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Primary Research Paper

Modelling effects of temperature and feeding level on the life cycle of the midge *Chironomus riparius*: an energy-based modelling approach

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Abstract

Survival, growth, emergence and reproduction were monitored during the life cycle of *Chironomus riparius* in the laboratory at five temperatures from 15 to 27 °C and two feeding diets (*ad libitum* and limiting). Data were analysed using an energy-based model. Survival was not affected. In *ad libitum* conditions, growth rate increased linearly with temperature as a consequence of quicker food ingestion. Our model parameterised using the data in *ad libitum* conditions could account for the data obtained in food limited conditions. Reproduction was not influenced by temperature because the decrease of the duration of the period of energetic investment into reproduction compensated for the increase of the feeding rate when temperature increased. Based on these results, we then built a model describing life cycles in the field which may contribute to the field assessment of the consequences of global warming or pollution.

Introduction

Temperature is a major environmental factor which affects many biological processes. It can influence growth at the individual level (Benider et al., 2002; Frouz et al., 2002; Hall & Burns, 2002) or cause changes in population abundance (Hall & Burns, 2002). Temperature may also enhance the toxicity of chemicals, either by weakening animals exposed to unfavourable temperatures (Jeyasingham & Ling, 2000) or by increasing chemical uptake (Bervoets et al., 1996) or biotransformation of chemicals into more toxic metabolites (Lydy et al., 1999). The effects of temperature on invertebrate growth are roughly as follows (Kooijman, 2000): growth is inhibited at very low temperatures (Benider et al., 2002; Frouz et al., 2002); developmental rate then increases with temperature (Benider et al., 2002); mortality occurs when temperature exceeds an upper limit (Benider et al., 2002; Hall & Burns, 2002).

Chironomus species, from the dipteran family Chironomidae, are non-biting midges widely distributed in the northern hemisphere at temperate latitudes. They can be found both in lentic and lotic environments, usually in organically enriched waters. Their life cycle comprises aquatic stages (egg, larval instars and a pupal stage) and an aerial adult stage. The larvae, which are collector–gatherers, feed on sediment-deposited detritus. Chironomidae represent a prominent part of benthic communities in virtually all freshwater habitats. For instance, Berg & Hellenthal (1992) reported an annual chironomid secondary production in an American stream (northern Indiana) that accounted for 80% of the total insect secondary production. Ectotherms like *Chironomus riparius* are animals that do not maintain their body at a constant temperature. Consequently, body

temperature usually follows that of the environment. They are thus likely to be sensitive to global warming or high temperature variations that can be observed nowadays.

Some studies of the growth pattern of Chironomidae under different temperature conditions are already available in the literature. The authors concluded that developmental rates increased with temperature until a certain limit (Hauer & Benke, 1991; Sankarperumal & Pandian, 1991; Frouz et al., 2002). Some also showed that females size and fecundity decreased for high temperatures (Frouz et al., 2002; Gong et al., 2002).

Recently, we developed a model to describe and predict growth, emergence and reproduction for *Chironomus riparius* (Péry et al., 2002). It is based on assumptions on the use of energy by Chironomidae. It was shown that: (i) the organisms were isomorphic during their development (i.e., the ratio length/width was constant), (ii) at least at 21 °C, the costs of maintenance (loss due to respiration) could be neglected compared to the costs of growth, (iii) there was a maximum length for males and females that was attained whatever the feeding regime. The growth pattern of the larvae for different starting densities and different amounts of daily feeding was predicted successfully and the model could be extended to account for different food qualities, from artificial fish food to field organic matter (Péry et al., 2003).

We have now developed the model to account for different temperatures. Experiments with growth, emergence and reproduction have been performed in our laboratory for five temperatures from 15 to 27 °C. As all the parameters of our models have a biological meaning, simple relationships could be found between the parameter values and temperature. We study two feeding conditions to assess if temperature and feeding act in an independent way, which would allow development of a life cycle model accounting for a large range of combinations of feeding and temperature parameters. Once achieved, we could use it to quantify the influence of temperature on the life cycle of *Chironomus riparius* and apply our results to actual field temperature data to evaluate the relevance of our modelling approach. Our study is original in three ways: (i) no study has ever taken into account the whole life cycle of Chironomidae, studying all the instars growth patterns and adults reproduction in the same experiment, (ii) little is known about the crossed influence of feeding and temperature although such a knowledge is crucial to fully understand field observations, (iii) the incorporation of temperature into our modelling framework could constitute a basis for modelling studies at population level which would permit a prospective approach to evaluate the effects of warming on ecosystems or to facilitate field evaluation of results obtained in the laboratory.

Materials and methods

Experiments

Chironomids were cultured prior to the experiments according to standard methods. For each experiment, 10 two-day-old organisms were added at random to 0.55 l beakers (0.11 l of silica sand and 0.44 l water). The beakers were set in a water bath at the chosen temperature with a 16:8 h light:dark photoperiod. We chose five nominal test temperatures around 21 °C, which is the usual choice for toxicity tests with *C. riparius*: 15, 18, 21, 24 and 27 °C. Conductivity, pH, amount of dissolved oxygen, nitrates and nitrites were measured daily. Temperature was measured three times a day (at 09:00, 13:00 and 18:00). As the amount of food could dramatically affect water quality, we used an aeration system.

Midges were fed with Tetramin® fish food (Tetrawerke, Melle, Germany). We used two feeding conditions in accordance with previous studies (Péry et al., 2002) and preliminary experiments, one *ad libitum* (0.6 mg/larva/d for temperatures below 21 °C and 1.2 mg/larva/d for temperatures above 24 °C) and one limiting (0.2 mg/larva/d). Each day of measurement, three beakers per feeding and temperature conditions were taken to measure length, under a binocular microscope fitted with a calibrated eye-piece micrometer. The organisms had to be killed, with formalin, before measuring their length. Measurements were performed on days 0, 2, 4, and each day after until the end of growth in *ad libitum* conditions.

For each temperature, six additional beakers were used to follow emergence and reproduction. These were covered to prevent adults from escaping. Emergence was measured every day. Feeding

was *ad libitum*. The females were then put into 1-l mating chambers, with 0.1 l water, with males from laboratory culture in a ratio of 3 males per female (Péry et al., 2002). Not more than six females were placed in the same bottle (we sometimes had to use five bottles for a given temperature). After mating and oviposition, each egg mass was removed and put into a 5 ml tube with 2 ml H_2SO_4, 2 N overnight. The following day, the tubes were agitated to dissociate the eggs which were counted under a binocular microscope. For each mass, measurements were made three times to reduce experimental errors.

Modelling growth

The model was described and parameterised earlier (Péry et al., 2002). It is based on two assumptions: (i) during growth, all the food assimilated is converted into biomass, (ii) during the growth period, length remains proportional to width (isomorphism). We use a discrete growth description with a time unit of one day. First, the photoperiod is a very important factor for chironomids and the day would be a relevant time unit with respect to the behaviour of these organisms. Secondly, we fed the animals once per day.

Under conditions of no food limitation, feeding and growth are continuous processes and length can be described by the following equation:

$$\frac{d}{\mathrm{d}t} l = a, \qquad (1)$$

where l is the mean length of the organisms and a is a constant depending on the instar and on the sex of the chironomids (during fourth instar, a is different between males and females) and where dt represents a one-day period. Equation (1) represents the uptake of energy, which is proportional to the surface of the organism, and its use to increase the volume, which is proportional to the cubic length of the organism because of isomorphism. Growth in length is assumed to stop as soon as a maximum length, $l_{\max}$, is reached. For second and third instars, growth was in accordance with Equation (1) with respective growth rates of 0.81 and 1.42 mm per day. For the fourth instar, the growth of males and females was in accordance with Equation (1) with respective growth rates 1.72 and 2.21 mm per day. The maximum larval length for males was 11.36 mm and for females 13.72 mm. The second and the third stage lasted 2 days each.

In the case of food limitation, feeding may not be a continuous process. As maintenance costs are low (assumption 1), the daily increase in weight is just equal to the daily amount of food introduced into the beaker. The equation describing the situation is thus:

$$W_{n+1} - W_n = \gamma \cdot ({l_{n+1}}^3 - {l_n}^3) = \frac{\theta}{N} \times Q, \qquad (2)$$

where Q (in mg) represents the daily quantity of food introduced into one beaker, N the number of larvae, l_n (in mm) the larval length at day n, W_n (in mg) the individual weight at day n, θ the percentage of Tetramin® that can effectively be incorporated by the chironomids and γ the proportionality factor between the weight and the cube of the length. The estimate of θ and γ were, respectively 0.691 and 0.523.

Here, we expected that temperature would only affect the parameter a, and that this effect would be the same for all instars. Consequently, the parameter a for a given temperature should be proportional to the parameter a for the reference temperature of 21 °C. This proportionality factor (let us call it μ) was estimated using least squares methods comparing actual data and model descriptions as a function of μ. A temperature effect on the parameters θ (food quality) and γ (ratio between weight and volume) makes little sense. Consequently, we should be able to deduce the effects of temperature on growth in limiting conditions only from the knowledge on parameter a. We checked this assumption by comparing the data obtained in limiting conditions with model predictions. To achieve this, we performed Student's t-tests for each temperature and day of measurement with the value predicted and the mean of the length measures. With three beakers, there were about 30 length measures per data point. We previously checked that there was no significant difference ($p > 0.05$) between the three beakers using one factor analysis of variance.

Analysis of emergence and reproduction data

For emergence data, Péry et al. (2002) showed that mean emergence time t_e was given by:

$$t_e = t_m + d, \quad (3)$$

where t_m is the time to reach $l_{\max}$ and d the delay between the moment when $l_{\max}$ is reached and emergence. We now examine how d depends on temperature. Reproduction measured in terms of number of eggs per female was proportional to the amount of food ingested by the females during these d days at 21 °C. This result is examined again here when temperature varies.

Results

During all the experiments, pH was constant (between 8.1 and 8.4). Conductivity was between 300 and 400 μS/cm, and the percentage of dissolved oxygen was always above 80%. Nitrates and ammonium level were always below 2 mg/l. Nominal mean temperatures were 15, 19.6, 21, 24.4 and 26.7 °C with a variation of less than 0.6 °C during the day.

No effect on survival was observed at any temperature. To study the growth curves under *ad libitum* conditions, we used our growth model for each instar, introducing a proportionality factor μ for the parameters a. We assumed μ not to depend on instars but only on temperature. For each temperature, the model was fitted to the data in order to estimate μ. Once this parameter had been estimated, the data were not significantly different from the model descriptions ($p > 0.05$ for all data points) (Fig. 1). Therefore, the larvae reached the same mean limit length (about 12.6 mm) and the influence of temperature was the same for each instar. There was a clear linear relationship between estimates of parameter μ and temperature between 15 and 26.7 °C (Fig. 2). When the data obtained under limiting feeding conditions were compared with the model predictions based on the results of the *ad libitum* experiment, the data were not significantly different from the model descriptions ($p > 0.05$) (Fig. 3). This confirmed the absence of the influence of temperature either on the parameters θ or γ. As a consequence, our modelling is able to account for the crossed influence of feeding and temperature.

The duration of the period between the end of growth and emergence (parameter d) was inversely proportional to the estimates of the parameter μ (Fig. 4). The slower the organisms ate, the more time they used to prepare for emergence and reproduction. Consequently, at low temperature, the increase in the value of d compensated for the fact that the ingestion rate by females was diminished during the period of energetic investment in reproduction. This was confirmed by the reproduction data. We obtained about 12 egg masses per temperature with the following numbers of eggs per mass: 15 °C: 370 ± 30; 19.6 °C: 362 ± 63; 21 °C: 312 ± 91; 24.6 °C: 321 ± 38; 26.7 °C: 270 ± 21. There was a slight decrease in egg

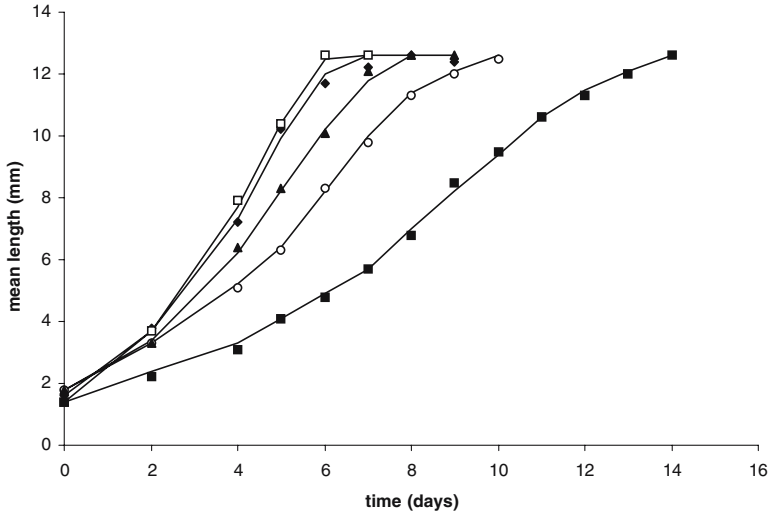

Figure 1. Growth in length under *ad libitum* feeding conditions as a function of temperature (black squares: 15 °C; circles: 19.6 °C; triangles: 21 °C; diamonds: 24.4 °C; white squares: 26.7 °C). Lines represent model descriptions.

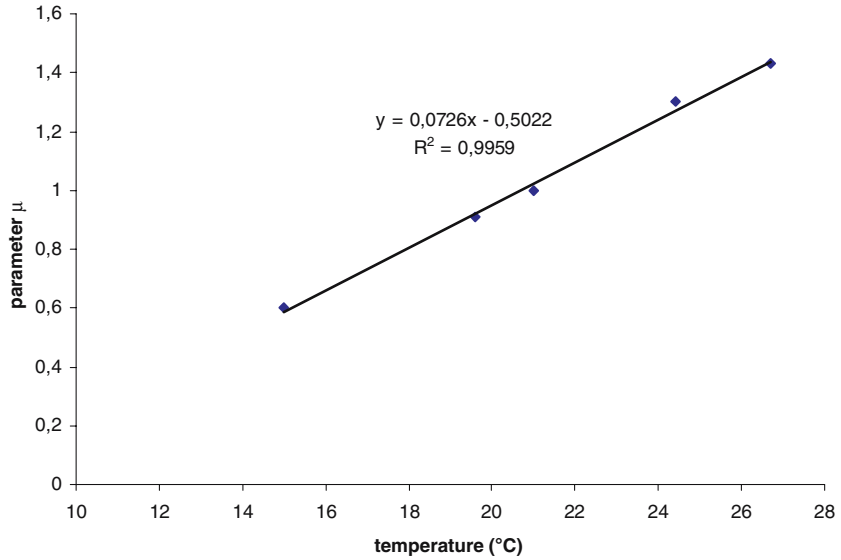

Figure 2. Estimates of parameter μ as a function of temperature.

number with increasing temperatures with the data obtained at 26.7 °C significantly lower than the data obtained for the other temperatures.

Discussion

In the range of temperature tested, food uptake and assimilation (accounted by parameter *a*) increased with temperature, this increase being similar for all instars. As expected, there was no effect of temperature on either the quality of the food or on the relationship between length and weight. The metamorphosis from one instar to the following one was also not affected. This result is in accordance with the works of Sankarpeumal & Pandian (1991) who showed absence of temperature influence on *Chironomus circumdatus*

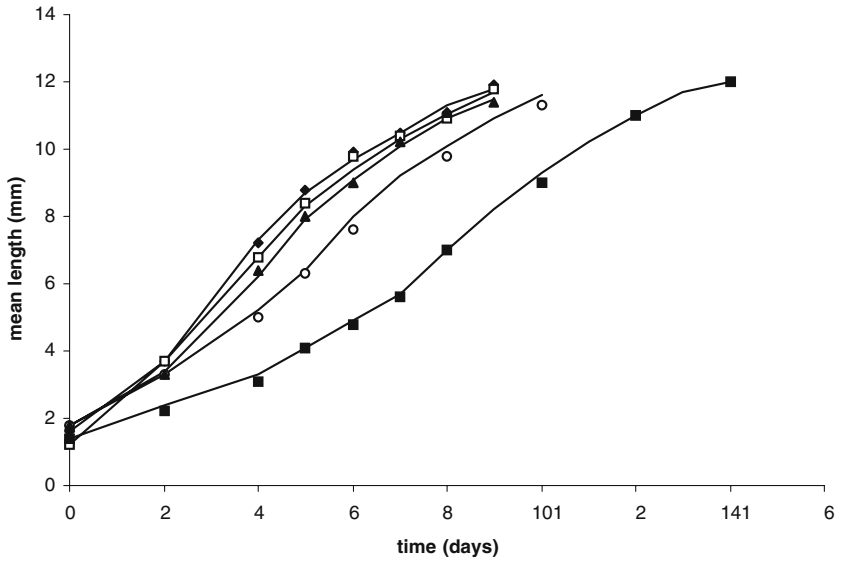

Figure 3. Growth in length under limiting feeding conditions as a function of temperature (black squares: 15 °C; circles: 19.6 °C; triangles: 21 °C; diamonds: 24.4 °C; white squares: 26.7 °C). Lines represent model predictions.

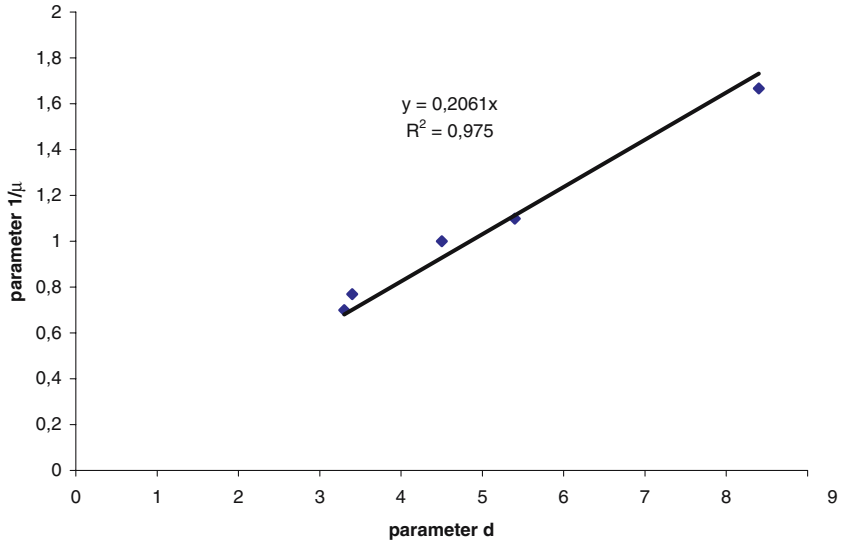

Figure 4. Relationship between estimates of parameter d and the inverse of estimates of parameter μ.

metamorphosis. Reproduction is only weakly affected by temperature, due to an increase in the duration of the pre-emergence period when temperature decreases. This influence of temperature on *Chironomus* growth and pre-emergence duration has also been shown by other authors (Sankarperumal & Pandian, 1991), who observed metabolic rate increase with increasing temperature without affecting metamorphic efficiency. The values we obtained are consistent with those obtained by other authors. Goddeeris et al. (2001) obtained a life cycle of 26 days at 15 °C. Here, the mean duration from hatching to pupation was 15 days at 21 °C, and 25 days at 15 °C.

There was a linear relationship between temperature and estimates of parameter a. Usually Arrhenius equation is used (Kooijman, 2000). This approach, based on thermodynamic theories, is certainly more relevant for large ranges of temperature variations but a linear approximation could be used in other cases. In our study, there was no need of the Arrhenius equation to fit the data. Other authors came to comparable conclusions with coleopteran invertebrates (Nava & Parra, 2003). They showed that, in the range 18–32 °C, the duration of the instars was inversely proportional to the temperature. In their models to account for the life history of mayflies species, Newbold et al. (1994) used a linear relationship in a certain range of temperatures between development rate and streamwater temperature. They were able to account for field data for six species.

The results of the present study can be combined with those previously obtained with different field sediments (Péry et al., 2003) to obtain a model accounting for field food condition and temperature. Light might also be incorporated, at least to estimate annual growth duration and deduce the number of generation produced per year. Goddeeris et al. (2001) showed that diapause could be induced by short day conditions, but that the diapausing threshold is temperature dependent. Without more precise information, let us just assume, in the following, that growth only occurs from March to October (duration about 180 days), which is usually observed in the field (Armitage et al., 1995; Goodeeris et al., 2001). As feeding, light and temperature are the main factors influencing the life cycle, we can build a relevant tool to account for what actually occurs in the field. This tool can be used to study two crucial environment issues: global warming and field ecotoxicity.

First, we can tackle the question of the changes in the ecosystem due to global warming. As the reproduction is not influenced by temperature, temperature influences the life cycle duration but not the number of organisms produced per generation. As the relationship between temperature and parameter a is linear in our study, the

temperature pattern is not necessary to evaluate the number of generations per year. We only need the mean temperature value during the growth period. We showed earlier (Péry et al., 2003) that field organic matter led to a growth 4.1 times slower than artificial fish food for second, third and fourth instars. With the results obtained here, this means that, with mean temperatures of 13, 15, 17 and 19 °C, the mean life cycle duration would be, respectively 122, 90, 74 and 62 days and the mean number of generations per year would be, respectively 1–2, 2, 2–3 and 3, assuming that the relationship we obtained in this paper between parameter *a* and temperature is also correct for temperature 13 °C. The order of these results is coherent with what is actually observed in the field at temperate latitudes (Armitage et al., 1995). It appears that an increase of the mean temperature by 4 °C adds one more generation per year. This means that, there is in the same time more food available per year for fish and birds, but also more organic matter required from the sediment as food for the chironomids.

Second, a modelling tool able to incorporate food and temperature can promote more relevant ecotoxicological studies at the population level. The protection of field populations is the goal of ecotoxicology, whereas most of the toxicological studies have focused on the individual (Congdon et al., 2001). This translation allows the integration of all the endpoints measured at the individual level in only one parameter, for instance population growth rate. It is a step towards more relevant endpoints but it still suffers from the fact that the parameters used in the modelling have been estimated under laboratory conditions. Together with data on the influence of temperature on the toxicity of the chemicals at individual levels, the results presented here can thus contribute to a better prediction of the consequences of contamination in the field.

Conclusion

In summary, temperature influences growth rate of *Chironomus riparius*, but has no effect on reproduction and survival in the range 15–27 °C. In this range, the relationship between growth rate and temperature is linear. Our energy-based modelling is able to account for the life cycle at different temperatures and under different feeding conditions. Our modelling could help to understand the consequences of global warming on aquatic ecosystems and to build more realistic population models in ecotoxicology.

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