

Seasonal synchronization of emergence in *Dolania americana* (Ephemeroptera: Behningiidae)

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This paper summarizes factors regulating seasonal emergence of *Dolania americana* in the Blackwater River, Florida, U.S.A. Emergence is temperature-dependent, and emergence on a given day can be predicted from the period of nymphal maturation and the pattern of temperatures on previous mornings. Development of the last two nymphal instars follows a pattern that can be interpreted linearly or by day-degree summations. Increases in water temperature at time of emergence (dawn) on the previous day provide the best correlation with emergence. Different responses to temperature events that cue emergence probably result from the effects of different temperature regimes in which the different populations develop. In experiments, males emerged equally 1 and 2 days after increases in the daily low water temperature, while females emerged more frequently after 2 days of increasing temperatures.

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Cet article résume les facteurs qui régularisent l'émergence saisonnière de *Dolania americana* dans le fleuve Blackwater, en Floride, E.-U. L'émergence dépend de la température et l'émergence un jour donné est prédictible en fonction de la période de maturation larvaire et des fluctuations de température les matins précédents. Les deux derniers stades larvaires suivent un modèle de croissance qui peut être interprété linéairement ou suivant la courbe cumulative des degrés-jours. C'est l'augmentation de la température de l'eau au moment de l'émergence (aurore) du jour précédent qui présente la plus forte corrélation avec l'émergence. Les réactions différentes des diverses populations aux fluctuations de température qui gèrent l'émergence dépendent probablement des régimes thermiques auxquels ces populations ont été exposées durant leur développement. Au cours des expériences, la proportion des mâles qui émergent un jour après l'augmentation de la température minimale de l'eau était égal à la proportion de ceux qui attendaient deux jours, alors que les femelles avaient plus tendance à attendre deux jours.

Introduction

Synchronization of emergence is common in mayflies (Ephemeroptera), and emergence patterns for species are widely reported and discussed (review in Brittain 1982). Although maturation, temperature, and light are of recognized importance, biologists are only beginning to understand factors influencing mayfly emergence at a given date and time (Riederer 1985).

Dolania americana Edmunds and Traver, the only North American member of the sand-burrowing family Behningiidae, has a highly synchronous seasonal emergence pattern (Peters and Peters 1977; Harvey et al. 1980; Sweeney and Vannote 1982). There is no evidence of parthenogenesis in the species (Peters and Peters 1977; J. G. Peters, W. L. Peters, and T. J. Fink, unpublished data). The adult life of mated females is less than 15 min, but can extend to 1 h for unmated females, and up to 2 h in special circumstances (Sweeney and Vannote 1982; J. G. Peters, W. L. Peters, and T. J. Fink, unpublished data). Thus, synchronized emergence of males and females is essential. In this paper, we use experimental data and 14 years of field records to summarize those factors involved in the seasonal timing of emergence.

Methods

Methods and localities are essentially as given or described in Peters and Peters (1977). The riverside study site on the Blackwater River, Okaloosa County, Florida, the source of quantitative field data, is abbreviated as R. Red Oak Bridge (RO), the farthest site upstream, is 1 km S of Alabama. Comparative data are available from Upper Three Runs (UTR), South Carolina, in Harvey et al. (1980) and Sweeney and Vannote (1982); one of us (T.J.F.) also recorded the 1978 UTR emergence.

All morning water temperatures were recorded with thermometers accurate to $\pm 0.1^\circ\text{C}$. All other temperature readings were also taken with these thermometers from 1983 to 1986, but before 1983, other readings depended on thermometers that were only accurate to $\pm 1^\circ\text{C}$. Sand temperature readings came from areas of 50–60 cm water depth and were taken 6–15 cm into the sand.

Weather records from Coldwater Tower, Division of Forestry, Florida Department of Agriculture and Consumer Services, 15 km W of the study site, include maximum and minimum air temperatures and rainfall from January 1975 to the fall of 1985, when the weather station was moved. Stage data from the Water Resources Division of the U.S. Geological Survey supplemented field records at the time of emergence. We continue to use the 22-year mean river depth to compare emergences between years, although mean depth has increased 6.7 cm since 1975; the median depth is about 20 cm less than mean depth.

Surface drift

We originally used a surface drift net of 1 m width (Peters and Peters 1977). In the middle of 1977, we changed to a net that collected only a 1/3-m section of drift. For comparison with other years, drift totals for 1976 were divided by 3. The estimate for exuviae in drift at mode + 4 days in 1976 was based upon total adults observed in drift from 50 min before sunrise until sunrise; adult numbers and percentages use these actual numbers.

The date of the largest number (mode) of adults in drift is treated as the date of peak emergence at the study site because it is least affected by predation (Sweeney and Vannote 1982) or by the upstream shift of emergence intensity, flow characteristics, and snags, all of which act to remove larger, broader objects such as winged adults from drift faster than smaller, streamlined objects such as exuviae (J. G. Peters, W. L. Peters, and T. J. Fink, unpublished data; Peters and Peters 1977). The adult mode is ineffective as an estimator if air temperatures are so low that males cannot complete the subimaginal molt (Peters and Peters 1986) or if air temperatures are cool (12°C) and adults modify their behavior to fly near the water surface where temperatures are higher (J. G. Peters, W. L. Peters, and T. J. Fink, unpublished data) and near the middle of the river, presumably for the same reason.

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Therefore, we supplemented all drift data with visual observations and light traps. Use of such methods verified that large numbers of exuviae may drift in the absence of any adult activity (rising water) and that a background exuvial drift (ca. 5/h) may continue for several days after large emergences. They further served as estimators on days when the bulk of emergence was slightly downstream of the drift net, or on days of high water when nets could not be used. The following visual estimates of emergence are compared against drift net totals for the 2.25-h period extending to 15 min after sunrise for 1-m nets (numbers adjusted for 1/3-m nets): + + +, large, exuvial drift total over 500, both sexes active and mating observed, or in times of adverse weather, numbers sufficient for mating; + +, moderate, exuvial drift total 101–500, as above; +, small, exuvial drift less than 100, as above; vs, very small, drift variable, little adult activity, as above. This category often includes special situations, e.g., temperatures near threshold, or emergence upstream with late arrival of males and females downstream; i, individuals, isolated individuals or all of one sex (usually male), or total number of opposite sex collected or observed ≤ 2 ; 0, no emergence (no adults present or observed).

Because exuviae continue drifting from upstream, we made approximations of sex ratio by stopping the count of male exuviae at sunrise and female exuviae 15 min later. This follows the different emergence patterns of each sex closely enough for comparisons between days within a season.

Day-degree estimates

The Blackwater River is a public recreation area and canoe trail, so thermometers or other equipment installed in the river are often lost. Day-degrees based on modified air temperatures, a method suggested by F. P. Ide (personal communication), were used to predict future emergence from past data. This "trial-and-error" method, developed for R in 1980 (from 1973–1979 data) and simplified in 1982, sums average daily air temperatures ((maximum + minimum)/2) and subtracts rainfall (1 cm = 3°C) for the period beginning February 1 until emergence. When mean daily January air temperatures exceed 11°C, the total number of degrees Celsius >11°C for January are added into the summation.

Morning and evening water temperature readings on the Blackwater River were available from February to emergence in 1981. We made water temperature readings for shorter periods in other years. Working from these data, we estimated average water temperatures from modified air temperatures to prepare day-degree summations.

Experiments

Nymphs were reared in 23- and 45-L aquaria with 2–3 cm of sand from the river bottom as substrate, air stones for aeration, Styrofoam coolers for insulation, and heaters, ice, ice packs, and water baths to modify temperature. Over the last 10 years, >1500 nymphs in >70 experiments and controls were used in these studies. Most data concern diel synchronization, although references are made to some of the data in this paper.

We reared small numbers of nymphs through the last instars in 5.5-L aquaria, with about 1250 cm³ sand and 2 L water; water was changed every 3 days. Nymphs were collected in early April in 1983–1986, and also in early March in 1984. About 10 nymphs were reared per aquarium with 14 replicates. Molts could be identified by cast exuviae on the surface or just under the surface of the sand. Experiments in 1983 were intended as controls for other work, therefore only mean values are available. When survival was high, we assumed that succession of molts into the last instar followed the same order as succession of emergence; when survival was low, we used the average between means for successive molts. Survival was highest in aquaria where nymphs were provided with weekly changes of river sand known to contain Chironomidae (Tsui and Hubbard 1979; Peters and Sponis 1983), although the exact level of food was not known. Sand in all aquaria was changed occasionally, usually twice a month. Water temperatures in the top centimetres of sand were recorded 2–6 times per day.

Other

Statistical comparisons use standard methods, χ^2 , t , binomial probabilities, paired comparisons, etc., as in Sokal and Rohlf (1969), and

the term "significant" is reserved for results where the probability of chance occurrence is <0.05. Day-degree lines were figured to the nearest 0.5°C critical temperature threshold, and best fit was calculated using the critical temperature giving the lowest percent standard deviation.

Some aspects of the biology of *Dolania americana* reported from both the Blackwater River (Peters and Peters 1977, 1986; Tsui and Hubbard 1979) and Upper Three Runs (Harvey et al. 1980; Sweeney and Vannote 1982) are generally accepted. References are given only when they refer to a particular study.

We use the term "adult" for all winged stages, i.e., male subimago and imago and female subimago (*D. americana* has no female imago, as the subimago is the reproductive stage). Unless temperature readings (air, sand, etc.) are identified, temperature refers to water temperature.

Review

Dolania americana is distributed in shifting-sand rivers and larger streams around the southeastern coastal plain from North Carolina to Louisiana (Edmunds and Traver 1959; Schneider 1967; Peters and Jones 1973; Ross and Jones 1979; Dakin and Felder 1981; Finn and Herlong 1980; Benke et al. 1984). However, large populations are known from only a few rivers in undisturbed condition, and the species has been included among the Rare and Endangered Biota of Florida (Peters 1982). Internal morphology was studied by Soldán (1979), protein composition by Basha and Pescador (1984), leg abscission by Peters and Peters (1986), life cycle and predatory habits by Tsui and Hubbard (1979), life cycle, emergence pattern, and bioenergetics by Harvey et al. (1980), and predator satiation and emergence synchrony by Sweeney and Vannote (1982).

Peters and Peters (1977) previously reported emergence patterns and adult behavior based on data for emergences from 1973 to 1975. Since then, additional research has shown some conclusions to be erroneous or incomplete, and the following corrections are necessary. (i) Emergence does not necessarily occur only when water is below mean depth (as in 1973–1975). We have since seen good emergences when depth was >1.25 m over mean depth, and peak emergence and most of the 1978 emergence occurred under flood conditions. (ii) Female subimagos and male subimagos and imagos can initiate flight from quiet water or from other stationary surfaces, as long as air temperatures are warm (>15°C). (iii) Male subimagos probably do not engage in patrol flights; our earlier interpretation confused emerging subimagos with imagos. (iv) It appears that male subimagos generally rest on vegetation or sand until they complete the subimaginal molt, although they sometimes molt on the water (Peters and Peters 1986). (v) Water temperature must be above 18°C the day before emergence, not on the day of emergence.

The following life cycle of *D. americana* is summarized from Tsui and Hubbard (1979), Harvey et al. (1980), and J. G. Peters, W. L. Peters, and T. J. Fink (unpublished data): synchronous adult emergence, mating, and oviposition; egg development lasting approximately 9–12 months, but prolonged recruitment that may carry a small part of the population to more or less than the 2-year egg to egg cycle²; nymphal growth in summer and fall, little to no overwinter growth (at which time development synchronizes), and rapid growth through spring until emergence. Populations in South Carolina differ from those in Florida in that a few, partially grown nymphs never mature to adults.

Nymphs feed largely in the top 5 cm of sand, where their prey

²We have seen a nymph hatch after 2 years in the egg, but the possibility of a shorter time is hypothetical.

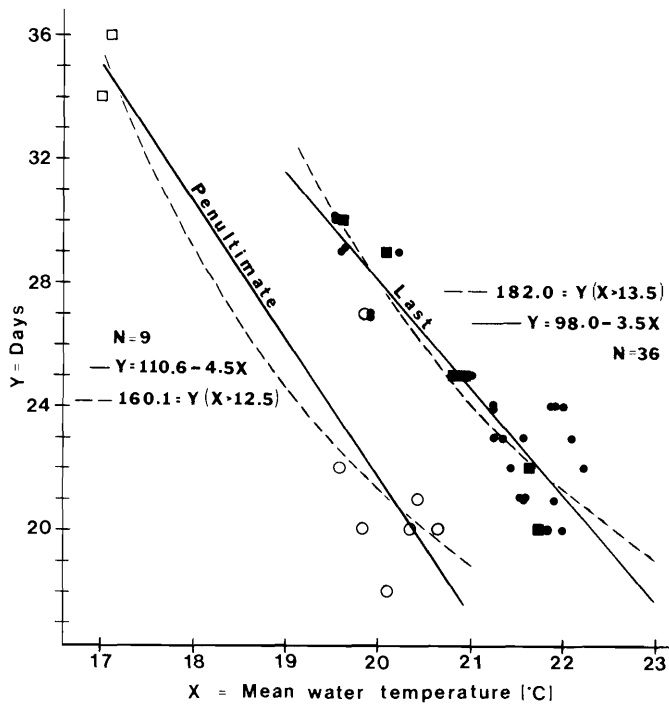


FIG. 1. Duration of development for aquarium-reared penultimate (○, □) and last (●, ■) nymphal instars of *D. americana*. For all lines, $r = 0.93$, $r^2 = 0.86$. Circles, individuals; squares, mean of several individuals (2–7).

(Chironomidae) are abundant. Near the middle of the last instar, nymphs cease feeding and move to deeper areas of the river and deeper into the sand (>10 cm), where they stay until emergence.

In experiments, we delayed emergence a week past natural emergence by exposing nymphs to temperatures below 18°C each morning, but we never continued these experiments long enough to measure survival. Similarly, experimental emergence could be advanced before natural emergence by rearing nymphs at warmer temperatures.

Results

Development of penultimate and last nymphal instars

In the Blackwater River, rapid maturation begins with the molt into the penultimate nymphal instar in March (Fink 1986). Figure 1 summarizes rearing data for several penultimate and last instar nymphs. Results can be interpreted either as linear within a temperature range or by the curvilinear day-degree pattern. Critical temperatures giving the best fit for day-degree models were 12.5°C for penultimate instars ($N = 9$) and 13.5°C for last instars ($N = 36$). Within the temperature ranges used (*similar to natural temperatures*), both linear and curvilinear formulas fit the data.

The total range of emergence times at any temperature was 4 days, at least 2 of which could be attributed to the absence of strong emergence-cueing water temperature changes. Diet was not standardized in the rearing experiments; however, we believe the growth data are accurate because (i) nymphs feed only in the first half of the final instar (Fink 1986), (ii) females maintain growth by ovariole resorption (Soldán 1979; Fink 1986), and (iii) day-degree figures for growth in experimental rearings matched estimates for growth based on water temperatures in the Blackwater River (see Discussion).

We counted eggs from mature female nymphs, reared only through the last instar, that died before or during emergence;

numbers averaged 39 ± 15 ($N = 13$) or 1/3 to 1/2 the number expected in natural populations (Peters and Peters 1977; Harvey et al. 1980; Fink 1986). Figure 1 does not include last instar growth data for nymphs reared through both the penultimate and last nymphal instars, because all males perished and ovariole resorption was severe in females. Females reared under lower temperatures died; development of those that emerged under higher water temperatures (21.2–21.0°C) required 26–28 days, 2–3 days more than other nymphs in Fig. 1, but apparently within the normal range, considering temperature patterns. The ability of the species to maintain consistent growth, even under severe stress, may contribute to synchrony of maturation and emergence.

Predictions of emergence based on day-degrees

Figure 1 demonstrates growth using either linear or day-degree formulas and gives no support to day-degree calculations starting at 0°C. However, in the Blackwater River, day-degree totals from 0°C predicted emergence more accurately than estimates using experimentally determined thresholds (Table 1). The summation of day-degrees is a curvilinear measure that applies over an “optimum” (Blunck 1923) or “medial” (Miller 1941) temperature range based on the relationship for any particular instar or stage (“duration in days \times temperature in °C (mean daily °C above critical cold point) = a constant” (Blunck 1923)). The method seems effective and is often used for mayflies, although growth is rarely consistent (Clifford et al. 1979), maximum development depends on optimum temperatures (Sweeney and Vannote 1978), and specific temperatures are often required at transitional stages (Clifford 1970; Svensson 1977).

A critical minimum temperature for *D. americana* growth is assumed, based on over-winter growth rates (Harvey et al. 1980), size-frequency histograms (Tsui and Hubbard 1979), and the fact that a correction was needed if mean January air temperatures exceeded 11°C/day. The threshold is probably between 11 and 12.5°C; also, 12.5°C is the threshold temperature that best fits developmental time of the penultimate nymphal instar (Fig. 1).

In 1981, 1450 water temperature day-degrees >0°C were accumulated from February 1 to peak emergence. Using these data and other readings, we estimated water temperatures for the 11 years of consistent temperature records (Table 1). We also refigured data from Fig. 1, combining the penultimate and last nymphal instars and assuming 12.5 and 11°C thresholds; at 12.5°C, mean time to emergence was 366 water temperature day-degrees, and at 11°C, the result was 439 day-degrees, similar to the mean of 437 day-degrees in Table 1.

Predictions of emergence using a 0°C threshold required a correction for years when average January water temperatures exceeded 12°C. Accuracy of day-degree totals >11°C beginning in March (the period of final maturation) can be improved to 11 days by deleting years with very warm temperatures in January and February. Without such modifications, thresholds from field data could not be used with any accuracy (Table 1). Clearly, day-degree totals did not measure development or developmental limits directly. They probably measured replicable seasonal patterns; within a narrow temperature range, these patterns would influence growth in a consistent manner (Sweeney 1984).

There were some data to support this suggestion. For 9 of the 11 years recorded, the range of predictive accuracy starting from 0°C was 6 days, or 3 days if we subtracted days in which water temperature patterns prohibited emergence. Eleven-year means

TABLE 1. Approximate water temperature day-degrees accumulated from winter to peak emergence at R, 1975–1985, using different possible thresholds (an average daily temperature of 21°C is used to estimate accuracy)

Threshold temperature (°C)	Starting in:	Day-degrees to emergence, $\bar{x} \pm SD$	Range	Range of accuracy (days)
0	Feb.*	1482 ± 57	1407–1593	9
	Mar.	1129 ± 96	917–1269	17
11	Jan.	437 ± 66	357–595	24
	Mar.	379 ± 63	246–464	22
12.5	Jan.	317 ± 58	252–412	19
	Mar.	289 ± 71	155–403	29

*Includes correction for high January water temperatures.

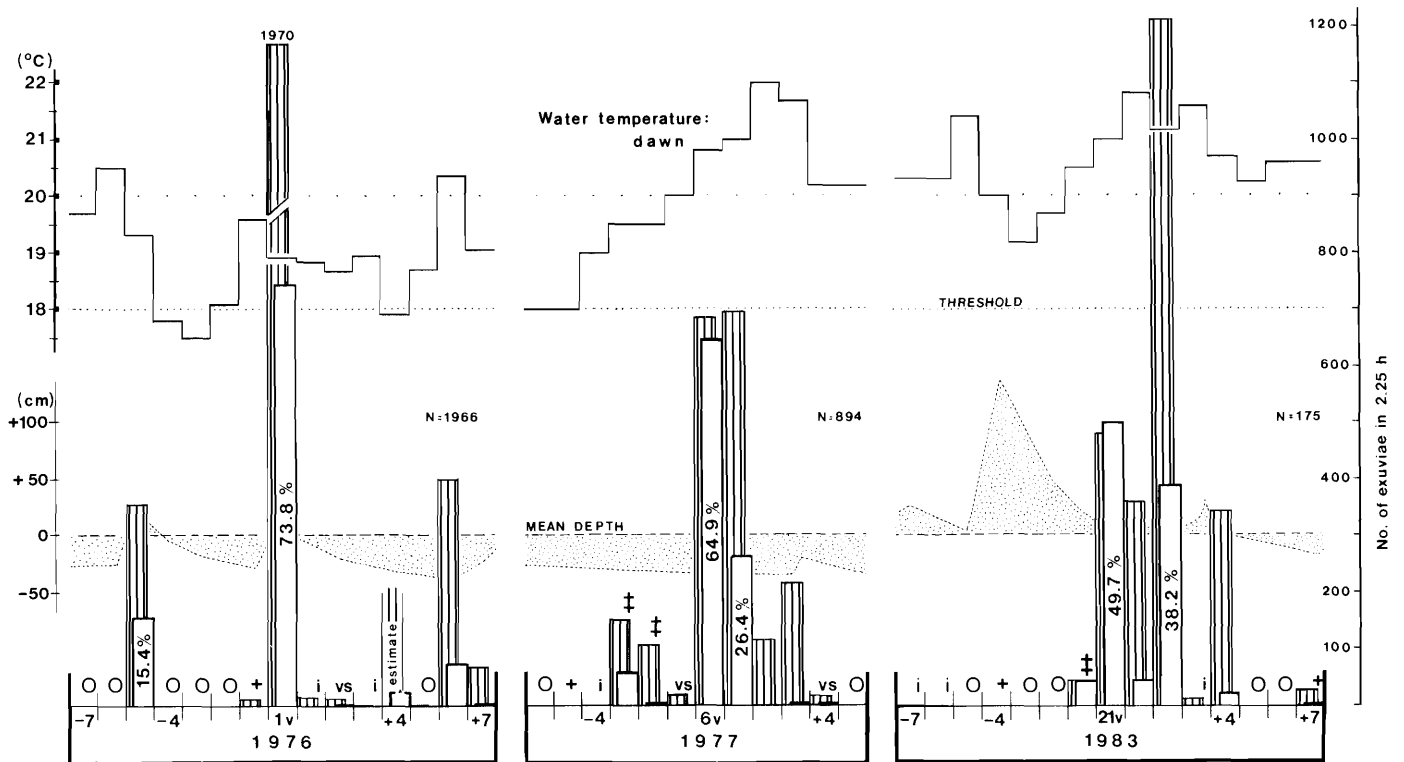


FIG. 2. Daily emergence patterns for *D. americana* at site R, Blackwater River, 1976, 1977, and 1983, based on numbers of exuviae and percent representation of adults in drift net (sunrise –120 to +15 min). Seasonal total of adults in drift (N) at right of each figure; date of adult mode on figure, other days numbered before or after mode. Dawn water temperatures were recorded 75 min before sunrise. Fluctuations in river depth are given in relation to 22-year mean depth. Visual estimate of emergence size: ++, moderate; +, small; vs, very small; i, individuals; 0, none. Dotted line at 20°C for orientation only.

in temperature and rainfall for the months of February, March, and April showed annual variations, but total variations for all 3 months exceeded the total seasonal standard deviations in 2 years only: 1982 was unusually warm and 1983 was unusually cool. In both years, emergence was delayed >3 days past the date predicted from water temperatures.

Emergence patterns

Figure 2 shows representative patterns for seasonal emergence of *D. americana* based on drift totals; the adult mode marks the date of peak emergence at the research site (R). Because drift actually measures the area immediately upstream, earlier dates are supplemented by visual records. In most years, the emergence mode and median coincided. However, in 1983 there were essentially two adult drift peaks, with the mode on the first peak (Fig. 2); a similar situation in 1975 produced a mode on the second peak.

From drift data, 2/3 or approximately ± 1 standard deviation of the emerging population at R emerged in 2 or 3 days. Based only on adult drift, 2/3 of the population on site emerged over two mornings, except in 1975 when emergence extended over three mornings (Peters and Peters 1977), and in 1976 (Fig. 2) when it appeared to be concentrated on a single day.

The patterns shown in Fig. 2 are sometimes treated as different emergence patterns: "sporadic" (1976) and "seasonal" with one (1977) and two peaks (1983) (Corbet 1964). For *D. americana*, these emergence patterns all resulted from responses to an environmental change in water temperature some 24 h before emergence.

Emergence cue

We have studied the effects of both light and temperature on emergence, but results showed that only temperature had any effect on the day emergence occurred (when nymphs were

TABLE 2. Relationship between changes in dawn water temperature (cue for emergence) from 48 to 24 h before emergence and size of emergence for *D. americana*, Blackwater River at R, 1976–1986 (only days within 7 days of mode and with above-threshold temperatures are included)

Size of emergence	% of emergences occurring when temperature (°C):					N
	increased, +1.7 to +0.4	was approximately equal			decreased, −0.4 to −2.4	
		+0.3 to +0.2	±0.1	−0.2 to −0.3		
Moderate–large (++, +++)	70.8	16.7	10.4	2.1	0	48
Small – very small (+, vs)	48.3	10.3	27.6	13.8	0	29
Individuals (i)	0	9.1	45.5	0	45.5	11
No emergence (0)	0	5.1	20.5	10.3	64.1	39
Average	37.8	11.0	20.5	7.1	23.6	127

mature). Nymphs reared experimentally at natural temperatures under constant darkness (five replicates), constant low light (0.02–0.03 lx, three replicates), and constant visible light (>1 lx, five replicates) emerged on the same day as controls.

Table 2 compares field data on emergence with temperature cues the previous morning, using all available data from R within 7 days of the adult emergence mode (1976–1986) where low temperatures were above threshold. Dawn water temperature changes from 48 to 24 h before emergence are treated as the emergence cue because they best predicted emergence.

If the average is treated as expected percentage representation, results obtained for emergence and nonemergence depart significantly from those expected (Table 2), except that the numbers for “individuals” were too low for analysis. Emergence was correlated with steady or rising dawn temperatures, and moderate to large emergences occurred significantly more often after temperatures increases $\geq 0.2^\circ\text{C}$.

Emergence is continuous as temperatures continue to rise (Fig. 2, 1977). From Table 2, emergence may also be continuous if temperatures remain constant. We have no field data, but emergence was continuous in constant-temperature experiments (J. G. Peters, W. L. Peters, and T. J. Fink, unpublished data).

An isolated individual, or several individuals of one sex, contribute nothing to the next generation. “Individuals” certainly occur more commonly than is recorded, but the chances of observation are low. Many records occurred outside the 7-day limits used for Table 2, the earliest being two males 17 days early in 1978 and one female 13 days early in 1976; the earliest record of one male and one female was 10 days before mode in 1976. The years 1976 and 1978 both had atypical weather patterns, 1976 (Fig. 5) with long cold periods, and 1978 with a cool period of record rainfall. Except for the cold-punctuated emergence of 1973 (Peters and Peters 1977), we have no records of individuals or emergence later than 9 days after mode (1984). For our studies, we consider the days where only individuals were present as days of nonemergence.

From data used for Table 2, the probability of emergence after temperature changes of $\geq 0.3^\circ\text{C}$ was almost 100% (54 of 55). The exception, an isolated female flying on the morning of 13 May 1984, occurred when temperatures were at threshold (low water temperature increase from 17.9 to 18.2°C). Proportions of emergence within the other intermediate categories were +0.2°C, 5 of 7; −0.2°C, 3 of 3; −0.3°C, 2 of 6; $\pm 0.1^\circ\text{C}$, 21 of 36. Results in some categories were pooled for Table 2 because of low numbers.

The threshold low water temperature (minimum necessary for

emergence) was reported as 18°C (Peters and Peters 1977). With the use of better thermometers in recent years, threshold for the population at R ranged from 17.8–18.2°C. Within this range, there was sometimes an emergence of individuals (often male) or a small emergence involving both sexes, but emergences of greater size only occurred when temperatures exceeded 18.2°C the morning before emergence.

Experiments with desynchronized temperature patterns

Delays between cue and event are implicit in studies of insect behavior and emergence (Corbet 1964; Nayar 1968; Saunders 1976; Beck 1980; Riederer 1985), and 24-h patterns are common. Time between cue and emergence for *D. americana* might be somewhat more or less than the observed 24 h.³

At R, the daily low water temperature usually occurred at sunrise; it occurred some hours later only if a strong cold front arrived overnight. As two potential marker events (dawn and daily low) occurred about the same time, with a similar degree of change from one day to the next, we could not distinguish the contribution of each.

We also questioned whether the change in temperature at the time of successive marker events, or mean temperatures over the 24-h period between markers, actually cued emergence. Under field conditions, these values frequently changed together. As the daily high water temperatures (used in the calculation of means) showed little correlation with emergence, it seemed that the actual temperatures rather than the means were most important.

Some resolution of these questions came from experiments with altered temperature and natural light. Figure 3, covering 4 hypothetical days, shows the method: nymphs were reared under natural daylight; water temperature was experimentally manipulated (continuous line) with elevated dawn temperatures and cold afternoon temperatures; emergence occurred at dawn for some individuals and near the time of the daily low for others. Marker events are labeled according to number of days before emergence, and possible cues are defined as the changes in water temperature between two successive markers, as follows: *low*, between lows on the 2nd and 1st day before emergence; *low-2*, between lows on the 3rd and 2nd day before emergence; *dawn*, between dawns on the 2nd and 1st day before emergence. Possible mean temperature values were measured

³The 12-h “gate” or phase shift to a dusk emergence never occurred in experiments with *D. americana*; in general, mayflies emerge around a single time of day, although flight activity times may be bimodal (Savolainen 1978).

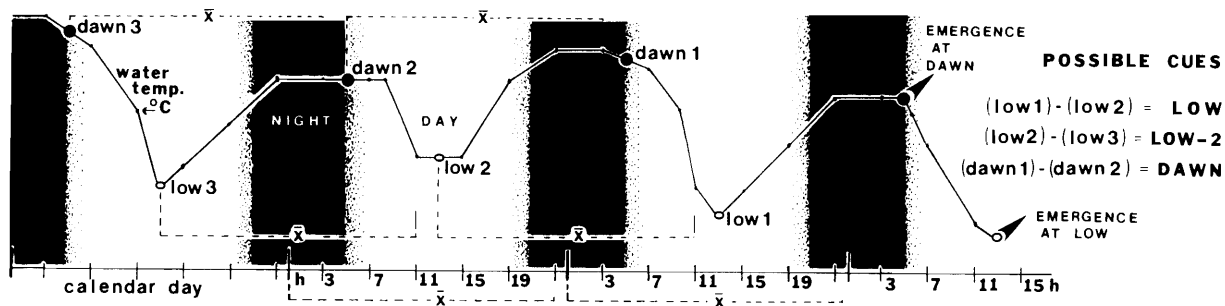


FIG. 3. Schematic of rearing experiments where daily water temperatures patterns were artificially manipulated. Marker events are labeled by number of days preceding emergence. Possible cues are defined as the changes in water temperature between successive marker events.

TABLE 3. Emergence of *D. americana* under natural light and manipulated water temperatures, 1979–1984; relationship between percent emergence and possible cues and mean temperatures over 24-h period between possible cue events

Possible cues positive or subequal ($\pm 0.2^\circ\text{C}$)	% emergence				Average ($N = 134$)
	at dawn		at low		
	♂ ($N = 42$)	♀ ($N = 56$)	♂ ($N = 13$)	♀ ($N = 23$)	
Cue, dawn	88.1	92.9	84.6	82.6	88.8
Cue, low-2	80.5 ^a	87.0 ^b	61.5	78.3	80.9 ^c
Mean, between lows	78.0 ^d	80.4	84.6	73.9	78.9 ^d
Mean, calendar day	76.2	80.4	92.3	56.5	76.1
Mean, between dawns	65.9 ^a	79.6 ^b	61.5	60.9	70.2 ^c
Cue, low	66.7	62.5	84.6	47.8	63.4

NOTE: Temperatures at natural dawn were elevated and lows occurred in the afternoon (see Fig. 3). Data given according to sex and time of emergence. See text for explanation of cues.

^a $N = 41$.

^b $N = 54$.

^c $N = 131$.

^d $N = 133$.

between dawn temperatures, between lows, and also for the calendar day.

Table 3 summarizes percentage frequency response to possible cue and mean temperature changes for material collected at R and RO in experiments through 1984, except for 13 adults that emerged within 2 days of collection. For each emerging adult, situations when the possible cue or mean temperature was in effect are totaled and expressed as a percentage. For adults that emerged at the low (in the afternoon), the previous low occurred 24 h earlier and there was a significant difference between male and female responses to cue low and to mean temperatures measured over the calendar day; for those that emerged at dawn, the cue low (from 13 to 17 h earlier, depending on the experiment) showed the poorest correspondence with emergence for both sexes. For dawn emergers, the cue low-2 (occurring an average of 39 h before emergence) was better correlated with emergence than the cue low. Mean temperatures calculated between lows were the best predictor of emergence among possible means, but the best single predictor of emergence was the temperature at dawn, no matter what time emergence actually occurred (Table 3).

However, when possible cues were analyzed individually (Table 4), isolated dawn temperature increases did not cue emergence. Table 4 uses the same data as Table 3, with the addition of one experimental replicate in 1986, and itemizes responses to possible cues in combination and individually (in

1986 we did not keep the kind of records necessary to also compute mean temperatures). There is a difference between male and female responses to an isolated low (Table 4, rows 3 + 5, male $N = 16$, female $N = 15$) compared with an isolated low-2 (rows 4 + 6, male $N = 13$, female $N = 34$). There were 12 replicates of these experiments, and we compared the 7 where a minimum of two males and two females emerged in the low or low-2 categories. When results are paired, $25 \pm 8\%$ fewer females than males emerged following a low cue ($t = 3.10$, $df = 5$, $p < 0.05$).

In Fig. 4, the total number of days with a potential emergence-cueing temperature change (low, low-2, or both) is compared with percentage emergence in each case. Male emergence was proportional to temperature cues, while females were underrepresented after temperature increases of 1 day and overrepresented on the 2nd day. Assuming a response to each potential opportunity is the expected norm, female delay was very significant ($\chi^2 = 12.20$, $df = 2$).

Note also in Table 4 a significant difference in response to cues involving only low temperatures (rows 3, 4, and 7) between material collected from RO and R. This difference (17.1 vs. 2.9%) is represented by low total numbers, but low temperature cues (in the absence of dawn temperature cues) seemed more effective in initiating emergence for populations at R than at RO.

We also looked at days without emergence. Considering only

TABLE 4. Emergence of *D. americana* under natural light and manipulated water temperatures, 1979–1986; numbers emerged are compared with combinations of temperature cues in effect

Row	Cues positive or subequal	Days		Days with emergence		% total emergence	No. emerged from:			
		N	%	N	%		R		RO	
							♂	♀	♂	♀
1	None	1	1.8	0	0	0				
2	Dawn only	4	7.1	0	0	0				
3	Low only	5	8.9	3	6.4	2.9	2	1		1
4	Low-2 only	1	1.8	1	2.1	2.2	1	2		
5	Dawn + low	12	21.4	11	23.4	19.4	8	8	6	5
6	Dawn + low-2	12	21.4	11	23.4	31.7	5	12	7	20
7	Low + low-2	5	8.9	5	10.6	5.0	3	3		1
8	All	16	28.6	16	34.0	38.8	14	11	11	18
Total		56		47			33	37	24	45

NOTE: R and RO, collection source of nymphs. For further explanation see Table 3.

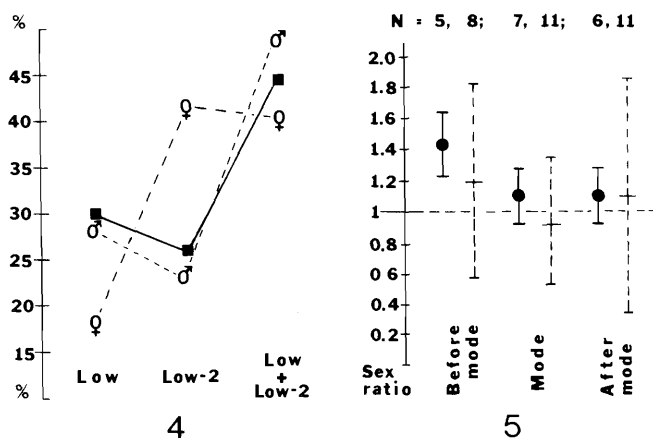


FIG. 4. Experiments with manipulated thermoperiod and natural light, 1979–1986: comparison of days temperature cue was in effect (■) and percent emergence of males and females. For terms see Fig. 3 and text; for numbers see Tables 3 and 4. FIG. 5. Observed sex ratio (*N* males:1 female) determined from exuviae (solid lines) and adults (broken lines) in surface drift, Blackwater River at R, 1975–1977 and 1979–1985. Mean and standard deviation, for adults, from 11 years' data; for nymphal exuviae, from 7 years' data. *N* = number of years with adequate data (≥ 10 males and ≥ 10 females) used for calculation.

days within the total experimental emergence period, a drop in low water temperature the previous day was the factor best correlated with an absence of emergence.

Nymphs in experiments excluded from Tables 3 and 4 emerged on the first opportunity after collection; low and dawn water temperatures in these experiments were below threshold (13–16°C) for 2–7 days, and most males and females emerged the day after temperatures rose above 18°C. Obviously, all cues and means increased (97–100%), except that the low-2 (85%) was below threshold. Similar results were obtained from other experiments, and most nymphs emerged at the first opportunity following days of below-threshold lows. However, in every case, a few delayed until the following day.

In one other experiment under natural temperature fluctuations and daylight, below-threshold temperatures of 16°C starting 6 h before and continuing through emergence did not prevent emergence.

Discussion

We can conclude that for mature nymphs, water temperature trends determined emergence, and dawn temperatures the previous morning were the best single predictor of emergence on a given day. An increase in the dawn temperature is the cue in effect 24 h before the time of emergence. However, this temperature increase does not operate in isolation but is normally accompanied by an increase in low (and other) temperatures over 1 or 2 days. Temperature on the morning of emergence is irrelevant. Riederer (1985) correlated emergence of *Rhithrogena semicolorata* (Curtis), *Ecdyonurus venosus* (Fabricius), *Baetis rhodani* (Pictet), and *Ephemerella ignita* (Poda) with the previous day's solar radiation, and obtained similar results. Water temperature trends will also explain the 1978 emergence of *D. americana* in UTR and more limited data from the Blackwater River at RO. Data are indistinct for the 1975 *D. americana* emergence at R, which probably reflects the poor precision of thermometers used that year rather than a different response by the mayfly. Temperature trends the previous day appear to account for the emergence pattern of *Ephoron album* (Say) documented in Britt (1962), although temperatures at critical times are not given. As *E. album* emerges at dusk, it would be interesting to learn if the low and dawn temperatures are also significant for *E. album*, or if the prediction of emergence is best reflected in the temperature 24 h before emergence, i.e., at dusk.

When water temperature changes were subequal ($\pm 0.2^\circ\text{C}$), we could not isolate any single factor that would conclusively predict emergence or its absence in any situation. Usually the mode and large emergences followed strong temperature cues (Fig. 2), and size of emergence showed a relationship to the amount of water temperature change (Table 2). In 1982, dawn water temperatures fluctuated just above threshold (18.4–18.8°C) for days before mode, and the mode was preceded by a small 2-day increase in dawn temperatures of only 0.2°C per day.

Another factor, presumably sand temperature, must be in operation. While awaiting emergence, nymphs are burrowed into the sand, not free in the water column.⁴ Water temperatures

⁴The actual water temperature threshold perceived at dawn by nymphs in an interstitial habitat is probably not 18°C but a higher value that is a function of surface water temperature; for practical purposes, we continue to refer to temperature without this qualification.

in sand are less extreme than temperatures of surface waters, higher than the low and lower than the high. Sand temperature fluctuations decrease with depth, and changes in water temperature are followed with some delay by changes in sand temperature (J. G. Peters, W. L. Peters, and T. J. Fink, unpublished data). Thus, when low water temperatures have increased for 2 days (even by a small amount, as in 1982), sand temperatures will also increase, but small fluctuations in water temperature will not necessarily be reflected in equivalent fluctuations in sand temperature.

Delays between cue and event may occur frequently in other mayflies, judging from numerous sources that match emergence with a "warming trend." However, as there is no female imago in *Dolania americana* (or *Ephoron album*), and females mate immediately after emergence, the cues initiating emergence also initiate mating and oviposition. In many other mayflies, there is a resting period during the subimaginal stage and a possible shift to other cues for swarming and oviposition. Even if the mechanism producing emergence is similar in genera with subimagos and imagos in both sexes, the cue sensitivity need not be as precise.

The short duration of the emergence season of *D. americana* results from tightly synchronized postwinter growth (Fig. 1). Based on limited data, it resembles the "staging" described by Svensson (1977) for *Ephemera danica* Müller. The fact that the second cohort of *D. americana* nymphs at UTR described by Harvey et al. (1980) lacked signs of sexual maturation, although they were physically as large as penultimate instar nymphs, may also indicate that a cold period at a critical stage is essential in the maturation of the nymph.

Acclimation to different thermoperiods may play a role in how *D. americana* responds to temperature cues. At R, the daily low water temperature normally occurred near sunrise. Upstream (RO), the river is canopied by trees and the daily low occurred some hours later. Temperatures have been recorded above 18°C at dawn but below 18°C later in the morning without seeming to affect the following day's emergence. Either this population had lower threshold requirements or the dawn temperature (not the low) operated as the threshold. We suspect the latter; nymphs in a different thermoperiod acclimated to the cue present at the time of emergence, i.e., the dawn temperature. Also, 97% of nymphs reared from RO (Table 4) emerged following dawn cues. According to Ward and Stanford (1982), "The thermal history to which an organism has been exposed shapes responses operative at the organismic, population, and community levels of organization"

Some males emerged days before females. Numbers were small and the overwhelming majority of both sexes emerged together, but proportions were not always equal: (i) seasonal representation of males, as expressed in the observed sex ratio in drift nets, was usually higher before the mode (Fig. 5); and (ii) in years where two large emergences occurred in sequence, the percentage representation of males was higher on the 1st day. Brittain (1982), reviewing emergence patterns of mayflies, stated, "There is a tendency for the cumulative emergence curve of males to lie somewhat ahead of the females'."

Early male emergence is common in insects, and the strategy is considered mutually beneficial to males and females, but in *D. americana* the terminology is somewhat inaccurate. Males do emerge earlier than females on a given day; however, experiments which accentuated the different responses of males and females showed females emerging later in seasonal patterns. Males tended to emerge in response to increases in the low

temperature 24 h or less before emergence, compared with 24 h or more for females. These differences were rarely so strong as to eliminate either sex, but there are many field records of days with visible shortages of females or males.

There are probably physiological differences; the male may be more sensitive to temperature cues or the female may require a longer period to complete the physical changes before emergence (for the male, some maturation occurs during the subimago stage). From the point of view of predator satiation (Sweeney and Vannote 1982), it is females participating in mass swarms that have the best chance of surviving to lay eggs. As early emergences are rarely very large (Fig. 2), there seems to be some reason for female delay.

Finally, the sexual difference in cue response is usually not such that the opposite sex is eliminated, and some individual variations in cue response of a population are necessary. Because temperatures that cue emergence occur 24–48 h earlier, and *D. americana* cannot anticipate or control climate at the time of emergence, adverse weather conditions might otherwise eliminate an entire population.

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- BASHA, S. M., and PESCADOR, M. L. 1984. Protein composition of the different life stages of *Dolania americana* (Ephemeroptera, Behningiidae). In Proceedings of 4th International Conference on Ephemeroptera, September 4–10, 1983, Bechyně, Czechoslovakia. Edited by V. Landa, T. Soldán, and M. Tonner. Czech. Acad. Sci. Inst. Entomol. (České Budějovice.) pp. 205–211.
- BECK, S. D. 1980. Insect photoperiodism. 2nd ed. Academic Press, New York.
- BENKE, A. C., VAN ARSDALL, T. C., JR., GILLESPIE, D. M., and PARRISH, F. K. 1984. Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. Ecol. Monogr. 54: 25–63.
- BLUNCK, H. 1923. Die Entwicklung des *Dytiscus marginalis* L. vom Ei bis zur Imago. 2. Teil. Die Metamorphose. Z. Wiss. Zool. Abt. A, 121: 171–391.
- BRITT, N. W. 1962. Biology of two species of lake Erie mayflies, *Ephoron album* (Say) and *Ephemera simulans* Walker. Bull. Ohio Biol. Surv. 1(5).
- BRITTAIN, J. E. 1982. Biology of mayflies. Annu. Rev. Entomol. 27: 119–147.
- CLIFFORD, H. F. 1970. Analysis of a northern mayfly (Ephemeroptera) population, with special reference to allometry of size. Can. J. Zool. 48: 305–316.
- CLIFFORD, H. F., HAMILTON, H., and KILLINS, A. 1979. Biology of the mayfly *Leptophlebia cupida* (Say) (Ephemeroptera: Leptophlebiidae). Can. J. Zool. 57: 1026–1045.

- CORBET, P. S. 1964. Temporal patterns of emergence in aquatic insects. *Can. Entomol.* **96**: 264–279.
- DAKIN, M. E., JR., and FELDER, D. L. 1981. A record of the mayfly *Dolania americana* in Louisiana (Ephemeroptera: Behningiidae). *Fl. Entomol.* **74**: 454–455.
- EDMUNDS, G. F., JR., and TRAVER, J. R. 1959. The classification of the Ephemeroptera. I. Ephemeroidea, Behningiidae. *Ann. Entomol. Soc. Am.* **52**: 43–51.
- FINK, T. J. 1986. The reproductive life history of the predacious, sand-burrowing mayfly *Dolania americana* (Ephemeroptera: Behningiidae). Ph.D. dissertation, Florida State University, Tallahassee.
- FINN, P. L., and HERLONG, D. D. 1980. New distributional record of *Dolania americana* (Ephemeroptera: Behningiidae). *Entomol. News*, **91**: 102–104.
- HARVEY, R. S., VANNOTE, R. L., and SWEENEY, B. W. 1980. Life history, developmental processes, and energetics of the burrowing mayfly *Dolania americana*. In *Advances in Ephemeroptera biology*. (Proceedings of 3rd International Conference on Ephemeroptera, July 4–10, 1979, Winnipeg). Edited by J. F. Flannagan and K. E. Marshall. Plenum Press, New York. pp. 211–230.
- MILLER, R. B. 1941. A contribution to the ecology of the Chironomidae of Costello Lake, Algonquin Park, Ontario. *Univ. Toronto Stud. Biol. Ser. No.* 49.
- NAYAR, J. K. 1968. The pupation rhythm in *Aedes taeniorhynchus*. IV. Further studies of the endogenous diurnal (circadian) rhythm of pupation. *Ann. Entomol. Soc. Am.* **61**: 1408–1417.
- PETERS, W. L. 1982. Phylum Arthropoda: class Insecta: order Ephemeroptera. In *Rare and endangered biota of Florida*. Vol. 6. Invertebrates. Edited by R. Franz. State of Florida Game and Fresh Water Fish Commission. University Presses of Florida, Gainesville. pp. 28–31.
- PETERS, W. L., and JONES, J. 1973. Historical and biological aspects of the Blackwater River in Northwestern Florida. In *Proceedings of 1st International Conference on Ephemeroptera*, August 17–20, 1970. Tallahassee, FL. Edited by W. L. Peters and J. G. Peters. Brill, Leiden. pp. 242–253.
- PETERS, J. G., and PETERS, W. L. 1986. Leg abscission and adult *Dolania* (Ephemeroptera: Behningiidae). *Fl. Entomol.* **69**: 245–252.
- PETERS, W. L., and PETERS, J. G. 1977. Adult life and emergence of *Dolania americana* in Northwestern Florida (Ephemeroptera: Behningiidae). *Int. Rev. Gesamten Hydrobiol.* **62**: 409–438.
- PETERS, J. G., and SOPONIS, A. R. 1983. A field method to quantitatively sample sand invertebrates. *Mem. Am. Entomol. Soc.* **34**: 241–247.
- RIEDERER, R. A. A. 1985. Emergence behaviour of some mayflies and stoneflies (Insecta: Ephemeroptera and Plecoptera). *Verh. Int. Ver. Theor. Angew. Limnol.* **22**: 3260–3264.
- ROSS, L. T., and JONES, D. A. 1979. Biological aspects of water quality in Florida. Part I. *Fl. Dep. Environ. Regul. Tech. Ser.* **4**(3). Tallahassee, FL.
- SAUNDERS, D. S. 1976. *Insect clocks*. Pergamon Press, New York.
- SAVOLAINEN, E. 1978. Swarming in Ephemeroptera: the mechanism of swarming and the effects of illumination and weather. *Ann. Zool. Fenn.* **14**: 17–52.
- SCHNEIDER, R. F. 1967. Mayfly nymphs from northwestern Florida. *Q. J. Fl. Acad. Sci.* **29**: 203–206.
- SOLDÁN, T. 1979. Internal anatomy of *Dolania americana* (Ephemeroptera: Behningiidae). *Ann. Entomol. Soc. Am.* **72**: 636–641.
- SOKAL, R. R., and ROHLF, F. J. 1969. *Biometry*. W.H. Freeman and Co., San Francisco.
- SVENSSON, B. 1977. Life cycle, energy fluctuations and sexual differentiation in *Ephemera danica* (Ephemeroptera), a stream-living mayfly. *Oikos*, **29**: 78–86.
- SWEENEY, B. W. 1984. Factors influencing life-history patterns of aquatic insects. In *The ecology of aquatic insects*. Edited by V. H. Resh and D. M. Rosenberg. Frederick A. Praeger Inc., New York. pp. 56–100.
- SWEENEY, B. W., and VANNOTE, R. L. 1978. Size variation and the distribution of hemimetabolous aquatic insects: two thermal equilibrium hypotheses. *Science (Washington, D.C.)*, **200**: 444–446.
- 1982. Population synchrony in mayflies: a predator satiation hypothesis. *Evolution (Lawrence, Kans.)*, **36**: 810–821.
- TSUI, P. T. P., and HUBBARD, M. D. 1979. Feeding habits of the predaceous nymphs of *Dolania americana* in northwestern Florida (Ephemeroptera, Behningiidae). *Hydrobiologia*, **67**: 119–123.
- WARD, J. V., and STANFORD, J. A. 1982. Thermal responses in the evolutionary ecology of aquatic insects. *Annu. Rev. Entomol.* **27**: 97–117.