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Life cycles and food habits of mayflies and stoneflies from temporary streams in western Oregon

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SUMMARY

1. Field data and results from laboratory rearing are combined to describe life cycles and food habits of the mayflies *Paraleptophlebia gregalis* and *Ameletus* n. sp., and the stoneflies *Soyedina interrupta*, *Ostrocerca foersteri*, *Sweltsa fidelis* and *Calliperla luctuosa*.

2. *P. gregalis*, *A. n. sp.*, *S. interrupta* and *O. foersteri* have univoltine life cycles which are characterized by a high degree of plasticity. *S. fidelis* and *C. luctuosa* have semivoltine life cycles which are more tightly synchronized.

3. Laboratory feeding trials and field observations characterize *P. gregalis* as a collector, *A. n. sp.* as a scraper, *O. foersteri* and *S. interrupta* as shredders and *C. luctuosa* as a predator mainly of midge larvae. Late-instar larvae of *S. fidelis* are believed to be scavengers.

4. Laboratory rearing yielded a negative correlation between growth rates (Y) and larval size in autumn (X) for *S. interrupta*. This indicates compensatory growth by small larvae in order to achieve synchronized emergence. The correlation can be described by the equation:

$$Y = 0.0053 - 0.0036X \quad (R^2 = 0.82; P < 0.01; n = 22)$$

5. The field and laboratory data indicate that photoperiod mainly determines the rate of development and size of emerging subimagos in *P. gregalis*.

Introduction

An extensive study of temporary headwater streams in western Oregon was initiated in 1988 to assess the value of these systems for conservation-orientated landscape management. Research focused on community composition and physico-chemical processes in different types of summer-dry headwaters.

In this paper we report on life cycles, growth patterns and food preferences of the mayflies *Paraleptophlebia gregalis* (Eaton) and *Ameletus* n. sp., and the stoneflies *Soyedina interrupta* (Claassen), *Ostrocerca foersteri* (Ricker), *Sweltsa fidelis* (Banks) and *Calliperla luctuosa* (Banks). Most of these were thought to be

uncommon species, but they accounted for more than 95% of the total mayfly and stonefly emergence from two temporary streams located in adjacent forested catchments.

Information on emergence patterns (Harper & Harper, 1986) and food habits (Mattingly, 1987) have been published for *P. gregalis*. There have been no thorough biological studies on the life history or food habits of *S. interrupta*, *O. foersteri*, *S. fidelis* and *C. luctuosa* (Stewart & Stark, 1988). Except for *Sweltsa*, these genera are not classified according to functional feeding groups in Merritt & Cummins (1984). How-

ever, Sweeney, Vannote & Dodds (1986) report on rearing experiments with *Soyedina carolinensis* (Claassen) which they characterized as a leaf-shredding stonefly.

Input of leaf litter into the temporary headwater streams was high, while primary production was low as a result of light limitation (Dieterich, 1992). Detritus, therefore, was expected to be the principal food source for the stream invertebrates. We were especially interested in determining whether the detritivorous species exploit the allochthonous organic material by shredding leaves (CPOM) or by collecting fine particles (FPOM). Thus, laboratory feeding trials were conducted in which larvae were provided with a choice of CPOM and FPOM.

Determination of food habits is a basic requirement for the assessment of possible interactions between members of the shredder and collector feeding guilds. It also provides information needed to compare temporary stream community structure to that postulated for permanent headwaters in the River Continuum Concept (Vannote *et al.*, 1980). This will be discussed in more detail in a subsequent paper. The comparison between laboratory rearing and life-history patterns observed in the field allows for the generation of hypotheses concerning the regulation of growth rates in mayflies and stoneflies.

Material and Methods

Study area

The field sites were located in, and adjacent to, the Oak Creek catchment in McDonald Forest, 8 km northwest of Corvallis, Benton County, Oregon. The climate of the Pacific Northwest is characterized by a distinct seasonality. Summers are warm and dry, winters are mild and wet. For Corvallis, Franklin & Dyrness (1973) gave the average July temperature as 18.9 °C (\bar{x} max, 27.1 °C), and January average as 4.0 °C (\bar{x} min, 0.6 °C). Mean annual rainfall is 1000 mm, with less than 50 mm falling from June to August. Because of the distinct seasonality with respect to precipitation, summer-dry streams are a common and predictable feature of the western Oregon landscape.

McDonald Forest, property of Oregon State University, is part of the eastern foothills of the Oregon Coast Range. The characteristic vegetation of the area is coniferous forest, primarily Douglas fir [*Pseudotsuga*

menziesii (Mirb.) Franco]. However, deciduous trees and shrubs are common along small headwaters. Bigleaf maple (*Acer macrophyllum* Pursh) accounted for about 65% of the litterfall (leaves and needles) in the temporary stream channels. In 1989 the mean dry mass input of leaf material (based on collections from litter traps) was 186 g m⁻² (Dieterich, 1992).

Both study streams have high gradients (11 and 20%). They are at altitudes of 250 and 350 m, respectively. Catchment areas of each stream are approximately 0.25 km². The temporary streams had continuous flow from about mid-November to May. Maximum discharge was 24.7 and 11.6 l s⁻¹, respectively (Dieterich, 1992). Although some permanent seeps and pools remained in both streams, most of the channel was dry during summer.

Field sampling

Collections were made from ten predetermined sample sites in each stream. A sample site was 2 m of stream channel. Because the streams were so small, limiting the amount of habitat disruption was important in choosing sampling methods. Each site contained two sediment baskets (150 cm³ of natural substrate) embedded into the stream bottom adjacent to each other, a leaf pack (about 5 g of maple leaves), and an emergence trap covering 0.3 m² (Fig. 1).

The sampling schedule for benthos collections was irregular and depended on flow conditions. Leaf-pack collections were obtained in December, February and monthly between April and October. Sediment baskets were sampled in December, April, August and October. Size measurements from larvae obtained in drift collections substituted for leaf pack and sediment-basket samples in March.

After 15–20 days of exposure, leaf packs and sediment baskets were collected from sites that had flow or water-saturated soil and were replaced with new samplers. Leaves and sediments were washed over sieves in the laboratory and animals collected on those with mesh openings of 250 µm or larger were identified and counted.

Five emergence traps containing a trough with ethylene glycol in the top section (Fig. 1) were placed into each study stream. Traps were emptied at 10–15 day intervals during winter and spring and at 4–6 week intervals thereafter. They were moved between sample sites after each trapping interval during the

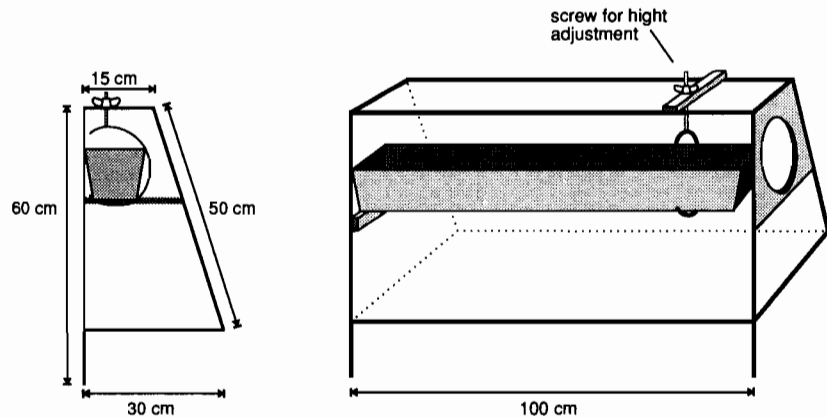


Fig. 1 Emergence trap design. A sleeve was used to close the trap opening and allow for gutter removal without escape of emergents.

lotic phase, but were permanently installed over seep areas and pools in summer and autumn.

To obtain size–weight functions, mayfly subimagos were collected and killed by freezing. Head-capsule width was measured to the nearest 0.02 mm. Specimens were then oven-dried to constant weight (45 °C, 24 h). Dry specimens were weighed to the nearest 0.001 mg on a Cahn electrobalance.

Field data reported to describe life cycles were obtained during the 1988/89 season from both streams. During that year both the benthos and the emerging adults were sampled intensively.

Laboratory rearing

Larvae used in rearing experiments were collected from one of the temporary streams. They were transported to the laboratory in containers with wet leaves. Larvae were picked from the detritus, and transferred to glass containers. To allow for growth from feeding in the field, mayflies were kept for 10 days without food prior to being used in the experiments. Trials with stonefly larvae were initiated within 5 days of field collection.

Larvae were reared at 10 °C under long-day conditions (16 L : 8 D). Experiments were conducted in shallow Petri dishes without aeration. Dishes had a single compartment (mayfly rearing) or two compartments separated by a plastic barrier about two-thirds the height of the dish (stonefly rearing). A single larva was placed in each dish with filtered stream water. Different food types (FPOM, CPOM, or FPOM and CPOM) were then assigned randomly to each larva.

The compartmentalized Petri dishes allowed for separation of food types within one dish while larvae still had access to both compartments and thus to both

food types. This helped reduce stonefly mortality; during pilot studies stonefly mortality was high in single-compartment dishes that only contained FPOM. Therefore, no feeding trials with FPOM as the only available food were conducted with stoneflies.

FPOM was obtained by decanting organic material (size classes 53–250 µm) from sediment collected in a McDonald Forest ephemeral stream. Maple leaves conditioned for 15 days in the field were used as the source of CPOM. The leaves were cut into 1-cm² squares. Two pieces from different leaves were added to each compartment in the trials containing CPOM. Larvae thereby could all be fed with CPOM from identical leaves although they were reared in individual containers. CPOM was maintained in excess throughout the feeding trials. Food and water were replaced every 10 days. At the same time, larval head capsules were measured to the nearest 0.02 mm, and leaf consumption was estimated visually (leaf area consumed).

To determine food preferences, average growth rates (increase of head-capsule width per day) on different food types were compared for all larvae independent of successful development to the subimago or adult stage.

Two-way ANOVAs (sex × treatment) for unbalanced data (SAS, 1991) were used to compare growth rates, size of last-instar larvae, leaf consumption and time for development to emergence. To test whether life cycle synchronization occurred via compensatory larval growth, the size of the animals at the beginning of the experiment and the corresponding growth rates were compared with a simple linear regression model. Larvae that completed development but failed to fully cast their last larval skin were included in the analysis.

The size of adults from rearing experiments and

Table 1 Developmental success of mayflies and stoneflies in laboratory feeding trials. Number of individuals in each treatment (*n*) and, in parentheses the percentage of larvae successfully completing development when fed on conditioned maple leaves (CPOM), fine particulate organic material (FPOM), or both foods

	FPOM		CPOM		Both	
	<i>n</i>	Emerged	<i>n</i>	Emerged	<i>n</i>	Emerged
<i>Ameletus n. sp.</i>	10	0 (0)	10	0 (0)	10	0 (0)
<i>Paraleptophlebia gregalis</i>	10	10 (100)	10	0 (0)	8	7 (88)
<i>Ostrocerca foersteri</i>	–	–	10	6 (60)	10	5 (50)
<i>Soyedina interrupta</i>	–	–	40	27 (68)	20	13 (65)

from field collections was compared with two-way ANOVAs (sex × origin) for unbalanced data (SAS, 1991). Only adults collected alive from the rearing chambers (Petri dishes) were considered for size comparisons.

Emergence data reported to compare results from laboratory rearing to development in the natural system were obtained during the 1989/90 season when the laboratory feeding trials were carried out. Emergence data are all from the stream where larvae were collected for the feeding trials.

Results

Ameletus n. sp. (Siphonuridae)

Ameletus n. sp. larvae took about 5–6 months to complete their development. Most larvae appeared in the streams at about the time when flow began in late autumn, but hatching continued long into the spring. As a result, larval size varied considerably throughout the flow period (Fig. 2a). Our data probably underestimate size variation because many large individuals escaped while the substrates were extracted. Larvae that hatched in spring survived the summer drought in the few permanent pools remaining in the channels. It is assumed that these larvae were the first to emerge in March and April.

The emergence period was from late March to August. However, very few individuals were collected during summer (Fig. 2a). Subimagos were much smaller later in the season. Head-capsule width of emergents in early April averaged 1.97 mm (SE = ± 0.03 mm; *n* = 21) compared with 1.04 mm (SE = ± 0.1 mm; *n* = 13) in July. As estimated from size-weight curves, this corresponds to a 2.6-fold difference in adult weights.

Although the genus *Ameletus* is listed as a collector-gatherer in Merritt & Cummins (1984) our feeding

trials demonstrated that *A. n. sp.* is not a detritivore (Table 1). Specimens survived for less than a month on either CPOM or FPOM. Larvae were observed scraping on small cobbles or pieces of wood. The species should be classified as a scraper, which is consistent with the results of the functional morphology study by Arens (1989).

Paraleptophlebia gregalis (Leptophlebiidae)

P. gregalis larvae are good swimmers and our benthic samples probably underestimated the abundance of the larger size classes. Most larvae emerged shortly after the onset of flow in late autumn and then took about 6–7 months to complete their development. Larval sizes were quite variable throughout the season and early stages were found almost year around (Fig. 2b).

There was an extended emergence period, with a distinct peak in June (Fig. 2b). Average size of emerging subimagos declined between April and early July and then increased again in the autumn. Mean head-capsule width was 1.53 mm (SE = ± 0.03 mm; *n* = 18) in April, 1.24 mm (SE = ± 0.02 mm; *n* = 48) in the first half of July and 1.28 mm (SE = ± 0.01 mm; *n* = 65) in September. As estimated from size-weight functions this corresponds to a 3.5-fold weight difference between spring and summer collections.

All larvae kept with CPOM in the rearing trials, died within 30–50 days, whereas only one individual died before emergence in the treatments containing FPOM (Table 1). Many larvae in the CPOM treatments moulted once accompanied by some growth, but ceased to grow thereafter. Growth rates were approximately the same in the FPOM only and the CPOM + FPOM treatments (Table 2). *P. gregalis* therefore belongs in the gathering-collector functional group.

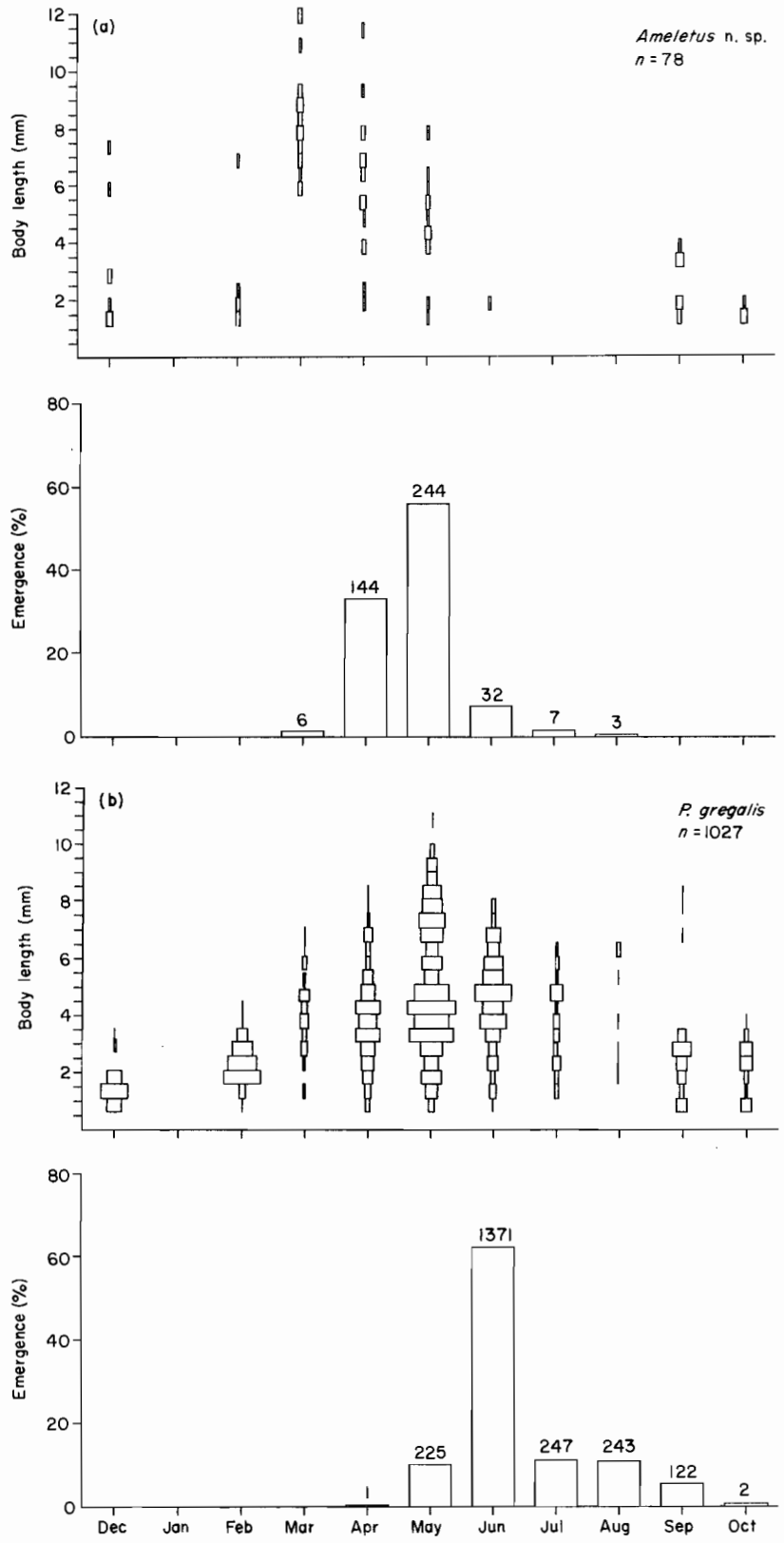


Fig. 2 Larval size distribution in benthic collections and emergence phenology of (a) *Ameletus n. sp.* and (b) *Paraleptophlebia gregalis*.

Most of the mayflies emerged within 70 days after the initiation of the experiment. During that period an average of 82% of the final larval body mass was gained. Male larvae had higher growth rates and shorter development times than did female larvae (Table 3). There was no negative correlation between larval size at the beginning of the feeding trials and growth rate ($R^2 = 0.09$; $P > 0.05$), and therefore no indication of compensatory growth by small larvae.

P. gregalis larvae used in the feeding trials were collected in late January. They were in the most common size class present at that time. Laboratory emergence was well synchronized (28 March–22 April), whereas field emergence was spread over more than 5 months and only 50% had emerged by mid-June (Fig. 3). Average subimago head-capsule width of reared animals was 1.19 mm (SE = ± 0.02 mm; $n = 12$). This was significantly less ($P < 0.01$) than the

size of early emerging subimagos. Laboratory-reared individuals also appeared to differ in size from the segment of the field population encountered in early July ($P < 0.07$).

Ostrocerca foersteri (Nemouridae)

O. foersteri eggs hatched shortly after the onset of flow in December and larvae completed their development within 5 months (Fig. 4a). There was some delayed hatching and early instar larvae were found until February. However, the presence of larvae in the temporary streams was restricted to the winter and spring flow period.

Emergence was comparatively well synchronized in *O. foersteri*. Adults first appeared in the traps in late March and continued to be collected through early June. More than 75% of the emergence was in April. Gravid females were encountered from mid-April to June (Fig. 4a).

Overall, 60% of the larvae reared in the CPOM treatment and 50% of the larvae fed both CPOM and FPOM, successfully completed development (Table 1). Larvae grew fastest on leaf material only, but the difference in growth rates between the two treatments was not significant (Table 2). The feeding trials demon-

Table 2 Comparison of larval growth on different food items. Growth is expressed as increase in head capsule width ($\mu\text{m day}^{-1}$) ± 1 SE

Species	FPOM	CPOM	Both
<i>Paraleptophlebia gregalis</i>	7.52 (± 0.25)	1.71 (± 0.17)	7.52 (± 0.12)
<i>Ostrocerca foersteri</i>	6.10 (± 0.46)	6.10 (± 0.46)	5.22 (± 0.42)
<i>Soyedina interrupta</i>	3.77 (± 0.14)	3.77 (± 0.14)	3.42 (± 0.18)

Table 3 Summary of results for growth rates, leaf consumption, time for development and adult size from two way ANOVAs (sex \times treatment, unbalanced data). Only individuals that successfully completed development are considered. Significance levels: * $P < 0.05$, ** $P < 0.01$

Species			Growth* ($\mu\text{m day}^{-1}$)	Size† (mm)	Duration‡ (days)	Consumption§ (cm^2)
<i>Paraleptophlebia gregalis</i> ($n = 16$)	Treatment	FPOM	7.63	1.32	62	–
		CPOM + FPOM	7.53	1.34	62	–
	Sex	Female	7.24**	1.31	66*	–
		Male	7.92**	1.34	58*	–
<i>Ostrocerca foersteri</i> ($n = 11$)	Treatment	CPOM	7.00	0.91	56	2.16*
		CPOM + FPOM	5.81	0.92	60	2.98*
	Sex	Female	6.08	0.95**	60	3.16**
		Male	6.73	0.89**	58	1.98**
<i>Soyedina interrupta</i> ($n = 35$)	Treatment	CPOM	3.69	1.43**	262	27.7
		CPOM + FPOM	3.58	1.47**	256	28.7
	Sex	Female	3.75	1.52**	272**	31.9**
		Male	3.52	1.37**	246**	24.5**

* Increase in head capsule width.

† Head capsule width of last instar larva.

‡ Duration from beginning of the experiment to emergence.

§ Leaf area consumed.

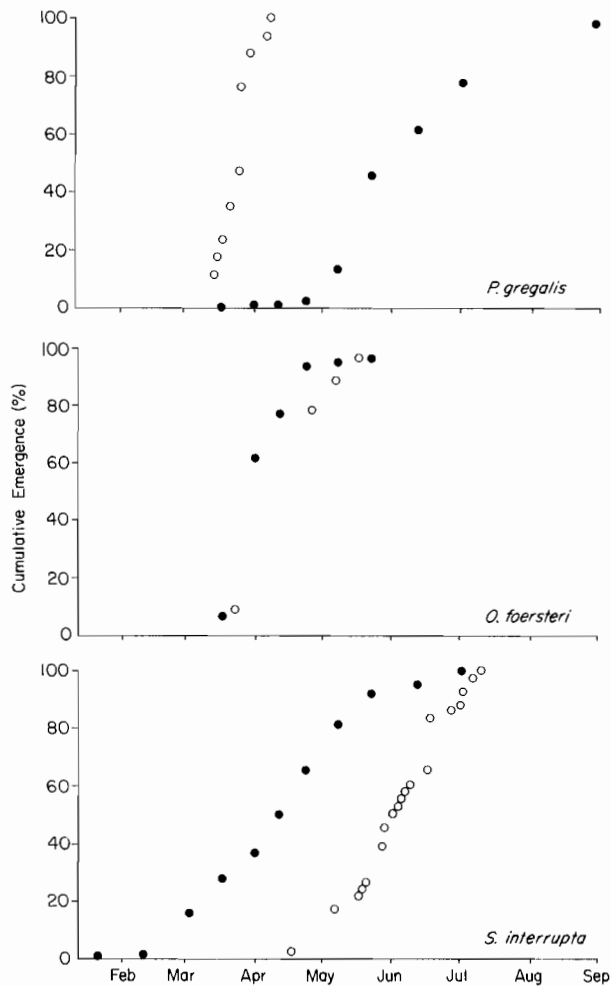


Fig. 3 Phenology of spring emergence in the feeding trials (○) and in the temporary stream (●).

strate that *O. foersteri* belongs to the shredder functional group.

Larvae matured within 60 days in the feeding trials. On average, they attained 83% of their body mass during that period. Female larvae consumed 3.2 cm² of leaf material. This corresponds to about 6.82 mg of conditioned leaf material as the leaf pieces offered in the trials averaged 2.13 mg cm⁻² (SE = ± 0.06 mg cm⁻²; n = 29). Consumption by male larvae was only 2 cm² of leaf material, and males were smaller than females at emergence (Table 3). There was no indication of compensatory growth by small larvae. Regression between larval size at the beginning of the experiment and growth rate did not yield a significant negative correlation ($R^2 = 0.21$; $P > 0.05$).

The timing of emergence was almost identical for *O. foersteri* from the temporary streams and for those

reared in the laboratory (Fig. 4a). Head-capsule width did not differ significantly between specimens from the laboratory culture ($\bar{x} = 1.04$ mm; SE = ± 0.02 mm; n = 6) and the natural system ($\bar{x} = 1.05$ mm; SE = ± 0.02 mm; n = 7). However, there was a difference in mass. Animals collected from the forest stream averaged 379 µg (SE = ± 32 µg), whereas mean mass was only 300 µg (SE = ± 12 µg) for adults reared in the feeding experiments ($P < 0.06$).

Soyedina interrupta (Nemouridae)

S. interrupta has an extremely variable life cycle. A wide range of larval sizes was present throughout the year. Early instar larvae were most abundant in May and June, but they also occurred from April to December (Fig. 4b). Spring hatchlings took about 10–12 months to mature. Field observations suggest that larvae survived the summer drought in moist, seep-like sections of the channels. Growth apparently is reduced or ceases in summer, but it is not clear whether diapause occurs.

The emergence period was extended, and included a major spring emergence and a minor autumn emergence (Fig. 4b). Gravid females were encountered from March to June and in September.

A high proportion of *S. interrupta* larvae completed development during the feeding experiment (68% in CPOM and 65% in treatments with CPOM and FPOM) (Table 1). Addition of FPOM did not enhance larval growth rates in the laboratory trials. Rather, average growth rates were slightly higher in the treatments lacking FPOM (Table 2). Thus, *S. interrupta* is considered to be a shredder breaking down CPOM by means of skeletonizing rather than biting chunks out of leaves.

Duration of development varied considerably but did not differ significantly between treatments. The first adult, a male, emerged after 185 days, whereas the last larva (a female) completed its development after 307 days. Female larvae on average took longer to mature, consumed more leaf material and grew significantly larger than did males, although sex differences in growth rates were minor (Table 3). A strong negative correlation was found between growth rate (Y) and initial larval size (X) (Fig. 5):

$$Y = 0.0053 - 0.0036X \quad (R^2 = 0.82; P < 0.01; n = 22)$$

Emergence of *S. interrupta* reared in the laboratory

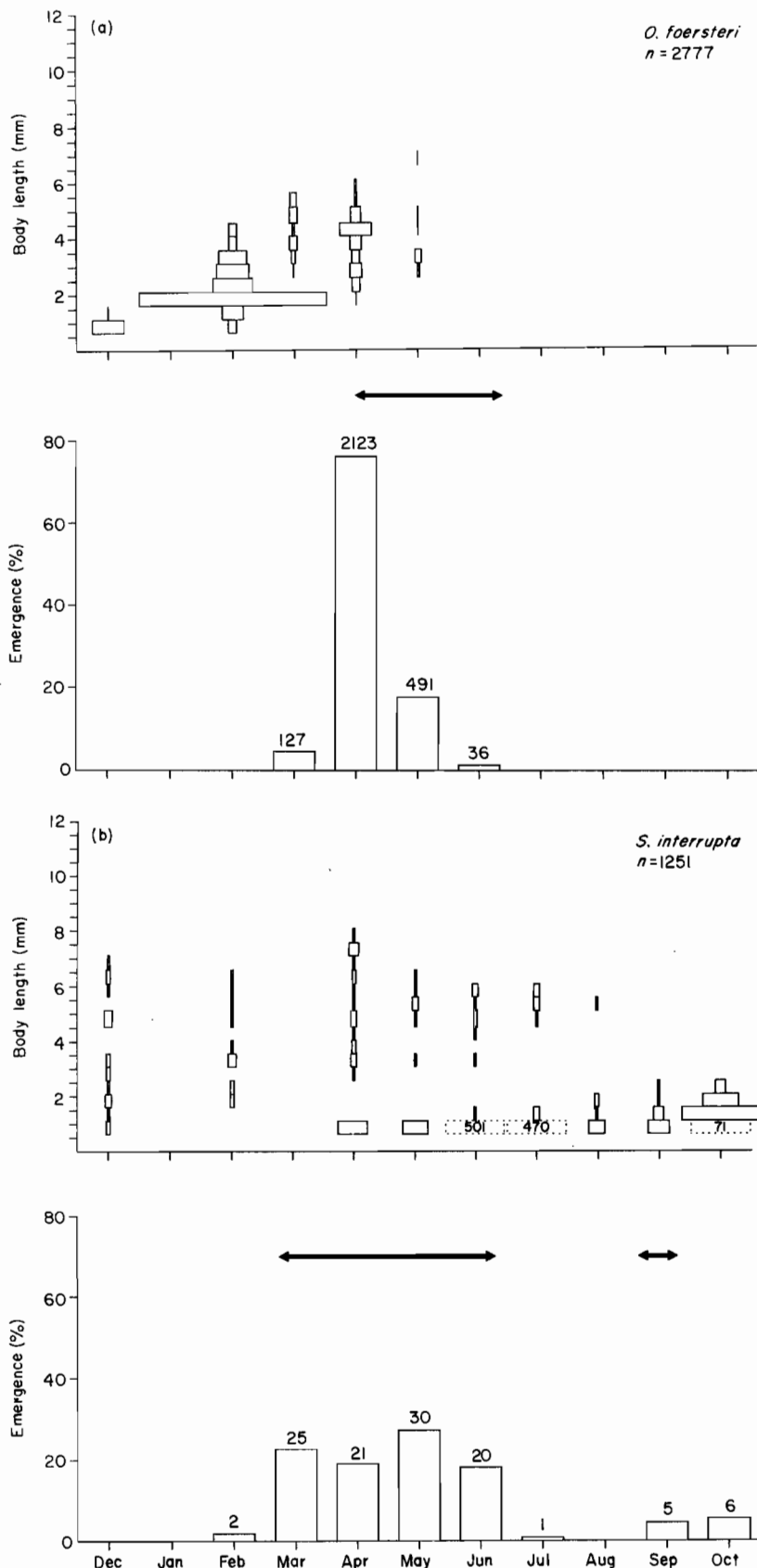


Fig. 4 Larval size distribution in benthic collections and emergence phenology of (a) *Ostrocerca foersteri* and (b) *Soyedina interrupta*. (The arrow indicates the period when gravid females were present.) In (b) dotted boxes represent numbers of larvae too large to be plotted on scale (actual numbers given in the boxes).

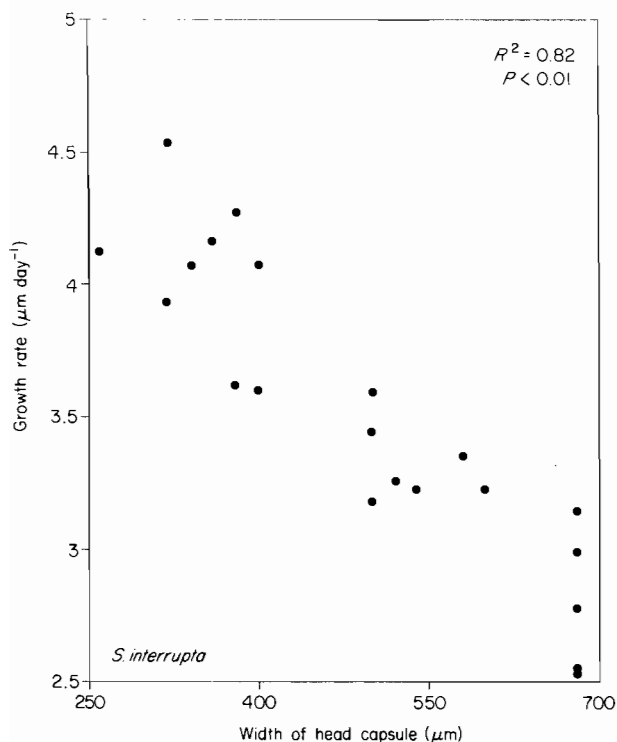


Fig. 5 Compensatory growth by *Soyedina interrupta* larvae. Correlation between head capsule width prior to the feeding experiments (September 1989) and growth rates during the trials (September 1989 – spring/summer 1990).

was delayed compared with that in the natural system (Fig. 3). Average head capsule width was 1.51 mm (SE = ± 0.02 mm; $n = 21$) for animals from the rearing trials and 1.50 mm (SE = ± 0.05 mm; $n = 6$) for animals collected in the field. Comparative weight data are not available.

Sweltsa fidelis (Chloroperlidae)

The life cycle of *S. fidelis* in the western Oregon temporary streams is rather complex. The common pattern was for eggs to hatch with the onset of flow in late autumn. Larvae then grew to about medium size before the following summer. The summer drought was spent in moist sections of the streams, presumably where the hyporheic zone was accessible. Growth was resumed in late autumn and completed by spring of the second year. The presence of early-instar larvae in April and the lack of a clear separation between generations in the December collection (Fig. 6a) suggests that some animals might have completed their life cycle within 1 year. This scenario

requires egg hatching in spring, larval growth until summer, a quiescent stage to survive the summer drought, resumption of growth in winter, and emergence of adults late in the following spring.

Emergence of *S. fidelis* was comparatively well synchronized, and restricted to 2 months in spring (mid-April–mid-June). Gravid females were encountered in May and June (Fig. 6a). Eggs were found before the onset of the summer drought. This supports the view that the species oversummers in the egg stage (regular pattern).

Attempts to keep *S. fidelis* larvae for an extended period in the laboratory were unsuccessful. Larvae did not ingest detritus or any kind of live prey. This suggests that *S. fidelis* could be a scavenger.

Calliperla luctuosa (Perlodidae)

C. luctuosa is semivoltine with a rather well-synchronized life cycle. Most larvae hatched in late autumn just after the onset of flow. However, early instar larvae were also found in spring (Fig. 6b). Growth continued throughout the year. The summer drought was survived in permanent pools or moist seeps. Mortality during the summer dry period appeared to be significant. Large larvae were rarely encountered in spite of the high numbers of small to medium-sized individuals present in the streams. About 100 larvae (average body length 5.5 mm) were collected in mid-July from a small puddle just about to dry out.

Adults emerged from late May until the end of July. Gravid females were collected in June and July (Fig. 6b) and eggs were found in the streams in late spring and early summer. The first year drought must therefore be survived in the egg stage.

Although no careful rearing was attempted, larvae could be maintained in the laboratory for several months. Larvae ingested live prey, preferably Chironomidae. Midge larvae trapped with the mandibles were seized and sucked into the gut within seconds, even those that were about the size of the predator. While *C. luctuosa* seemed to actively search for midges, mayfly larvae apparently were caught incidentally as they swam by.

Discussion

It has been proposed that ecological generalization is the best adaptation for life in temporary waters

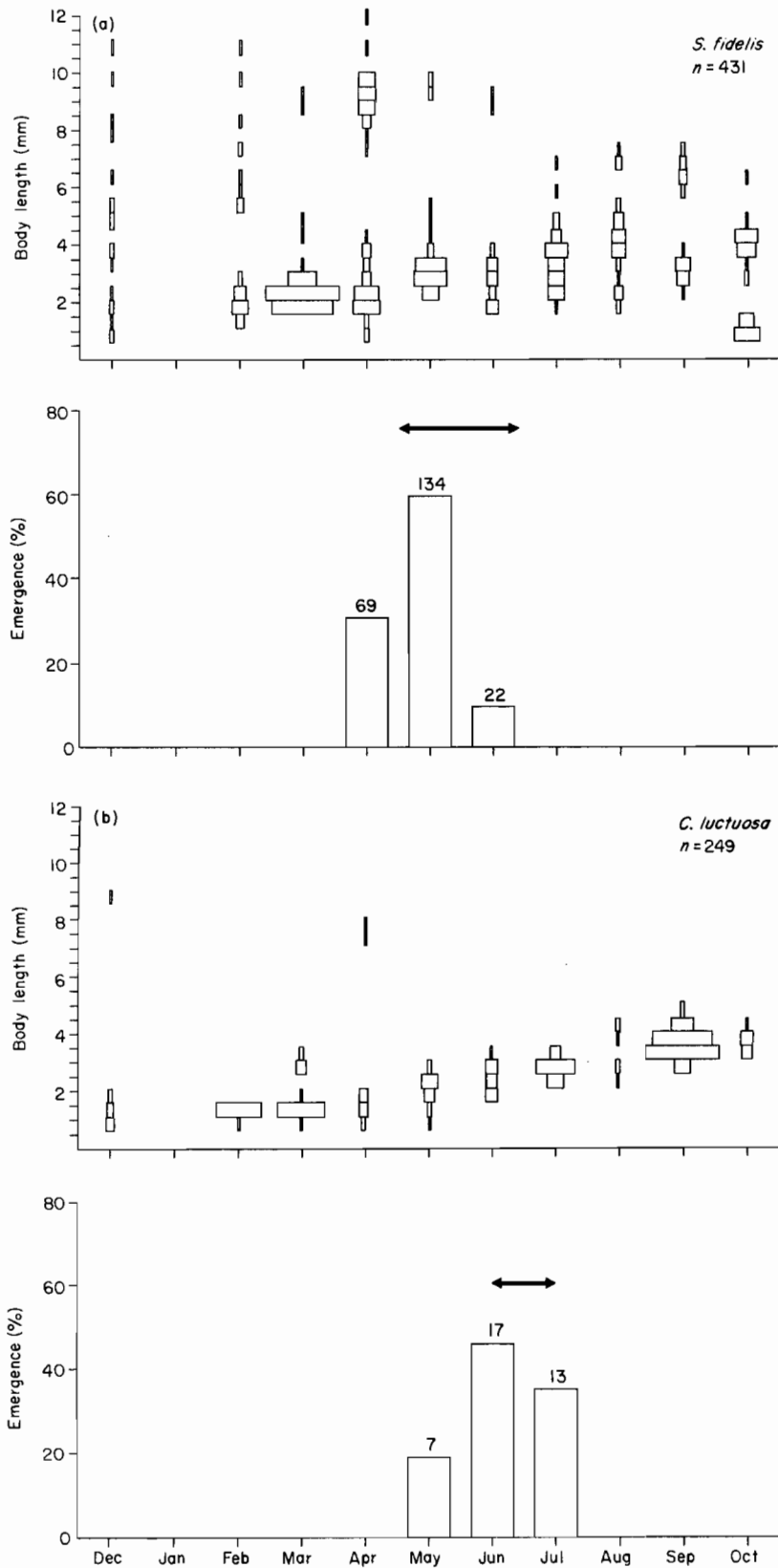


Fig. 6 Larval size distribution in benthic collections and emergence phenology of (a) *Sweltsa fidelis* and (b) *Calliperla luctuosa*. (The arrow indicates the period when gravid females were present.)

(Wiggins, Mackay & Smith, 1980; Boulton & Suter, 1986). The high degree of asynchrony that characterizes the life cycles of most mayflies and stoneflies common in western Oregon temporary streams is in accord with this supposition. Prolonged hatching and emergence periods, and the presence of a wide range of larval stages at any given time are basic components of life cycle plasticity.

Asynchronous development spreads life stages over time, thereby decreasing the risk of eradication by short-term catastrophic events (Hynes, 1970; Stewart & Stark, 1988). The spread of life stages over time may be particularly important in habitats such as temporary streams because there is the risk of premature drought in both winter and spring. During this study a drought in March/April 1990 resulted in the complete loss of the aquatic fauna in large sections of the channels. A pool of drought-resistant eggs present in the channels at any given point in time will allow for rapid recolonization.

In contrast to the annual summer drought, winter and spring droughts result from climatic stochasticity, and therefore are not predictable. The lack of predictability does not allow for life-cycle specialization to develop as a suitable means of winter and spring drought avoidance. Furthermore, drought during the main growth period of the aquatic organisms could be labelled a 'complete disaster'. It appears unlikely that organisms could broaden their short-term range of physiological responses enough to be able to cope with the complete and unpredictable loss of the aquatic milieu. The lack of predictability, combined with the severity of the catastrophic event for the stream benthos may provide a powerful force towards the maintenance of life-cycle plasticity and thus adaptability at the population level.

The tension between selection-caused optimization at the individual level, and the need to retain the highest possible degree of plasticity at the population or species level is an unresolved issue in ecological and evolutionary theory. This tension may be one of the root causes of ecological unpredictability in general.

Life cycle plasticity was pronounced in *A. n. sp.*, *P. gregalis* and *S. interrupta*. An extended hatching period in these species resulted in the presence of early-instar larvae during most of the year, and was the key to asynchronous development and prolonged emergence periods.

Differences in larval growth rates in *S. interrupta*

provided for some synchrony in emergence; larvae that were small at the beginning of the flow period grew faster than did larger individuals. A similar observation has been reported for black fly larvae by Zwick (1974). In the case of *S. interrupta*, however, complete synchronization at emergence was not achieved. As a result, there was a major emergence from mid-March to early June and a minor second emergence occurred during the autumn. This rather peculiar emergence pattern was also noted for *S. interrupta* by Kerst & Anderson (1974).

Synchronized emergence is a widespread phenomenon among insects. It facilitates the finding of mates, which is especially important in short-lived species (Downes, 1969; Savolainen, 1978), and reduces the exposure of adult individuals to predation (Corbet, 1957). The life cycle of *S. interrupta* can be regarded as a strategy to combine the advantages of asynchronous development with those of synchronized emergence.

The life cycle of *S. interrupta* contrasts with that of *Protonemura intricata* (Ris) reported by Marten & Zwick (1989). Variability in larval growth rates introduces asynchrony into the life cycle and differences in the duration of egg dormancy then help to synchronize hatching of *P. intricata*. Synchronized hatching in autumn will allow for effective resource use when food is plentiful. Asynchronous development then may allow for better use of resources when food supplies are low in summer and thus reduce intraspecific competition (Marten & Zwick, 1989). Furthermore, it will lead to risk spreading at the population level as different life stages are less likely to be affected in the same way by any particular kind of disturbance (Marten & Zwick, 1989).

In contrast, plenty of leaves and thus resources are available for *S. interrupta* larvae during their main growth period in spring. Leaves are not flushed out of these small retentive streams and the snail *Juga silicula* (Gould) is absent or in very low numbers in summer-dry headwaters. *J. silicula* is highly effective at shredding leaves and has been considered a competitive dominant in many streams of the Pacific Northwest (Hawkins & Furnish, 1987). The need for resource partitioning therefore does not appear to exert a strong selective force towards the maintenance of a desynchronized life cycle in *S. interrupta*.

Because of a prolonged egg diapause in summer, *O. foersteri* larvae were only found in the temporary channels during the 6-month flow period. Considering

the short time span that larvae were present in the system, a 3-month hatching and a 3–4 month emergence period can be classified as extended. In addition, variation of larval sizes in benthic samples increased rapidly as the season progressed. The life cycle of the species therefore is characterized by a high degree of plasticity within the constraints of its overall brevity.

Life-cycle patterns of *S. fidelis* and *C. luctuosa* contrast with those described for the univoltine species. Hatching occurred at about the time that flow began in late autumn, and emergence was restricted to 2–3 months in the spring. Both species depend on moist sections in the channel (seeps, summer pools) for first-year larvae to survive the summer drought. Size-class variation mainly resulted from two generations being present in the streams for most of the season. However, in *S. fidelis* the presence of early instar larvae in April and the wide variation of larval sizes in December suggest that both univoltine and semivoltine life cycles could occur. This would represent a somewhat different form of plasticity in this species. Similarly, *Leuctra ferruginea* (Walker) in eastern Canada is primarily a semivoltine species with a variable proportion of the population being univoltine (Harper, 1973).

The feeding trials show that larvae have to be reared to emergence for an adequate assessment of food requirements. Leaf material was consumed by *P. gregalis* larvae when no other food was available. As a result of what has been termed 'echo moulting' (Willoughby & Hurley, 1987) larvae reared on a CPOM diet moulted and grew during the initial phase of the experiments. But about 2–3 weeks after collection they ceased to grow and finally starved. Mattingly (1987) conducted her experiments for just 2 weeks without prior acclimation and erroneously concluded that *P. gregalis* was a shredder. Demonstrating that *P. gregalis* larvae are able to shred leaves does not by itself warrant the conclusion that they can actually grow on a CPOM diet. Rather, the ability to shred leaves allows *P. gregalis* larvae to self-condition their habitat by converting CPOM into faecal FPOM (M. Dieterich, unpublished data).

In *P. gregalis* and *S. interrupta* considerable differences were found in the duration of development between individuals reared in the laboratory, and those emerging from the stream. In *O. foersteri* the duration of development was similar for the laboratory and the field population. However, individuals from

the temporary stream were heavier than those successfully completing development in the feeding trials.

The rearing experiments were conducted under long-day conditions at 10 °C. The winter and spring temperature (December 1989–June 1990) in the stream from which the larvae had been obtained ranged between 6.0 and 12.0 °C (average 9.0 °C). Degree-day accumulation therefore cannot account for the observed differences in adult size and duration of development.

Photoperiod rather than temperature best explains the rapid development of *P. gregalis* larvae in the experimental trials. Dingle (1972) showed that increase in day length was negatively correlated with the time needed for development in the milkweed bug *Oncopeltus fasciatus* (Dallas). Accelerated development under long-day conditions has also been observed for several damselfly species (Ingram & Jenner, 1976; Procter, 1973) and the caddisfly *Chaetopteryx villosa* (Fabr.) (Wagner, 1990). In contrast to a temperature-based model, regulation of development by photoperiod would also explain why size of *P. gregalis* subimagos first decreased as the season progressed, and then increased slightly after a minimum in early July.

P. gregalis was the last of the major lotic taxa to emerge from the temporary streams and therefore was most vulnerable to mortality caused by the onset of the summer drought. Acceleration of development as day length increases enables this species to reduce the risk of death from drought at the expense of small adult size. In contrast, short days in spring allow for the continuation of growth, resulting in large adults when drought is least likely to occur.

The risk of unsuccessful development from an early summer drought is low in *O. foersteri* because emergence peaks in April. Thus, there is no strong selective force to develop sensitivity to increasing photoperiod. The change to long-day laboratory conditions did not appear to affect the duration of development. Reduced weights of adults may be a result of either oxygen stress or low food quality in the experimental trials. *O. foersteri* occurs only during the lotic phase of the temporary stream and is absent from summer pools or muddy seeps. The species therefore may be more susceptible to oxygen stress than either *P. gregalis* or *S. interrupta*. The higher growth rate and lower mortality in CPOM as compared to the CPOM + FPOM treatment supports this conclusion.

Both photoperiod and food quality appear to govern the rate of development in *S. interrupta*. Photoperiod is believed to induce egg dormancy and thereby differential growth rates in *P. intricata* (Marten & Zwick, 1989). Similarly, stage-specific sensitivity (egg stage or early-instar larvae) to photoperiod may have induced the different growth rates observed for *S. interrupta* larvae. However, there is as yet no direct experimental evidence to support this hypothesis.

Food quality has been shown to affect the growth rates of many detritivores (Anderson & Cargill, 1987). Time for development increases as food quality decreases. In their natural habitat, *S. interrupta* larvae can be selective with respect to choosing food particles. In the laboratory experiments the choice was between two 1-cm² pieces from just two different leaves. A consistent preference for pieces originating from one particular leaf was often observed in the assays. Larvae apparently discriminate between food items suggesting the capability of selecting between food qualities. The choice in the experiments was limited, whereas in the field larvae can choose between numerous leaves and thus food qualities. The wider range of choice may allow for more efficient foraging and thus faster development.

Oxygen deficiency is believed to have hampered the rate of development of *S. interrupta* less than that of *O. foersteri*. The former is frequently encountered in muddy seeps and therefore has to be able to withstand low dissolved oxygen concentrations. Mortality of *S. interrupta* in the rearing experiments was low. However, as in *O. foersteri*, growth rates were somewhat lower in treatments containing FPOM than in those with leaf material only, and adult size differed significantly between treatments. Thus, oxygen stress may depress growth rates but by itself it appears to be insufficient to explain a developmental delay of almost 2 months for the laboratory-reared individuals.

The comparison of results from laboratory rearing and field collections illustrate the difficulty of elucidating which factors are dominant determinants for rates of development in aquatic insects. Food quality, photoperiod, temperature, oxygen availability and other variables may be involved. The dominant determinant, however, will probably be species-, and possibly site-specific. In particular, the effects of temperature and photoperiod are difficult to separate from field data alone, because of the mutual dependency of these parameters.

Stoneflies and mayflies from temporary streams proved to be well suited for laboratory rearing mainly because the animals are easily maintained in artificial environments. Much may yet be learned concerning the regulation of stonefly and mayfly life cycles using temporary stream species in controlled experiments specifically designed to assess the effects of temperature, photoperiod or food quality on larval development.

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