Food preference and relative influence of temperature and food quality on life history characteristics of a grazing mayfly, *Ephemerella ignita* (Poda)

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In choice experiments, starved larvae of *Ephemerella ignita* (Poda) moved preferentially to compartments with a diatom-rich diet rather than to those with a detritus diet. Growth rate, mortality rate, larval developmental time, adult size, and fecundity of *E. ignita* were assessed in response to rearing on two diets (diatoms and detritus) at four constant temperatures (4.5–18°C). On each diet, growth rate (range 0.30–6.2% length/d) increased with increasing temperature according to a power law ($Y = ax^b$). At any temperature, growth rate was significantly higher on the diatom diet than on the detritus diet. Mortality rate (range 0.2–6.5%/d) increased with increasing temperature and was higher on the detritus diet than on the diatom diet. Developmental time varied significantly with temperature for animals fed diatoms according to a hyperbolic relationship. The thermal requirement for completing larval growth from hatching to emergence on a diatom diet was estimated at about 950 degree-days above a threshold of 3.5°C (range 9.5–18°C). Very few larvae reared on detritus achieved the adult stage and their developmental time seemed longer. Subimago weight did not vary significantly with temperature, but fecundity (range 435–1320 eggs per female) was significantly lower at 9.5°C than at 14.5 and 18°C in larvae fed diatoms. Fecundity of females from larvae fed detritus was very low (range 5–150 eggs). The reproductive effort (number of eggs per milligram of subimago weight; range 66–125) followed a clear linear increasing relationship with temperature (9.5 to 18°C) for animals reared on diatoms. Poor food quality could probably restrict distribution of *E. ignita* by reducing fecundity. In conclusion, these results show that the thermal equilibrium hypothesis must be extended to other environmental factors. They also support the hypothesis of a bivoltine cycle of *E. ignita* under favorable thermic and food conditions.

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Des expériences de choix alimentaires ont montré que des larves à jeun d'*Ephemerella ignita* (Poda) se dirigent préférentiellement vers une nourriture riche en diatomées que vers une nourriture riche en détritus. L'influence du régime alimentaire (diatomées et détritus) et de la température (quatre températures constantes; 4,5 à 18°C) sur le taux de croissance, le taux de mortalité, la durée du développement larvaire, la taille des adultes et la fécondité a été estimée par élevage en laboratoire. Pour chaque régime alimentaire, le taux de croissance augmente avec la température selon une relation $Y = ax^b$. À toute température, le taux de croissance est significativement plus élevé chez les larves nourries avec des diatomées que chez celles nourries avec des détritus. Le taux de mortalité (0,2 à 6,5%/jour) augmente avec la température et il est plus élevé chez les larves nourries avec des détritus que chez celles nourries avec des diatomées. La durée de développement varie significativement avec la température chez les individus nourris avec des diatomées; la relation peut être approximée par une hyperbole. Le développement complet depuis l'éclosion jusqu'à l'émergence a été estimé à environ 950 degré-jours au-dessus d'un seuil de 3,5°C (intervalle: 9,5 à 18°C). Très peu d'animaux élevés sur détritus ont atteint le stade adulte et la durée de développement est apparue plus longue. Le poids des subimagos ne semble pas varier avec la température, mais la fécondité (435 à 1320 oeufs/femelle) est significativement plus faible à 9,5°C qu'à 14,5 et 18°C chez les animaux consommant des diatomées. La fécondité des femelles provenant de larves alimentées avec des détritus est extrêmement faible (5 à 150 oeufs/femelle). L'effort de reproduction (nombre d'oeufs/mg de poids frais; intervalle : 66–125) suit une relation linéaire et positive avec la température (de 9,5 à 18°C) pour les animaux élevés sur diatomées. Une nourriture de pauvre qualité peut probablement réduire la distribution d'*E. ignita* par une forte réduction de sa fécondité. En conclusion, ces résultats montrent que l'hypothèse de l'équilibre thermique devrait tenir compte d'autres facteurs de l'environnement et ils corroborent l'hypothèse d'un cycle bivoltin d'*E. ignita* dans des conditions thermiques et alimentaires favorables.

Introduction

Temperature and food quality are known as important factors regulating the life history characteristics of aquatic insects, but experiments have usually focused on the effect of a single factor at a time (for synthesis see Sweeney 1984). Only recently have attempts been made to assess the interaction of both parameters (Sweeney et al. 1986a, 1986b). In addition, the effect of food has been investigated mostly in shredder and collector species (Otto 1974; Ward and Cummins 1979; Fuller and Mackay 1981; Vannote and Sweeney 1985; Sweeney et al. 1986a, 1986b). Similar observations for grazer– scrapers are scarce.

In natural populations, gut contents of scraper–grazers usually contain variable proportions of two main kinds of food: periphyton and fine amorphous detritus (Chapman and Demory 1963; Anderson and Cummins 1979; Hawkins 1985, Yule 1986; Wallace and Gurtz 1986). An increase of larval growth rate often occurs concomitantly with an increase of temperature and a shift in ingested food (Brown 1961; Gibbs and Mingo 1986). It is then difficult to relate growth rate modifications to one or the other factor.

This paper focuses on the relative importance of temperature and food quality (diatoms versus detritus) to life history characteristics of *Ephemerella ignita* (Poda), a scraper–grazer mayfly. *Ephemerella ignita* is widespread in Europe and its life cycle has been studied by many authors (see Rosillon 1986b). Most of them described *E. ignita* as a univoltine, rapidly growing summer species but in better thermic conditions larvae occurred throughout the year and emergence

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extended from spring to late autumn (Thibault 1971; Neveu *et al.* 1979). The life history of this species seems very flexible. The time required for egg hatching has been elucidated by Elliott (1978) but very little is known about larval growth rate.

Materials and methods

Animals and diets

Material used in the experiments was obtained from different hard-water chalk streams in Dorset (southern England). Larvae of *E. ignita* were collected from Bere Stream (National Grid Reference: SY856930) in April–May 1986, when a large population with a wide range of sizes occurred (Bass 1976). The diatom diet was obtained by washing samples of *Ranunculus penicillatus* var. *calcareus* (R. W. Butcher) C. D. K. Cook taken from Waterston Stream through a 125-μm sieve. The detritus diet was obtained by washing deposited organic matter collected from the River Frome through the same sieve. Both foods were maintained in culture in stream water at 15°C, in constant light for diatoms and in darkness for detritus. The stream water in diatom cultures was replaced about twice a week. The cultures were replaced by new material from the field every 3–4 weeks.

Food quality was assessed by microscopic analysis of both diets by the following procedure. Ten drops of sedimented food were diluted in 10 mL of water, the solution was vigorously stirred, and four drops were placed on a cavity slide. Ten fields were selected at random and observed through a 10 × 10 cell ocular grid. The number of cells with diatoms and fine amorphous detritus were counted. Two slides were examined for each diet on three occasions.

Food preference experiment

With a view to determining whether larvae of *E. ignita* preferred to feed on one or the other of the two diets, choice chambers were made similar to those used by Haynes and Taylor (1984) for *Potamopyrgus jenkinsi*. The chamber was a circular plastic tray 15 cm in diameter and 2 cm high, having a central area and eight radial compartments each of equal area (20 cm²). Stream water was added, to a height of about 1 cm, and each diet was placed in four randomly selected compartments. This experiment was carried out in a constant temperature room (15°C) under constant light. Animals were acclimatized under these conditions for at least 2 days. At the beginning of the experiment, 15 to 25 larvae, which had been starved for 24 h, were placed in the centre of the chamber. The number of animals in each compartment was counted after 15, 20, 45, 60, 90, 120, and 180 min. The mean number of animals per compartment was calculated. Five replicates were carried out and a two-way analysis of variance was performed to test the effects of diet (factor 1) and experiment (factor 2) on the distribution of nymphs between the compartments.

Laboratory rearing experiments

Two rearing experiments were carried out in the laboratory. To estimate growth rate of *E. ignita*, tiny nymphs, (1–2 mm) were maintained individually in stream water in small plastic petri dishes (diameter 7 cm, water depth 7 mm). Twelve individuals were used in each of the eight treatments: four constant temperatures (4.5, 9.5, 14.5, and 18°C), two diets (diatoms and detritus). The food was deposited in each dish with a fine pipette; no aerator was used. The quantity of food varied with the size of the larvae but it was always maintained in excess to avoid a limiting factor of food quantity. Water and food were changed every week when animals were measured (total body length from head to the tip of the abdomen) using a microscope with an ocular micrometer under 50, 25, or 12× magnification according to animal size. For this purpose, animals in a drop of water were transferred with a pipette or flexible forceps onto a microscope slide. When nymphs were very close to emergence (black wing pads) they were transferred to a larger plastic box (15 × 15 cm, water depth of 7 cm) to facilitate emergence.

In a second experiment started at the same time as the first, a group of about 30 tiny larvae were maintained in each of the same eight temperature–diet treatments in stream water in a plastic container

TABLE 1. Analysis of diets: number of cells of a 10 × 10 grid containing diatoms and fine amorphous detritus for the two laboratory diets (collected from the field on different dates) and for the sediment taken from the cage used for the field experiment ($n = 10$ ocular fields)

	Diatoms		Detritus	
	$\bar{x}$	SD	$\bar{x}$	SD
Diatom diets				
15 May	22	14	15	13
	26	11	17	10
31 July	39	5	12	4
	36	9	7	3
28 August	24	3	7	3
	22	4	8	3
Detritus diets				
15 May	2	2	53	7
	3	2	50	6
7 June	3	2	98	3
	2	1	96	5
30 August	0.2	0.4	45	15
	0.2	0.4	59	13
Field expt. (No. 2) sediment				
19 June	3	2	38	8
	3	2	44	8

(15 × 15 cm, water depth of 7 cm). Aeration was provided by means of a hypodermic needle. Food given in excess and water were replaced every 10 days when all animals were counted and measured following the procedure described above. This trial was performed to assess mortality rate but a mean growth rate for the group of larvae could be also calculated.

Subimagos obtained from both experiments were weighed alive on a Unimatic CL 41 balance (precision 0.1 mg) and kept in the laboratory at room temperature until the final moult. The subimago and imago females were dissected and the number of eggs (fecundity) was determined for each.

Field rearing experiment

To compare the laboratory values for growth and mortality rates with field values, three groups of 15 to 20 larvae (see Table 3) were reared in metal cages (7 cm in diameter, 6 cm high, with mesh size 0.4 mm) partially immersed in a small secondary channel of the River Frome. The water level in the cages was about 3 cm. Food was provided only by drift; no supplementary food was added. The surviving animals were counted and measured every week over a month (19 May to 20 June). To assess the quality of available food, the fine sediment (< 0.250 mm) present in a rearing cage collected on 19 June was analysed by the same procedure as that used in the food choice experiment.

Results

Diet characterization

Microscopic examination at different times showed a marked difference between the two diets (Table 1). Diatoms were almost completely absent in the detritus diet and largely predominated in the diatom diet in spite of the presence of some detritus in the latter. The composition of each diet probably changed between months but similar differences occurred between the two kinds of food.

Food preference

A two-way analysis of variance performed on the number of animals per compartment (Table 2) revealed a highly significant effect of food ($F_{1,30} = 38.9$, $p < 0.001$) and no significant difference between experiments ($F_{4,30} = 2.48$, $p > 0.05$)

TABLE 2. Number ($\bar{x} \pm$ SD) of *E. ignita* larvae per compartment in the five replicates of the food preference experiment (in each replicate there were 4 compartments with each food type)

	Repl. 1	Repl. 2	Repl. 3	Repl. 4	Repl. 5
Detritus compartments	1.63±0.66	1.99±1.85	1.64±1.10	0.85±0.88	0.72±0.51
Diatoms compartments	3.89±2.63	3.44±1.17	3.75±1.13	2.10±1.87	3.51±1.23

TABLE 3. Initial size, instantaneous growth rate, and mortality rate of larvae of *E. ignita* reared in the laboratory on two diets at four constant temperatures or reared in the field

	Initial size (mm)			Instantaneous growth rate (% length/d)			Mortality rate (%/d)
	$\bar{x} \pm$ SD	Range	N	$\bar{x} \pm$ SD*	Range	N	
Diatom diet							
Reared individually							
4.5°C	1.70±0.49	1.0−2.8	12	0.66±0.19a	0.45−0.87	8	—
9.5°C	1.54±0.32	1.1−2.0	12	1.88±0.20b	1.6−2.2	12	—
14.5°C	1.50±0.31	1.1−2.0	12	3.89±0.43c	3.4−4.5	12	—
18°C	1.50±0.32	0.9−2.0	12	4.60±0.76d	3.9−6.2	12	—
Reared in groups							
4.5°C	2.02±0.48	1.0−3.1	31	1.54±0.62			6.5
9.5°C	1.97±0.68	1.0−3.5	30	1.74±0.18			0.2
14.5°C	2.03±0.62	1.2−3.8	31	3.01±0.38			0.5
18°C	2.04±0.65	1.0−3.2	31	3.57±0.63			2.3
Detritus diet							
Reared individually							
4.5°C	1.74±0.81	1.1−3.8	12	0.36±0.04a	0.30−0.42	5	—
9.5°C	1.49±0.27	1.2−1.8	12	0.91±0.21b	0.67−1.13	7	—
14.5°C	1.42±0.32	0.8−1.8	12	1.06±0.37b	0.64−1.6	11	—
18°C	1.54±0.34	1.0−2.0	12	1.52±0.32c	1.8−2.0	10	—
Reared in groups							
4.5°C	2.02±0.62	1.0−3.1	31	0.95±0.08			1.6
9.5°C	1.93±0.57	0.9−3.4	32	0.86±0.08			2.0
14.5°C	2.05±0.67	1.1−3.9	30	1.8±0.14			2.8
18°C	1.95±0.49	1.2−3.0	14	1.0±0.29			5.5
Field expt. (14.2°C)							
Replicate 1	3.57±0.20	3.2−3.9	15	1.47±0.17			0.8
Replicate 2	4.35±0.27	4.0−4.9	15	1.16±0.26			1.0
Replicate 3	2.79±0.41	2.0−3.3	22	1.14±0.30			1.7

NOTE: Values followed by the same letter within a diet treatment are not significantly different ($p > 0.05$) according to a t-test performed on growth rate for animals reared individually.

*For larvae reared in groups, $\bar{x} \pm$ SD relate to the b coefficient of a single relationship, $L = ae^{bt}$, calculated from all individuals of a group.

as well as no significant interaction ($F_{4,30} = 0.79$, $p > 0.05$). Starved larvae of *E. ignita* preferentially moved to compartments containing diatoms.

Growth rate

Specific growth rates (G, % length/d) of single larvae and groups of larvae were determined by assuming an exponential relationship between body length (L, mm) and time (t, days): $L = ae^{bt}$ and $G = 100b$. Because of a cessation of growth in length for 1 (at 18°C) or 2 weeks (14.5 and 9.5°C) before emergence, body lengths measured for this period were ignored. Mean individual growth ranged from 0.3 to 6.2% length/d.

For animals on each diet, there was a significant increase in the instantaneous growth rate with increasing temperature and at each temperature, growth rate was significantly (t-test, $p < 0.01$) higher on diatoms than on detritus (Fig. 1; Table 3). The relationship between growth rate (G, % length/d) and temperature (T, °C) followed a power law for animals on each diet: $G = aT^b$; the values of the constants a and b (with 95% CL)

were $a = 0.0686$ (0.0524−0.0899) and $b = 1.48 \pm 0.11$ on diatoms ($N = 44$, $R^2 = 94\%$), and $a = 0.0917$ (0.0527−0.1596) and $b = 0.936 \pm 0.22$ on detritus ($N = 32$, $R^2 = 70\%$). Both relationships were highly significant ($p < 0.01$) and within a single diet, temperature was the main factor affecting growth. Proportion of the variability of mean G accounted for by mean temperature was 94 and 70% on diatoms and detritus, respectively. Comparison of the two regression lines (t-test) showed a significant difference between the slopes ($p < 0.01$) but not between the values of a ($p > 0.05$). G increased more quickly with temperature for animals eating diatoms than it did for those eating detritus. A portion of residual variability of G could be related to the initial size of the animals. In spite of a narrow range of size at the beginning of the experiment (Table 3) a significant linear relationship of G with increasing initial size was observed at 18°C ($R^2 = 90\%$) and 14.5°C ($R^2 = 70\%$) for animals on the diatom diet and at 18°C ($R^2 = 61\%$), 14.5°C ($R^2 = 67\%$), and 9.5°C ($R^2 = 64\%$) for animals on the detritus diet. This observation suggested a decline in growth rate with size but for each indivi-

dual the relationship was rarely significant. Therefore the exponential model of growth was applied (Kaufmann 1981).

A mean value of G was calculated for groups of larvae reared under different conditions of temperature and food (expt. 2; Table 3). The same tendency occurred as in individual rearing (Fig. 1): better growth was obtained with the diatom diet than with the detritus diet and a positive effect of temperature was apparent. Nevertheless, some divergences occurred between the animals reared individually and those reared in groups. Different factors could be involved, such as differential mortality rate according to size, a negative effect of interaction between individuals within the group, or an effect of the water current generated by aerators.

Growth rates for larvae reared in the stream at fluctuating temperature (mean 14.2°C, range 11−21°C) were 1.5, 1.2, and 1.1% length/d in the three experiments (Fig. 1). These values were very close to those obtained at constant temperature in the laboratory. They were intermediate between values obtained with the diatom and detritus diets but were closer to the latter. Food quality seemed to be the limiting factor for larval growth in our field experiment, as the analysis of fine sediment from the cages indicated that food quality was similar to that of the detritus diet (Table 1).

Mortality

A significant decreasing linear relationship was observed between the logarithms of the number of surviving animals (N) and time (t, days) in seven of eight groups of larvae. The number of surviving animals was then an exponential function of time: $N = ae^{-bt}$ and the mortality rate (M, %/d) was $M = 100b$ (Table 3). Except for the very high value for larvae held at 4.5°C on the diatom diet, the mortality rate was higher for larvae on the detritus diet than for those on the diatom diet and it seemed to increase with increasing temperature for both diets (Table 3).

Mortality rates in field experiments at fluctuating temperatures were within the range of values in the laboratory at constant temperature (Table 3).

Developmental time

The number of subimagos from different experiments is shown in Table 4. A large proportion of larvae fed diatoms reached the adult stage at 18, 14.5, and 9.5°C but none of those held at 4.5°C had reached the adult stage by 4 months, when the experiment was stopped; only three animals were still alive. On the other hand, the percentage of animals achieving emergence was very low on detritus, only one and three individuals in the groups reared at 18 and 14.5°C, respectively, and no larvae reared individually in petri dishes emerged. For animals on the diatom diet held at any temperature, developmental time seemed longer for females than males but the difference was only significant at 14.5°C (Mann−Whitney test). Developmental time decreased with increasing temperature regardless of sex or the type of rearing. There was no significant difference between larvae reared individually and larvae reared in groups at the same temperature and on similar food (Table 4). Because of these results the relationship between development time (t, days) and temperature (T, °C) was established for each sex from pooled data of both experiments (Fig. 2). That relationship was well described by a hyperbola and therefore the relationship between the reciprocal of time (rate of development, day^{-1}) and temperature was linear over the temperature range 9.5−18°C: $1/t = a +$
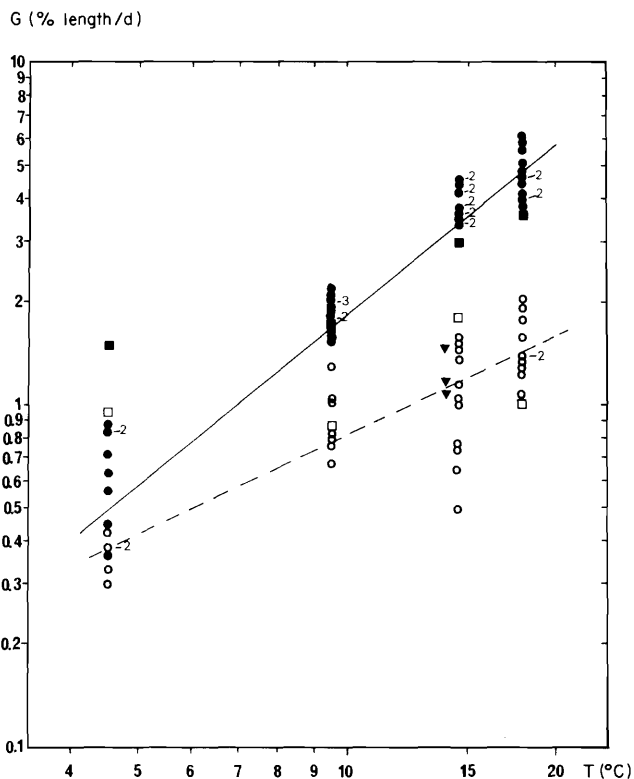
G (% length/d)

FIG. 1. Relationship between mean specific growth rate (% length/d) and mean water temperature (T, °C) for $E.$ $ignita.$ Data are for (i) larvae reared individually in the laboratory on diatoms (● and solid line) or detritus (○ and broken line), (ii) in groups in the laboratory on diatoms (■) and on detritus (□), and (iii) in the stream (▼). When more than one larva had the same data point, the number of larvae is indicated.

bT; the values of coefficients a and b (with 95% CL) were $a = (-6.6 \pm 3.0) \times 10^{-3}$ and $b = (1.80 \pm 0.22) \times 10^{-3}$ ($N = 46$, $R^2 = 85\%$, $p < 0.001$) for males, and $a = (-5.0 \pm 2.5) \times 10^{-3}$ and $b = (1.60 \pm 0.17) \times 10^{-3}$ ($N = 51$, $R^2 = 87\%$, $p < 0.001$) for females. This kind of relationship means that the time taken for development can be expressed as a number of degree-days above a threshold temperature. The threshold temperature (T_0) is the temperature at which the developmental rate ($1/t$) is zero and the number of degree-days (D) is the reciprocal of the regression coefficient (b^{-1}); another formulation of the previous equation is $t = D/(T-T_0)$. The value for D (with 95% CL) was 556 (495−633) degree-days above 3.67°C for males and 625 (578−699) degree-days above 3.15°C for females. This number of degree-days is not the actual number of degree-days required by larvae of $E.$ $ignita$ fed on diatoms to complete development from hatching to emergence, because the mean size of animals at the beginning of experiments was 1.5 mm. Despite few emergences of detritus-reared animals (Table 4) it seemed that, under the same temperature conditions, the developmental time was slightly longer than it was on diatoms.

Adult size

Adult size was estimated from the wet weight of living subimagos a few hours after emergence. In all treatments, females were significantly larger than males but there was no consistent effect of temperature on adult weight (Table 4). A higher weight at 14.5°C was observed for groups of females reared on

TABLE 4. Developmental time, subimago weight, fecundity, and reproductive effort

	Developmental time (d)						Wet wt. of		
	Female			Male			Female		
	$\bar{x} \pm$ SD	Range	N	$\bar{x} \pm$ SD	Range	N	$\bar{x} \pm$ SD	Range	N
Diatom diet									
Reared individually									
9.5°C	$115 \pm 16a$	93 – 130	4	$96 \pm 8.0a$	85 – 108	8	$8.7 \pm 1.14a$	7.9 – 10.0	3
14.5°C	$56 \pm 1.8b$	54 – 58	5	$50 \pm 3.0b$	45 – 53	7	$10.5 \pm 0.33a$	10.1 – 10.9	4
18°C	$44 \pm 1.8c$	41 – 47	8	$42 \pm 1.5c$	41 – 44	4	$9.7 \pm 1.36a$	8.4 – 11.7	7
Reared in groups									
9.5°C	$97 \pm 13a$	78 – 125	13	$101 \pm 17a$	77 – 123	9	$7.1 \pm 0.62a$	6.1 – 7.9	8
14.5°C	$55 \pm 8.0b$	40 – 65	11	$50 \pm 6.8b$	40 – 60	12	$8.3 \pm 0.63b$	7.5 – 9.0	4
18°C	$42 \pm 6.6c$	33 – 59	11	$40 \pm 8.5c$	32 – 54	6	$7.6 \pm 0.51a$	5.7 – 8.1	10
Detritus diet									
Reared in groups									
14.5°C	79 ± 3.5	77 – 82	2	80		1			
18°C	51		1						

NOTE: Values within the same treatment followed by the same letter are not significantly different ($p > 0.05$) (t-test, except for developmental time, Mann–Whitney test).

diatoms, but this trend was not confirmed for individually reared females or for males. The effect of rearing temperature on adult size of *E. ignita* fed on diatoms appeared very weak. But at any temperature, animals reared individually were larger than those reared in groups.

Fecundity

Contrary to adult size, fecundity exhibited variations according to temperature conditions for animals on a diatom diet (Table 4). Females reared individually were less fecund at 9.5°C than at 14.5 and 18°C. The same trend occurred in females reared in groups although the difference between 9.5 and 18°C was not significant. At any temperature, females reared individually were more fecund than those reared in groups. The three subimago females obtained from larvae on a detritus diet showed a very low fecundity (Table 4). In spite of few data, females had much lower fecundity levels when they were fed detritus than when they were fed diatoms.

Reproductive effort

The different responses to temperature exhibited by adult size and fecundity can be accounted for by a significant increase in the reproductive effort (number of eggs per milligram of wet weight) with increasing temperature. The proportion of total weight allocated to egg production increased with temperature and was not affected by the kind of rearing (individually or in groups). The relationship between reproductive effort (RE, eggs/mg) and temperature (T, °C) was well described by a linear regression: $RE = a + bT$; the values of coefficients a and b (with 95% CL) were $a = 50.1 \pm 12$ and $b = 3.49 \pm 0.83$ ($N = 26, R^2 = 74\%$, p < 0.001) in animals fed diatoms (Fig. 3).

Discussion

Our results for *E. ignita* show that temperature, diet, and rearing conditions affect life history parameters such as larval growth rate, adult size, developmental time, and fecundity. Effect of temperature on insect dynamic parameters has previously been studied in several species (for synthesis see Sweeney 1984). On the other hand, the effect of food quality is

well known for shredders (Otto 1974; Vannote and Sweeney 1985; Sweeney et al. 1986a, 1986b), but data for grazer–scrapers are more scarce (Sweeney and Vannote 1984; Storey 1987).

The feeeding preference experiment indicates that the preferred food (diatoms) yields the best growth rate and the most fecund adults. Although food preference has been reported for other species (Cianciara 1980; Haynes and Taylor 1984) a positive relationship between food preference and growth rate has rarely been described (Vannote and Sweeney 1985). Contrary to observations of Bird and Kaushik (1984) of an American mayfly, *Ephemerella subvaria*, mortality rate was lower on the diet that yielded better growth in *E. ignita*.

Growth rate increases with increasing temperature regardless of diet. A similar positive relationship between growth rate and temperature over a range of field temperatures has usually been reported in aquatic insects (Humpesch 1979, 1981; Elliott 1984) and the relationship was also well described by a power law for the mayfly *Ecdyonurus dispar* on a diet of periphyton (Humpesch 1981). Interaction of food quality and temperature indicates that the rate of acceleration of growth with temperature depends on diet. At low temperature, the effect of food on growth is very low and is probably obscured by the effect of temperature. Growth rate observed in the field experiments was within the range of laboratory values and it seems that in those experiments the limiting factor was food quality.

In natural insect populations, a positive correlation has often been observed between larval growth and water temperature (Humpesch 1979; Elliott 1982; Lavandier 1981; Welton et al. 1982) but change in food quality was also suggested to account for modifications in growth rates (Gibbs and Mingo 1986; Rosillon 1986a). From our results on *E. ignita* both factors appear important; the value of the mean growth rate obtained at 18°C (4.6% length/d) on the diatom diet is probably very close to the maximum potential growth of the species and it is certainly higher than the highest values calculated for other Ephemeroptera (Humpesch 1979, 1981; Welton et al. 1982; Rosillon 1986a). Because of the problem of separating different cohorts, only Welton et al. (1982) reported an estimation of growth rate for *E. ignita* in field populations. They obtained

of *E. ignita* reared in the laboratory on two diets at four constant temperatures

subimagos (mg)			Fecundity (no. of eggs per ♀)			Reproductive effort (no. of eggs/mg wet wt.)		
Male								
$\bar{x}$ ± SD	Range	N	$\bar{x}$ ± SD	Range	N	$\bar{x}$ ± SD	Range	N
7.0±0.75a	6.0−7.8	7	747±62.8a	696−817	3	86±5.1a	82−92	3
7.4±0.58a	6.6−8.1	7	1095±67.0b	1004−1184	5	103±4.3b	99−109	4
6.9±0.14a	6.8−7.0	2	1098±1.36b	909−1320	8	112±6.1c	101−118	7
6.6±0.84a	5.9−7.7	4	548±121a	435−744	5	80±12a	66−95	4
6.5±0.55a	5.5−7.0	7	867±116b	732−998	5	107±6.7ab	98−111	4
5.6±0.85a	5.0−6.2	2	729±116ab	630−915	5	112±10b	99−125	4
3.5		1	102±74	50−154	2			
			5		1			

a mean value (±95% CL) of 3.26 ± 0.49% length/d over the period of 3 April − 15 May at a mean temperature of 11.9°C. The estimated value at the same temperature from our equation for a diatom diet is 2.69 ± 1.06% length/d. These two values are not significantly different.

The final size of larvae before emergence varied from 7.3 to 8.6 mm (mean = 7.8, SD = 0.4, N = 36) for animals reared individually on diatoms. These values were similar to those measured in natural populations with a maximum larval size of about 8 mm (Jazdzewska 1980; Wise 1980; Rosillon 1986b). Values for growth and final size prove that the experimental conditions were adequate for the development of *E. ignita*.

A decrease of development time with temperature is also generally observed in aquatic insects but the mathematical relationship is rarely established. In our experiment a hyperbolic relationship is suggested. Larval development thus requires a constant number of degree-days above a threshold temperature to achieve emergence. This number was estimated to be about 600 degree-days above 3.5°C for tiny larvae of an initial mean size of 1.5 mm, fed on a diatom-rich diet. By assuming a size of 0.6 mm at hatching and a constant instantaneous growth rate(% length/day) over size, the total number of degree days is estimated to be 900 above 3.5°C for completing larval development from hatching until emergence. At mean water temperatures of 10, 14, and 18°C, cohort production interval (CPI) can be estimated as 138, 86, and 62 days, respectively.

From these results and those for hatching time (Elliott 1978), the life history of the species can be elucidated. Under suitable temperature and food conditions (e.g., southern France: Thibault 1971; Neveu *et al.* 1979; southern England: Bass 1976; Welton *et al.* 1982), eggs laid in spring or early summer can yield a second generation which can complete its development during the same year. That scenario accounts for the presence of mature larvae or subimagos in late autumn or even in winter (Thibault 1971; Neveu *et al.* 1979; Welton *et al.* 1982). Under such favorable conditions *E. ignita* is probably partially bivoltine, as suggested by Thibault (1971).

Adult size and fecundity usually show the same pattern of variation with temperature in aquatic insects and in field popu-

lations of bivoltine species (e.g., *Baetis rhodani*), with adults of winter generations both larger and more fecund than those of summer generations (Benech 1972; Rosillon 1986b). Sweeney and Vannote (1978) suggested that for hemimetabolous insect species there is an optimum temperature for larval growth, which yields the largest and most fecund adults. In our experiments, adult size did not vary significantly with temperature (range 9.5−18°C) but fecundity decreased at 9.5°C. On the other hand, reproductive effort showed a marked relationship with temperature; the proportion of total production allocated to eggs increased with increased temperature in *E. ignita*. In addition, a clear effect of food quality was demonstrated with very low fecundity in animals fed detritus because of a very small reproductive effort. Reproductive effort is rarely estimated in aquatic insects. Sweeney *et al.* 1986b) observed an increase in proportion of weight allocated to eggs with increasing temperature and increasing size in the mayfly *Leptophlebia intermedia*. Benech (1972) described constant relationships over the year between fecundity and larval or adult measurement in *Baetis rhodani*, though egg volume varied extensively over seasons. The relationship between fecundity and adult size (weight or length) seems not to be constant in all species but could depend on larval growth conditions, contrary to a general assumption of many authors (see Sweeney and Vannote 1978).

Animals reared in groups showed substantially lower adult size and fecundity and higher mortality than those reared individually. Competition between individuals within the group could account for these differences, but other factors could also be involved, such as the effect of the water current generated by aerators and the energy spent to face it.

In conclusion, our results from rearing *E. ignita* under different conditions of temperature and food quality reveal the importance of both factors on life history parameters. In addition to confirmation of their influence on growth rate and duration of development, it appears that fecundity and especially reproductive effort can vary extensively with temperature and food quality. Although *E. ignita* can survive and complete its larval growth until emergence on detritus, this diet could probably limit the distribution of the species by reducing success of
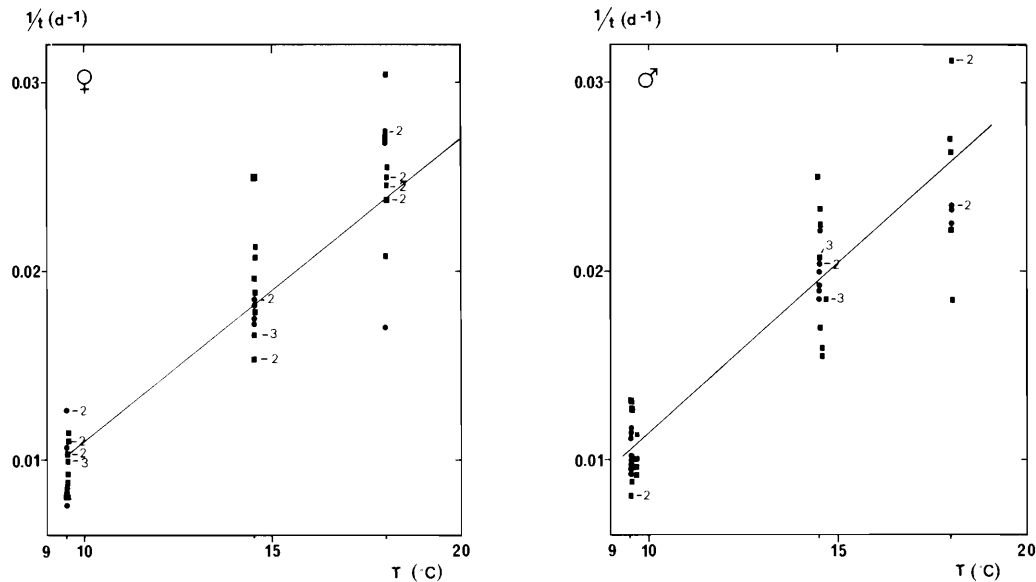
FIG. 2. Relationship between rate of development ($1/t$, d^{-1}) and water temperature (T, °C) for *E. ignita*. Data are for larvae reared individually (●) or in groups (■) on diatoms in the laboratory. Regression lines are given for each sex. When more than one larva had the same point, the number of larvae is indicated.
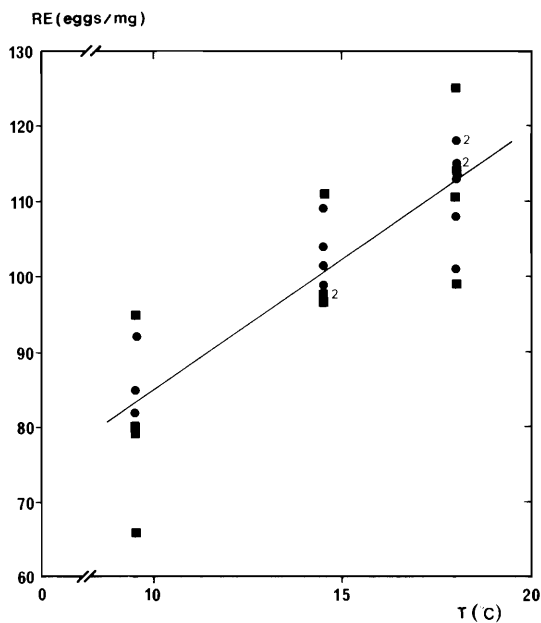

FIG. 3. Relationships between reproductive effort (RE, number of eggs per milligram of wet weight) and water temperature (T, °C) for *E. ignita*. Animals were reared individually (●) or in groups (■) on diatoms in the laboratory. When more than one larva had the same data point, the number of larvae is indicated.

reproduction. Our results, as well as those of Sweeney *et al.* (1986*b*) on *Leptophlebia intermedia*, indicate that the thermal equilibrium hypothesis of Sweeney and Vannote (1978) should be improved to take into account effects of food quality and variability in reproductive effort with both factors.

Acknowledgements

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