Effects of Temperature and Food Quality on Growth and Development of a Mayfly, *Leptophlebia intermedia*

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Larval development, adult size, and fecundity of *Leptophlebia intermedia* were assessed in response to rearing on five diets (hickory, white ash, red oak, chestnut oak, and American beech leaves) at each of three temperature regimes (ambient White Clay Creek temperatures (WCC) and 3 and 6°C above WCC). Developmental time was shortened about 40−50 d by elevating creek temperatures 6°C, but varied only about 20−30 d over the range of diets for any given temperature. Adult size was influenced more by diet than temperature. Adult female weights differed among diets by about 1.5 mg for any given temperature regime. In contrast, female weights varied by only about 0.6 mg among temperatures for any given diet. The proportion of total female weight allocated to eggs increased with adult size and ranged from 0.12 to 0.45 depending on diet and temperature. In general, hickory and white ash diets consistently yielded the highest survival and largest adults, while the highest mortality and poorest growth occurred on the red oak and American beech diets.

On a évalué la réaction de *Leptophlebia intermedia* du point de vue du développement des larves, de la taille des adultes et de la fécondité en soumettant cette espèce à cinq régimes alimentaires différents (feuilles de caryer, de frêne d'Amérique, de chêne rouge, de chêne châtaignier et de hêtre à grandes feuilles) à chacun des trois régimes de température (températures ambiantes du ruisseau White Clay (RWC) et températures de 3 et 6°C supérieurs à celles du RWC). Le temps de croissance a été réduit de 40 à 50 jours en élevant la température du ruisseau de 6°C mais n'a varié que de 20 à 30 jours environ pour toute la gamme de régimes alimentaires à n'importe quelle température. Le régime alimentaire a influé davantage sur la taille des adultes que la température. Le poids des femelles adultes différait selon le régime alimentaire de 1,5 mg environ pour tout régime de température donné. Par contre, le poids des femelles n'a varié que de 0,6 mg environ en fonction de la température pour tout régime alimentaire donné. La partie du poids total des femelles consacrée à la formation des oeufs a augmenté proportionnellement à la taille des adultes et a varié de 0,12 à 0,45 selon le régime alimentaire et la température. De façon générale, le taux de survie a été plus élevé et les adultes étaient plus gros lorsque le régime alimentaire était constitué de feuilles de caryer ou de frêne d'Amérique, tandis que le taux de mortalité était plus élevé et la croissance plus faible avec les feuilles de chêne rouge ou de hêtre à grandes feuilles.

The seasonal pattern of temperature and nutritive value of food significantly affects the life history characteristics of a variety of aquatic insect species (see Sweeney 1984 for review). It is difficult, however, to design experiments to adequately test the relative importance of these two factors because temperature can affect the growth and development of insect larvae both directly, through metabolic processes, and indirectly, by affecting the quantity or quality of food. Thus, most studies have focused on either temperature or food as an experimental variable, and the interaction of these two factors has only been tested to a limited extent on a few shredder and collector species (e.g. Anderson and Cummins 1979; Ward and Cummins 1979).

For aquatic detritivores, studies of food quality have largely involved rearing larvae for various lengths of time on different species of deciduous leaves (Wallace et al. 1970; Iversen 1974; Otto 1974; Grafius and Anderson 1979; Anderson and Sedell 1979). Leaf species often differ from one another in terms of biochemical composition (i.e. proportions by weight of lipids, fats, and carbohydrates) and associated microflora (i.e. quantity and quality of colonizing bacteria and fungi), both of which affect the nutritive quality of the leaves. Larval feeding and growth rates often vary significantly with the species of leaf provided as food (Cummins et al. 1973; Iversen 1974; Otto 1974; Anderson and Cummins 1979).

This paper focuses on the relative importance of temperature and nutrition to certain life history characteristics of *Leptophlebia intermedia* (Traver), a leaf-shredding mayfly. We assessed development, size, and fecundity of larvae reared on five diets (i.e. hickory, white ash, red oak, chestnut oak, and American beech leaves) at each of three temperature regimes: ambient White Clay Creek temperature (WCC) and when WCC was increased constantly by 3 and 6°C.

Materials and Methods

Test Species

Leptophlebia intermedia occurs in slow flow areas of small to intermediate streams in the eastern and southeastern region of the United States (Berner 1950, 1975). The species seems to

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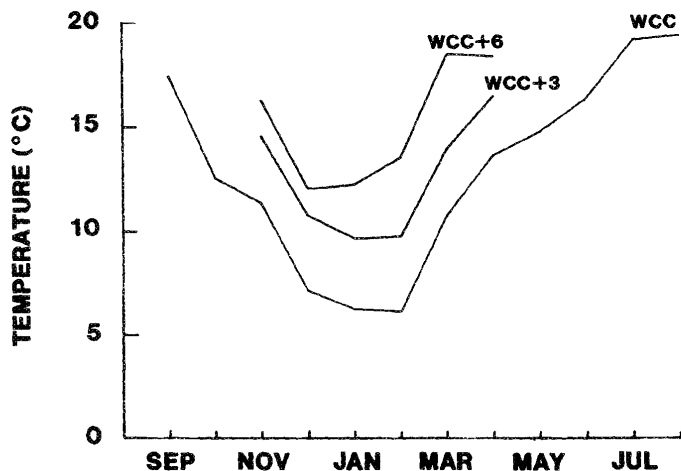*Can. J. Fish. Aquat. Sci., Vol. 43, 1986*

FIG. 1. Mean monthly temperatures for each of the three experimental regimes used for rearing experiments on *Leptophlebia intermedia*.

be univoltine throughout its range, with adult emergence occurring from early February in the south to late March in the north. In White Clay Creek, larvae are often found in accumulations of deciduous leaves. Although we have no direct evidence that *L. intermedia* larvae actually shred leaves in the field, we have observed it directly (visual) and indirectly (large quantities of fecal pellets in trays containing only larvae and leaves) in the laboratory. We have not attempted to determine whether *L. intermedia* prefers certain particle sizes of leaves. Larvae probably also ingest algae (diatoms) and fungi associated with the leaves in the field. The overall ecology and life history appears similar to congeneric species occurring in North America (*L. cupida* (Say): Clifford 1969, 1970a, 1970b; Clifford et al. 1978) and Europe (*L. vespertina* (L.) and *L. marginata* (L.): Brittain 1972, 1976). In White Clay Creek, larvae apparently hatch from eggs in late August and emerge as adults in late March.

Larval Growth and Adult Emergence

Larvae were collected on December 31 from first- and second-order tributaries of White Clay Creek in Londonderry township, Chester County, Pennsylvania (39°51'47"N; 75°47'07"W). They were divided into groups of 150 individuals, and each group was placed into a separate flow-through tray (23 × 45 × 22 cm deep) for rearing. One group of larvae was reared on each of the following diets at each temperature regime: American beech (*Fragus grandifolia*), chestnut oak (*Quercus prinus*), red oak (*Quercus rubra*), hickory (*Carya ovata* and *C. ovalis*), and white ash (*Fraxinus americana*). These species were carefully chosen to represent a nutritional gradient ranging from poor to good in White Clay Creek (Sweeney and Vannote 1985; Vannote and Sweeney 1985). There were three temperature regimes (Fig. 1): (i) ambient White Clay Creek temperatures (WCC); (ii) White Clay Creek warmed about 3°C (WCC + 3°C); and (iii) White Clay Creek warmed about 6°C (WCC + 6°C).

The average size of larvae at the start of the experiment was estimated by killing and dry weighing (60°C, 48 h) 100 larvae that were collected at the same time and location as the experimental larvae. Larvae were slightly less than half grown when collected on December 31 and none showed any signs of matu-

rity (e.g. well-developed wing pads). Larvae were reared in the trays until metamorphosis. During the emergence period, subimagoes were collected daily beneath netting that was fastened tightly over each tray. Male subimagoes were killed and dry weighed. Female subimagoes (hereafter called adults) were frozen immediately and subsequently dissected to determine fecundity (see Materials and Methods).

For each temperature regime, water was pumped to the rearing trays from a separate 800-L reservoir. The diel and seasonal cycle of temperature in the creek was reproduced in the laboratory by constantly pumping creek water through Pyrex® heat exchange coils submerged in each reservoir. Aquarium heaters were used to add the 3 and 6°C of heat needed to produce the WCC + 3°C and WCC + 6°C thermal regimes. The water in each reservoir was replaced weekly with fresh stream water.

At the start of the experiment, leaves were soaked in stream water for 1 wk at 20°C and then in the rearing trays for 1 wk before adding the larvae. During the study, leaves were kept in aerated 120-L reservoirs with stream water (changed twice a week) and periodically added to trays to keep food levels nonlimiting.

Protein levels associated with each leaf diet were measured in the three thermal regimes. Each leaf type was placed into a separate mesh bag and submerged for 6 wk in each reservoir. Leaves were then removed, dried, and ground in a Wiley mill. The amount of protein was determined using the method of Lowry et al. (1951). We emphasized protein levels among diets because protein is the principal component of aquatic insect eggs which contribute greatly to the weight of mature females (Harvey et al. 1979; unpubl. data).

Fecundity

The eggs were removed, placed on a preweighed glass coverslip, dried for 48 h at 60°C, and the mass (milligrams) determined by reweighing the coverslip with attached eggs. A dry mass was also obtained on each female body after removing the eggs. The total mass of each female was estimated by summing the egg and body masses.

The number of eggs per female was estimated from egg mass with the following equation: $Y = 7.934 + 1192.2\ (X)$, where Y = number of eggs and X = mass of eggs (milligrams) ($r^2 = 0.98$). This relationship was derived by removing eggs from 10 females (two chosen at random from each of the five diets), counting out various quantities of eggs for each female (i.e. 25−1200 in increments of about 50), and obtaining the dry mass of each quantity.

Mean reproductive effort of females was estimated as described by Tinkle and Hadley (1975). Reproductive effort in this context refers to the ratio of egg biomass to total female biomass (including eggs).

Results and Discussion

Larval Mortality

Mortality during the experiment tended to be higher on leaf species that produced small adults (chestnut oak, red oak, and American beech) and lower on diets yielding large adults (hickory and white ash) for all temperature regimes (Table 1). Mortality also seemed to decrease with increased temperature on diets producing large adults (hickory and white ash) and

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TABLE 1. Adult size, reproductive potential, and emergence of *Leptophlebia intermeida* reared on five leaf diets at three experimental HI = hickory, WA = white ash, RO = red oak, CO = chestnut oak, AB = American beech.

| Temperature regime | Leaf diet | Adult dry weight (mg) | | | | | | | | No. of eggs per female | | | |
| | | Male | | | | Female | | | | | | | |
		n	$\bar{x}$	SD	Range	n	$\bar{x}$	SD	Range	n	$\bar{x}$	SD	Range
WCC	HI	14	1.90	0.47	1.29−2.65	16	3.70	1.14	1.34−5.22	12	1064	471	28−1507
	WA	17	2.51	0.42	1.52−3.07	11	3.27	0.90	2.10−4.89	6	831	480	469−1388
	RO	11	1.37	0.17	1.09−1.68	6	1.69	0.51	1.22−2.66	3	272	470	0−815
	CO	18	1.48	0.34	0.79−2.13	17	1.82	0.50	1.22−2.14	9	223	188	0−553
	AB	12	1.36	0.14	1.18−1.65	8	1.63	0.41	1.07−2.18	6	212	156	0−410
WCC + 3°C	HI	40	2.01	0.34	1.37−2.92	34	3.23	0.90	1.93−5.29	26	939	474	159−1996
	WA	27	2.30	0.63	1.13−3.42	27	3.91	1.09	2.22−6.04	22	1079	588	183−2265
	RO	11	1.55	0.37	1.12−2.38	6	1.92	0.96	1.14−3.46	3	732	312	446−1066
	CO	11	1.73	0.36	1.03−2.34	12	3.11	1.14	1.77−5.77	11	787	613	0−2163
	AB	6	1.66	0.35	1.32−2.06	6	2.67	1.31	1.38−5.00	6	641	733	0−1996
WCC + 6°C	HI	24	2.06	0.40	1.55−2.88	34	2.61	0.52	1.60−3.80	28	479	349	3−1412
	WA	12	2.31	0.45	1.35−2.78	25	3.80	1.16	1.92−6.55	21	1329	643	116−2748
	RO	5	1.47	0.13	1.27−1.58	5	2.84	1.18	1.39−4.16	4	865	742	1−1531
	CO	4	1.66	0.39	1.43−2.23	6	2.65	1.28	1.59−4.84	5	774	775	0−1948
	AB	2	1.17	0.23	0.99−1.34	2	2.04	0.57	1.64−2.44	1	307	—	307

increase with temperature on diets producing small adults (red oak, chestnut oak, and American beech). There was, however, no statistical correlation between daily mortality rate and either larval growth rate, adult size, or developmental time.

Larval Development

The amount of time needed to complete larval growth (i.e. developmental time) was affected significantly by both temperature and diet. Larvae of both sexes completed development and emerged as adults earlier from the WCC + 3°C and WCC + 6°C regimes relative to WCC (Table 1). For example, females completed development 38−54 d earlier (depending on diet) at WCC + 6°C than at ambient WCC. Mean developmental time of both sexes significantly decreased with increased temperature for the hickory, white ash, chestnut oak, and American beech diets (ANOVA, Scheffe test, $p <$ 0.05; see Table 2). Mean developmental time for larvae on the red oak diet was statistically the same for the ambient WCC and WCC + 3°C regimes but significantly shorter for WCC + 6°C (ANOVA, Scheffe test, $p < 0.05$). Results from a two-way ANOVA comparing all diets and temperatures revealed no significant interaction of temperature and diet on mean developmental time.

A significant diet effect was observed for mean developmental time at each of the three temperature regimes (ANOVA, $p < 0.05$). The only consistent pattern, however, was the significantly shorter mean development time for hickory and/or white ash relative to the other diets (Scheffe test; Table 3). In general, the response of developmental time to diet was substantially less than the response to temperature, even though temperature regimes differed by 6°C or less and the range of diets was deliberately chosen to include a gradient from good to poor in terms of overall nutrition or growth response. For example, the fastest and slowest median developmental time differed on the average by about 37% among diets for a given temperature regime. In comparison, the fastest and slowest median developmental time differed on the average by about

TABLE 2. Results of Scheffe multiple range tests used to compare the relative effects of temperature within a given diet on developmental time, adult biomass, and fecundity for *Leptophlebia intermedia*. Although each leaf diet was tested separately, diets are presented together when the results were identical. Temperature regimes connected by solid lines did not differ significantly for the parameter being tested. The broken line connects two temperatures that did not differ significantly but could not be presented in adjacent columns. a = insufficient data for statistical comparison.

| Leaf diets | Temperature regime | | |
	WCC	WCC + 3°C	WCC + 6°C
	Developmental time (females)		
HI, WA, CO	—————	—————	—————
RO	—————	—————	—————
AB	—————	—————	a
	Developmental time (males)		
HI, WA, RO, CO	—————	—————	—————
AB	—————	—————	a
	Adult female biomass (mg)		
HI	—————	—————	—————
WA, RO	—————————————————		
CO	—————————————————		
AB	—————	—————	a
	Adult male biomass (mg)		
HI, WA, RO, CO	—————————————————		
AB	—————	—————	a
	Fecundity		
HI	—————	—————	—————
WA, RO, CO	—————————————————		
AB	—————	—————	a

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temperatures, beginning January 2 (initial larval size: $\bar{x} = 2.61$, SD $= 1.03$, range $= 0.50-5.95$).

| Mean reproductive effort | | | | Larval mortality (%) | Developmental time | | | | | |
| | | | | | Days to first adult | | Days to median adult | | Mean | |
n	$\bar{x}$	SD	Range		Male	Female	Male	Female	Male	Female
12	0.21	0.07	0.02−0.27	80	77	83	92	97	94	96
6	0.17	0.08	0.08−0.25	81	58	92	92	97	88	102
1	0.26	—	0.26	88	83	97	118	118	118	119
7	0.11	0.05	0.05−0.18	77	97	92	112	115	113	114
5	0.12	0.05	0.06−0.18	85	92	97	118	115	114	114
23	0.21	0.07	0.07−0.32	50	54	55	77	71	74	74
20	0.21	0.06	0.07−0.30	64	54	50	70	73	73	77
3	0.22	0.04	0.18−0.26	88	90	81	103	102	103	101
10	0.21	0.07	0.12−0.32	84	77	85	90	97	95	96
4	0.22	0.10	0.10−0.34	92	85	55	90	9?	93	90
4	0.22	0.03	0.20−0.27	61	43	45	55	55	54	57
7	0.31	0.03	0.26−0.35	75	43	43	50	50	53	51
2	0.31	0.03	0.29−0.33	93	59	44	69	59	70	68
3	0.26	0.09	0.16−0.34	93	56	43	69	63	70	66
—	—	—	—	97	69	43	69	43	81	44

71% among temperature regimes for a given diet. This suggests that the rate of larval development was determined largely by the seasonal pattern and magnitude of temperatures, with diet playing a modifying role.

Adult Size

The white ash and hickory diets generally produced larger male and female adults than other diets within each thermal regime (Table 1). At WCC, female adults from the white ash and hickory diets were about the same size and significantly larger than adults reared on the other diets (Table 3). The only significant differences for adult weights among diets at higher temperatures was between white ash and red oak at WCC + 3°C and white ash and hickory at WCC + 6°C. Adult males reared on white ash leaves were significantly larger than males reared on chestnut oak or red oak leaves at all temperatures, and also larger than males reared on hickory and American beech leaves at WCC. No significant differences were observed for the size of males reared on the American beech, chestnut oak, and red oak diets at any temperature. Thus, male and female adults reared on chestnut oak, red oak, and American beech leaves were about the same size at all temperatures and were generally the smallest adults produced during the experiment.

Male and female weights were significantly larger at WCC relative to WCC + 3°C when the data were combined for all diets (ANOVA, $p < 0.05$). The effects of temperature, however, varied greatly among males and females and from diet to diet. For example, female weights significantly decreased with increased temperatures for hickory leaves but significantly increased with temperatures for all other diets (Table 2). Although males reared on hickory, white ash, red oak, and chestnut oak seemed to increase in weight from ambient WCC to WCC + 3°C and then decrease at WCC + 6°C, the differences were not significant. Adult males reared on American beech were significantly larger at WCC + 3°C relative to WCC.

The data suggest that both temperature and diet can significantly affect adult size of L. intermedia. For females, a two-way ANOVA revealed that temperature and diet interact significantly in producing the observed changes in adult size. However, no significant interaction was observed for the males.

Fecundity

We expected a priori that fecundity would exhibit the same response pattern to temperature and diet as adult weight because of the obvious correlation between the two parameters. Although both fecundity and female size generally decreased with increased tempeature for all diets except hickory, the levels of significance of these patterns often differed for the two parameters. For example, adult females from the white ash diet were significantly heavier than females from most of the other diets at all temperatures. Fecundity levels for females reared on white ash, however, were not significantly different from any other diet at WCC + 3°C as well as most other diets at WCC (except chestnut oak and American beech) and WCC + 6°C (except hickory). Similarly, fecundity levels for the chestnut oak diet did not vary significantly among any of the temperature regimes, even though significant differences were observed for female size (Table 2).

The observed differences in the response of adult size and fecundity to temperature and/or diet are undoubtedly related to changes in the relationship between fecundity and size for each experimental population (Table 1; Table 4 contains the specific equations). A comparison of the slopes for regressions relating egg number and adult female biomass indicated significant differences among diets only for the WCC regime (ANCOVA, $p < 0.05$). A similar analysis revealed significant temperature effects on regression slopes only for the chestnut oak diet (ANCOVA, $p < 0.05$). The underlying factors causing the changes in the slopes of these regressions are unknown. We did not attempt to measure differences in mean egg size or egg mass for females from the different treatments.

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TABLE 3. Results of Scheffe multiple range tests used to compare the relative effects of diet within a given temperature regime on developmental time, adult biomass, and fecundity for *Leptophlebia intermedia*. Diets connected by a solid line did not differ significantly for the parameter being tested. The broken line connects two diets that did not differ significantly but could not be presented in adjacent columns. a = insufficient data for statistical comparison.

Temperature regime	Leaf diets				

Developmental time (females)

Temperature regime	HI	WA	AB	RO	CO
WCC					
WCC + 3°C					
WCC + 6°C			a		

Developmental time (males)

Temperature regime	HI	WA	CO	RO	AB
WCC					
WCC + 3°C					
WCC + 6°C					a

Adult female biomass (mg)

Temperature regime	WA	HI	AB	CO	RO
WCC					
WCC + 3°C					
WCC + 6°C			a / a		

Adult male biomass (mg)

Temperature regime	WA	HI	AB	CO	RO
WCC					
WCC + 3°C					
WCC + 6°C			a		

Fecundity

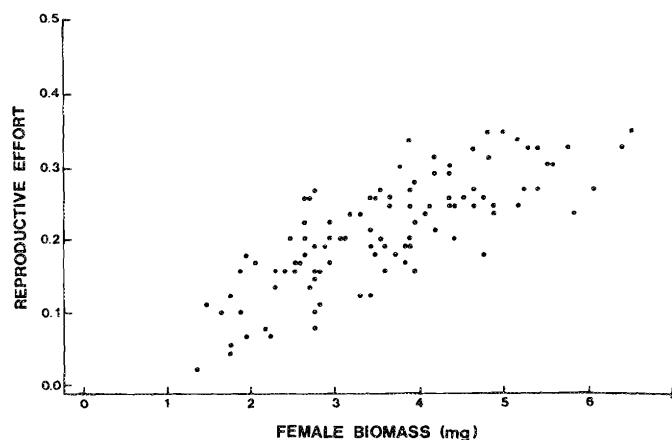| Temperature regime	HI	WA	RO	CO	AB
WCC					
WCC + 3°C					
WCC + 6°C					a

FIG. 2. Reproductive effort of *Leptophlebia intermedia* (total egg biomass/total adult female biomass including eggs) versus adult female biomass.

white ash, which consistently resulted in the highest survival and best overall larval growth regardless of temperature, seemed to provide superior nutrition to larvae relative to the other leaf diets. In contrast, the consistently high mortality and poor larval growth associated with red oak and American beech diets suggest a low nutritive quality. Protein levels were substantially higher for hickory and white ash relative to other diets but protein levels were not checked throughout the experiment and we do not know what proportion of the protein was associated with live (microbes) versus dead (leaf) biomass.

It is unclear whether diet is generally more important than temperature with respect to larval growth and adult size of *L. intermedia*. In these experiments, five diets were deliberately chosen to represent a nutritional range from poor to good (based on laboratory results on other aquatic species). Our design, however, did not include a range of temperature regimes from lower lethal to upper lethal for comparison. Our experimental temperature regimes differed at most by only 6°C (e.g. WCC vs. WCC + 6°C) but the actual temperatures when larvae did most of their growth probably differed by less than 6°C. For example, adding 6°C in midwinter to natural stream temperatures caused larvae to resume growth and emerge about 7 wk earlier than normal. At natural winter temperatures, larvae are in a facultative diapause and do not grow; growth resumes only after temperatures rise to about 10°C. In the WCC regime, larvae did most of their growth several weeks later than larvae in the WCC + 6°C regime but probably at comparable temperatures. Thus, the experimental design was biased towards evaluating the absolute effect of diet (not temperature) on larval growth and adult size and fecundity of *L. intermedia*.

The results of this experiment strongly suggest that (i) temperature is the principal factor determining the overall length of the larval growth period and (ii) the ultimate size that a given larva attains (i.e. adult size) depends on how fast and efficiently it can grow in the available time period. Our experiment confirms that diet can strongly influence the magnitude of growth (see Anderson and Cummins 1979). However, the full effects of temperature on the growth of this species still need to be properly tested.

The data base on *L. intermedia*, and for aquatic insects in general, needs to be expanded considerably before speculating on the relative importance of temperature and nutrition to the life history characteristics and geographic dispersal of aquatic

The proportion of total female weight allocated to eggs (i.e. reproductive effort) ranged from 0.12 to 0.45 depending on diet and temperature (Table 1). Reproductive effort (RE) generally increased with temperature (e.g. overall average RE for WCC, WCC + 3°C, and WCC + 6°C was 0.21, 0.28, and 0.39, respectively) and adult size (correlation coefficient = 0.78, $p < 0.001$; Fig. 2). It appears that in nonoptimal conditions, a premium is placed on attaining a certain physical adult size, even if only a small amount of energy can be allocated to reproduction. In optimal conditions for growth, larvae attain a certain size and then allocate disproportionately large amounts of energy to eggs rather than further increasing in size.

Conclusions

A few general conclusions can be made concerning the nutritive quality of the five diets that were tested. Hickory and

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TABLE 4. Parameters of regression equations ($Y = a + bX$) relating egg number (Y) to female biomass (X) in milligrams for *Leptophlebia intermedia*. Parameters are given separately for each combination of diet and temperature as well as for data combined for all diets at each temperature. Not enough data were available to perform regressions for the red oak diet at all temperatures and the American beech diet at WCC + 6°C.

Temperature regime	Diet	b	s_b	a	s_a	r^2	df	F-ratio	p
WCC	HI	394.8	43.9	−517.6	182.0	0.89	1,10	80.9	0.0001
	WA	604.9	66.0	−1463.6	254.5	0.95	1,4	84.1	0.0008
	CO	280.2	63.1	−343.1	132.1	0.73	1,7	19.7	0.0030
	AB	308.7	169.4	−340.3	307.7	0.45	1,4	3.3	0.1424
	Pooled	393.5	21.27	−552.2	69.8	0.91	1,31	342.2	0.0001
WCC + 3°C	HI	535.0	42.5	−939.3	153.1	0.86	1,24	158.5	0.0001
	WA	481.1	45.2	−886.0	191.1	0.85	1,20	113.4	0.0001
	CO	501.4	39.5	−776.3	130.5	0.94	1,9	160.8	0.0001
	AB	552.6	46.6	−833.8	136.2	0.97	1,4	140.7	0.0003
	Pooled	474.0	23.0	−753.2	85.5	0.87	1,63	426.3	0.0001
WCC + 6°C	HI	482.8	108.9	−781.2	288.6	0.43	1,26	19.7	0.0001
	WA	506.6	25.6	−642.7	104.4	0.95	1,19	391.1	0.0001
	CO	586.9	20.9	−902.4	64.6	0.99	1,3	789.1	0.0001
	Pooled	559.5	28.3	−915.2	93.4	0.88	1,52	391.9	0.0001

insects. It appears, however, that even when food quantity is nonlimiting, changes in food quality can cause significant changes in larval growth and survival. Our understanding of these processes will have direct bearing on existing models concerning environmental variation and its effect on aquatic insect populations. For example, to what degree should the thermal equilibrium hypothesis (Sweeney and Vannote 1978; Vannote and Sweeney 1980) be modified to take into account food quality along natural thermal gradients? It is certainly known that plant communities change along temperature gradients associated with latitude and/or altitude. It is unknown, however, to what degree parallel gradients of water temperature and tree species along stream corridors interact to cause observed changes in life history characteristics of resident populations.

Acknowledgements

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