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Interactive effects of diet and thermal regime on growth of the midge *Pseudochironomus richardsoni* Malloch

SUSAN E. GRESENS
Department of Integrative Biology, University of California, Berkeley, CA 94720, U.S.A.

Present address: Department of Biological Sciences, Towson University, Towson, MD 21252, U.S.A.

SUMMARY

1. Larvae of *Pseudochironomus richardsoni* were reared to pupation in individual enclosures, in one of three thermal habitats in a northern California stream. The average temperature range in cold seeps was 15–21 °C, while the main channel ranged from 20 to 27 °C, and side pools ranged from 18 to 33 °C. Diet consisted of either diatoms or algal detritus.
2. Specific growth rate ranged from 0.057 to 0.267 day^{-1}. Specific growth and developmental rates were highest on a diatom diet, and increased with temperature. Regressions of growth rate on mean microsite temperature were also significantly altered by diet. Differences in specific growth rate due to diet are magnified at higher temperatures.
3. Pupae reared on diatoms were larger than those reared on detritus. The mass of pupae reared on detritus decreased with increasing temperature. However, there was no significant relationship between pupal mass and temperature for larvae reared on diatoms.
4. The combined effects of food quality and thermal environment on growth of the midge *P. richardsoni* are significantly different from the independent effects of diet and temperature. Interactive effects of food quality and temperature may influence the contribution of certain aquatic habitats (algal mats) to invertebrate secondary production.

Introduction

Food and temperature are the primary factors determining aquatic insect growth and life history (Sweeney, 1984). Human alteration of watersheds can drastically change both food quality and thermal regime in rivers (Petts, 1989); for example, loss of riparian canopy can raise stream temperatures above the thermal tolerance of salmonids (Barton, Taylor & Biette, 1985; Armour, Duff & Elmore, 1991; Li *et al.*, 1994). In this situation, the direct effect of temperature on top-level consumers is clear. In contrast, population-level responses of primary consumers to changes in thermal and nutritional environment are not well understood.

In order to design research to answer this question, one needs to know whether the effects of temperature on an organism can be predicted without a knowledge of diet, and vice versa. This study demonstrates the existence of interactions between the effects of diet and thermal regime on growth of the midge *Pseudochironomus richardsoni* (Diptera: Chironomidae).

Reports of rapid growth and high production to biomass ratios for midge larvae imply that midge populations have the potential to influence cycling of materials and energy in some lotic systems (Fisher & Gray, 1983; Stites & Benke, 1989). *Pseudochironomus richardsoni* can influence community structure in a

seasonal river: field experiments by Power (1990a) showed that *P. richardsoni* is the herbivore link in a trophic cascade. Although predator control of *P. richardsoni* populations has been demonstrated (Power, Marks & Parker, 1992), the intrinsic limitations to growth and development of *P. richardsoni* under different environmental conditions are unknown.

Larvae of *P. richardsoni* are found in the littoral of lakes and ponds, and the margins of slow-flowing rivers and streams. Gravel or other hard substrates overgrown with algae appear to be preferred habitats (Saether, 1977). In northern California, *P. richardsoni* is multivoltine. Gut contents of larvae include diatoms, green filamentous algae and detritus (Power, 1991).

Materials and methods

The experiment was conducted at the Angelo Coast Range Preserve (Mendocino Co., CA), in Ten Mile Creek, a second-order tributary of the South Fork Eel River. *Pseudochironomus richardsoni* larvae were reared individually in small enclosures in Ten Mile Creek. The experiment employed a 2×3 factorial design: larvae were reared on one of two diets, and in one of three thermal habitats in the creek.

Larval diet consisted of either epiphytic diatoms or algal detritus. Diatoms (primarily *Epithemia* spp. and *Rhopalodia* sp.) were collected from the macroalga *Cladophora glomerata*. Following the growth and decline of macroalgal populations, flocculant detritus becomes abundant in depositional areas during late summer. Microscopic analysis of this detritus shows that grey amorphous material and empty diatom frustules are the dominant constituents (Fig. 1), implying that it is of algal origin. Green and blue-green algae were minor components of both diatom and detritus diets. Green algae were mostly desmids (especially *Scenedesmus*). Blue-green algae included small cocci, and filaments of *Phormidium*, *Lyngbya* and *Calothrix*. A Carlo Erba C N analyser was used to measure the percentage organic content, percentage nitrogen content and the carbon : nitrogen ratio of diatom and detritus diets prepared on three dates. Diatom diet contained an average ($\pm$ 1 SE) of 31.6% (2.68) organic matter and 2.2% (0.15) nitrogen, with a C : N ratio of 6.4 (0.79). Detritus diet averaged 20% (0.29) organic matter and 1.5% (0.06) nitrogen, with a C : N ratio of 5.6 (0.40). Diatom diets contained 58% more organic matter and 47% more nitrogen, on average, than did detritus diets.

Fresh food was collected prior to each feeding, so that all larvae in a diet treatment received food of similar quality. Diatoms were collected by shaking *Cladophora* filaments in a jar, and filtering detached epiphytes through a 64-μm mesh sieve. Detritus diets were prepared by pipetting detritus from depositional areas in the main channel of the creek, where accumulations of the flocculant detritus formed distinct greyish patches. Detrital material was shaken and filtered as above. Filtration removed midge larvae and other macroinvertebrates. Food suspensions were concentrated to a similar degree by decanting excess water. All larvae received 2 ml of the appropriate diet, which was sufficient to maintain food in excess.

To ensure a wide range of mean temperature within the experimental design, three thermal habitats were defined, based on consistent differences in temperature: (i) cold seeps, where groundwater enters the creek; (ii) the main channel; and (iii) shallow, semi-isolated side pools, which become quite warm during the day. *Pseudochironomus richardsoni* larvae occurred naturally in all three habitats.

Individual larvae were housed in enclosures made from plastic jars (4×4.5 cm diameter) with 53-μm mesh windows in the sides and lid. Larvae were initially collected from pools along the margin of Ten Mile Creek, often in *Cladophora* filaments. Under 16× magnification, larvae were gently teased from their retreats and their length was measured with an ocular micrometer. Length measurements were converted to estimates of larval ash-free dry mass (AFDM) using a length-mass regression based on second to fourth instar *P. richardsoni* larvae ($r^2 = 88\%$, $n = 106$, $P = 0.0001$). These larvae were killed by freezing, their lengths were recorded, and AFDM was measured on a microbalance. The regression relationship which gave the best prediction of larval AFDM was:

$$\log (\text{AFDM, mg}) = -5.13993 + 0.49877 \text{ (length, mm)}.$$

Most larvae began the experiment in their third instar, a few in late second or early fourth instars, based on size and degree of sclerotization of the head capsule.

After the initial length measurement, individual larvae were placed in numbered enclosures. Larvae were then randomly assigned to a diet and a thermal habitat (microsite). Twelve individual larvae were reared at each diet × thermal habitat combination. Enclosures were placed in the creek on 5 August 1992,

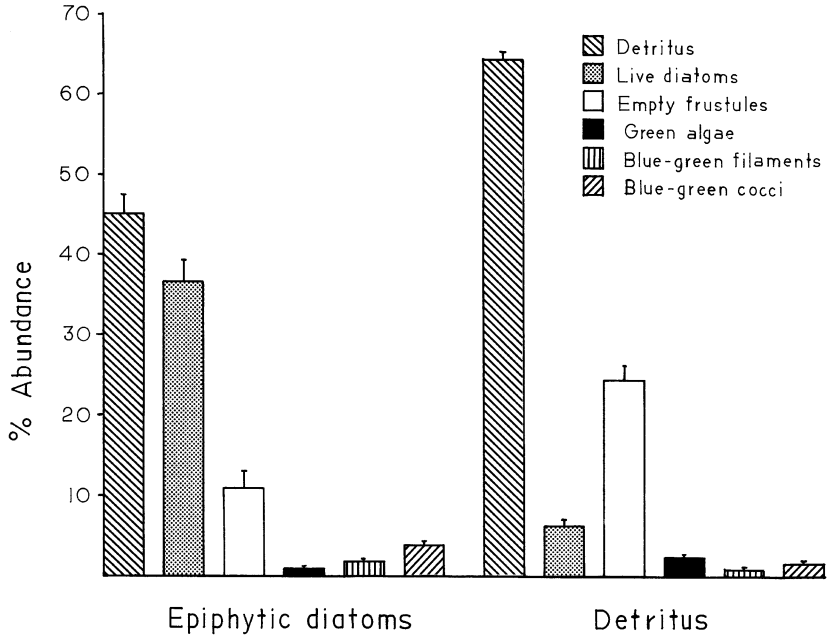

Fig. 1 Percent composition of epiphytic diatom and detritus diets. Diet suspensions were examined in a Palmer-Maloney chamber at 200× magnification. Using a gridded reticule, the identity of diet components was recorded at over 400 grid intersections per sample. Means and standard errors for diets from three different dates are presented.

and larvae were fed and their lengths measured, in the field, every 3–4 days until pupation (the experiment ended on 2 September 1992). At each monitoring interval, all old food was removed, and an excess of fresh food was added. Given the flocculent nature of both diets, the fine mesh enclosures and the slow ambient water velocities, exchange of food particles between the enclosures and the stream was assumed to be insignificant. Water velocities adjacent to the enclosures ranged from undetectable up to 14 cm s^{-1}, although at the majority of microsites, water velocity was less than 3 cm s^{-1}. There was no precipitation during the experiment, and little fluctuation in baseflow.

Temperatures were recorded automatically every 2 h by an Outdoor Weather Logger (EME Systems, Berkeley, CA) using an array of thirty-six thermistors. Each experimental microhabitat was marked by a thermistor, and two midge enclosures (one of each diet). Mean microsite temperature experienced by an individual larva during the course of the experiment was calculated as:

$$2 \times (\text{total degrees recorded})/(\text{total h to pupation}).$$

The pupal stage lasted from 3 to 4 days. The time of pupation could be estimated to the nearest day, because the colour of pupae changed from red to black at a consistent rate (based on laboratory observation). Pupae were collected and frozen until AFDM measurement.

Results

Thermal regimes in cold seeps, side pools and the main channel of Ten Mile Creek were distinctly different. Mean microsite temperatures were estimated as the sum of degree-hours accumulated at a site, divided by the number of hours required for a larva to reach pupation. Mean temperatures (± 1 SE) were: cold seep, 15.9 °C (0.38), main channel, 21.5 °C (0.15), side pool, 24.3 °C (0.44). A Kruskal–Wallis test indicated that there were significant differences in average temperature of each habitat ($P < 0.05$, $n = 60$, $K = 50.2$). Associated tests for multiple comparison of means (Devore, 1982) showed that each habitat had a significantly different (alpha = 0.05) mean temperature.

The most striking pattern was the high diurnal variation in temperature in side pools, compared to cold seep and main channel habitats. Representative daily thermal variation in habitats is presented in Fig. 2. Note that by 6.00 h (dawn) side pools were nearly as cold (mean minimum = 17.6 °C) as cold seeps (mean minimum = 14.9 °C), but by 14.00 h (mid-afternoon) the mean maximum temperature of side pools was 33 °C.

Despite thermal variation and repeated measurement, larval survival was high in all treatments: between 83% and 92% of larvae survived to pupation. The correlation between specific growth rate and pupal AFDM was small ($r = 0.331$, $n = 60$) but significant ($P = 0.01$). Mass-specific growth rate (G) decreased

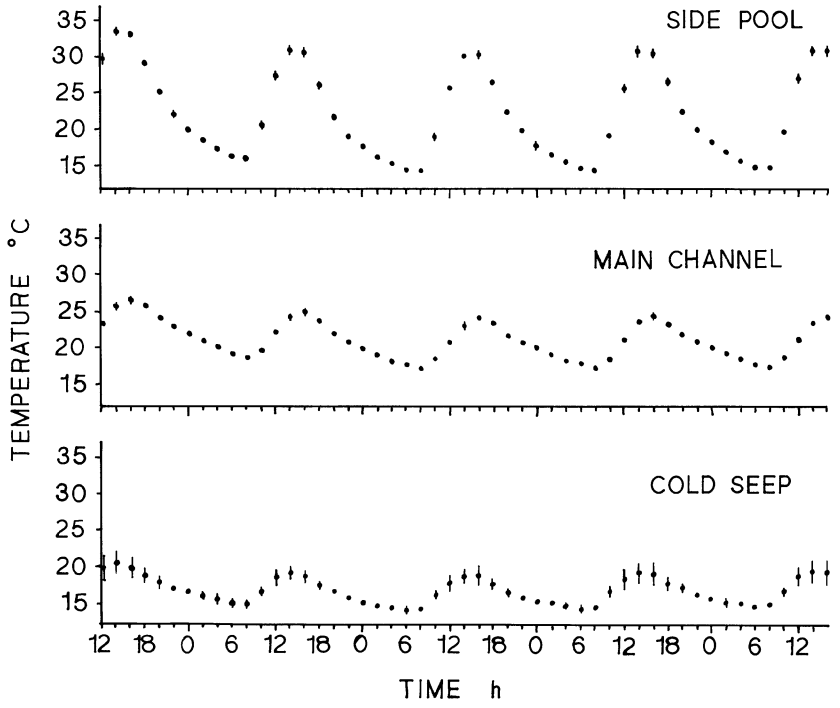

Fig. 2 Representative temperature regimes in three habitats in Ten Mile Creek. Means and standard errors for twelve microsites are plotted. These data were collected from 20–24 August 1992; weather conditions varied little during the experiment.

with larval biomass, following the Gompertz model (Kaufmann, 1981):

$$G = -0.300 - 0.103 \ln(\text{geometric mean biomass}).$$

Because the majority of larvae began the experiment as third instars, growth rate estimates will be biased to lower values, and pertain to fourth instar *P. richardsoni*.

The mass-specific growth rate of larvae during the experiment was estimated according to Kaufmann (1981):

$$G = [\ln(\text{final mass}) - \ln(\text{initial mass})]/(\text{days to pupation})$$

Specific growth rates of larvae were subject to a two-way factorial ANOVA (Table 1a). A significant interaction between diet and habitat effects existed. Therefore, the large main effects of diet and habitat need to be interpreted together.

Is the effect of habitat on growth actually associated with temperature, or with other unknown habitat characteristics? To determine this, regressions of specific growth rate (G) on mean microsite temperature (TEMP), were performed for each diet. Analysis of residuals indicated fit to a linear model. The data and fitted regression lines are shown in Fig. 3. For a diatom diet, growth is predicted by the equation:

Table 1 ANOVA of (a) specific growth rate of larvae, and (b) biomass of pupae

(a) Specific growth rate

Source	d.f.	SS	*F*	*P*
Food	1	0.0532	84.19	0.0001
Habitat	2	0.0617	48.84	0.0001
Food × habitat	2	0.0057	4.54	0.0150
Error	54	0.0341		

(b) Final ash-free dry mass of pupae

Source	d.f.	SS	*F*	*P*
Food	1	0.4578	36.47	0.0001
Habitat	2	0.1761	7.01	0.0020
Food × habitat	2	0.0718	2.86	0.0660
Error	54	0.6778		

$$G = -0.0349 + 0.01025 \text{ (TEMP)},$$
(with $r^2 = 66\%$, $n = 31$, $P = 0.0001$).

For a detritus diet:

$$G = 0.0011 + 0.00546 \text{ (TEMP)},$$
(with $r^2 = 43\%$, $n = 29$, $P = 0.0001$).

For both diets, specific growth rate increased with

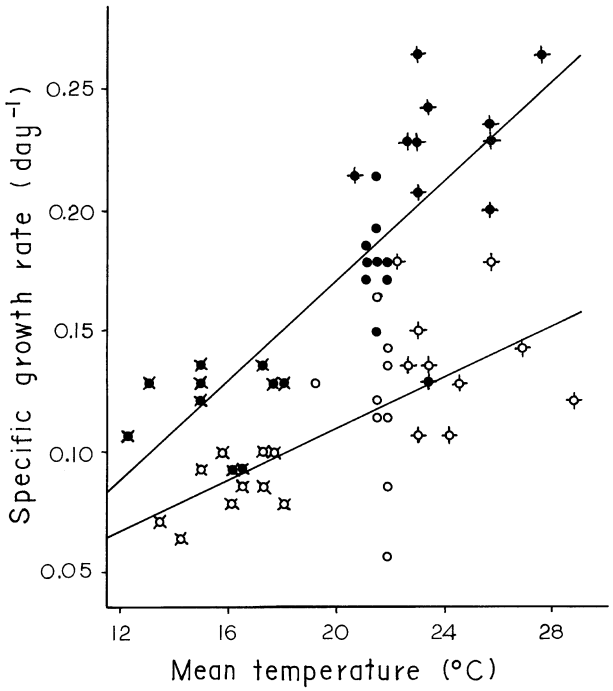

Fig. 3 Average specific growth rate of individual larvae vs. mean microsite temperature. Cold seep microsites are designated by 'circle-with-X', main channel by ● ○, and side pools by 'circle-with-cross'. Closed symbols indicate diatom diet, open symbols indicate detritus diet. Growth rates predicted by linear regression (see text) are plotted for both diets.

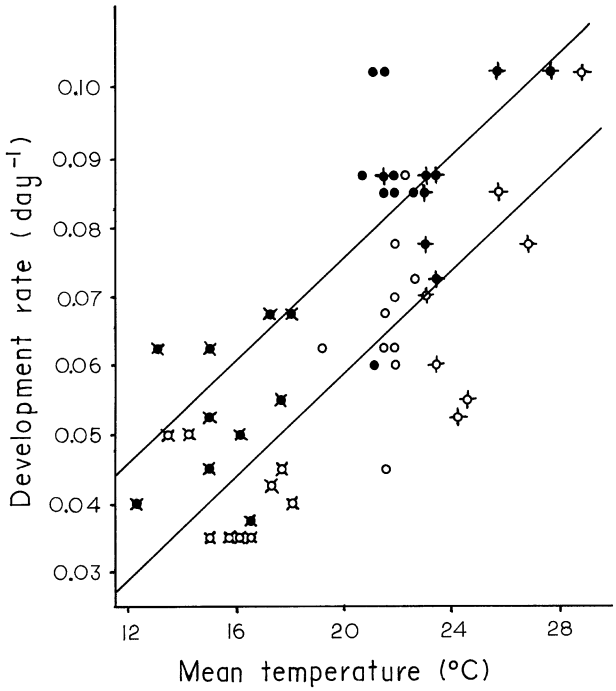

Fig. 4 Developmental rates of larvae, expressed as (days to pupation)$^{-1}$. Symbols as in Fig. 3. Developmental rates predicted by regression (see text) are plotted for both diets.

mean microsite temperature. However, comparison of the slopes of regression lines (Zar, 1984) revealed that a significant interaction between diet and temperature also existed ($t = 2.004$, $0.01 < P < 0.025$). Therefore, the difference in growth rates on the two diets increased with mean temperature.

The rate of development of larvae was expressed as (days required to reach pupation)$^{-1}$. Despite some variation in initial age/size of larvae, developmental rate was highly correlated with specific growth rate ($r = 0.728$, $P = 0.0001$), but not with pupal mass ($r = -0.113$, $P = 0.392$). For both diets, linear regressions adequately described the relation between developmental rate (DEV) and mean temperature (Fig. 4). For a diatom diet:

$$\text{DEV} = -0.00145 + 0.003814\ (\text{TEMP}),$$
$$(\text{with } r^2 = 62\%,\ n = 31,\ P = 0.0001).$$

For a detritus diet:

$$\text{DEV} = -0.01592 + 0.003673\ (\text{TEMP}),$$
$$(\text{with } r^2 = 62\%,\ n = 29,\ P = 0.0001).$$

Comparison of these regression lines showed that the slopes were not significantly different ($t = 0.178$, $P > 0.50$). Developmental rates for diatom diets were significantly greater than rates on detritus diets ($t = 5.795$, $P < 0.001$). Mean development rate was 0.0768 day^{-1} for diatom diets and 0.0602 day^{-1} for detritus diets.

Pupal AFDM showed significant responses to both diet and thermal habitat (Table 1b). A greater portion of total variation was related to diet than to habitat. The interaction of these factors was marginally significant, $P = 0.066$. A diatom diet produced larger pupae than did a detritus diet (Fig. 5). Within the detritus diet, average pupal mass consistently decreased across habitats with increasing mean temperature, from 0.450 mg AFDM in cold seeps to 0.352 mg in side pools. This negative relationship was not evident within the diatom diet: pupae from the main channel were smaller on average (0.454 mg) than pupae from cold seeps (0.647 mg), but pupae from warm side pools were larger than expected (0.598 mg). Scheffe's test for multiple comparison of thermal habitat means, averaged across diet, indicated that pupae reared in cold seeps were significantly larger than those from the main channel. However, mean pupal AFDM of

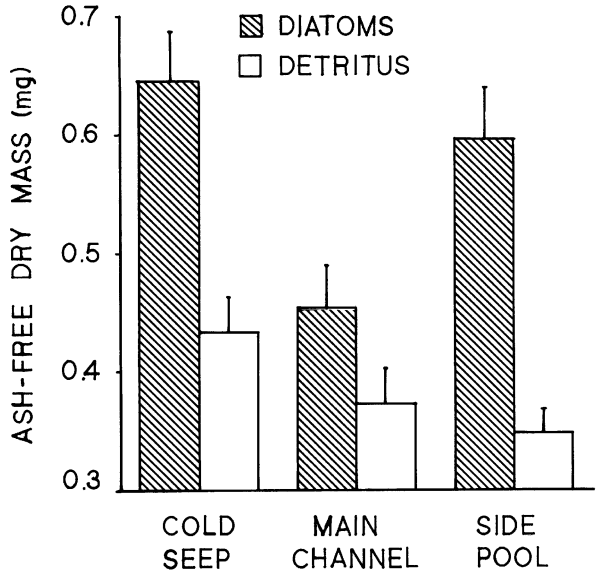

Fig. 5 Means and standard errors of final ash-free dry mass (AFDM) of pupae, grouped by diet and thermal habitat.

side pools was not significantly different from that of other habitats.

Mean temperature does not predict pupal mass as well as it predicts growth and development rates. For detritus diets, a linear relation between mean temperature and pupal AFDM was indicated by the regression:

$$\text{AFDM} = 0.6216 - 0.0110\ (\text{TEMP}),$$
$$(\text{with } r^2 = 21.5\%,\ n = 29,\ P = 0.0113).$$

For the diatom diet, in contrast, regression of pupal AFDM on temperature was not significant ($P = 0.219$). More importantly, a linear model was unacceptable: residual analysis suggested a non-linear trend in the data, corresponding to the distribution of mean AFDM in Fig. 5. Thus, larval diet determines whether or not pupal mass exhibits a simple response to temperature.

Discussion

Relatively few studies have measured *in-situ* growth rates of lotic midges. Specific growth rates of *P. richardsoni* larvae ranged from 0.057 day^{-1} to 0.267 day^{-1}. This overlaps the range of midge growth rates reported from a forested stream (Huryn & Wallace, 1986), and a desert stream (Fisher & Gray, 1983). Hauer & Benke (1991) found much higher growth rates (up to 0.60 day^{-1}) for chironomids in a high-order blackwater river. Because in this study growth rates were averaged over approximately the fourth instar, the measurements of G underestimate the growth rate of earlier instars.

In a field study, it is difficult conclusively to isolate one environmental factor, such as temperature, from all other unknown habitat features. Nevertheless, mean microsite temperature was a statistically significant predictor of specific growth and development rates of larvae in Ten Mile Creek.

For *P. richardsoni*, the observed interaction of diet and temperature effects means that differences in larval growth rates due to diet will be magnified at higher temperatures. At 14 °C, regression models predict $G = 0.109$ day^{-1} on a diatom diet, and $G = 0.078$ day^{-1} on detritus. At 28 °C the predicted growth rate on diatoms is $G = 0.252$ day^{-1}, while $G = 0.154$ day^{-1} on detritus. The difference in predicted growth rates at 28 °C is over three times greater than the difference at 14 °C. At low temperature, growth may simply be limited by low metabolic rates, while at higher temperatures, nutritional inadequacy may become the dominant limitation to growth.

The relative quality of diatom vs. detritus diets should gradually change over time. Temperature should accelerate this process through its effects on microbial metabolism. Heterotrophic bacteria will metabolize labile organic compounds, leaving their own biomass plus refractory detritus for midges to consume. In contrast, autotrophic diatoms would continue to produce new organic matter, so that a 'diatom diet' should retain higher quality than detritus, especially at elevated temperatures. Enclosures receiving diatom diet often had noticeable growths of *Epithemia* on the inside walls, suggesting that diatoms were continuing to grow.

Review of other studies of diet and temperature effects on aquatic insects suggests that interaction between these factors may be common. Most studies did not test directly for interaction effects (as in an ANOVA design). However, if comparison of means showed that significant differences in response to temperature depended on diet, the present study assumed that interactive effects may have existed. Diet × temperature interactions influenced the growth rates of mayflies offered diatoms or detritus (Sweeney & Vannote, 1984; Sweeney, Vannote & Dodds, 1986; Rousillon, 1988), tipulids feeding on leaf detritus (Vannote & Sweeney, 1985) and midges grazing periphyton (Storey, 1987). Larvae of *Eukiefferiella ilkleyensis* exhibited optimal growth at 14 °C; at this temperature,

diet quality had little impact on midge growth (Storey, 1987). A detritus-rich diet supported poor survival and growth at temperatures above and below optimum. Performance of larvae on a diatom-rich diet was superior, and much less responsive to temperature. The energy content of detrital diets may have been insufficient to support rapid larval metabolism at warmer temperatures (Storey, 1987), but other factors apparently limited the ability of midges to utilize detritus at cold temperatures.

Diet × temperature interactions are not universal, however. Neither this study, nor others, reported interaction effects on development rates of insects. Ward & Cummins (1979) found that interaction effects on midge growth were not significant. Growth of midge larvae was associated with bacterial biomass and respiration on different types of detritus. This result would be expected if larvae are primarily assimilating bacterial biomass, and not the detrital substrate.

Adult size, and fecundity, of hemimetabolous aquatic insects decreases both above and below a thermal optimum (Sweeney & Vannote, 1978). It is not clear whether this pattern characterizes holometabolous groups, such as chironomids (Mackey, 1977; Rempel & Carter, 1987), where size decreases with increasing temperature. Adult size was not associated with fecundity of midges reared under different thermal regimes (Rempel & Carter, 1987).

Diet determined whether or not there was a significant association between pupal size of *P. richardsoni* and temperature. The AFDM of pupae reared on detritus showed a negative linear regression on mean temperature. In contrast, the size of pupae reared on diatoms did not show a linear relation to mean temperature, but there was evidence that a more complex relation might exist (at high temperatures, pupae were larger than expected).

For larvae feeding on diatoms, thermal regime may be a better predictor of pupal mass than mean temperature. Side pool habitats exhibited a much larger absolute variation in daily temperature (Fig. 2) than did the other habitats. Considerable research shows that insects reared under fluctuating temperature regimes have increased growth and development rates, compared to constant mean temperature (Huffaker, 1944; Hagstrum & Hagstrum, 1970). Different metabolic and developmental processes within an insect may have different temperature optima (Huffaker, 1944; Sweeney & Vannote, 1978). Fluctuating temperatures may help to integrate these processes, and allow for increased growth and performance of an insect (Huffaker, 1944), providing that nutrition is adequate. Growth and development of aquatic insects were predicted better by maximum temperature, rather than mean temperature (Sweeney & Schnack, 1977; Sweeney, 1978). For *P. richardsoni*, the correlations of specific growth rate with mean temperature ($r = 0.577$) and with maximum temperature ($r = 0.603$) are similar. Likewise, the association of development rate with maximum temperature ($r = 0.657$) was no greater than the correlation of development with average temperature ($r = 0.704$).

A review of experimental studies (Atkinson, 1994) concluded that in 83% of cases, temperature and organism size at maturity showed a negative relationship. Berrigan & Charnov (1994) noted that temperature and food quality have very different effects on age and size at maturity. However, neither study considered that food quality might alter the effects of temperature on life history characteristics. The relationship between adult size and fecundity within a species may also depend on food quality (Sweeney *et al*., 1986; Rousillon, 1988).

Streams and rivers which receive considerable sunlight should exhibit high local variability in both temperature and food quality. Absorption of solar energy directly increases both diel and microspatial thermal variation, especially in small streams (Wiley, Osborne & Larimore, 1990), or in the shallow margins of larger ones. Solar energy can also indirectly increase thermal variation by stimulating growth of plants. Dense patches of macrophytes or macroalgae trap solar energy as heat and create local 'hot spots', where fluctuating temperatures prevail (Dale & Gillespie, 1977; Power, 1990b).

Reduction of canopy cover also increases variation in food resource quality, by increasing the availability of live algae and algal detritus, relative to vascular plant detritus (Hawkins & Sedell, 1981; Bilby & Bisson, 1992; Tait *et al*., 1994). Primary consumers assimilate algae and algal detritus more efficiently than vascular plant detritus (Mann, 1988).

The results of this study suggest that such small-scale food and temperature variation within a stream may effect the dynamics of some invertebrate populations. Spatial variation in temperature and food will limit the distribution of species with strict microhabitat requirements. Among primary consumers that occupy

a variety of stream micro-habitats, the effects of diet and temperature on growth and development should reduce the synchrony of cohorts in multivoltine species.

Interactive effects of food quality and temperature on insect growth and size may also magnify the contribution of certain habitats to secondary production. Power (1990b) proposed that floating algal mats are important in channelling aquatic insect production to terrestrial vs. aquatic predators. Algal mats provide midge larvae a refuge from fish predation, compared to benthic algal turf habitats. Algal mats were also warmer than benthic turfs, and had higher insect emergence rates than mats, over a 2-day period (Power, 1990b). The high growth rates and large size of *P. richardsoni* larvae fed diatoms in side pool habitats probably reflect those of *Pseudochironomus* larvae in floating mats (another diatom-rich habitat, with warm, fluctuating temperatures). If midges from mat-like habitats not only grow more rapidly, but are also more fecund, they are more likely to influence the dynamics of other consumer and producer populations, both in the river and its watershed, as hypothesized by Power (1990b).

This experiment demonstrates that food quality significantly influences the pattern of growth of chironomid larvae in different thermal habitats. In natural aquatic habitats, thermal regime and food quality are often linked. Therefore, interactive effects should be considered in the design of field studies which assess the effects of temperature or diet on the growth of aquatic insect populations.

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