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Influence of food quality and temperature on life history characteristics of the parthenogenetic mayfly, *Cloeon triangulifer*

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SUMMARY. 1. Laboratory and field data indicate that *Cloeon triangulifer* McDunnough has at least three generations per year in White Clay Creek (Pennsylvania, U.S.A.).

2. The duration of the egg stage ranged from 5 days at 30°C to about 90 days at 10°C.

3. Larvae completed development (i.e. first instar to adult) in 27 days at 25°C, 45 days at 20°C, and 179 days at 10°C on an algal diet dominated by diatoms.

4. Larvae reared on hickory leaves completed development in 30 days at 25°C but died prior to metamorphosis at 10, 15 and 20°C.

5. Adult size (i.e. body length, wing length and dry mass) and fecundity were inversely related to rearing temperature for all laboratory and field experiments.

6. The significant interaction of food quality and temperature suggest that these factors may be important in understanding geographic variation in the life history of *C. triangulifer*.

Introduction

Cloeon triangulifer McDunnough (Ephemeroptera: Baetidae) inhabits slow flow or quiet water areas along the margin of White Clay Creek in Southeastern Pennsylvania, U.S.A. (39°51′N, 75°47′W). The species is known to occur throughout the northeastern United States and eastern Canada and can become abundant especially in impounded areas of small to intermediate sized rivers (Gibbs, 1973, 1977). Obligatory parthenogenesis seems to be the mode of reproduction for all populations studied to date. The absence of males was noted by both McDunnough (1931) and Ide (1937) when they described the adult and larva respectively. Gibbs (1977) confirmed parthenogenetic reproduction in *C. triangulifer* and discussed the possible effects of parthenogenesis on its emergence period.

This paper describes the life history of this species in White Clay Creek and provides experimental data concerning the possible influence of food quality and temperature on various life history characteristics.

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Methods

Egg development

The duration of egg development was studied by incubating individual egg clutches (≈300–1000 eggs per clutch) in glass museum jars (6.5 cm deep; 5.5 cm diameter) containing about 50 ml filtered (0.45 μm) stream water. Adult females deposited eggs into the jars almost immediately after the tip of their abdomen touched the water surface. Hatching success for each experimental temperature was much high-

er (generally >90%) when females were manipulated to oviposit directly rather than dissecting the eggs and placing them in jars. Eggs were incubated in environmental chambers kept at various temperatures (i.e. 10, 15, 20, 25, 30, 35±1°C) and at a constant 11 h photoperiod. Eggs were inspected daily for hatching; at least two egg clutches (range: two to ten) were incubated at each temperature. Although most eggs in a given clutch hatched during a 2–3 day period, a small percentage (i.e. ≈10–20%) hatched during the subsequent 4–6 weeks depending on temperature. This skewness for the frequency distribution of egg hatch within a clutch was the reason we chose 'days to first hatch' as the statistic to describe the duration of embryonic development. Hogg & Craig (1970) have shown the first day to be a sufficient statistic for a delay parameter.

The pattern of larval growth for the natural population during the autumn–winter–spring period was determined by periodically (every 2–8 weeks depending on season) collecting at least forty larvae from stream margin and pool habitat and determining the dry mass (60°C for 48 h) of each individual. Summer field samples, however, were difficult to interpret because larvae representing all sizes and stages of development were present throughout the summer.

Rearing experiments: White Clay Creek temperatures

To estimate the number of summer generations and pattern of larval growth during the summer, first instar offspring from the winter generation were reared to maturity in three polypropylene trays (45×24 cm, 20 cm deep) that were maintained at ambient stream temperatures by being partially submerged in a laboratory experimental stream continuously supplied with water pumped from White Clay Creek (150 l min^{-1}). About 200–400 first instar larvae were placed in each tray at the start of each rearing cycle. Temperatures within the trays were always within ±0.5°C of the creek which exhibits a 5°C diurnal temperature change in summer months and which ranges seasonally from 0 to 24°C.

An algal diet dominated by diatoms was provided as food for the larvae in most rearing trays. Diatoms were cultured on Plexiglass® plates (23×6 cm) by continuously pumping fresh stream water over their surface. The plates were kept on a wooden rack (1.2×2.4 m) at about a 45° angle facing South in a glasshouse. Depending on seasonal water temperature, approximately 2–6 weeks are needed to culture enough algae on a plate to make it suitable for use in rearing trays. One algal plate was placed in each tray. All plates were exchanged after 1 week, suggesting that food was not limiting in the trays. One plate was taken at random each week from the diatom culture system and the associated algae were preserved in Lugols solution. Microscopic examination of the preserved algae indicated a diatom-dominated community at all seasons. The principal species of diatoms were: *Achnanthes minutissima* Kütz., *Synedra rumpens* v. *familiaris* (Kütz.) Hust., *Synedra ulna* v. *oxyrhynchus* (Kütz.) Van Heurck, *Nitzschia frustulum* (Kütz.) Grün., *Nitzschia admissa* Hust., *Nitzschia kutzingiane* Hilse and *Nitzschia tropica* Hust.

Hilse and *Nitzschia tropica* Hust.

Three flourescent lights (40 W vita-lite®; Duro Test Co.) were suspended about 45 cm above each rearing tray. Lights were programmed with timers to provide photoperiods similar to ambient field conditions. White polyester screening fastened over each tray kept emerging adults confined until they were collected each day. Eggs taken from females of the first summer generation were hatched at creek temperatures and the larvae were reared to maturity as described above for the offspring of the overwintering generation. Thus, the number of summer generations was determined at natural temperatures and with diatoms provided as food.

Rearing experiments: constant temperature

Larval growth studies at constant temperatures (i.e. 10, 15, 20, 25 and 30°C) were performed in static, plastic trays (37×7 cm, 5 cm deep; Rubbermaid Co.) kept in environmental chambers at a constant 11 h photoperiod. One hundred first instar larvae were placed in each tray at the start of the experiment. At each temperature, two trays were provided with plates containing diatoms (cultured as described above) and two other trays were provided with hickory (mixture of *Carya ovata* (Mill.) Koch. and *C. ovalis* (Wangenh.) Sarg.) leaves. All

leaves were leached in stream water for several days and allowed to become colonized in the dark with microbial populations (i.e. bacteria, fungi, protozoa) prior to use as food.

Subsamples of larvae were taken at random from the rearing trays at various time intervals and measured (dry mass) to characterize the magnitude of larval growth for each temperature–diet combination. Netting above each tray captured emerging adults. Each adult was measured (wing length, total body length) and then carefully dissected and the dry mass of eggs and non-egg adult components (head, thorax, wings, etc.) was determined. The number of eggs per unit dry mass (mg) of egg tissue was predicted from the following equation which was derived empirically by counting out various numbers of eggs and determining dry mass (mg) on them (number of eggs $=44.6+0.1517$ (egg dry mass); $r^2=0.94$).

Experimental trays containing plates of diatoms were illuminated directly with a flourescent light (20 W at 12 cm distance), while experimental trays containing hickory leaves received indirect lighting. Filtered (0.45 μm membrane) creek water was used for all rearing trays. Water was changed twice a week. One glass microscope slide (5×7.5 cm) was placed in each tray at the start of the experiment in order to monitor possible algal contamination of the hickory leaf trays and to determine the viability of cells in the algal trays. Slides were collected and replaced every 21 days; slides were then extracted for 24 h at 4°C in 90% acetone. After centrifugation (10,000 *g* for 10 min at 4°C), chlorophyll *a* in the supernatant fluid was determined using the analytical protocol of Lorenzen (1967).

The degree of microbial (non-algal) colonization of whole leaf substrates was determined by taking ten 0.78 cm^2 cores of the leaves from each tray and extracting the ATP using the cold 1.0 M H_3PO_4 procedure of Karl & Craven (1980). ATP was assayed in a liquid scintillation counter operated in the non-coincidence mode (Stanley & Williams, 1969).

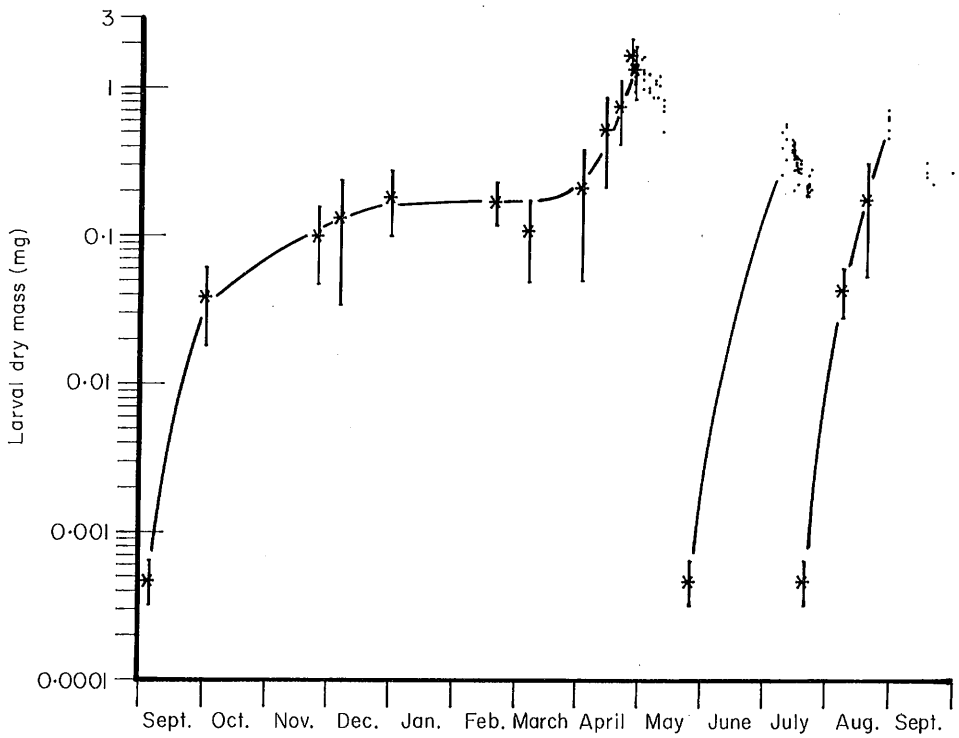

FIG. 1. Life history of *Cloeon triangulifer* in White Clay Creek showing the seasonal pattern of larval growth for each of the three generations. Asterisks and vertical bars indicate the mean and range of larval dry mass measurements; each small dot represents the dry mass for a single adult female.

Results

Life history

In White Clay Creek, *C. triangulifer* has a relatively long overwintering generation followed by at least two summer generations (Fig. 1). Adult emergence is synchronous for the overwintering generation. Most eggs from overwintering females are deposited during the first week of May and require about 18 days to hatch when kept at ambient creek temperatures (average daily temperature statistics for White Clay Creek from 1 to 18 May were: min. 11.0, avg. 13.9, max. 16.8°C). Larvae hatching in late May matured in about 43 days, with adults emerging during the second and third week of July. Eggs taken from these adults hatched in 9 days (average daily temperature statistics for White Clay Creek from 13 to 22 July were: min. 18.2, avg. 19.9, max. 21.9°C) and the larvae matured in about 37 days. Adult emergence of this second summer generation continued from late August until late September in our rearing trays. A few large mature larvae were also found occasionally in creek populations in October (not plotted in Fig. 1). We collected some of these large larvae on 1 October and attempted to rear them at ambient White Clay Creek temperatures but all specimens died by late autumn. No large larvae were present in field samples taken in late autumn.

In addition to obvious differences in the duration of each generation, adult size also varied considerably. overwintering females had 3 times the mass of summer generation females [average (SD)=1.21 (0.28) versus 0.37 (0.13) mg] which was highly significant statistically (t-test; $P<0.001$). No significant difference was found between average adult size for the two summer generations.

Egg development

Development time for eggs ranged from 5 days at 30°C to about 90 days at 10°C (Table 1). Eggs failed to hatch at 35°C even though partially developed embryos were observed. A power function best described the response of development time (days) to temperature (development time = 41165 (temperature)$^{-2.713}$; $r^2=0.96$). No significant difference in the rate of embryonic development was observed when eggs from the overwintering generation were compared with those from the summer generation at the same temperatures (e.g. 20 and 25°C). Thus, we combined these data in Table 1.

The length of the hatching period for *Cloeon* eggs decreased with increased temperature (Table 1). This suggests that eggs from the overwintering generation probably hatch less synchronously than eggs laid during the sum-

TABLE 1. Duration of the embryonic and hatching period as a function of temperature for *Cloeon triangulifer*

	Development time (no of days to first hatch)			Length of hatching period (days)	
Temperature regime	No. of egg batches	Avg. (SD)	Range	Avg. (SD)	Range
10°C	2	90.0 (4.2)	87–93	34.0 (14.1)	24–44
15°C	7	28.0 (6.8)	18–37	29.0 (11.3)	21–37
20°C	7	10.5 (1.2)	8–12	17.8 (7.5)	10–27
25°C	10	6.9 (1.5)	6–11	7.0 (1.7)	5–10
30°C	2	5.0 (—)	5	7.5 (0.7)	7–8
35°C	2	100% mortality			
WCC*	1	15.0 (—)	—	Not determined	
WCC†	10	9.2 (0.4)	9–10	19.2 (8.4)	7–34

* Eggs from overwintering generation incubated in May; average (SD) daily temperature (°C) statistics for the incubation period were: minimum 11.9 (1.3), average 14.5 (1.3), maximum 17.1 (1.8).

† Eggs from first summer generation incubated in July; average daily temperature (°C) statistics for the incubation period were: minimum 17.8 (0.9), average 19.6 (1.4), maximum 21.4 (1.9).

TABLE 2. Chlorophyll *a* and ATP levels measured for each diet–temperature combination during the experiment. Chlorophyll *a* determinations were performed about every 21 days. Most ATP measurements were made during the initial 52 days of the experiment.

		Chlorophyll *a* (μg dm^{-2})		ATP (ng mg^{-1} dry mass*)	
Temperature	Diet	*n*	Avg. (SD)	*n*	Avg. (SD)
10°C	Diatoms	14	0.26 (0.12)	5	263.6 (63.8)
	Hickory leaves	2	0	6	27.8 (7.1)
15°C	Diatoms	4	0.25 (0.18)	4	212.9 (66.0)
	Hickory leaves	2	0	4	37.6 (7.1)
20°C	Diatoms	2	0.13 (0.056)	2	337.0 (19.2)
	Hickory leaves	2	0	4	75.8 (27.3)
25°C	Diatoms	2	0.019 (0.000)	2	286.2 (11.0)
	Hickory leaves	2	0	4	35.1 (11.9)

* Dry mass of diatoms or hickory leaf depending on diet.

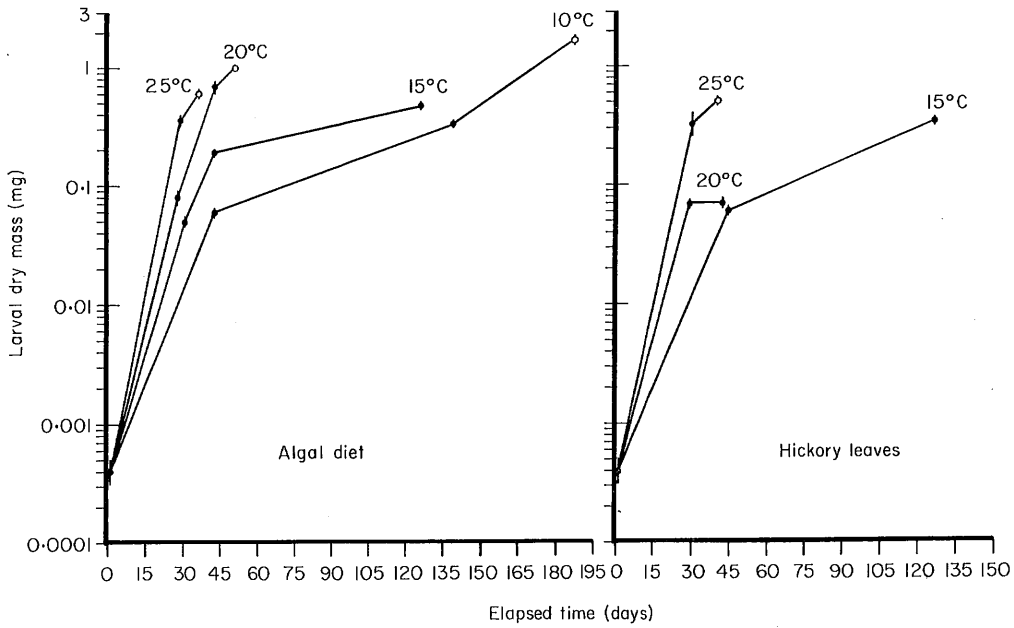

FIG.2. Pattern of larval growth and adult size for *Cloeon triangulifer* reared at different temperatures and diets. Mean and two standard errors of larval (closed circles) and adult (open circles) biomasses are shown for each temperature–sample date combination.

mer. Considerable variation in hatching synchrony may also occur from one marginal area to another along the stream due to thermal gradients caused by differences in flow rate and circulation through marginal alcoves and the amount of canopy shading. The prolonged recruitment of new larvae from the overwintering generation during May and June might partially explain why summer field collections had a wide size range of larvae and why adult emergence seems to be continuous during the summer in White Clay Creek and elsewhere (e.g. see Gibbs, 1973).

Larval growth studies

C. triangulifer larvae generally feed by gathering or scraping fine particles of organic material from the steam bottom or submerged structures.

The larvae do not utilize whole leaves directly as food, but readily ingest fine particulate floc composed of shredded leaves, algae and associated microbes. In our experiments, either algae (mainly diatoms) or whole hickory leaves colonized with microbes were provided as food to larvae at each of the experimental temperatures. We quantified microbial levels for both diets, using ATP analysis, and found that microbial levels did not vary significantly with temperature among algal diets (ANOVA; $P=0.15$). However, ATP levels were significantly different among hickory leaf diets (ANOVA; $P<0.05$), with leaves at 20°C having significantly higher ATP levels than at any other temperature (Scheffe test; $P<0.05$). We assume that ATP associated with leaves did not originate from algae because chlorophyll *a* was not detected on glass microscope slides incubated on the surface of hickory leaves in the trays (Table 2). Thus, there may have been a nutritional gradient among the hickory leaf diets due to the effects of temperature on growth rates of microbes.

The duration of the larval growth period decreased with increased temperature for all diets (Fig. 2). On algae, larvae completed development and began emerging as adults in 27 days at 25°C, 45 days at 20°C, and 179 days at 10°C. We report in Fig. 2, however, the median number of days until adult emergence because the frequency distribution of emerging adults was not consistently skewed to the right. A few larvae were approaching maturity by day 126 at 15°C, but mortality was increasing significantly among the larger specimens for some unknown reason. We decided to sacrifice all remaining larvae at 15°C for dry mass determination on Day 127 in order to gain as much information as possible concerning larval growth. Similarly, a subsample of specimens at 10°C was taken on Day 139 to characterize larval growth because we thought that all larvae would die before they were ready to emerge. We did, however, eventually get thirty-three adult specimens at 10°C for dry mass analysis.

Larvae reared on hickory leaf diets completed development and emerged at 25°C in about the same time (i.e. 30 days) as those reared on the diatom diet. However, larvae fed hickory leaves at lower temperatures either died shortly after the start of the experiment (e.g. 10°C) or during the experiment (e.g. sometime after Day 43 for larvae kept at 20°C). Growth was much slower

TABLE 3. Adult female size and fecundity measurements for individuals reared at various constant temperatures while feeding on either algae (mainly diatoms) or microbes (bacteria and fungi) associated with hickory leaves

	Algae, 10°C			Algae, 20°C			Algae, 25°C			Hickory leaf microbes, 25°C			
Study parameter	*n*	Avg.	(SD)	Range	*n*	Avg.	(SD)	Range	*n*	Avg.	(SD)	Range	*n*	Avg.	(SD)	Range
Wing length (mm)	29	6.9	(0.3)	6.3–7.5	46	5.5	(0.2)	5.0–6.0	67	4.8	(0.3)	4.3–5.6	16	4.5	(0.2)	4.2–4.9
Body length (mm)	33	6.9	(0.4)	5.8–8.1	50	5.4	(0.4)	4.3–6.1	69	4.6	(0.4)	3.7–5.6	17	4.1	(0.6)	3.2–5.5
Dry mass (mg)	32	1.8	(0.4)	1.1–3.2	50	1.0	(0.1)	0.5–1.4	73	0.6	(0.1)	0.4–1.1	20	0.5	(0.1)	0.3–0.7
Fecundity	32	1275	(485)	667–3231	49	937	(180)	348–1546	71	574	(142)	272–1061	20	456	(87)	302–666

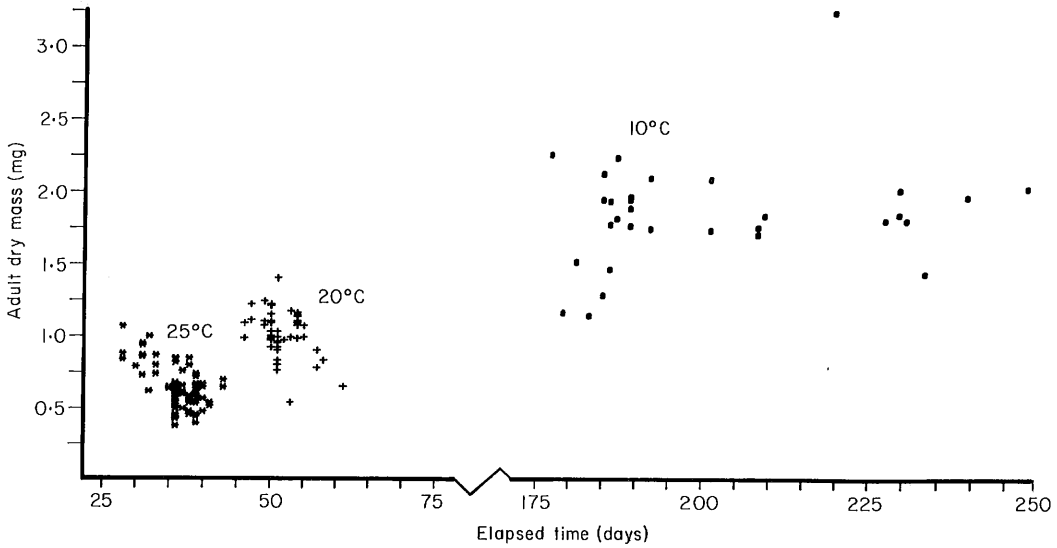

FIG. 3. The dry mass (mg) of adult *Cloeon triangulifer* when reared at different temperatures on an algal diet. Elapsed time indicates the number of days that were required for each individual to mature at a given temperature. Adult fecundity (Y) can be predicted from female dry mass (X) using the following equation: $Y=160.7+662.4(X)$, $r^2=0.78$.

and mortality higher at 15°C on the hickory leaf diet than on the diatom diet. For example, the rate and magnitude of larval growth on hickory leaves at 15°C was about the same as those at 10°C on the diatom diet by Day 126.

Adult size (wing length, body length and dry mass) and fecundity were very similar for individuals reared at 25°C on either hickory leaves or diatoms (Table 3). Adults reared at 20°C on diatoms, however, were significantly larger and produced more eggs per individual than adults reared at 25°C on either diatoms or hickory leaves (Scheffe test; $P<0.05$). Instantaneous growth rates (mg mg^{-1} day^{-1}) were higher for larvae reared at 25°C (relative to 10 and 20°C) but metamorphosis occurred before the larvae could attain a large size. Thus, larvae kept at 10 and 20°C grew at a slower rate but were able to grow larger because the onset of metamorphosis was delayed.

Although each experimental treatment was started on the same day with newly hatched larvae of similar size, there was considerable variation in adult size and fecundity as well as the timing of metamorphosis among the individuals. For example, adult emergence lasted about 2 weeks and adult size and fecundity decreased gradually during emergence at both 20 and 25°C on diatom diets (Fig. 3). At 10°C, emergence lasted almost 10 weeks but adult size did not decline. Because food was kept non-limiting throughout the experiment, variation in growth might be attributed to genetic differences among individual larvae, especially as all larvae in a given treatment were not necessarily siblings. We have no measure of genetic variability for *C. triangulifer* in White Clay Creek.

Discussion

Our results for *C. triangulifer* indicate that life history parameters such as larval growth, adult size and fecundity were affected significantly by both temperature and nutrition. It is difficult, however, to differentiate experimentally the relative importance of temperature and nutrition because temperature affects larval bioenergetics as well as the quantity and/or quality of food materials. For example, temperature can affect larval growth in natural populations directly by its influence on rates of feeding, assimilation and respiration, food conversion efficiencies, enzymatic kinetics and endocrine processes (Vannote & Sweeney, 1980; Sweeney & Vannote, 1981) or indirectly by altering the quantity (e.g. density and/or productivity of periphyton algae) and quality (e.g. microbial populations associated with detritus) of avail-

able food material (Cummins & Klug, 1979). In our study, microbial levels associated with hickory leaves varied with temperature. Thus, the failure of larvae to complete their growth in water <20°C on hickory leaves might have been due indirectly (poor nutrition) or directly (reduced feeding rates, low food conversion efficiencies) to rearing temperature.

Numerous workers have observed a positive correlation between larval growth rates of natural insect populations and water temperature (e.g. Humpesch, 1979; Mackay, 1979; Johannson, 1980). Controlled growth experiments in the the laboratory have also confirmed that larval growth rates generally increase with increased temperatures (e.g. Sweeney & Vannote, 1978; Ward & Cummins, 1979).

The effects of food on insect life histories have also been examined, with most aquatic studies focusing on larval growth of species that feed on whole leaf substrates (see Anderson & Cummins, 1979, for recent review). These studies have shown that larval growth can vary by a factor of 2 or more depending on the species of leaf that is provided as food (Cummins *et al.*, 1973; Iversen, 1974; Otto, 1974; Anderson & Cummins, 1979). The high preference and growth rates exhibited by aquatic insect species for certain leaf types may be related to the degree of colonization by microbes. Thus, a positive correlation between selective feeding and density of microbial flora, nitrogen content and respiration rate and ATP content per unit mass of leaf has been observed (see Anderson & Cummins, 1979; Ward & Cummins, 1979, for references).

The importance of associated microbes relative to the leaf itself with respect to larval growth is difficult to assess. Cummins & Klug (unpublished data cited in Cummins & Klug, 1979) report for a stream cranefly, *T. abdominalis,* that only 8.3% of the observed larval growth could be attributed to microbial biomass, even when the assimilation efficiency was assumed to be 100%. They also reported that *T. abdominalis* had nearly the same growth rate on sterile leaves as on leaves heavily colonized with microbes. Our data for *C. triangulifer* suggest that microbes associated with hickory leaves can supply a significant portion of their overall nutrition. For example, larvae grew, matured and metamorphosed successfully at 25°C when fed hickory leaves, even though no leaf shredding by larvae was observed and chlorophyll samples indicated no detectable contamination by algae. We assume that microbes were the primary source of nutrition in these experiments because ATP levels on the dead leaves were relatively high.

The unsuccessful growth of *C. triangulifer* larvae at low temperatures is not consistent with recent data on other aquatic insects. For example, Hanson *et al.* (1983) show that the caddisfly *Clistoronia magnifica* grew on alder leaves at 8.5°C but not at 17°C. They conclude that the 'dietary inadequacy' of alder leaves becomes *more* severe at high temperatures because of the increased metabolic demands of the larvae. For *C. triangulifer,* hickory leaves seemed to be *less* inadequate at higher temperatures. This suggests that the nutritive quality of hickory leaves may have increased with increased temperature, perhaps due to increased population levels of microbes.

The magnitude of larval growth was similar at 25°C regardless of diet. Temperatures below 25°C, however, resulted in either increased larval growth (diatom diet) or mortality levels at or near 100% (hickory leaf diet). Thus, growth of *C. triangulifer* on the two food types varied over the range of study temperatures. In contrast, Ward & Cummins (1979) reported that growth rates of a stream midge, *Paratendipis albimanus,* remained similar over a 10°C range of temperature.

The importance of diatoms in the diet of *C. triangulifer* was especially evident at intermediate temperatures (i.e. 15 and 20°C). For example, larval growth was substantially lower on hickory leaves (relative to diatoms) at 20°C. Other studies on aquatic insects have shown that larval growth rates can be increased significantly when detrital diets are supplemented with either animal material (Mackey, 1977; Anderson, 1978; Anderson & Cummins, 1979; Fuller & Mackay, 1981), algae (Fuller & Mackay, 1981) or wheat (Hanson *et al.*, 1983). We did not attempt to supplement the hickory diet with algae in any of our experiments.

Variation in adult size of *C. triangulifer* probably reflects the interaction of two highly temperature dependent processes—the duration of the larval growth period and the rate of larval growth during the period. Theoretically, if growth and development rates were affected to the same relative extent by a given change in

water temperature, then adult size would not vary significantly with rearing temperature. Available data, however, indicate that adults (or pupae) vary significantly in size with rearing temperature for *C. triangulifer* and a wide variety of other species (for references see Sweeney, 1984).

Our field and experimental data indicate that generation time (i.e. from egg deposition to adult emergence) for *C. triangulifer* can range from a minimum of about 30–35 days at 25–30°C to ≈270 days at 10°C. In White Clay Creek, we demonstrated that three generations per year is probably the maximum number possible within the constraints of the existing thermal conditions. Four generations per year might be possible in warmer streams at lower latitudes (i.e. <39°N). However, thermal regimes that are warm enough to support four generations per year might reduce adult size and fecundity below the threshold levels needed to maintain a viable population. Our results predict that in colder, northern streams, *C. triangulifer* may only have one or two generations per year. For example, Gibbs (1973) data from Ontario indicate two generations per year for *C. triangulifer,* with the species overwintering mainly as eggs which hatch in late May and mature by early July. Using our data concerning egg development and larval growth at specific temperatures and Gibbs (1973) data on ambient temperatures for the Ontario habitat, we predict that eggs from adults ovipositing in July would hatch in about 10 days and complete their larval growth by about late August. This coincides with the second peak of adults observed by Gibbs (1973) in late August and early September. The general agreement of predicted and observed geographic variation in the life history of *C. triangulifer* may be fortuitous, but may also reflect the relative importance of environmental gradients such as temperature and food quality to life history characteristics of this species in eastern North America.

Acknowledgments

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