Influence of temperature and food quality on the life history of an epiphytic chironomid

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First instar larvae of the epiphytic chironomid, *Eukiefferiella ilkleyensis* (Edwards) were collected from the field and reared until pupation. 4 temperature regimes and food sources of varying quality were combined to study their effects on larval growth dynamics. On both a low quality "winter" diet and a higher quality "spring" diet survival to the second instar and to pupation demonstrated a positive relationship with temperature up to 14° C, above which survival was reduced. At 5° C, 9° C and 18° C survival was increased on the higher quality diet. Growth rates showed a similar response. On the "winter" diet growth rate increased from 0.57% length day $^{-1}$ at 5° C to 1.77% length day^{-1} at 14° C. At 18° C growth was reduced to 1.1% length day^{-1}. On the "spring" diet growth rate increased over the range of temperatures from 0.47% length day^{-1} at 5° C to 2.05% length day^{-1} at 18° C. Growth rates at 9° C and 18° C were significantly higher on the "spring" diet than the "winter" diet. At 5° C and 14° C growth rates were similar on both diets. A supplement of macrophyte tissue to the "spring" diet resulted in increased growth rates at all temperatures. Decreased growth rate at a high temperature, on a low quality diet, is discussed in relation to the energetic cost of "maintenance metabolism". Overall results are discussed in relation to the population dynamics of the species in the field.

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It is generally accepted that temperature and nutrition are 2 of the prime factors influencing lifehistory patterns of aquatic insects (Sweeney 1984). In recent years many workers have investigated the effects of either temperature or food quality on rates of growth and development of aquatic insects. Some of these studies have involved the Chironomidae, with either temperature (Danks 1978, Graham & Burns 1983, Konstantinov 1958, Mackey 1977, Menzie 1981, Swanson & Hammer 1983) or food quality (Biever 1971, Davies 1975, King 1978, Mattingly et al. 1981) being investigated. Few authors have attempted a multivariate approach, in which several factors have been investigated simultaneously (Mackey 1977, Ward & Cummins 1979).

Many workers have assumed food quantity not to be limiting, placing more importance on the quality of the available food source (McMahon et al. 1974, White 1978). Various techniques have been used to assess the relative quality of food items, such as C/N ratio (McMahon et al. 1984), calorific equivalents (Cummins & Wuycheck 1971), ATP content (Ward & Cummins 1979) and percentage organic matter (Mattingly et al. 1981). In most cases the aims of the investigator, or the food item in question, have determined which technique has been employed.

The present study is part of a larger project on the population dynamics and production of 3 species of epiphytic chironomid, and was primarily designed to provide the data necessary for the estimation of production. The effects of temperature and food quality on the growth and survival of *Eukiefferiella ilkleyensis* (Edwards) are examined. The biology of *E. ilkleyensis* in the English chalk stream environment is well documented. The habitat requirements of this species have been studied by Pinder (1980) and its dietary requirements were examined by Williams (1981).

Methods

First instar larvae of *Eukiefferiella ilkleyensis* were obtained by washing samples of *Ranunculus penicillatus* var. *calcareus* (R. W. Butcher) C. D. K. Cook, taken from the Tadnoll Brook (Pinder 1974), through a series of sieves of decreasing mesh-size. The majority of first instar chironomid larvae were retained at the 70µm stage (Storey & Pinder 1985). With practice, it was possible to identify first instar larvae of *E. ilkleyensis* on the basis of head capsule size, head and body colour and behaviour.

Larvae were reared in incubators at constant temperatures of 5° C, 9° C, 14° C and 18° C (±1° C). This is approximately the range of mean temperatures likely to be experienced in the river. A 12 hour light: dark photoperiod was used throughout. Individual larvae were placed in rearing pots of 40 ml volume containing river water and an excess of food. 20 larvae were reared at each temperature.

The initial length of each larva was measured to the nearest 0.05 mm at x20 magnification. Larvae maintained at 14° C and 18° C were measured once every 3-4 days, and those at 5° C and 9° C, once every 7 days. To reduce bacterial and fungal growth, especially at the higher temperatures, food and water were changed weekly.

Two food sources, intended to represent a winter and a spring diet, were selected for growth experiments. Each diet consisted of "Aufwuchs" collected from *R. calcareus*, but at different times of the year. "Aufwuchs" is here regarded as the flora of diatoms, blue-green algae, other single-celled algae and filamentous algae, and the fauna of bacteria, fungi, protozoa and other microscopic invertebrates associated with allochthonous and autochthonous organic matter, occurring on the surface of *R. calcareus*. The "winter-diet" was collected during mid-October to late January, the period of minimal diatom growth and the "spring-diet" was collected from early April until mid-June, covering the period of the spring diatom bloom (Marker et al. 1984, Williams 1981).

Before being added to the rearing pots the "Aufwuchs" was passed through a 50µm mesh aperture plankton net to remove all other chironomid larvae and macroinvertebrates. Excess "Aufwuchs" was maintained in culture, continually aerated at 14° C under a 12 hour light: dark regime, and used to replenish the food in the rearing pots. Cultures were discarded every 14-21 days and replaced with fresh "Aufwuchs" from the field.

The spring diet, of 10 of the replicates at each temperature, was supplemented with fragments of young leaves of *R. calcareus*.

The C/N content of each diet was used as an indication of food quality (McMahon et al. 1974). Estimates of total carbon (C) and total nitrogen (N) were made on a Carlo Erba analyser.

Mean growth rates at each temperature and for each diet were calculated according to Humpesch (1979). The relationship between the body len[gth] (L, mm) of a single larva and the time from [the] start of the experiment (t, days), was found to be rectilinear on a semi-logarithmic scale. Therefore, growth was assumed to be exponential during each experiment and the relationship between L. and t. is given by:

$$L_t = L_0 e^{bt}$$

converting to logarithms $\log_e L_t = \log_e L_0 + bt$, where L_0 is the body length of the larvae at the start of the experiment, L_t is the body length after t. days, and the constant b is the relative rate of growth in length (mm. mm^{-1}day^{-1}). Final values were expressed as specific growth rates, G, % day^{-1}, where G = 100.b.

Mean rates of development and survivorship were determined for larvae at each temperature and for each diet. Also the mean body lengths of each instar of larvae reared in the laboratory were compared with those of larvae taken from the field in mid-June.

Results

The percentage C, percentage N and C:N ratios of samples of the winter and spring diets are presented in Tab. 1. Differences in C and N values between diets were compared using a pooled t-test. Both percentage C and percentage N were significantly higher in the spring diet than in the winter diet ($p < 0.05$). The same test indicated no significant differences in C:N ratio values between the 2 diets.

C/N analysis was also carried out on cleaned sections of *R. calcareus* (Tab. 1). Sections were separated into 4 categories on the basis of increasing leaf age. The percentage C and percentage N

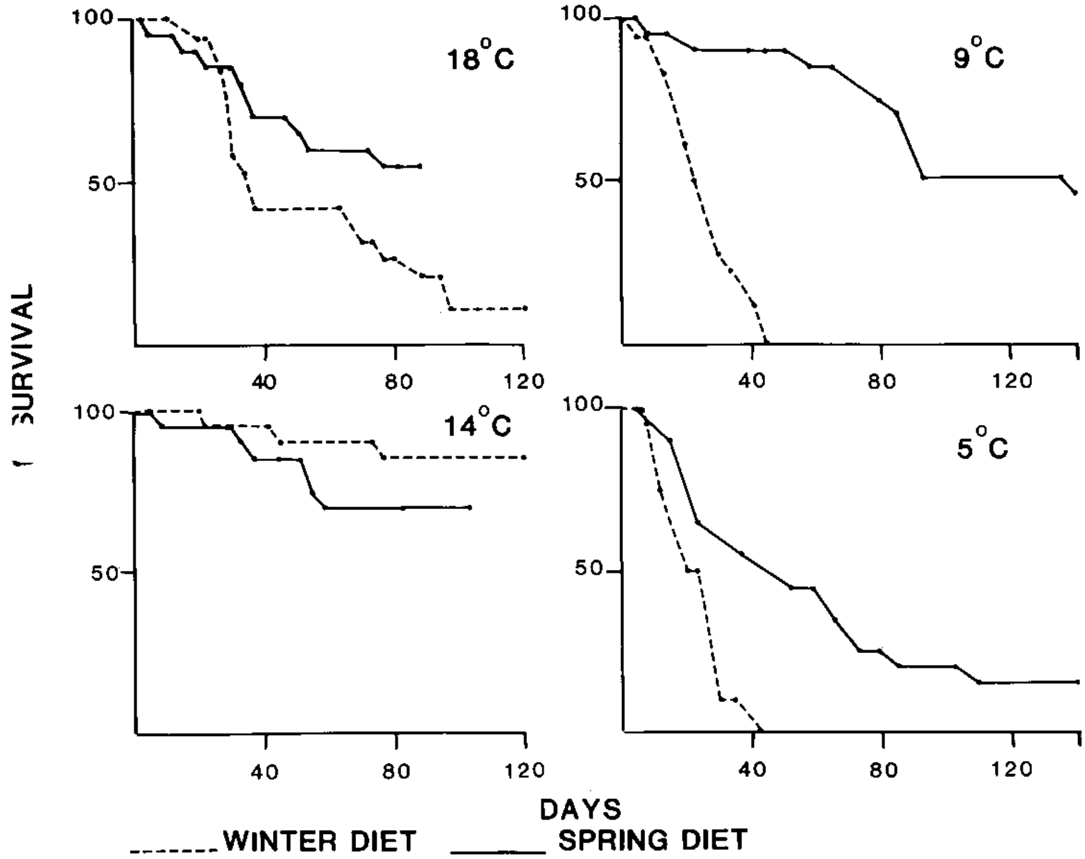

Fig. 1 Influence of diet and temperature on larval survival.

Table 1. Food quality: percentage nitrogen, percentage ·rbon and carbon: nitrogen ratios of samples of "Auf- _ ıchs" and *R. calcareus*.

Diatom/Detritus				
Date sampled	%N	%C	C:N ratio	
15.10.84	1.13	11.28	9.99	
10.12.84	1.11	11.34	10.22	Winter
diet				
8.5.85	1.24	12.61	10.16	
28.5.85	1.42	13.08	9.21	Spring
diet				
19.6.85	1.35	13.83	10.28	
Ranunculus calcareus				
Section of plant	%N	%C	C:N ratio	
Budding leaves	6.11	45.05	7.38	
Young leaves	4.44	41.38	9.32	↓Increasing
Mid-leaves	3.75	40.62	10.85	leaf age
Old leaves	2.96	37.46	12.72	

Table 2. Percentage of larvae surviving to second instar.

Temperature (°C)	Winter diet	Spring diet
18	72.0	86.7
14	100	92.3
9	16.6	78.1
5	13.3	46.9

values decreased progressively with increasing leaf age. The C:N ratios similarly showed a response to the age of leaves with significant successive increases with increasing age.

The percentage survival plotted against time (day) at each temperature and for each diet is

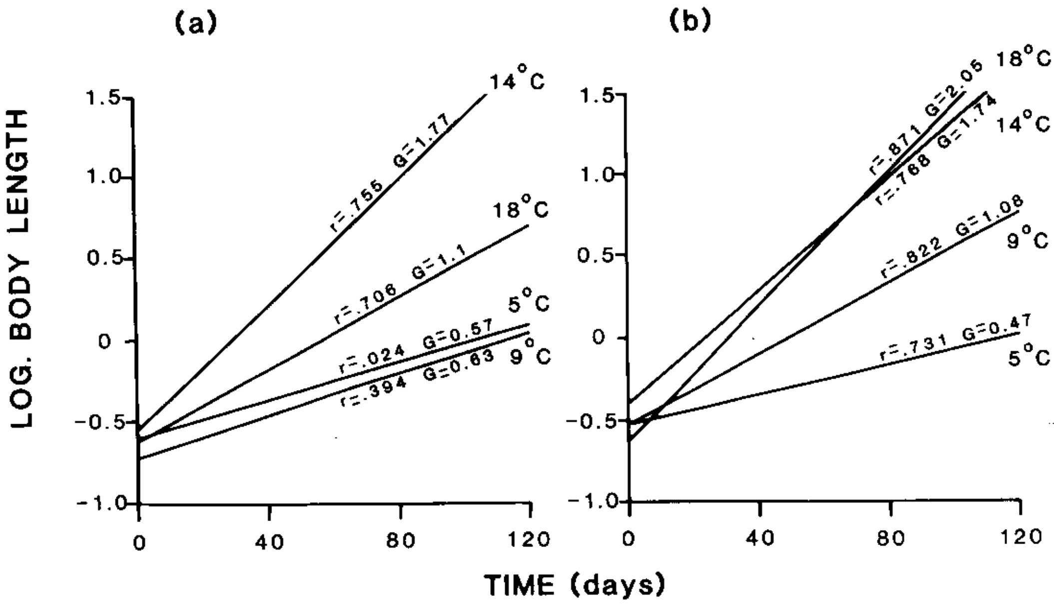

Fig. 2 Effect of temperature on mean larval growth rates, (a) winter diet and (b) spring diet, where G = specific growth rate (% length day^{-1}), and r = correlation coefficient between log. body length and time (days). The relationship between body length (L, mm) and dry weight (W, mg) may be expressed by the equation $W = aL^b$, where $a = 4.427 \times 10^{-3}$ and $b = 2.46$.

shown in Fig. 1. On the winter diet, survival at 18° C was low, with about 20% of larvae pupating, while at 14° C approximately 80% of larvae reached pupation. Survival on the winter diet at 9° C and 5° C was poor, with total mortality at 40-45 days, with no larvae pupating.

On the spring diet the percentage surviving to pupation was 55%, 70% and 45% at 18° C , 14° C and 9° C respectively. At 5° C no larvae developed to pupation, but c. 20% of larvae which survived to the second instar, appeared to diapause, with development ceasing. The experiment was terminated after 140 days.

A comparison of diets revealed better survival to pupation on the spring diet than on the winter diet at 18° C, 9° C and 5° C. The greatest degree of mortality occurred within the first instar (Tab. 2). At 5° C, 9° C and 18° C survival to second instar was better on the spring diet than the winter diet, with the greatest differences occurring at 5° C and 9° C. At 14° C the percentage surviving to second instar and to pupation differed little between diets.

At each temperature and for each diet the mean specific growth rates of all replicates were determined. Figs. 2 (a) and 2 (b) illustrate the effects of increased temperature on the mean specific growth rates (G) for the winter and spring diets respectively. The results of this analysis are summarised in Tab. 3. On the winter diet, values of G increased with increasing temperature to a maximum of 1.77% day^{-1} at 14° C. The value of G at 18° C was significantly lower than at 14° C. On the spring diet G increased with increasing temperature throughout the entire range of temperature.

A comparison of diets showed increased mean specific growth rates on the spring diet at 18° C and 9° C. Diet did not significantly affect G either 5° C or 14° C.

Mean specific growth rates were also calculated for the third and fourth instar stages of larvae reared on the spring diets with and without *R. calcareus*. On both diets, i.e. spring "Aufwuchs" with macrophyte and without macrophyte, growth rates showed a positive relationship with temperature. A comparison of diets revealed that at each temperature growth rate in the third and fourth instar stages (Tab. 4) and overall larval growth rates (Tab. 3) were higher when the diet was supplemented with *R. calcareus*.

Mean developmental periods, time in days taken to reach pupation, were estimated at each temperature and for each diet (Tab. 5). On the

Table 3. Influence of diet and temperature on mean larval growth rates, expressed as specific growth rate (G) (where G = % increase body length day^{-1}), with correlation coefficients between log.body length (mm) and time (days) in parenthesis.

Temperature (°C)	Winter diet	Spring diet	Spring diet + macrophyte
18	1.1 (r=0.706)	2.05 (r=0.871)	2.25 (r=0.866)
14	1.77 (r=0.755)	1.74 (r=0.768)	1.92 (r=0.746)
9	0.63 (r=0.394)	1.08 (r=0.822)	1.32 (r=0.916)
5	0.57 (r=0.024)	0.47 (r=0.731)	—

winter diet no larvae pupated at 5° C and 9° C. Larvae at 14° C and 18° C took 67.1 and 97.5 days respectively to reach pupation. On the spring diet, no larvae completed development at 5° C. At 9° C, 14° C and 18° C larvae had mean developmental periods of 110.9, 71.1 and 74.9 days, respectively. 95% confidence limits were fitted to each mean developmental period as an indication of the significance of changes between temperatures and diets.

The mean body length of larvae showed a geometric rate of increase in relation to instar, with the mean body lengths for each instar, of larvae reared in the laboratory, similar to those of larvae taken from the field (Fig. 3).

Discussion

The majority of past studies on the effects of food quality have focused on macroinvertebrate species using whole leaf substrates (shredders). Such studies on the Chironomidae have tended to

Table 4. Effect of macrophyte on growth of the 3rd/4th instar stage, expressed as specific growth rate (G) (where G = % increase body length day^{-1}), with correlation coefficients between log. body length (mm) and time (days) in parenthesis.

Temperature (°C)	Spring diet	Spring diet +macrophyte
18	1.91 (r=0.886)	3.64 (r=0.833)
14	1.56 (r=0.813)	3.03 (r=0.884)
9	0.97 (r=0.773)	1.33 (r=0.89)

Table 5. Mean duration of larval development (days), with 95% confidence limits.

Temperature (°C)	Winter diet	Spring diet
18	97.5 (±30.03)	74.88 (±8.59)
14	67.06 (±9.27)	71.08 (±11.68)
9	—	110.88 (±26.02)
5	—	—

look at detritivores, such as *Stictochironomus annulicrus* (Townes) (Mattingly et al. 1981) and *Paratendipes albimanus* (Meigen) (Ward & Cummins 1979). These species depend upon particulate organic matter and its associated microbial fauna and may be classified as collectors/gatherers. This present study, apparently for the first time, examines a scraper/herbivore, largely dependent upon primary production for its food supply.

Sweeney (1984) suggested that it is only through experiments which include an array of food qualities and a broad range of temperatures that it will be possible to determine the relative importance of each variable to a life history.

Temperature is a relatively simple parameter to investigate in the laboratory since it may be easily quantified and maintained. The assessment of food quality is much more difficult. Ward & Cummins (1979) reported a positive relationship between growth rate and food quality for *Paratendipes albimanus*. They based quantitative estimates of quality on the ATP content of the substratum. Higher quality, conditioned, leaves supported a higher microbial fauna, as indicated by higher ATP values. Iversen (1974) also worked with conditioned leaves, but used nitrogen content as a measure of quality. He observed faster growth of the trichopteran, *Sericostoma personatum* (Spence) on leaves with a higher organic nitrogen content. More recently, Taylor & Roff (1984) compared the use of both ATP and C:N ratio as indicators of quality of stream detritus, and found both methods to be useful but they preferred the former.

Few growth studies have involved the qualitative description of "Aufwuchs". McMahon et al. (1974) looked at variations in "Aufwuchs" in terms of C:N ratios. They reported C:N ratios ranging from 3.7:1 to 10.1:1, with higher growth rates and fecundity of the snails *Laevapex fuscus*

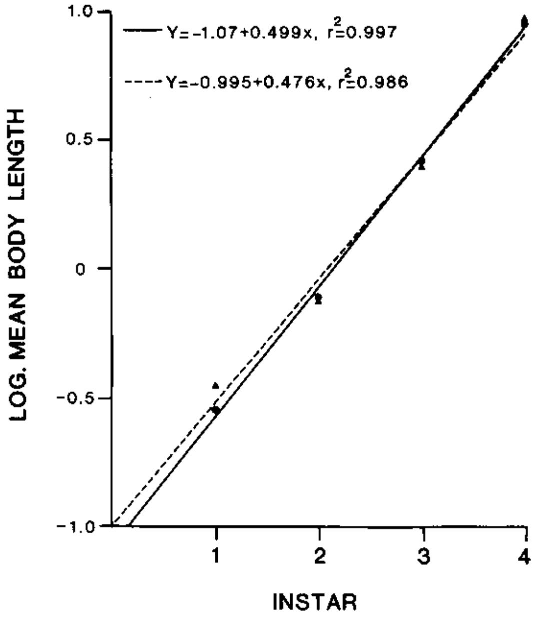

Fig. 3 Linear regressions of log.mean body length against instar for laboratory reared larvae (—, •) and larvae collected from the field (- - - , ▲) with regression equations and values of r^2.

(Adams) and *Lymnaea palustris* (Muller) correlated with lower C:N ratios.

Since this study was also based on feeding experiments with differing qualities of "Aufwuchs", it was decided to assess food quality through the determination of C/N contents. C/N analysis of the diets (Tab. 1) does not show the expected decrease in C:N ratio from the winter to the spring (McMahon et al. 1974). But there is a significant increase in the percentage N content in the spring diet. This increase in the amount of available nitrogen per unit of food ingested is an indication of the increased quality.

Anderson & Cummins (1979) proposed the following relative nutritional gradient for different food items from lowest to highest quality: wood, terrestrial leaf litter, fine particulate organic matter (FPOM), decomposing vascular hydrophytes and filamentous algae, living algae (primarily diatoms) and animal tissue. On this basis the spring, diatom dominated, "Aufwuchs" would be of a higher quality than the winter diet in which detritus predominates (FPOM and decomposing vascular hydrophytes). Analysis of the survival, growth and development of larvae reared on the 2 diets, in the laboratory, tend to support this proposition.

Total survivorship and percentage survival by first instar larvae showed a response to both temperature and food quality, although the latter appeared to exert the major influence. First instar larvae survived better on the spring diet, especially at the lower temperatures (5° and 9° C). This supports the work of White (1978) who suggested that the single most important factor limiting the abundance of certain herbivorous invertebrates was a relative shortage of nitrogenous food for the very young. He proposed "that animals live in a variably inadequate environment wherein many are born but few survive", with "populations being limited from below rather than controlled fror above". Dempster & Pollard (1981) came to a similar conclusion, for the responses of a range of invertebrates to food supply, suggesting that population sizes were dependent upon the carrying capacity of the environment, which, in turn, was usually determined by the availability of a suitable food source. Williams (1981) looked at the dietary requirements of *E. ilkleyensis* in the field and noted positive selection by first instar larvae for diatoms. Even when diatoms were scarce during winter, the guts of first instar larvae were full of diatoms. The greater availability of diatoms in the spring diet, as compared with the winter diet, may well have a major influence on first instar survival, either through the higher nutritional value of diatoms or possibly as a result of diatoms being more easily ingested because of their size.

Attempts were made to differentiate between the effects of temperature and nutrition on rates of growth and development. Larvae on the spring diet demonstrated a positive correlation between growth rate and temperature, previously observe for a range of species, in the laboratory and in the field (Sweeney 1984). On the winter diet this positive correlation held over 3 temperatures (5°, 9° and 14° C), but at the highest temperature growth rate was reduced. Decreased growth rates at "abnormally high" temperatures have been reported by several authors (Brust 1967, Heiman & Knight, Konstantinov 1958, Nebeker 1973). In this study, the change in response to increased temperature was most probably related to the change in diet. At 9° C and 18° C mean specific growth rates were significantly higher on the spring diet than the winter diet. At 5° C there was little difference between diets, with growth rates in each instance being very low. Growth rates at 14°

C were also similar on both diets. This may indicate that larvae are adapted to an optimum field temperature close to this value. The mean spring/summer field temperature is in fact 13.1° C. The response to temperature and diet at 18° C was most interesting. It would appear that on the winter diet the upper developmental threshold temperature was about 14° C, whilst on the spring diet it was greater than 18° C. It is suggested that at 18° C larvae have a high metabolic rate, independent of diet. On the winter diet the low energy content of the food source was sufficient for larvae to sustain maintenance metabolism but not to promote growth. On the higher quality spring diet there was a sufficiently high energy content to sustain maintenance metabolism and promote near optimum growth, leading to the observed higher growth rate. Presumably at a higher temperature growth rates would again decrease with metabolic rate outstripping the energy content of the food source. This leads to the hypothesis that the upper developmental threshold temperature of a species may be modified by food quality. Reduced growth rates at high temperatures, due to the combination of high maintenance metabolism and a low quality diet, have previously been noted for Trichoptera (Hanson et al. 1983) and Ephemeroptera (Sweeney & Vannote 1978) but not for the Chironomidae.

Past investigations of the effects of temperature on growth have considered the role of acclimation. It is often assumed that individuals of a species, taken from the field, are acclimatized to the temperature range under which they have developed. It could be argued that larvae reared on the winter diet demonstrated a different growth response, compared to larvae on the spring diet, due their acclimation to a lower temperature regime. Larvae reared on the winter diet were taken from the field in early October. The mean daily water temperature for the preceding 4 weeks was 14.11° C, with a range of 11.4-16.8° C. For larvae on the spring diet, collected in late April, the mean daily water temperature for the preceding 4 weeks was 10.73° C, with a range of 7.2-13.8° C. So larvae on the spring diet were, if anything, acclimatized to a low temperature range than those on the winter diet, so that the observed effects are not explainable on this basis.

Mean developmental periods, even at high temperatures and on the spring diet, tended to be longer than expected. From field data, and from past studies of chalk stream chironomids (Mackey 1977, Williams 1981), mean developmental periods of about 40 days at 14° C on the spring diet would have been expected. The unsuitability of conditions in the laboratory is a possible explanation for the extended developmental periods. Stable temperature regimes and photoperiods and reduced oxygen levels may all inhibit growth. This is an aspect in need of further investigation.

Williams (1981) observed a change in gut contents of *E. ilkleyensis*, at about the third instar stage, from a mixture of diatoms and detritus to a preponderance of macrophyte tissue. By the fourth instar stage macrophyte comprised 70-80% of the gut contents. During winter, the quantity of macrophyte in the guts was lower, with a higher proportion of detritus. This was possibly due to the relative unpalatability of older leaves.

At each experimental temperature the growth rates over the third and fourth instar stages were significantly higher on the spring diet supplemented with *R. calcareus*, compared to that without C/N analysis of *R. calcareus* (Tab. 1) indicates the high nutritional quality of this food source, with a C:N ratio for young leaves of 7.38:1 and a N. content of 6.11%. *Eukiefferiella ilkleyensis* would appear to have adapted to take advantage of this readily available resource. A dietary switch late in development has been observed in other macroinvertebrates and may be attributed to a requirement for protein or lipoid to prepare the larvae for pupation or reproduction (Anderson 1976, Hanson et al. 1983).

This study suggests that there is generally faster growth and development on the higher quality food source. This supports work by Bird & Kaushik (1984) who observed highest growth rates of *Ephemerella subvaria* (McDunnough) fed on periphyton as compared with nymphs fed diets of conditioned leaf discs and faecal material. Fuller & Mackay (1981) similarly reported higher growth rates in *Hydropsyche* spp when a detritus diet was supplemented with diatoms.

From the results of this study it is possible to infer how fluctuations in temperature and food quality may influence the population dynamics of *Eukiefferiella ilkleyensis* in the field.

Larval densities of *E. ilkleyensis* exhibit a late spring - early summer period of abundance with numbers rapidly increasing from overwintering levels in mid-April to a maximum density in mid-June. This is followed by a steady drop in numbers, with overwintering levels again being reached by late August (prs. obs.). The spring increase in larval numbers is correlated with increasing water temperature, the spring diatom bloom and the spring increase in macrophyte biomass. It is probable that the spring increase in water temperature and food quality lead to increased larval survivorship, especially at the first instar stage, and to increased rates of growth and development. A combination of these responses would explain the population dynamics of *E. ilkleyensis* recorded from the field.

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