

# The combined effects of temperature and food consumption on body weight, egg production and developmental time in *Chaoborus crystallinus* De Geer (Diptera: Chaoboridae)

## Some new evidence for the adaptive value of vertical migration

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**Summary.** *Chaoborus crystallinus* fourth-instar larvae were reared individually at 14°, 17° and 20° C under different food conditions. *Daphnia magna* of 1.25 mm average length served as prey. The following were measured: amount of prey ingested, larval weight gain, duration of fourth instar, body weight of the adults, and egg number per female. At a given temperature, the body weight, egg-number and developmental rate increased with food consumption. At a given food consumption, higher temperatures caused a decrease in body weight and egg number, and an increase in developmental rate. Gross production efficiencies for fourth-instar larvae were highest at temperatures around 17° C. The results clearly indicate that from an energetic point of view higher temperatures are disadvantageous. In *C. crystallinus* vertical migration is evidently a way of lowering the temperature to which the animals are exposed and hence optimizing food conversion into biomass and offspring production, especially if prey densities are below the saturation level.

**Key words:** Temperature – Relative food saturation – Development – Reproduction – Vertical migration

In aquatic communities, the larvae of the phantom midge *Chaoborus* are considered as important predators, which are able to affect the abundance of zooplankton species (Pastorok 1978, 1980a, b; Kajak and Rybak 1979; Yan et al. 1991). Among insects, only the genus *Chaoborus* undergoes diurnal vertical migration like many zooplankton organisms (*C. punctipennis*: LaRow 1968, 1969; *C. flavicans*: Goldspink and Scott 1971; *C. trivittatus*: Pastorok 1980a; *C. crystallinus*: Erb et al. 1979; Ratte 1986). The adaptive value of vertical migration is

still controversial, and may also be different for different species (for current hypotheses see Kerfoot 1985; Haney 1988).

*C. crystallinus* larvae inhabit shallow waters, which are characterized by the absence of large visual predators and by more or less stable thermal gradients in which the surface temperatures may be up to 7° C higher than those at the bottom. Consequently, by vertical migration the larvae of *C. crystallinus* are exposed to varying temperatures. Laboratory experiments in which abundant prey was supplied showed that in *C. crystallinus* varying temperatures can evoke faster development and affect adult body weight and egg production (Ratte 1979, 1985). The effects on population dynamics were further investigated by an outdoor mesocosm experiment in 5-m<sup>3</sup> tanks. Two *C. crystallinus* populations were compared, one of which was exposed to thermal stratification during migration (migrants), and the other to thermally homogeneous conditions where the temperature was similar to the surface temperature of the stratified tank (“non-migrants”). Thus, only the migrants were exposed to varying temperatures, whilst the “non-migrants”, though they did migrate, were exposed to surface temperatures throughout the day-night cycle (for details see Ratte 1986). Prey density was nearly equal for migrants and non-migrants but markedly lower than that in the laboratory experiments. Both populations of midges had nearly equal developmental times, as was expected from the laboratory experiments, but the migrants proved to be heavier and laid markedly larger egg clutches than those living at constant higher temperatures; this was not predicted from the laboratory experiments. These effects were interpreted as being due to the interaction of the limited food supply and the temperature.

In order to analyze these effects further, we started an investigation on the combined effects of temperature and food on development and reproduction. The results obtained so far are presented here.

## Materials and methods

For every test condition stock cultures of *C. crystallinus* were established and grown under the test conditions at least 2 months before the experiments started (photoperiods of LD 16:8, 800 lx light intensity (white neon tubes) and temperatures of 14°, 17° and 20° C; for rearing method see Ratte 1979). The test larvae were derived from several egg clutches that had been laid on the same day in the corresponding stock culture and were mixed after hatching. During the first to third instars, the larval test populations were kept in 5-L polyethylene containers and were abundantly fed with *Paramecium* and nauplii of *Artemia salina* rinsed with fresh water. After reaching the third instar, individual larvae were isolated and further reared singly in 100-ml glass beakers. To time the start of the fourth instar, the developmental stage of every individual was checked daily by measuring the head capsule length. (In contrast to the gradually increasing length of the whole larvae, the length of the chitinized head capsule increases suddenly after molting.)

The experiments were conducted with fourth instar larvae, beginning with the day of molting from third to fourth instar (day 1). The larvae were grown in water from an artificial outdoor pond, in which a population of *C. crystallinus* was established some years ago. The water was changed daily and not pretreated with the exception of glass-fibre filtering (Whatman GF/C), temperature control and aeration. The volume of the culture medium was adjusted so that in every experimental condition for all larvae an equal prey concentration of 1 *Daphnia* per 2 ml and thus an equal predator-prey encounter rate, was provided. This was done to obtain the same energy efforts in prey capture for all larvae.

Each day, every larva received a defined number of *Daphnia magna* specimens (size class 1–1.5 mm). Daily food intake was measured by counting the non-ingested prey after 24 h. To test whether all larvae started the experiment at the same weights, each individual was weighed when entering the fourth instar (for method see below). This procedure was repeated shortly before the onset of metamorphosis in order to measure the weight gain of every larva (the approaching change to pupae was easily recognized by a yellowish colour of the larvae and clearly visible thoracic horns). The adults were narcotized with ether and weighed. Thereafter the females were returned to the glass beakers together with some males from the stock cultures. Most of them produced an egg clutch within 1 or 2 days. The clutch was photographed so that eggs could be counted later.

A micro-balance MP 4501 (Sartorius) was used to measure the life weights of the larvae to a precision of 1 µg. Before weighing, the larvae were placed on filter paper to remove the water. With careful handling the larvae could be weighed without injury. In an independent experiment we found no statistically significant difference in mortality, developmental time, or body weight between unweighed larvae and those weighed twice by the method described. We may therefore assume that the life-history parameters of the larvae are not affected by the weighing procedure.

In describing the experimental parameters and results the following terms will be used:

*Amount of food*: total number of prey items (e.g. 15 daphnids) either supplied or consumed during a given time period.

*Maximum feeding rate*: maximum amount of food consumable per time unit (e.g. 10 daphnids/day). The maximum feeding rate is related to sex, temperature and prey size (Pastorok 1980a, 1981; Riessen et al. 1984; Wiertz 1984; Spitze 1985). With all other factors remaining constant, the maximum feeding rate of female *C. crystallinus* larvae increases with rising temperature (Wiertz 1984; Ratte et al. in prep). For this investigation the maximum feeding rate of males was assumed to be half that of females, because males achieve about half the body weight of females during approximately the same developmental time (Ratte 1979, this study).

**Table 1.** Mean maximum feeding rates (daphnids/day) of *Chaoborus crystallinus* fourth-instar larvae. *Daphnia* size 1–1.5 mm, photoperiod LD 16:8; values for males are estimated (see text); data from Wiertz (1984)

Temperature [°C]	Items per day	
	Males	Females
20	17.8	35.5
17	14.5	29.0
14	11.5	23.0

*Food saturation*: By this expression a given amount of food consumed is related to the maximum feeding rate under the prevailing conditions. Food saturation becomes 100% if the amount of food consumed per time unit equals the maximum feeding rate. This parameter was introduced in order to describe the nutritional state of a larva. Depending on temperature, the same amounts of food may mean different levels of food saturation.

Based on the data given by Wiertz (1984) maximum feeding rates for both male and female *C. crystallinus* larvae were calculated for the test conditions; the resulting values are summarized in Table 1. By means of these values the measured number of prey eaten per day can be expressed as values of food saturation.

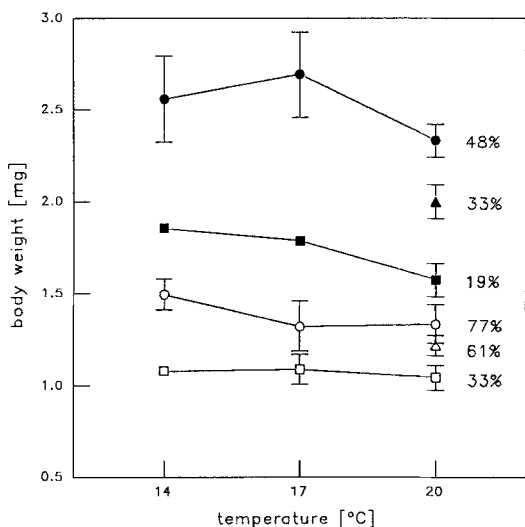
## Results

### Initial weight

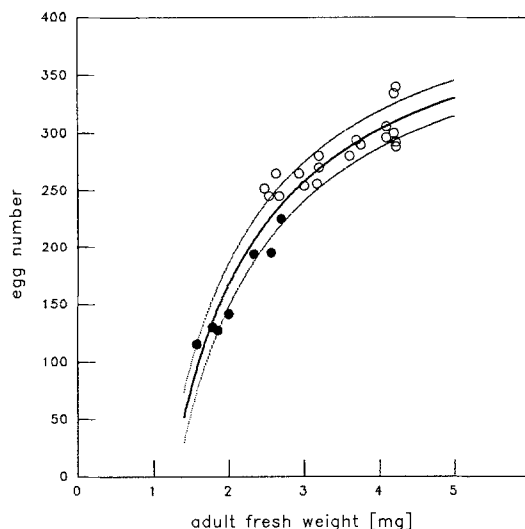
On the day of molting from third to fourth instar, the mean body weights of male and female larvae were about 1.8 mg (males) and 2.5 mg (females), independent of the rearing temperature (*t*-test,  $P > 0.05$ ). Therefore, any effects on body weight measured later on must be due to the different test conditions during the fourth instar.

### Final weight

In Fig. 1, the body weight of the adults is plotted against temperature for different levels of food saturation. To aid in understanding the following, it should be kept in mind that at different temperatures the *same food saturation* corresponds to *different amounts of food consumed* (see Table 2, and definitions given above). At a given food saturation, the body weights were quite similar and were not markedly affected by temperature, which was confirmed by regression analysis. Only the females show a slight, but statistically significant, decrease in body weight with increasing temperature ( $P = 0.046$ ). At the same time, at a given temperature the body weight was higher at higher food saturation. Though this was statistically significant for both sexes, the effect was much more distinct in females. The relationship obtained was approximately linear (for males:  $r^2 = 0.80$ ; for females:  $r^2 = 0.86$ ). According to this, the body weight of *C. crystallinus* is mainly affected by the level of food saturation.



**Fig. 1.** Adult fresh weight of *Chaoborus crystallinus* in relation to temperature and food saturation level. Mean and 95% confidence interval are shown: *open symbols*, males; *filled symbols*, females carrying an egg-clutch. For the saturation percentages see Table 2



**Fig. 2.** Relationship between egg number and fresh weight of adult females. *Open circles*, results from Ratte (1979); *filled circles*, results from the present study; *thick line*, curve fitted to data; *thin lines*, 95% confidence limits. Every point represents the average of a test group

**Table 2.** Results of the feeding experiments; for an explanation see text; the mean % saturation is used for the graphical presentation (Figs. 1, 3, 4)

T [°C]	20°		17°		14°		Mean % saturation	
	Males	Females	Males	Females	Males	Females	Males	Females
Prey items								
– supplied	20	20	18	18	15	15		
– consumed	13.8	17.9	11.4	14.1	8.4	10.6		
% saturation	78	50	79	49	73	46	77	48
Sample size	11	21–24	8–9	5–7	11–12	8–10		
Prey items								
– supplied	13	13						
– consumed	10.9	11.8						
% saturation	61	33					61	33
Sample size	23	8–10						
Prey items								
– supplied	7	7	6	6	5	5		
– consumed	6.1	6.6	4.5	5.4	3.9	4.5		
% saturation	34	19	31	19	35	20	33	19
Sample size	10–12	10–15	12–13	2–4	5	3–8		

*Egg number*

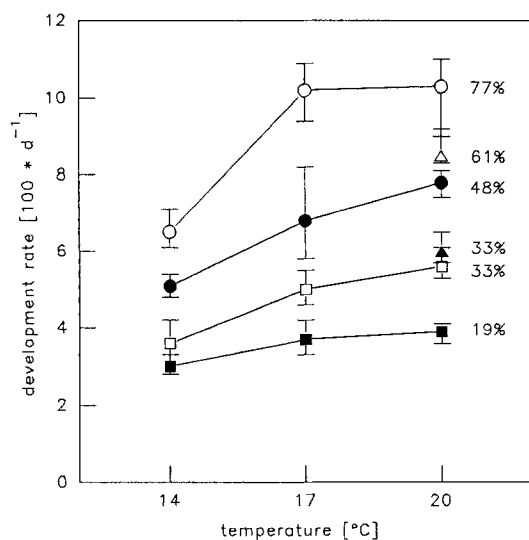
*C. crystallinus* showed a distinct numerical response; within the range of food quantity tested, the egg number changed from 120 to 230 eggs per female (Fig. 2). Using these data and those from Ratte (1979), a functional relation between egg number and body weight (Eq. 1) was derived by linear regression analysis which covers a wider range than that given by Ratte (1979). Equation 1 indicates that a slight increase in body weight (e.g. due to improved food conditions) evokes a great change in the offspring number.

$$E = 438.01 - 540.81/BW \quad (r^2 = 0.91) \quad (1)$$

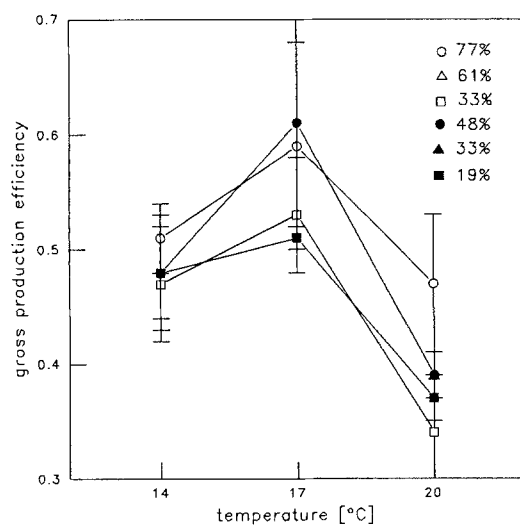
with  $E$ =egg number;  $BW$ =female fresh weight (mg) Comparing Eq. 1 and the relationship between body weight, food saturation and temperature (Fig. 1), the relation of egg number to both factors appears similar (not shown).

*Developmental time*

At the lower saturation levels, the developmental rate (1/developmental time) of fourth instar larvae was found to be nearly linearly dependent on both food saturation and temperature (Fig. 3), as was confirmed by multiple linear regression analysis. At the highest saturation level, it exhibited a saturation curve.



**Fig. 3.** Development rate of fourth instar larvae in relation to temperature at different levels of food saturation. *Open symbols*, males; *filled symbols*, females. For the saturation percentages see Table 2



**Fig. 4.** Effects of temperature and level of food saturation on gross production efficiency (mean and 95% confidence interval). *Open symbols*, males; *filled symbols*, females. For the saturation percentages see Table 2

### Energetics

From the gain of dry weight (production) and amount of food ingested (consumption, as dry weight), for the different temperature- and food-conditions, gross production efficiencies ( $K_1$ ) were calculated as production divided by consumption (Ivlev 1945, from Wieser 1986). For this, the larval weight gain was reduced to dry weight using the function: dry weight =  $0.3 \times$  fresh weight (according to Ratte 1979); dry weights of the ingested daphnids were calculated according to Eq. 2 (from Wetzel and Likens 1979).

$$DW = 0.0052 \times L^{3.012} \quad (2)$$

where DW = dry weight (mg),  $L$  = length (mm). The resulting curves (Fig. 4) show optima, indicating that the most favourable energetic conditions occur at an intermediate temperature (around 17° C). Consequently, higher temperatures and hence higher feeding rates are not optimal from an energetic point of view.

### Discussion

It has been shown that (1) body weight, egg production and developmental time of *C. crystallinus* are determined by food saturation, and (2) that food conversion into biomass, measured as gross production efficiency, follows an optimum curve with maximum efficiency around temperatures of 17° C. How can we explain these findings and what are the logical consequences?

The key for understanding the interaction of food amount and temperature is the food saturation, which takes into account metabolic needs. At a given temperature, it relates the actual food consumption to the maximum possible food consumption. This latter itself depends on temperature due to the temperature dependence of the metabolic rate. The primary effect of rising temperature is an increase in both the metabolic rate and the metabolic needs. The final body weight, then, depends on the extent to which these metabolic needs can be fulfilled by the actual food consumption. Earlier reports assumed a direct action of the temperature on body weight in *C. crystallinus* (Ratte 1979, 1985). These data should be reconsidered and interpreted in terms of food saturation. For the discussion of the benefit of vertical migration it should be kept in mind that at a given level of food consumption below the saturation level, lower temperatures *increase* the body weight.

The gross production efficiencies found for *C. crystallinus* range from 0.35 to 0.57 (males) and 0.37 to 0.61 (females) and were not markedly affected by sex. They are in line with results from other *Chaoborus* species: Cressa and Lewis (1986) found a gross production efficiency of 0.46 and a corresponding assimilation efficiency of 0.61 (fourth instar larvae of *C. brasiliensis*, grown at 26° C). In *C. trivittatus*, the assimilation efficiency ranged from 0.69 (Swift 1976) to 0.87 (Giguere 1981). Compared with other small aquatic organisms, the gross production and assimilation efficiency of *Chaoborus* species seems exceptionally high (for review see Cressa and Lewis 1986; Calow 1977).

So far as we are aware, curves with optima for the dependence of the gross production efficiency on temperature have not previously been reported. A similar relationship between assimilation efficiency and temperature has been found in some other small aquatic organisms (e.g. *Daphnia pulex*, Lampert 1977a). The temperature optimum curves are seen to be due to several separate processes. On the one hand, as the temperature rises, the feeding rate and thus the energy input increases. On the other hand, there are three antagonistic effects: (1) The assimilation efficiency is a function of meal size.

It decreases with increasing meal size due to faster food transport through the gut which reduces food utilization (Giguere and Dill 1980; Giguere 1981, in *C. trivittatus*). Similar effects have also been observed by Krishnan and Chockalingham (1988) in the lepidopteran *Pericallia* sp. and by Roe et al. (1980) in *Acheta domesticus*. In the monarch butterfly, *Danaus chrysippus*, Mathavan and Pandian (1975) found that a feeding rate that has increased by 50% may yield a gain of assimilated food of only 30%. (2) There is an increase in metabolic rate when processing a meal, known as specific dynamic action (SDA). Giguere (1980) found increased metabolic expenditures with higher feeding rates in *C. trivittatus* larvae. (3) There is an energy loss because of respiration rates increasing with rising temperature (Weber 1974).

In summary, above a critical temperature, additional food ingested due to an increased feeding rate (e.g. at higher temperatures) cannot be as efficiently utilized. Therefore, larval growth is achieved more efficiently at intermediate temperature conditions.

There are important logical consequences with respect to vertical migration in *Chaoborus*, which are probably significant for the selection of this behaviour. The latter is only possible if the benefits of migration exceed the costs (measured in terms of individual fitness). We shall show that this is indeed the case in *C. crystallinus*.

Firstly, one has to consider that the larvae of *C. crystallinus* and *C. americanus* are known to be continuous feeders and food consumption is not affected by photoperiod (Bradshaw 1970; own measurements). Secondly, the larvae of *C. crystallinus* settle in shallower waters and migrate diurnally through thermal gradients. The migration pattern switches from upward migration in the afternoon, performed by the overwintering generation shortly before emergence in spring, to upward migration at night during later seasons (own observations in mesocosm experiments). In *C. crystallinus* larvae the diurnal migration leads to a decrease in the mean temperature to which they are exposed and hence to an increase in the food saturation at a constant prey density. This would only appear if the amount of prey ingested lies below the saturation level. This should occur frequently under field conditions (Parma 1969; Pastorok 1980a, b, 1981; Riessen et al. 1984). Furthermore, the prey distribution should be either homogeneous or correspond to that of the larvae. During most seasons, this condition is fulfilled, as *Chaoborus* shows a nocturnal migration into the surface layer as do many prey organisms and planktivores (Haney 1988).

Our results clearly indicate that under these conditions the benefits of the downward migration into cooler water and the following increased level of food saturation are higher body weights and higher egg numbers (Figs. 1 and 2). What are the costs? Normally, the costs of vertical migration are assumed to be mainly the costs of living at lower temperature and of energy consumption for the movements. In *Chaoborus*, the latter is negligible because the upward and downward movements are achieved by regulating the gas volume in the tracheal bladders (Franke 1983). With respect to the

developmental costs, previous laboratory experiments have shown that in *C. crystallinus* at temperatures between 14° and 25° C, the developmental time can be considerably shortened by thermoperiodic effects and that developmental rates could be reached that were nearly equal to those shown at the upper temperature of the thermoperiodic cycle (Ratte 1979, 1985). In addition, the increase in food saturation due to downward migration shortens the developmental time (Fig. 3) and in part compensates for the developmental retardation. So, developmental costs are low or even non-existent. *C. crystallinus*, therefore, is able to increase individual fitness and, as a consequence, population growth by migration into cooler waters. Our hypothesis is clearly supported by the mesocosm experiment described initially: the predicted increases in weight and egg production were in fact observed, and development was found to proceed as fast as at surface temperatures.

Our findings are in line with the predictions of the metabolic hypothesis of McLaren (1963), but the physiological mechanisms invoked as explanations are somewhat different. McLaren suggested that a migrant can gain an energy bonus by feeding efficiently at high temperatures near the surface and digesting at low metabolic rates in cooler water. As yet, this hypothesis has not been supported by experiments (McLaren 1974; Orcutt and Porter 1983; Stich and Lampert 1984; Lampert et al. 1988; Frost 1988). Further, our findings confirm the theoretical work of Giguere and Dill (1980) who computed the energy budget of *C. trivittatus* by a simulation model including different temperature-dependent metabolic rates and costs of swimming and attacking prey. It was run with different prey densities utilizing two alternative migratory tactics (which were observed in *C. trivittatus* as well as in *C. crystallinus*). The energy benefits to the larvae were found to reach a maximum when they were migrating at low prey density and staying at the warmer surface in other conditions. A comparison with field data did provide evidence that the seasonal changes in migration pattern of *C. trivittatus* are correlated with seasonal changes in prey densities.

There has been an earlier attempt by Swift (1975) to simulate the optimal migration behaviour of *C. trivittatus*. The results are in contradiction to the migration pattern exhibited in the field. We suppose this is due to mainly two facts: firstly, Swift's assumption that feeding occurs primarily at night is not true, at least in *C. crystallinus*; secondly, in the model only surface prey densities were varied regardless of prey densities in deeper water and the actual place of the larvae. This is in contradiction to the above mentioned necessary prey distribution.

Generally, one might counterargue that the nocturnal upward migration performed more frequently than other patterns indicates a predator avoidance mechanism and, moreover, is in contradiction to the hypothesis presented here. In order to gain maximum metabolic benefits, a diurnal migration pattern is not necessary. However, any other kind of migration pattern requires a temperature or metabolic "memory" which controls the migration pattern such that the average temperature of exposure

and food concentrations lead to the suggested benefits. As yet, such a mechanism is unknown. However, obviously the diurnal migration rhythm corresponding to the photoperiod is indeed a mechanism which ensures that during summer, with long days, the larvae of *C. crystallinus* spend more than 12 h in cooler waters. So the migration pattern does not conflict with our hypothesis.

In our opinion, the hypothesis may also be extrapolated to other vertical migrants because basic metabolic processes are involved which are common to all poikilotherms. As yet, however, only few investigations have been conducted on this topic (Haney 1988). The importance of food effects was shown for different herbivorous crustaceans migrating in the Bodensee, Germany (Geller 1986). In this lake the occurrence of migration behaviour proved to be dependent on the species-specific threshold food concentration. Geller suggests that the vertical migration behaviour is a starvation avoidance mechanism at low food concentrations. From our own laboratory experiments with *Daphnia magna* there is evidence for effects quite similar to those obtained for *C. crystallinus* (Dülmer and Ratte, in prep.). The effect of food concentration as a selective factor has been pointed out by several investigators in the context of intra- and interspecific competition (Lampert 1977b; Lampert and Schober 1980; Romanovsky and Feniova 1985). According to the low-food-efficiency hypothesis of Lampert and Schober (1980) the fitness of a species depends on the survival probability when food is limited. There is evidence that food concentration is involved in the adaptive value of vertical migration.

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## References

- Bradshaw WE (1970) Interaction of food and photoperiod in the termination of larval diapause in *Chaoborus americanus* (Diptera: Culicidae). *Biol Bull* 139:476–484
- Calow P (1977) Conversion efficiencies in heterotrophic organisms. *Biol Rev* 52:385–409
- Cressa C, Lewis WM Jr (1986) Ecological energetics of *Chaoborus* in a tropical lake. *Oecologia* 70:326–331
- Erb D, Neumann D, Ratte HT (1979) Tagesperiodische Vertikalwanderungen der in Flachgewässern beheimateten Larven von *Chaoborus crystallinus* (Diptera: Culicimorpha). *Entomol Gen* 5:163–168
- Franke C (1983) Eine Modellvorstellung zum Schwebeverhalten der Larvalstadien von *Chaoborus flavicans* (Diptera, Chaoboridae). *Zool Beitr NF* 28:231–252
- Frost BW (1988) Variability and possible adaptive significance of diel vertical migration in *Calanus pacificus*, a planktonic marine copepod. *Bull Mar Sci* 43:675–694
- Geller W (1986) Diurnal vertical migration of zooplankton in a temperate great lake (L. Constance): a starvation avoidance mechanism? *Arch Hydrobiol Suppl* 74:1–60
- Giguere LA (1980) Metabolic expenditures in *Chaoborus* larvae. *Limnol Oceanogr* 25:922–928
- Giguere LA (1981) Food assimilation efficiency as a function of temperature and meal size in larvae of *Chaoborus trivittatus* (Diptera: Chaoboridae). *J Anim Ecol* 50:103–109
- Giguere LA, Dill LM (1980) Seasonal patterns of vertical migration: a model for *Chaoborus trivittatus*. In: Kerfoot WC (ed) *The evolution and ecology of zooplankton communities*. University Press of New England, Hanover, pp 122–128
- Goldspink GR, Scott DBC (1971) Vertical migration of *Chaoborus flavicans* in a Scottish Loch. *Freshw Biol* 1:411–421
- Haney JF (1988) Diel patterns of zooplankton behavior. *Bull Mar Sci* 43:583–603
- Kajak Z, Rybak J (1979) The feeding of *Chaoborus flavicans* Meigen (Diptera, Chaoboridae) and its predation on lake zooplankton. *Int Rev ges Hydrobiol* 64:364–378
- Kerfoot WC (1985) Adaptive value of vertical migration: comments on the predation hypothesis and some alternatives. *Contrib Mar Sci, Suppl* 27:91–113
- Krishnan M, Chockalingham S (1988) Influence of temperature on the bioenergetics of a tropical moth. *J Therm Biol* 13:149–155
- LaRow EJ (1968) A persistent diurnal rhythm in *Chaoborus* larvae I. The nature of the rhythmicity. *Limnol Oceanogr* 13:250–256
- LaRow EJ (1969) A persistent diurnal rhythm in *Chaoborus* larvae. II. Ecological significance. *Limnol Oceanogr* 14:213–218
- Lampert W (1977a) Studies on the carbon balance of *Daphnia pulex* de Geer as related to environmental conditions. II. The dependence of carbon assimilation on animal size, temperature, food concentration and diet species. *Arch Hydrobiol Suppl* 48:310–335
- Lampert W (1977b) Studies on the carbon balance of *Daphnia pulex* de Geer as related to environmental conditions. IV. Determination of the “threshold” concentration as a factor controlling the abundance of zooplankton species. *Arch Hydrobiol Suppl* 48:361–368
- Lampert W, Schober U (1980): The importance of “threshold” food concentrations. In: Kerfoot WC (ed) *The evolution and ecology of zooplankton communities*. University Press of New England, Hanover pp 264–267
- Lampert W, Schmitt RD, Muck P (1988) Vertical migration of freshwater zooplankton: test of some hypotheses predicting a metabolic advantage. *Bull Mar Sci* 43:620–640
- Mathavan S, Pandian TJ (1975) Effect of temperature on food utilisation in the monarch butterfly *Danaus chrysippus*. *Oikos* 26:60–64
- McLaren IA (1963) Effects of temperature on growth of zooplankton and the adaptive value of vertical migration. *J Fish Res Bd Can* 20:685–727
- McLaren IA (1974) Demographic strategy of vertical migration by a marine copepod. *Am Nat* 108:91–102
- Orcutt JD, Porter (1983) Diel vertical migration by zooplankton: constant and fluctuating temperature effects on life history parameters of *Daphnia*. *Limnol Oceanogr* 28:720–730
- Parma S (1969) The life cycle of *Chaoborus crystallinus* (De Geer) (Diptera, Chaoboridae) in a Dutch pond. *Verh Internat Verein Limnol* 17:888–894
- Pastorok RA (1978) Predation by *Chaoborus* larvae and its impact on the zooplankton community. Ph. D. thesis, University of Washington, Seattle
- Pastorok RA (1980a) Selection of prey by *Chaoborus* larvae: a review and new evidence for behavioral flexibility. In: Kerfoot WC (ed) *The evolution and ecology of zooplankton communities*. University Press of New England, Hanover pp 538–554
- Pastorok RA (1980b) The effects of predator hunger and food abundance on prey selection by *Chaoborus* larvae. *Limnol Oceanogr* 25:910–921
- Pastorok RA (1981) Prey vulnerability and size selection by *Chaoborus* larvae. *Ecology* 62:1311–1324
- Ratte HT (1979) Tagesperiodische Vertikalwanderung in thermisch geschichteten Gewässern: Einfluß von Temperatur- und Photoperiodezyklen auf *Chaoborus crystallinus* De Geer (Diptera: Chaoboridae). *Arch Hydrobiol Suppl* 57:1–37

- Ratte HT (1985) Temperature and insect development. In: Hoffmann KH (ed) Environmental physiology and biochemistry of insects. Springer Verlag, Heidelberg pp 33–66
- Ratte HT (1986) Vertical migration and population dynamics of *Chaoborus crystallinus* (Diptera, Chaoboridae) in thermally stratified waters. Proc 3rd Europ Congr Entomol, Amsterdam, pp 125–128
- Riessen HP, O'Brien WJ, Loveless B (1984) An analysis of the components of *Chaoborus* predation on zooplankton and the calculation of the relative prey vulnerabilities. Ecology 65:514–522
- Roe PM, Clifford CW, Woodring JP (1980) The effect of temperature on feeding, growth and metabolism during the last larval stadium of the female house cricket, *Acheta domesticus*. J Insect Physiol 26:639–644
- Romanovsky YE, Feniova IY (1985) Competition among Cladocera: effect of different levels of food supply. Oikos 44:243–252
- Spitze K (1985) Functional response of an ambush predator: *Chaoborus americanus* predation on *Daphnia pulex*. Ecology 66:938–949
- Stich HB, Lampert W (1984) Growth and reproduction of migrating and nonmigrating *Daphnia* species under simulated food and temperature conditions of diurnal vertical migration. Oecologia 61:192–196
- Swift MC (1975) Simulation studies of *Chaoborus* vertical migration. Verh Internat Verein Limnol 19:3120–3126
- Swift MC (1976) Energetics of vertical migration in *Chaoborus trivittatus* larvae. Ecology 57:900–914
- Weber H (1974) Grundriß der Insektenkunde. Gustav Fischer Verlag, Stuttgart
- Wetzel RG, Likens GE (1979) Limnological analysis. W.B. Saunders Company, Philadelphia, London, Toronto
- Wiertz S (1984) Funktionelle Reaktion bei den Larven der Mücke *Chaoborus crystallinus* (Diptera, Chaoboridae) unter besonderer Berücksichtigung der Temperatur und Photoperiodeabhängigkeit. Diplomarbeit, RWTH Aachen
- Wieser W (1986) Bioenergetik: Energietransformation bei Organismen. Thieme Stuttgart
- Yan ND, Keller W, MacIsaac HJ, McEachern LJ (1991) Regulation of zooplankton community structure of an acidified lake by *Chaoborus*. Ecol Applications 1:52–65