

## Temperature-dependent energetics of *Chaoborus* populations: hypothesis for anomalous distributions in the great lakes of East Africa

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### Abstract

*Chaoborus*, the phantom midge (Insecta, Diptera, Chaoboridae), has a widespread distribution, commonly occurring in lakes and ponds all over the world. In the great lakes region of East Africa *Chaoborus* is present in Lakes Victoria, Albert, Edward, Malawi and George, but absent from Lakes Tanganyika, Kivu and Turkana. Tropical lakes typically have water temperatures in the range of 22–26 °C year round. Lakes Tanganyika and Kivu have only 20% of their bottom sediments oxygenated during full circulation, contrary to 95–100% in all of the other lakes, excluding Lake Malawi (45%) (Hecky & Kling, 1987). Planktivorous fish are present in all lakes (Lehman, 1995). We hypothesized that the absence of *Chaoborus* larvae from some lakes of East Africa may be the result of interaction among high temperatures, low oxygen levels, and fish predation.

We developed a model to estimate energetic costs for *Chaoborus* larvae at temperatures greater than 14 °C. We hoped to shed light on the bioenergetics of *Chaoborus* populations, and the possibility that extant distributions of *Chaoborus* larvae are the result of energetic constraints.

We found that relative respiratory and growth costs of *Chaoborus* larvae are highest in the early stages of development. We estimated that non-feeding instar I larvae living in 25 °C water will starve to death in less than one day. It is possible that *Chaoborus* populations are prevented from establishing in certain areas because high energetic costs condemn young larvae to death by either predation or starvation.

### Introduction

*Chaoborus*, the phantom midge (Insecta, Diptera, Chaoboridae), has a cosmopolitan distribution. The winged adult stage has allowed *Chaoborus* to disperse into the majority of lentic systems worldwide, where its larvae are important predators. However, *Chaoborus* is not present in all lakes. The reasons for the discontinuous distribution of *Chaoborus* are a subject of debate. Eccles (1985) suggested that high salinities may exclude chaoborids from certain East African lake habitats. High temperatures, low oxygen concentrations, and fish predation (Pope et al., 1973; Northcote et al., 1978) are other possible factors limiting the distribution of *Chaoborus*. At warm water temperatures, the oxygen demand of *Chaoborus crystallinus* larvae

is elevated and the development time is decreased compared to demands at cooler temperatures (Ratte, 1984).

In tropical systems, year round water temperatures average 22–26 °C or more. Respiratory and growth demands of *Chaoborus* at warm temperatures may strain rates of possible energetic input. In order to meet energetic demands, larvae may have to spend most of their time foraging and may have little scope to seek refuge from predators. *Chaoborus* larvae in high temperature environments, moreover, may be under too much energetic stress to survive conditions of temperature anoxia.

*Chaoborus* larvae exhibit the four stages typical of a holometabolous insect life cycle, egg, larva, pupa, and adult. The larval stage consists of four discrete instars, instars I and II in which larvae are plankton-

ic, and instars III and IV in which larvae exhibit diel vertical migration and spend a considerable amount of time in the sediments (Stahl, 1966). *Chaoborus* larvae in Lake Victoria reside near the bottom of the lake (approximately 55 m) during the day and up at the surface during the evening (MacDonald, 1956). Adults are short-lived and typically do not feed.

Third and fourth instar *Chaoborus* larvae usually spend the daylight hours in the sediments in temperate (Swift, 1976) and tropical lakes (MacDonald, 1956). It is important to the survival of these larvae that either the bottom waters are oxygenated, or that the larvae are able to withstand periods of temporary anoxia. At high temperatures, the energetic demands of respiration may be too great for the larvae to withstand prolonged periods of temporary anoxia. If there is no available oxygen in the sediment, the larvae may have to remain in the water column. Larow (1970) found that *Chaoborus punctipennis* larvae in low oxygen conditions (3% saturation), showed an increase in activity by 1.82-fold over larvae in higher oxygen conditions (68–90% saturation), and the former larvae remained planktonic for a longer period. Larvae that remain in the water column are more susceptible to fish predation. The interaction between fish predation, food availability, and oxygen demands at high temperatures may exclude *Chaoborus* from establishing populations in certain environments.

In the great lakes region of East Africa *Chaoborus* is found in Lake Victoria, Lake Albert, Lake Edward, Lake Malawi and Lake George. Because of the adult winged stage, *Chaoborus* should be able to disperse throughout the region. However, *Chaoborus* is absent from Lake Tanganyika, Lake Kivu, and Lake Turkana. Lakes Kivu and Turkana have much higher conductivities, 1300  $\mu\text{S}$  and 3000  $\mu\text{S}$  respectively, than the other lakes where conductivities are less than 1000  $\mu\text{S}$  (Lehman, 1995). Lake Tanganyika and Lake Kivu have only 20% of their bottom sediments oxygenated during full circulation; the others, except for Lake Malawi (45%) have 95–100% of the bottom sediments oxygenated during full circulation (Hecky & Kling, 1987). Planktivorous fish are present in all forementioned African Lakes (Lehman, 1995) including Lake Kivu in which *Limnothrissa* was introduced during the 1980's.

We developed a model to evaluate the effect of temperature on the energetic demands of a generalized *Chaoborus* larvae. The model calculates minimum daily ingestion rate required by a *Chaoborus* larva at different, constant temperatures ( $>14$  °C). We wanted to

quantify respiration and growth demands of *Chaoborus* at warm temperatures, 22–25 °C, to help evaluate the hypothesis that bioenergetics may constrain the distribution of the taxon and may help explain the apparent absence of *Chaoborus* from certain lakes in the East African region.

## Methods

We calculated daily ingestion rate required by *Chaoborus* larvae at different, constant temperatures according to the general mass balance equation

$$\text{IR} = (R + G) \div \text{AE}, \quad (1)$$

where

- IR = ingestion rate ( $\mu\text{g}$  carbon/day);
- R = respiration rate ( $\mu\text{g}$  carbon/day);
- G = growth rate ( $\mu\text{g}$  carbon/day);
- AE = assimilation efficiency, approximately 0.8 for *Chaoborus trivittatus* fed on small food items (Giguere, 1981).

Our estimate of ingestion rate can be considered conservative because we do not account for the activity rate of *Chaoborus* larvae. Because we obtained most of our data from the literature, it was sometimes necessary to use data from different species of *Chaoborus* to develop our model. We used data on *Chaoborus* from studies conducted in East Africa or in other tropical regions as much as possible.

## Respiration

We expressed respiration according to the variables of larval weight ( $\mu\text{g}$  carbon) and water temperature (°C). Berg & Jonasson (1965) measured the respiration rate of *Chaoborus flavicans* larvae at different, constant temperatures (8–24 °C). We optically scanned and digitized data points for respiration rates at certain temperatures from fig. 6 of Berg & Jonasson (1965) using a Microtek 600G flatbed digital scanner. We expressed the measured respiration rates,  $R_0$ , in terms of  $\mu\text{g}$  carbon/day, according to the following relationship:

$$R_C = (R_0 * 24 * 12\text{gC} * \text{RQ}) \div 22.4, \quad (2)$$

where

- $R_O$  = Respiration rate,  $\mu\text{L}$  oxygen/hour;  
 $R_C$  = Respiration rate,  $\mu\text{g}$  carbon/day;  
 $RQ$  = 0.949, standard value for ammonotelic animals (Downing & Rigler, 1984).

We fit the temperature and oxygen consumption data to an exponential function ( $n = 8$ ,  $R^2 = 0.993$ ) using SYSTAT version 5.0.

$$R_C = \alpha * W^\beta * e^{k*T}, \quad (3)$$

where

- $W$  = dry weight of a larvae ( $\mu\text{g}$  carbon);  
 $\beta$  = 0.75, standard value for poikilotherms (Peters, 1983);  
 $T$  = temperature ( $^\circ\text{C}$ );  
 $\alpha$  = 0.0272 (SE = 0.0003);  
 $k$  = 0.143 (SE = 0.008).

#### Growth

We expressed growth according to the variables of larval weight, water temperature, and relative age of a larva in its life cycle. Total development time is influenced by temperature. Ratte (1984) measured total development time of *Chaoborus crystallinus* larvae from the egg through the fourth and final larval instar at different temperatures (14–27  $^\circ\text{C}$ ). We scanned and digitized data points for development rates ( $\text{day}^{-1} * 100$ ) at fixed temperatures from fig. 2.3 of Ratte (1984). We fit the temperature and development data to a linear regression model ( $n = 5$ ,  $R^2 = 0.998$ ) to obtain the following equation:

$$D = 100 \div (0.254 * T - 2.04), \quad (4)$$

where

- $D$  = total development time (days);  
 $T$  = temperature ( $^\circ\text{C}$ ) for temperatures  $>8$   $^\circ\text{C}$ .

In order to facilitate calculations, it is convenient to express the age of a larva in units of relative time,  $t'$ , scaled as a fraction of total development time. We assumed that larval instar durations scale linearly with total development time, so that the percentage of time spent in each instar is constant, regardless of total development time. Because our model is for a tropical chaoborid, the development times that we used in our simulations ranged from 23–57 days.

We used length, instar, and duration of instar data for *Chaoborus anthracinus* from Lake Victoria, Ugan-

da (MacDonald, 1956) to develop an equation expressing growth of a *Chaoborus* larva over time. MacDonald (1956) found that the approximate duration of the egg stage and four instars was as follows, egg: 2–4 days, instar I: 4–6 days, instar II: 6–10 days, instar III: 12–16 days, and instar IV: 25–30 days. We converted total lengths of *Chaoborus* larvae as given by MacDonald (1956) to standard lengths, the length between the midpoints of each segment containing an air bladder (Lewis, 1975). We measured thirty *Chaoborus* larvae (lengths ranging from 4.1–8.1 mm) taken from Lake Victoria, Uganda on August 24, 1992, obtaining an average ratio of standard length/total length = 0.6714 (SD = 0.056). We converted standard lengths (mm) into dry weights (mg) according to the following relationship for *Chaoborus* larvae (Lewis, 1975):

$$\text{Log}(Y) = 3.10 * \text{Log}(X) - 2.71, \quad (5)$$

where

- $Y$  = dry weight (mg);  
 $X$  = standard length of a larva (mm).

We wanted to express the model in terms of carbon thus, we converted dry weights to  $\mu\text{g}$  of carbon assuming 50% of the dry weight can be attributed to carbon. We used a nonlinear regression model in SYSTAT to fit the data for mass in carbon and time to the following equation ( $n = 9$ ,  $R^2 = 0.950$ ):

$$C = C_0 * e^{\alpha*(1-e^{-\lambda*t'})}, \quad (6)$$

where

- $C$  = total carbon accumulation at age  $t'$ ;  
 $C_0$  = 0.251  $\mu\text{g}$  C, egg weight of a *Chaoborus anomalus* egg expressed in  $\mu\text{g}$  carbon (McGowan, 1974);  
 $t'$  = unit of relative age;  
 $\gamma$  = 5.633 (SE = 1.365);  
 $\alpha$  = 2.874 (SE = 0.149).

Equation 6 can be rearranged algebraically to express relative age as a function of carbon content,

$$t' = -\frac{1}{\gamma} * \ln \left[ \frac{\alpha - \ln \left( \frac{C}{C_0} \right)}{\alpha} \right]. \quad (7)$$

We used Microsoft Excel to calculate growth, the change in body carbon mass of a *Chaoborus* larva over time. Total development time, as calculated from Eq. 4, was divided into 40 equal intervals. The increment

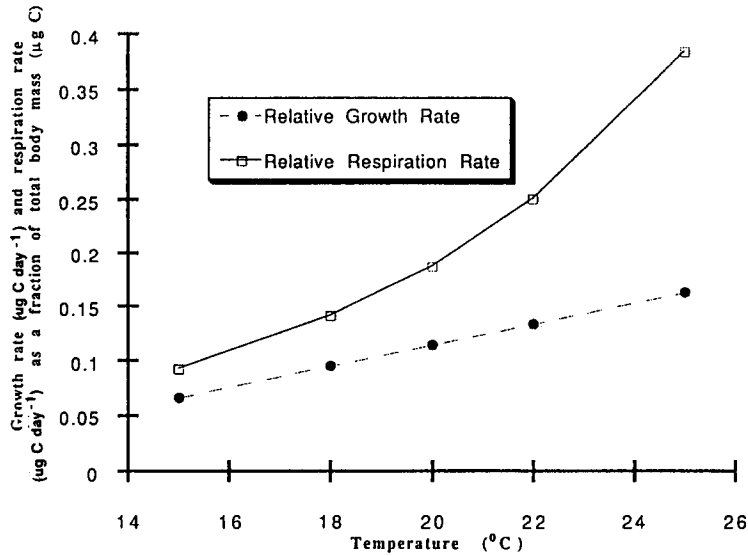


Figure 1. Minimum ingestion rate ( $\mu\text{g C day}^{-1}$ ), amount of carbon a *Chaoborus* larva must ingest to account for respiratory and growth costs, as a function of total body mass ( $\mu\text{g C}$ ) at different temperatures ( $^{\circ}\text{C}$ ) and at different stages in development.

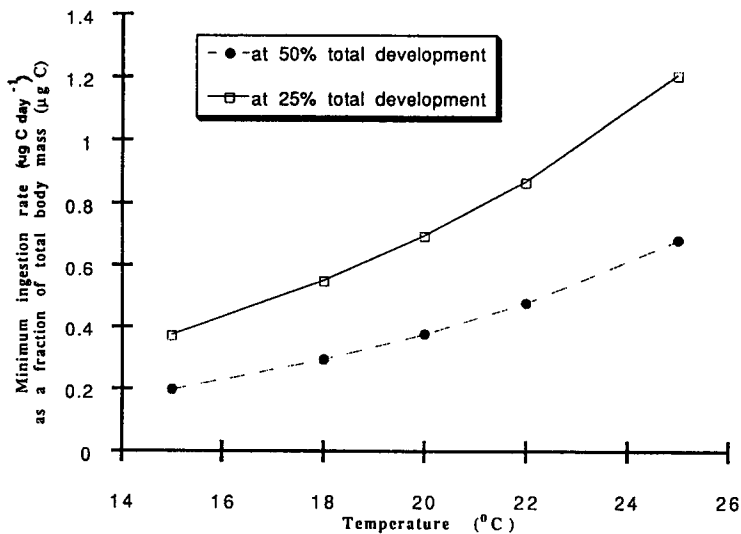


Figure 2. Respiratory ( $\mu\text{g C day}^{-1}$ ) and growth ( $\mu\text{g C day}^{-1}$ ) rates relative to body mass ( $\mu\text{g C}$ ) at different temperatures ( $^{\circ}\text{C}$ ) for *Chaoborus* larvae at 50% total development.

in body carbon over each interval was calculated by Eq. 6. We thus calculated a discrete measure of growth for each interval of development time.

## Results

Minimum ingestion rate, the amount of carbon that a larva must ingest to account for respiration and growth

requirements, increases with temperature as a function of body mass (Figure 1). The rate at which ingestion rate as a function of total body carbon increases with temperature is much more rapid for a larva at 25% total development than for a larva at 50% total development. The percentage of body mass that a larva must ingest each day increases more rapidly with temperature for larvae in early stages of development.

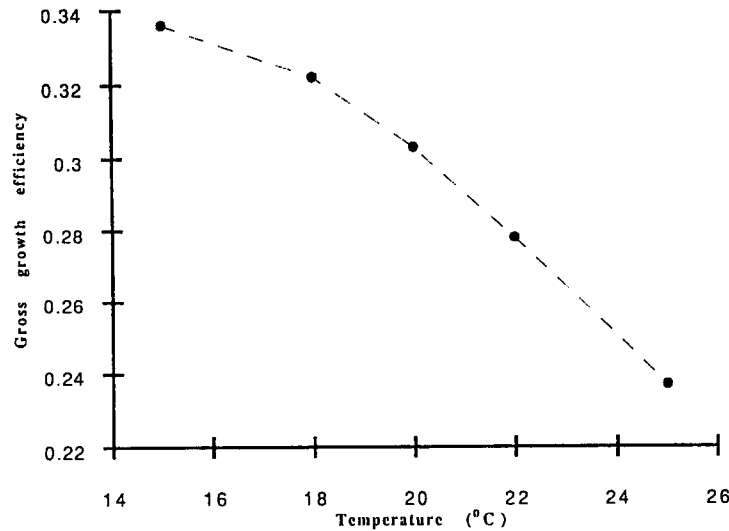


Figure 3. Gross growth efficiency (growth rate/ingestion rate), as a function of temperature ( $^{\circ}\text{C}$ ), for *Chaoborus* larvae at 50% total development.

Table 1. MTS (mean time to starvation in days), amount of time for a non-feeding *Chaoborus* larva to respire 50% of its body mass ( $\mu\text{g C}$ ), for each instar at different temperatures ( $^{\circ}\text{C}$ )

Instar	15 $^{\circ}\text{C}$	18 $^{\circ}\text{C}$	20 $^{\circ}\text{C}$	22 $^{\circ}\text{C}$	25 $^{\circ}\text{C}$
	MTS (SE)	MTS (SE)	MTS (SE)	MTS (SE)	MTS (SE)
I	2.3 (0.43)	1.5 (0.28)	1.2 (0.21)	0.9 (0.16)	0.6 (0.10)
II	3.4 (0.72)	2.2 (0.47)	1.7 (0.35)	1.3 (0.26)	0.8 (0.17)
III	4.8 (0.89)	3.1 (0.58)	2.3 (0.44)	1.8 (0.33)	1.2 (0.21)
IV	6.0 (0.43)	3.9 (0.28)	2.9 (0.21)	2.2 (0.16)	1.4 (0.10)

Respiration and growth rates as functions of body mass both increase with temperature (Figure 2). For a larva at 50% total development, growth rate increases nearly linearly with temperature and respiration increases at an exponential rate. At low temperatures, respiration and growth increases with temperature at about the same rate, but at high temperatures respiration rate increases much faster with temperature than does growth rate.

Gross growth efficiency, growth rate/ingestion rate, of a *Chaoborus* larva at 50% total development decreases with increasing temperature (Figure 3). Less carbon is allotted for growth at higher temperatures.

Mean time to starvation, calculated subjectively as the amount of time for a non-feeding *Chaoborus* larva to lose 50% of its body mass, decreases with increasing temperature (Table 1). Young larvae are more likely to starve when not eating for a short period than are older larvae. At tropical lake temperatures (25  $^{\circ}\text{C}$ ), the

minimum estimated starvation time for larvae at 25% total development is less than one day.

## Discussion

*Chaoborus* larvae in high water temperature environments have to eat much more food each day in order to survive than do larvae inhabiting water of lower temperatures. Thus, larvae living in warm temperature water have to spend more time capturing and ingesting food items. *Chaoborus* larvae living at high temperatures are probably forced to be more active for a greater period each day than are chaoborids living at lower temperatures. Increasing the amount of energy spent on activity may reduce the amount of energy available for growth. Ratte (1984) found that as temperature increases, the final adult size of *Chaoborus crystallinus* decreases. With an increase in temperature, growth may be hindered.

Our model assumes that temperature governs the schedule of development for *Chaoborus* larvae. Because chaoborids have a synchronous emergence period, a fixed period of time is allotted for larval growth and development. For most insects, as body size increases, fecundity and reproductive success increase as well (Thornhill & Alcock, 1983). It will be advantageous for a *Chaoborus* larva to achieve the largest size possible, conferring greater reproductive success, before emerging as an adult. Growth requires food,

and food is up in the water column as are predators. *Chaoborus* larvae must risk predation when feeding.

If *Chaoborus* larvae at high temperatures have to remain active for most of each day to obtain sufficient food for survival and growth, foraging larvae may be more susceptible to fish predation than larvae remaining in the sediments. *Chaoborus* larvae in tropical systems may chance death by predation over death by starvation. Fish predation is generally recognized as a likely cause for the suppression or extinction of larger, visible members of the planktonic community in lentic systems. Gliwicz (1985) reasoned that the disappearance of *Daphnia lumholtzi* from a tropical reservoir was due to the interaction between fish predation and starvation. Intense predation forced the *Daphnia* into food limited refuges where they eventually starved. *Chaoborus* larvae in tropical systems similarly face the risk of starvation if they do not feed; thus, the larvae may have to risk exposure to predators in order to obtain food.

As temperature increases, younger larvae must ingest a greater percentage of their body weight than most older larvae. First and second instar larvae may be under extreme stress to consume enough food to fuel their metabolism and growth at high temperatures. Larvae consuming less carbon than needed for respiratory costs must catabolize carbon reserves in the body.

It is possible that even in systems where *Chaoborus* is absent, eggs are occasionally introduced by natural means. Populations may not become established because energetic constraints due to temperature and oxygen levels may be too great for the young larvae to survive for more than a few days. Conditions of temporary anoxia may prevent *Chaoborus* populations from establishing or persisting in new environments, particularly if abundant planktivorous fish eliminate them from oxygenated, food-rich regions.

High, constant temperatures are characteristic of tropical, lentic systems. Larvae in tropical systems are constantly exposed to high temperatures, unable to enter an 'metabolic refuge' like that of the lower temperature hypolimnion of temperate systems. *Chaoborus* larvae in tropical systems are constantly running full speed ahead towards emergence, with little time or energy for interruptions. It is possible that *Chaoborus* may enter certain systems where energetic constraints are too great for a population to establish. The interaction between oxygen content of the water, fish predation, food levels and ability of *Chaoborus* to survive is a fine line at high temperatures. Low levels of oxygen and limited access to food may prevent

*Chaoborus* larvae from taking refuge from fish predation in bottom areas. High temperatures, predation risk, and low oxygen conditions may interact to limit the distributions of *Chaoborus* in the great lakes region of East Africa.

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