period of malfunction of the temperature data-logger, we estimated water temperatures by linear regression with air temperature. Temperatures of the Schunter River (annual mean ± s.d.=10.9±4.9°C) fluctuated to a larger degree than temperatures of Wabe River (11.15±1.85°C; see supplementary material Fig. S2).

Models

PSPMs (De Roos, 1997) generally comprise reproduction, mortality and changes in the physiological state considered. The model applied here comprises only mortality and growth, considering size as physiological state:

$$\frac{\partial n(l,t)}{\partial t} = -\frac{\partial G(T,l)n(l,t)}{\partial l} - \mu(T)n(l,t) , \quad (3)$$

where $n(l,t)$ (mm^{-1}) is population density per body length l (mm) depending on time t (days); $G(T,l)$ is growth (mm day^{-1}) depending on temperature T (°C) and body length; and $\mu(T)$ is the temperature-dependent mortality rate (day^{-1}). The total number of individuals is given as the integral of $n(l,t)$ with respect to length and will be referred to as abundance [for a derivation of $n(l,t)$ from data see the previous section].

We described growth, $G(T,l)$, by a hump-shaped temperature response $\Phi_G(T)$ modulating only net growth $g(l)$:

$$G(T,l) = \Phi_G(T)g(l) . \quad (4)$$

Net growth was defined as the differential form of the von Bertalanffy equation (Bertalanffy, 1957):

$$\frac{\mathrm{d}l}{\mathrm{d}t} = r\left(l_{\max} - l\right) = g(l) \text{ with } l(0) = l_0 , \quad (5)$$

where r is the growth rate (day^{-1}) and $l_{\max}$ is the maximum body length (mm).

We assumed that overall mortality can be described by two independent factors: (1) a constant intrinsic mortality rate μ_0 and (2) an additional temperature response of mortality $\varphi_M(T)$. The latter was described through its complement, the temperature response of survival $\Phi_S(T)$=1–$\varphi_M(T)$, because we expected it to be hump-shaped and preferred identical temperature response functions for both processes:

$$\mu(T) = 1 - (1 - \mu_0)\Phi_S(T) . \quad (6)$$

In order to describe the hump-shaped temperature response of growth and survival, we applied the O'Neill function (Krenek et al., 2011):

$$\Phi(T) = \left(\frac{T_{\max} - T}{T_{\max} - T_{\text{opt}}}\right)^p e^{p\frac{T - T_{\text{opt}}}{T_{\max} - T_{\text{opt}}}} , \quad (7)$$

with

$$p = \frac{1}{400}W^2\left(1 + \sqrt{1 + \frac{40}{W}}\right)^2 , \quad (8)$$

and

$$W = (Q_{10} - 1)(T_{\max} - T_{\text{opt}}) , \quad (9)$$

where $T_{\max}$ and T_{opt} are maximum and optimum temperatures (°C), respectively; Q_{10} is the determining response change ($°C^{-1}$), i.e. it describes the slope of the temperature response.

Data from mesocosm experiments differed in two respects from the two other data sets: (1) mass was measured instead of size, (2) measurements revealed dynamic fluctuations in mass (loss–gain–loss) instead of a steady increase. Accounting for (1), a mass-structured population model was applied here. Size-related parameters can be deduced from mass-related parameters through allometric functions (see e.g. Kooijman, 2010). For the population of *G. pulex* at hand, laboratory experiments as described in 'Laboratory: monitoring growth at fixed temperature' revealed a functional relationship between mass (m) and size: m=cl^3, where c is the size to mass coefficient and has a value of approximately 0.0119 mg mm^{-3} (L.M. and L.R., unpublished); consequently, size-related parameters could be deduced from mass-related parameters. Accounting for (2) and speaking in terms of von Bertalanffy growth, mass loss is the result of anabolic processes being smaller than catabolic processes. Consequently, an additional factor was required that allowed to separately activate the anabolic term. The dominant environmental factor activating anabolism is food, such that for the sake of simplicity we introduced a term $F(t)$, called the food response. Eqn 5 thus changed to:

$$\frac{\mathrm{d}l}{\mathrm{d}t} = r\left(F(t)l_{\max} - l\right) = g(l) . \quad (10)$$

We assumed $F(t)$ to be a response function in the sense that it has a value of 1 under optimum conditions and 0 under unviable conditions:

$$F(t) = \left(1 - e^{-\left(\frac{t}{t_1}\right)^{\alpha_1}}\right) \cdot e^{-\left(\frac{t}{t_2}\right)^{\alpha_2}} . \quad (11)$$

In the given measured dynamics, optimum conditions were present during midterm only and an adequate description was as follows with t_1 (days) being the point in time of the response increase and t_2 (days) being the point in time of the response decline. α_1 and α_2 are design parameters for inflections.

Parameter identification

We assumed that the temperature response of growth and survival could be described by the O'Neill function. Hence, we quantified temperature response by identifying the respective response parameters T_{opt} and Q_{10} for growth and survival. Temperature response modulates net rates of either process; consequently, these rates, r and μ_0, were also determined during parameter identification. Parameter fitting was carried out with the subspace trust region optimisation algorithm implemented in MATLAB version 9b, allowing for nonlinear optimisation. Standard deviations of data, where available, were used as inverse weights in the objective function, i.e. samples with large standard deviations were given small weight. The algorithm furnishes local optima only and manual checking and repetition was applied where necessary.

Differences in experimental design as well as differences in process assumptions result in different approaches for parameter identification (see Table 1). If temperature is constant over the course of the experiment, a two-step fitting is required: rates are first fitted as temperature-specific rates $r(T)$ and $\mu(T)$, which then serve for response parameter fitting. If temperature is not constant, rates and response parameters must be fitted simultaneously. If growth and mortality are independent, which is the case in our model, both processes can be fitted separately: growth through body length $l(t)$ and mortality through abundance $N(t)$. If the processes are not independent, for instance if juvenile mortality is expressed as mortality dependent on body length, both processes must be fitted simultaneously *via* fitting of population density $n(l,t)$. Simultaneous fitting of a set of parameters generally is accompanied by the risk that correlations between individual parameters are high, i.e. different combinations of parameters explain the data equally well (Beven and Freer, 2001; Sokal and Rohlf, 1995). Fortunately, growth and mortality could be considered to be independent here (A.-K.S., unpublished). However, in order to pinpoint the effect of simultaneous fitting, we deliberately transformed the measured variables from length frequencies to mean body length and abundance, or *vice versa*. Although body length data and abundance data were fitted directly, length frequency data were fitted indirectly: they were transformed to normal distributions of population densities per length. These were homogeneously sampled (see supplementary material Fig. S3 for a visualisation). For identical quantities, goodness of fit was compared *via* the coefficient of determination, R^2, and reliability of parameter estimates *via* Pearson correlations (Sokal and Rohlf, 1995).

Subsequently, we will list all parameter identification strategies applied and finish the section assigning the strategies to the four questions raised in the introduction.

The laboratory (L) data set was the most comprehensive because: (1) individual growth and survival was tracked and (2) temperature-specific rates and related response parameters could be fitted successively. This allowed us to apply different strategies to identify temperature-specific rates, coming forth from specific assumptions. We describe here the underlying assumptions and corresponding strategies.

L1: growth rates were individually fixed and showed a normal distribution among individuals. Individual growth (time course of size) was fitted separately for each individual. These individual growth rates were divided into temperature-specific sets whose means were identified as temperature-specific growth rates.

L2: growth rates were temperature dependent only and identical for all individuals surviving until the end of the experiment. Individual growth was fitted at once for all living individuals in one temperature treatment, resulting in temperature-specific growth rates.

L3: growth rates were temperature dependent only and identical for all individuals, including moribund animals. This strategy resembles L2, but comprises moribund animals.

L4: both growth and mortality rates were temperature dependent only and identical for all individuals, including moribund animals. Size-structured population densities were determined per temperature and sample date and fitted, resulting in temperature-specific growth and mortality rates.

L5: mortality rates depended on temperature only. The dynamics of abundance were fitted, resulting in temperature-specific mortality rates.

Note that the strategies basically differ in the underlying assumptions of the causes for deviations. In L1 to L3, size sampling is assumed to have a normally distributed error. In L4, population density per body length is assumed to have a normally distributed error. Finally, in L5, abundance is assumed to have a normally distributed error.

For mesocosm (M) data, the following assumptions and strategies were applied:

M1: no prior assumptions could be considered. Mass-structured population densities were determined per tank and sample date and fitted, delivering all rates and all response parameters simultaneously.

M2: food response was identical for all temperature regimes. It was fixed to be 1 between sampling days t_1=81 and t_2=104, with a steeper inflection at its decrease than at its increase, i.e. $\alpha_1<\alpha_2$. Mean mass dynamics was determined for each tank and fitted, resulting in growth rates and the temperature response of growth.

M3: temperature response parameters from laboratory experiments were applicable. Mean mass dynamics were determined

Table 1. Effects of experimental design and process assumptions on parameter fitting procedure

		Temperature course	
		Constant	Natural
Process assumption	Effect	Two-step fitting	Simultaneous fitting
Size-independent mortality	Separate fitting of growth	L1, L2, L3	M2, M3
	Separate fitting of mortality	L5	M4
Size-dependent mortality	Simultaneous fitting of growth and mortality	L4	M1, F1, F3, F4

Parameter identification strategies are abbreviated as laboratory (L), mesocosm (M) and field (F) and numbered serially. F2 and F5 are excluded because no temperature dependence was fitted.

for each tank and fitted, resulting in growth rate and the temperature response of food, i.e. t_1 and t_2.

M4: mortality rates depended on temperature only. The dynamics of abundance were calculated for each tank and mortality rates and the temperature response of mortality were fitted.

Field (F) data were used for four strategies. These strategies imply either presence or absence of temperature dependencies, i.e. the underlying models differ in complexity. Consequently, we additionally applied Akaike's information criterion (AIC) for model comparison (Akaike, 1973).

F1: all rates and all response parameters were fitted simultaneously.

F2: growth and mortality were assumed to be temperature independent. Consequently, all response parameters were neglected.

F3: only mortality was assumed to be temperature independent.

F4: only growth was assumed to be temperature independent.

F5: temperature response parameters from laboratory experiments were applied and only rates were fitted.

Additionally, laboratory parameters (including rates) were applied to mesocosm and field data to quantify deviations.

Assuming that laboratory experiments, although artificial, serve best for parameter identification, we will answer question 1 based on strategies L1 to L3 for growth and L5 for mortality. Transferability considerations (question 2) will, on the one hand, be based on respective strategies, i.e. M3 and F5, and, on the other hand, be compared with method-specific strategies, i.e. M4 and F2 to F4. We will analyse whether the population level itself impedes identification by comparing the results of L4 with those of other laboratory strategies (question 3). Finally, we will analyse emerging ambiguities and shortcomings where applicable, especially with M2 and F4 (question 4).

RESULTS

Laboratory experiments

Fitting of growth

All four strategies used for temperature-specific growth fitting (L1–L4) were similarly successful (Fig. 1): the coefficients of determination varied from 0.86 to 0.90. A comparison of the temperature-specific rate estimates of the four strategies (see supplementary material Table S1) showed that their minima were similar in magnitude and were reached at identical temperatures, i.e. at both 8 and 24°C. A distinct peak rate was found only for strategies L1 and L4 at 16°C. Fitted rates for specific temperatures were identical for strategies L2 and L3 only (omission *versus* inclusion of dead individuals). An O'Neill response curve fitting (Fig. 2 and Table 2) yielded similar T_{opt} and Q_{10} values for strategies based on the assumption of identical growth rates for all individuals (L2–L4). In contrast, for L1 a higher Q_{10} was found due to the distinct peak.

Fitting of mortality

Temperature-specific mortality rates found in L5 were generally higher than those of L4 (see Fig. 3 and supplementary material Table S1), and L5 overestimated mortality rates at smaller temperatures and L4 underestimated mortality rates at higher temperatures. As no hump shape was found, the minimum mortality rate, found at 8°C, was considered to be the extreme in the first step of the fitting, i.e. $\mu(8°C)=\mu_0$. However, in the second step, the minimum temperature for mortality (i.e. the maximum temperature for survival, T_{opt}) was estimated to be lower and the constant mortality rate μ_0 hence overestimated. An O'Neill response curve fitting for survival yielded similar T_{opt} and Q_{10} (see Table 2).

Mesocosm experiments

While parameterising mesocosm data we were confronted with fluctuating mass dynamics, which cannot be modelled with the general von Bertalanffy growth curve. Applying it nevertheless yielded a coefficient of determination of –1.33 (data not shown). Furthermore, parameterisation strategy M1 did not succeed because of too many and too high correlations: rates and response parameters of both growth and mortality could not be identified simultaneously. Growth parameters could only be identified through strategies M2 and M3 (Fig. 4) and mortality parameters only through strategy M4 (Fig. 3). Structured population simulations (Fig. 5) were based on M3 and M4 and serve for visual control only.

Both growth-related strategies, M2 and M3, led to a successful parameterisation of the experimental data (Table 2), with coefficients of determination of 0.95 and 0.97. Respective growth rates were of the same order of magnitude, which was higher

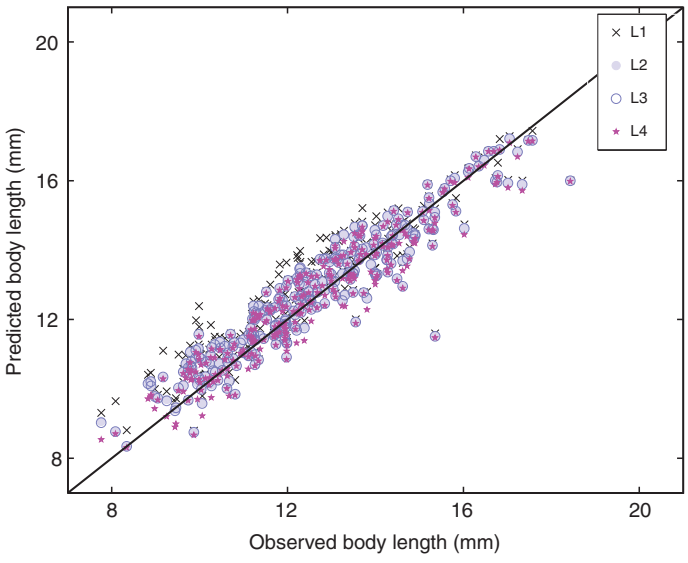

Fig. 1. Scatter plot of individual length of *Gammarus pulex* at the end of the laboratory experiments for all parameterisation strategies (L1–L4).

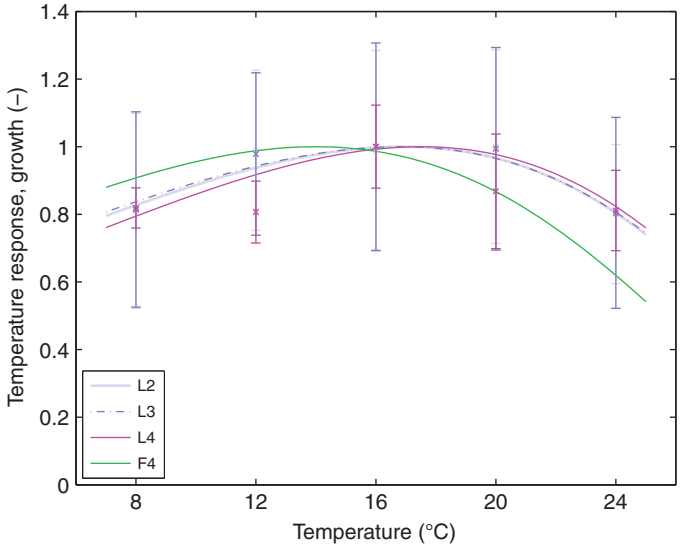

Fig. 2. Temperature response of individual growth of *G. pulex*. Data points with accompanying error bars are mean temperature-specific rates ±s.d.; curves are fitted O'Neill responses.

Table 2. Fitted rates and temperature response parameters for all data sets [laboratory (L), mesocosm (M) and field (F)] and all fitting strategies

	Growth				Mortality				PSPM
Parameter identification strategy	r (day^{-1})	T_{opt} (°C)	Q_{10} (°C^{-1})	R^2	μ_0 (day^{-1})	T_{opt} (°C)	Q_{10} (°C^{-1})	R^2	R^2
L1	0.0091±0.019	16.46±0.43	2.11±0.10	0.86	–	–	–	–	–
L2	0.0062±0.002	16.74±0.15	1.46±0.01	0.9	–	–	–	–	–
L3	0.0062±0.002	16.8±0.13	1.45±0.01	0.9	–	–	–	–	–
L4	0.0061±0.001	17.51±0.00	1.49±0.00	–	0.004	5.02±1.01	1.01±0.00	–	0.99
L5	–	–	–	–	0.01	3.79±0.01	1.003±0.00	0.96	–
M2	0.045	21.6	2.5	0.97	–	–	–	–	–
M3	0.024	17	1.5	0.95	–	–	–	–	–
M4	–	–	–	–	0.003±0.00	6.5±1.73	1.06±0.02	0.95	–
F2	0.0034±0.000	–	–	–	0.007±0.000	–	–	–	0.97
F3	0.0035	14	1.5		–	–	–	–	0.98
F4	–	–	–	–	0.005±0.007	3±0.036	1.13±0.017	–	0.98
F5	0.0035	16.8	1.45	–	0.007	3.79	1.003	–	0.98

Data are presented ±s.d. where applicable; coefficients of determination are also shown where applicable.
PSPM, physiologically structured population model.
r, individual growth rate; Q_{10}, temperature coefficient; T_{opt}, optimum temperature; μ_0, constant mortality rate.

compared with laboratory-related rates. In M2 (fitting of temperature response parameters), both T_{opt} and Q_{10} were higher than in the laboratory experiments. In M3 (fitting of food response parameters), t_1 increased with increasing tank temperature whereas no clear picture was revealed for t_2. However, both parameterisations were most sensitive to food response parameters t_i (see supplementary material Table S2). For M4, mortality rate and the related temperature response resembled those of the laboratory experiment strategy L5 (see Fig. 3 and Table 2); solely Q_{10} was markedly higher.

Field monitoring

As for mesocosm data, it was not possible to identify the parameters simultaneously (F1); for all parameters except growth rate at least one Pearson correlation coefficient higher than 0.85 appeared. The complete application of laboratory (L3) parameters resulted in moderate fits (R^2≈0.77 for both rivers, data not shown). The application of mesocosm parameters resulted in minor fits ranging from R^2=0.29 to R^2=0.51 (data not shown). As described in Materials and methods, Parameter identification, three alternative parameterisation strategies were tested. Temperature independence of both growth and mortality (F2) resulted in acceptable parameterisations (R^2=0.98 and 0.99 for Schunter and Wabe Rivers, respectively; see Table 2 and Fig. 5) and similar rate estimates for both rivers. The maximum growth rate was smaller than that of both the laboratory and the mesocosm experiments, although the mortality rate was higher.

Inclusion of the temperature response of either process (F3 and F4) did not result in better fits. Coefficients of determination were identical (see Figs 2 and 3 and Table 2), whereas correlations remained high for Wabe River because of the small temperature range. Similar goodness of fit (R^2=0.98) was reached when applying the temperature response parameter of laboratory experiments and fitting of rates only (F5).

For both rivers, AIC values were lowest for the temperature-independent model F2. The manually calibrated fully temperature-dependent model according to F1 exceeded this minimum by ΔAIC≈7 and models according to F3 and F4 exceeded it by ΔAIC≈4.

DISCUSSION

The multitude of parameter identification strategies were motivated by four questions that we reconsider here.

1. What is the temperature response of *G. pulex* with respect to growth and mortality?

Laboratory experiments suggested that a temperature response of growth exists for *G. pulex*, with an optimum temperature of approximately 17°C. A Q_{10} of 1.5°C^{-1}, as found in strategies L2 to L4, indicates that the growth rate decreases slowly with decreasing temperature. In contrast, fitting growth individually (L1) resulted in a comparably large Q_{10} of 2.1°C^{-1}. At the same time, the standard deviations related to the temperature-specific means of individual growth rates were too high to consider the means to be significantly different (see supplementary material Table S1). The fact that the difference in individual growth rate estimates between the five temperatures was not statistically significant indicates a small slope of the temperature response over these temperatures and therefore confirms the smaller value for Q_{10} of 1.5°C^{-1}. The high standard deviations of the growth rate estimates were caused by two technical outliers: here, size was close to the assumed maximum of 20 mm and the observed growth could only be represented by extremely high growth rates. Although we did not remove the outliers in further

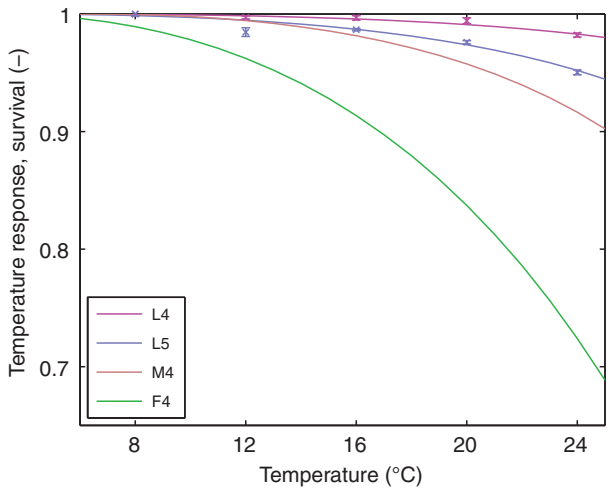

Fig. 3. Temperature response of survival of *G. pulex*. Data points with accompanying error bars are mean temperature-specific rates ±s.d.; curves are fitted O'Neill responses.

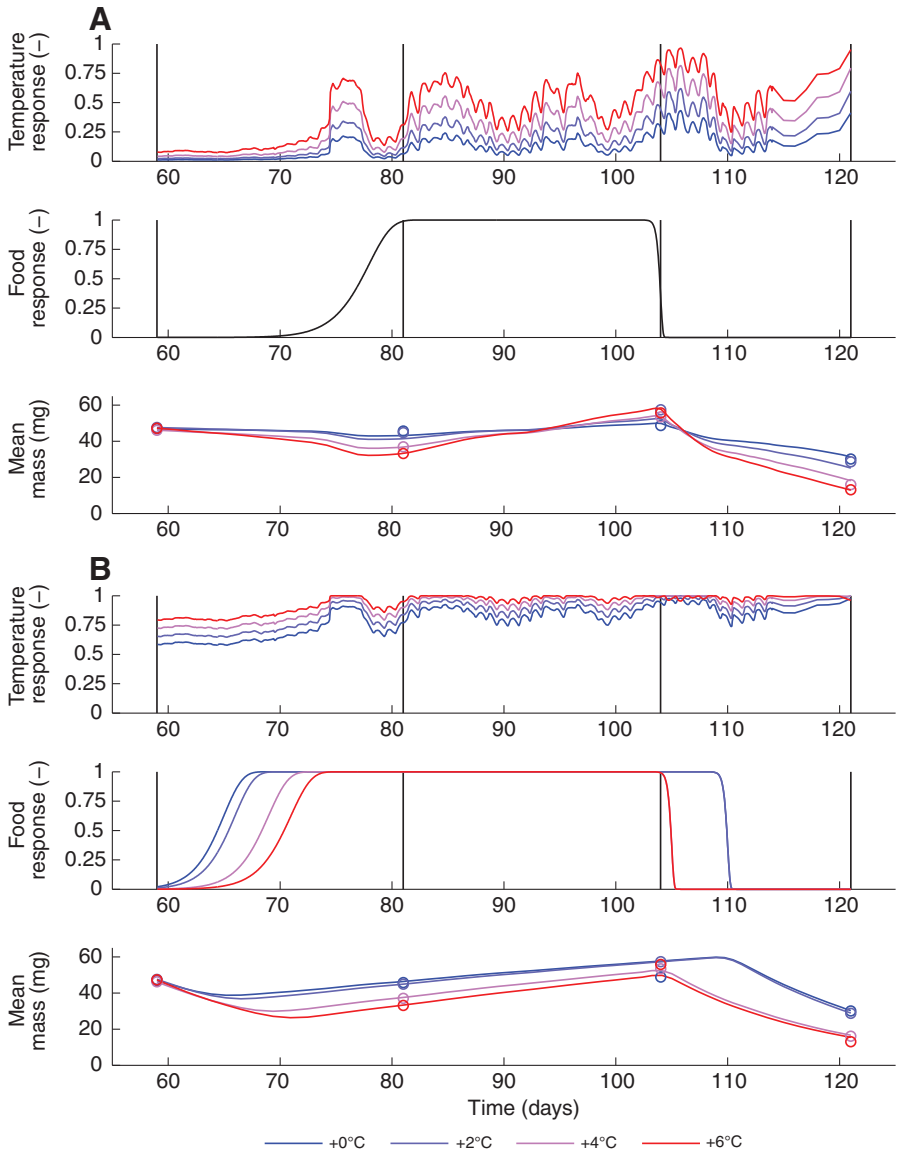

Fig. 4. Growth dynamics of *G. pulex* in mesocosms. (A) Parameterisation strategy M2; (B) parameterisation strategy M3. For each strategy, the temperature response (top), food response (centre) and resulting mean mass dynamics (bottom; where circles are observed values and lines are simulated values) are shown. Vertical black lines in the temperature and food response panels indicate sampling dates.

analyses (to save comparability with other strategies where it was impossible to identify the outliers), removing them resulted in a Q_{10} of 1.8°C^{-1} (data not shown). Sutcliffe et al. (Sutcliffe et al., 1981) identified a T_{opt} of 15°C in similar temperature-dependent growth experiments; however, they did so through visual fitting. Generally, the temperature response curve found here resembles theirs and applying our parameter identification to their data resulted in T_{opt}=17.6°C and Q_{10}=1.66°C^{-1}, i.e. similar values.

The temperature response of survival was weak, with a Q_{10} less than 1.01°C^{-1}. The optimum temperature of approximately 4°C was below the temperature range taken into consideration, such that the value remains debatable.

2. Can temperature response parameters derived from laboratory conditions be applied unambiguously under natural conditions?

Laboratory experiments yield a parameterisation of response for the most controlled conditions. Thus, laboratory-based response parameters should be applicable under natural conditions, but could need to be modified to account for the temperature response of additional effects. Consequently, we here consider unknown effects that might have been influential in mesocosms and field monitoring, first for growth and later for survival.

In mesocosm experiments, food availability probably exerted additional influence. Food response parameters yielded from strategy M3 (application of laboratory temperature response parameters) suggest that food requirements differed between the mesocosms, possibly because the metabolic rate increases with increasing temperature (Enquist et al., 2003; Gillooly et al., 2001). Considering a time-dependent food conditioning process (Alemanno et al., 2007), this process would reach the required level for the coldest mesocosms first and for all others consecutively thereafter. With respect to food shortage at the end of the experiments, two aspects might cancel each other out. On the one hand, a higher metabolic rate for higher temperatures leads to the assumption of earlier food shortage. On the other hand, higher mortality rates for higher temperatures leads to the assumption of decreasing food demand through decreased population density. Moreover, dead individuals were likely turning into food for the remaining *G. pulex*. However, as this process was fitted only indirectly and yielded the highest sensitivity, it remains highly speculative. Finally, the growth rate identified in

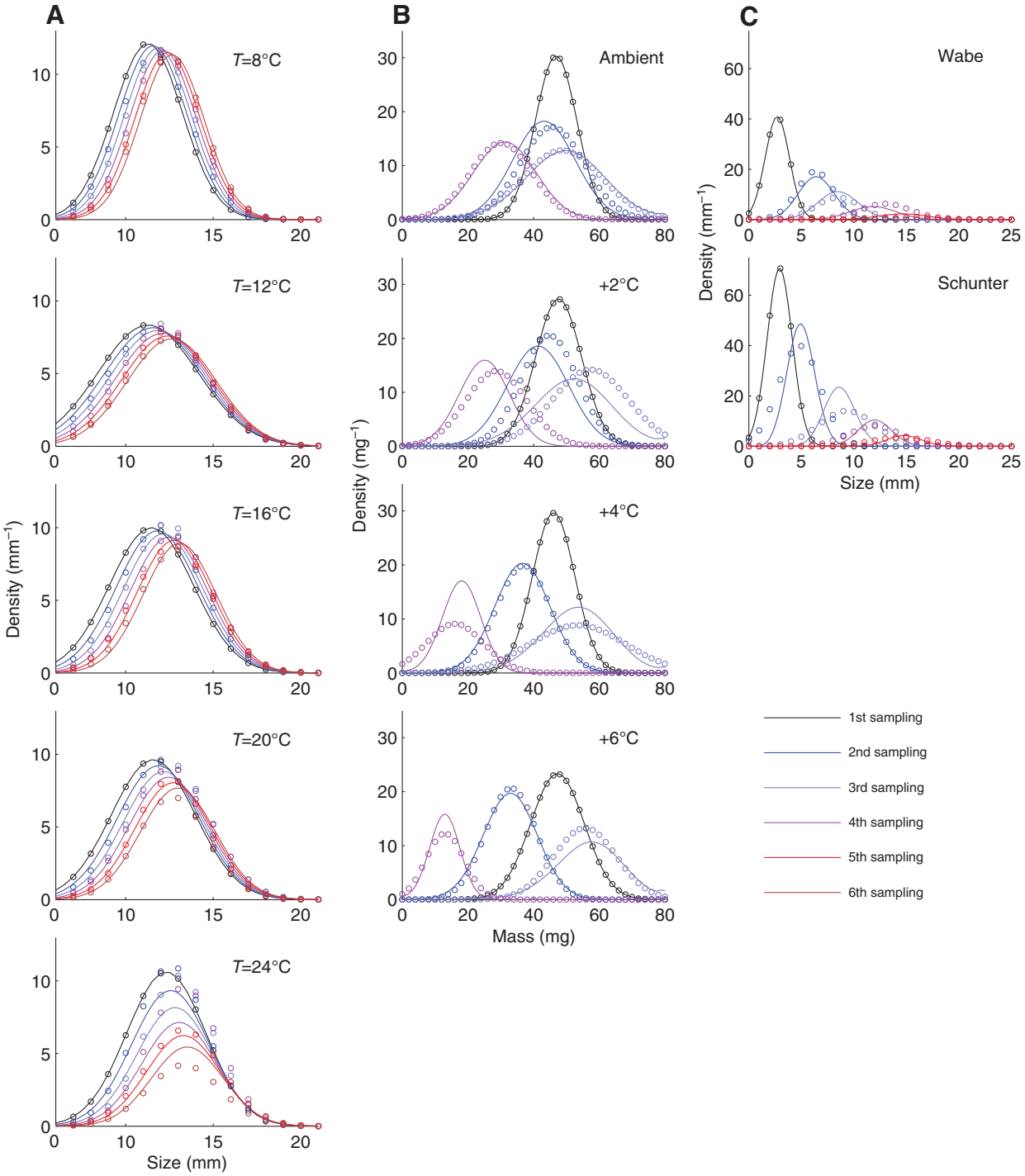

Fig. 5. Population dynamics of *G. pulex* for all experimental setups. Circles are samples of normal distributions fitted to observed data. Lines represent simulated dynamics. Sampling times can be found in the Materials and methods. (A) Size-structured populations in laboratory experiments, comprising five constant temperatures. (B) Mass-structured populations for the four temperature scenarios of the mesocosms. (C) Size-structured populations for field monitoring data of the Wabe and Schunter Rivers.

mesocosms was large compared with laboratory results. We assume that the time-invariant relationship between body length and mass applied here in order to deduce a length growth rate is not valid under food stress, as occurred during the experiment (Kooijman, 2010), and its comparability cannot be reached.

In the field parameterisations, F2 (omission of temperature response), F3 (consideration) and F5 (laboratory temperature response) yielded similar coefficients of determination. At the same time, the maximum growth rate in the field was approximately 50% smaller than in the laboratory. We conclude that, because of adverse effects, peak growth rates were dampened to such an extent that omission of temperature response is applicable. One such adverse effect could again be food shortage (Flenner et al., 2010).

The optimum temperature of survival (T_{opt}) ranged between 3 and 6.5°C, whereas the temperature coefficient of survival (Q_{10}) increased from 1.003 to 1.13°C^{-1} from the laboratory to the field. One coherent interpretation of this result could be a consecutive addition of temperature effects as follows: a primary minor response to temperature in laboratory might have been induced from stress related to temperature dependence of the metabolic rate. In mesocosms, the same increase in metabolic rate with temperature might have induced a food demand that was not met there (M4). Consequently, temperature-dependent starvation caused an amplified temperature response of mortality (Enquist et al., 2003; Gillooly et al., 2001). In field monitoring, food shortage could be thought of as being more severe because of competition with other shredders (F4). Additionally, a temperature-dependent increase in the food demand of predators, for instance by fish (Bakker et al., 1997), could amplify the temperature response of mortality of their prey. Moreover, cannibalism (MacNeil et al., 1997) may vary depending on temperature and food availability.

Although this interpretation is not unlikely, the overall reliability of parameters is somewhat debatable. Firstly, note that a clear trend of an increase in temperature emerged over the course of the mesocosm experiment: at the beginning of the experiment it matched the temperature optimum and became increasingly unfavourable as the experiment progressed. Hence, the temperature response could partly be a wrongly attributed experiment duration response. Secondly, a set of additional hypotheses on the shape of temperature response of mortality were tested for the field data set (A.-K.S., unpublished). From these, only a sigmoidal temperature dependence of mortality improved the coefficient of determination; however, model efficiency (given by AIC) was not increased.

3. Can we identify physiological parameters of growth at the population level?

Considerations at the population level are complicated by: (1) the difficulty or impossibility of tracking individuals, (2) the difficulty or impossibility of identifying dead or moribund individuals, and (3) the presence of interaction between individuals. In strategy L4, we transformed data of growth derived from individually raised *G. pulex* to size-structured population dynamics. Thus, we identified parameters at the population level without the confounding factor of interaction. The resulting response parameters were identical for growth (L2) and similar for mortality (L5). Consequently, we assume that identification of these parameters at the population level is feasible. In other words, it is not necessary to track individuals or to identify dead or moribund individuals. The latter could also be concluded from a comparison of L2 und L3 (inclusion *versus* omission of moribund individuals): temperature dependence of growth of moribund individuals did not differ significantly from that of surviving individuals.

In other words, the only drawback of parameter identification at the population level is the presence of interaction. Consequently, if physiological parameters of growth can only be determined at the population level, e.g. if it is impossible to mark individuals or to raise them individually, the temperature-driven effects of interaction must be either known or minimised. For instance, density-dependent mortality or cannibalism as a consequence of a temperature-dependent increase in food demand could be excluded through provision of food *ad libitum*. In contrast, if physiological parameters identified at the population level differ from previously known values, interaction can be assessed (see the discussion of mesocosm parameterisation for question 2).

4. Can we identify physiological parameters under natural conditions?

Identifying parameters from natural conditions comprises: (1) the need to track populations instead of individuals and (2) the lack of control of environmental effects. In question 3 we discussed that tracking populations does not hinder parameter identification. Lack of control, however, may do so if unknown processes interfere and if the prevailing environmental conditions allow for ambiguous interpretation of the monitored dynamics.

An example of the former can be found in the parameterisation of the mesocosm experiments. Here, the temperature response of growth yielded from M2 probably took over other, indirect effects of temperature on growth, e.g. the food response. However, the mass dynamics of both parameterisations (Fig. 4) diverge over long periods of time and coincide over short periods only, i.e. around sampling dates. Additional sampling between the sampling dates would have helped to select the right parameterisation (or lead to yet another). If interference of unknown processes is likely, frequent sampling at regular intervals remains the only way out.

In contrast, ambiguous interpretations due to prevailing environmental conditions might be limited through other means. Results of the temperature response of survival in the field may serve as an example. Omission and inclusion of the latter in the population model showed a similar goodness of fit. Omission was accompanied by an elevated intrinsic mortality rate, which could be interpreted as an averaging over time of the temperature-dependent mortality. Additional sampling over temperatures with diverging mortality could have led to a lower goodness of fit for the omission model. As the sampling procedure represents disturbance, which should be minimised, it should be reduced to cardinal dates. We suggest determining these dates through virtual monitoring: simulations can be run for first estimates of the temperature dependence of growth, mortality and reproduction, with a representative annual course of water temperature and of food availability. Signal phases can thus be identified and, ultimately, captured during sampling in the actual field monitoring. Such signal phases comprise extremes in population density or body size distribution, as well as extreme changes in the latter.

If the temperature course does not exhibit the optimum temperature sufficiently long, the peak of the temperature response may be estimated erroneously in magnitude or position. Errors in magnitude might lead to an erroneously low Q_{10}, while errors in position may lead to an erroneous rate constant. As it is impossible to separate the identification of temperature-specific rates, r and μ_0, and resulting temperature response $\Phi(T)$ under natural conditions (see Materials and methods, Parameter identification), previous information on probable value ranges is a prerequisite in simultaneous fitting.

Conclusions

Our central issue was whether the population level was adequate to identify parameters of temperature-dependent size growth and mortality. Three main conclusions were drawn. Firstly, length–frequency data of a population can suffice for identification of physiological parameters. This might be especially useful when treating species that are difficult to individualise. The only drawback is that temperature dependence of intraspecific interaction must be minimised, confining the strategy to laboratory experiments. Secondly, applying the strategy to field data results in net parameters of temperature-dependent size growth and mortality only. Consequently, if purely physiological parameters were identified in independent laboratory experiments, field data serve for

quantification of superposing effects. However, thirdly, as field monitorings are associated with fluctuating environmental conditions, well-designed sampling schemes are needed in order to avoid possible parameter correlations. Such sampling schemes might be designed through virtual monitoring based on modelling physiologically structured population dynamics.

LIST OF SYMBOLS

c	size to mass coefficient ($0.0119\,mg\,mm^{-3}$)
l	size (mm)
l_0	initial size (mm)
l_{max}	maximum size (20 mm)
F	food response function
G	net growth ($mm\,day^{-1}$)
m	mass (mg)
M	number of generations
n	population density (Mm^{-1})
N	abundance
Q_{10}	temperature coefficient ($°C^{-1}$)
r	individual growth rate (day^{-1})
t	time (days)
t_i	shape parameter for food response (days)
T	temperature (°C)
T_{max}	maximum temperature (°C)
T_{opt}	optimum temperature (°C)
α_i	shape parameter for food response
μ	net mortality (day^{-1})
μ_0	constant mortality rate (day^{-1})
Φ	O'Neill temperature response

ACKNOWLEDGEMENTS

We thank three anonymous referees for very valuable comments and Katharina Braunmiller and Klaus Schmalstieg for complementary analyses.

FUNDING

This study was funded by the German Science Foundation within the priority programme 1162 AQUASHIFT [Ri 534/11-1,2].

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