Life-Cycle and Production of the Burrowing Mayfly, Ephemera danica: A New Method for Estimating Degree-Days Required for Growth

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LIFE-CYCLE AND PRODUCTION OF THE BURROWING MAYFLY, *EPHEMERA DANICA*: A NEW METHOD FOR ESTIMATING DEGREE-DAYS REQUIRED FOR GROWTH

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SUMMARY

(1) Growth, life-cycle and production of the burrowing mayfly *Ephemera danica* were investigated by taking monthly samples from April 1983 to June 1984 in the River Tud in Norfolk, U.K.

(2) A maximum likelihood method was used to estimate the number of degree-days required to complete nymphal growth. Minimum threshold temperatures for growth were estimated to be 2·6 °C for males and 3·1 °C for females. From the estimates of degree-days required to reach maturity and the temperature regime of the study site, it was concluded that some larger males should emerge as adults in 1 year, whereas the rest, and all females, should take 2 years to mature. This agrees with the pattern observed in size–frequency distribution of *E. danica* nymphs throughout the year.

(3) Predictions of time to emergence based on temperature data from other sites in Europe agree well with published accounts of the life-cycle of *E. danica*.

(4) Annual population production of the 2 year-classes of *E. danica* combined was 5·58 g dry weight m^{-2} $year^{-1}$, with the older year-class contributing about 85% of the total. Females accounted for 60–70% of production. Monthly production in summer was as much as ten-times that in winter. Production–biomass ratios showed relatively low values ($<2·1$), a pattern that may be general in semi-voltine species.

(5) The maximum likelihood method for estimating minimum threshold temperature and degree-days to complete growth can be used for aquatic and terrestrial insects in the field or laboratory.

INTRODUCTION

The mayfly *Ephemera danica* (Müller) is widely distributed in Europe. The nymphs inhabit both lakes and rivers with a sandy or gravelly bottom (Macan 1979). Various aspects of its biology have been reported, including adult emergence (Percival & Whitehead 1926; Harris 1956; Müller-Liebenau 1960; Thomas 1969), fecundity and oviposition behaviour (Percival & Whitehead 1926; Harris 1956; Landa 1969; Whelan 1980), life-cycles (Pleskot 1959; Landa 1968; Thibault 1971a; Sowa 1975; Svensson 1977) and long-term population dynamics (Wright, Hiley & Berrie 1981).

Despite this wealth of literature, no comprehensive understanding has emerged of the growth and life-cycle of *E. danica* over its whole range. Svensson (1977) reported that a fraction of the population in a southern Swedish stream completed a generation in 2 years, while the rest took 3 years. Thibault (1971a), studying in the Pyrenees, considered that some individuals completed their life-cycle in 1 year while the rest took 2 years to mature. In central Europe Landa (1968) in Czechoslovakia and Sowa (1975) in Poland reported a

2-year life cycle, whereas Pleskot (1959) in Austria and Jazdzewska (1971) in Poland suggested one generation per year. In Britain and Ireland, a 1-year life cycle was indicated by Peart (1916), Walker (1978) and Whelan (1980), all of whom studied lentic populations, whereas a 2-year life cycle was evident in the population of a southern English stream (Wright, Hiley & Berrie 1981).

The present study deals with the growth and production of *E. danica* in a stream in eastern England and introduces a new maximum likelihood method for determining the number of degree-days required to complete nymphal growth. The results are used in an attempt to account for variation in duration of the life cycle of *E. danica* in different parts of its range.

METHODS

Study site

The study was carried out in a wooded stretch of the River Tud (National Grid Reference TG 135 115), a tributary of the River Wensum that flows west to east for about 25 km before joining the latter near Norwich in Norfolk. The catchment area consists mainly of arable land and pastures. The study site was 40 m in length, with a width of 2–2·5 m and a depth of 30–50 cm although greater depths were recorded in winter with a maximum of 110 cm in early February. The substrate was composed of a layer, approximately 10 cm in depth, of silt with sand and gravel above an anaerobic layer of decaying organic matter. *Ephemera danica* nymphs occurred only in the top layer. pH ranged between 6·2 and 6·4 through the year and the flow velocity was normally between 30 and 60 cm s^{-1} at 60% of the depth. Temperature was recorded at 4 h intervals by a Grant Instruments automatic recorder and the weekly maximum and minimum temperatures are shown in Fig. 1.

Sampling methods

A random sample of ten sampling units was taken between the 4th and 8th day of each month from April 1983 to June 1984 using a box-type sampler that completely enclosed an
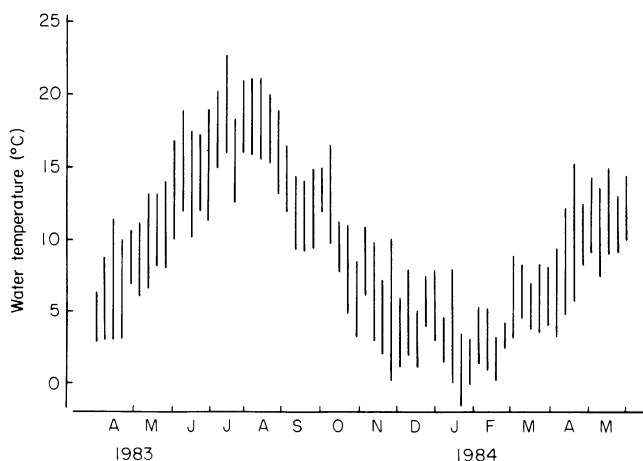

FIG. 1. Weekly maximum and minimum water temperatures throughout the study period.

area of 15 × 15 cm to a depth of approximately 10 cm. Additional samples were taken during the emergence period in summer 1983. The samples were sorted live in the laboratory and *E. danica* nymphs were placed individually in glass vials kept at 0–2 °C. Within 48 h of collection, measurements were made of body length (from the front of the head to the posterior edge of the last abdominal segment—to the nearest 0·1 mm) and of head capsule length (from the anterior to posterior edge—to the nearest 0·05 mm). Preservation in alcohol was avoided because of its distorting effect; some specimens shrink and others expand.

Measured specimens, starved for 48 h to evacuate gut contents, were dried at 60 °C for 24 h and weighed to the nearest 10 μg using a Kahn electronic microbalance. Dry weight (W mg) was related to body length (X mm) thus:

$$\log_{10} W = -2{\cdot}501 + 2{\cdot}860 \log_{10} X \quad (r^2 = 0{\cdot}86)$$

This equation is almost identical to that reported by Svensson (1977) in southern Sweden.

Nymphs more than 8 mm in length were sexed by examining the external genitalia on the ninth abdominal segment. The development of wing pads was also recorded.

Maximum likelihood estimates of the minimum threshold temperature and degree-days required for growth

Taking the August 1983 sampling occasion as the starting point ($t = 0$), sums of daily mean water temperatures over a given minimum threshold temperature for growth (MT) were computed for the September 1983 sample ($t = 1$) to the May 1984 sample ($t = 9$) for each sex of the 1982 year-class separately. August 1983 was chosen as the starting point because prior to that date it was impossible to sex every individual of the cohort. The sums obtained in this procedure, which constitute cumulative degree-days since August 1983, were designated as DD(0) (=0 for August 1983), DD(1), DD(2), . . ., DD(9). The analysis was repeated for a range of values for *MT*, at 1 °C intervals between −2 and +10 °C (and subsequently narrowed to 0·1 °C intervals between 2·5 and 3·5 °C). In each case, linear regression analysis was performed between the mean body length (*BL*) and the derived number of degree-days (DD). The value of *MT* which yielded the highest coefficient of determination (r^2) in the regression analyses was assumed to be the true minimum threshold temperature and was obtained for each sex separately. Note that linear regression proved appropriate in the present study, though there is no a priori reason to assume a straightforward linear relationship between body length and cumulative degree-days.

This procedure yielded estimates of degree-days above the minimum threshold required for nymphs of each sex to complete their second year of growth and reach maturity at a range of body lengths observed in the field. The regression line was then extrapolated back to provide an estimate of degree-days required from hatching (when body length is 0·6 mm, as determined in the laboratory) to achieve the body length recorded in August. The period of hatching was prolonged and, in addition, the smallest nymphs taken in the field were 1·5 mm long. Thus, a reliable estimate of degree-days required before the August sampling occasion could not be derived directly from temperature and size–frequency data.

Estimation of production

Monthly production was calculated using the formula of Ricker (1946):

$$P = \bar{B}G$$

where $\bar{B}$ is the arithmetic mean population biomass (dry weight) of the 2 adjacent months and G is the instantaneous growth rate given as:

$$G = \ln W_1 - \ln W_0$$

where W_1 and W_0 denote the geometric mean individual dry weight in month 1 and month 0, respectively. Calculations were made separately for different year-classes and, where possible, for different sexes. On occasions when negative production values were obtained, as a result of negative values for G, production was taken to be zero. Reductions in mean individual dry weight between months can be attributed to emergence, as adults, of larger nymphs.

RESULTS

Life-cycle and growth

Throughout the study period the population of *Ephemera danica* consisted of two year-classes. Within the older year-class, males and females differed in size. Thus, a trimodal size–frequency distribution was apparent, particularly from September 1983 onwards (Fig. 2). Nymphs with fully developed wing pads were present from the beginning of May until the end of August. Mass emergence of adults was observed in the first week of June; thereafter emergence continued at a low level until the end of August. Recruitment of newly hatched nymphs started in mid-summer and continued through to the next spring. Evidently, the bulk of the population passes through a nymphal life of approximately 2 years.

Increase in mean individual dry weight of both males and females was rapid between spring and autumn but almost ceased in winter (Fig. 3). Note that clear separation of year-classes was made possible after plotting body length and head capsule length together. Mean individual dry weight of females declined between May and June in both 1983 and 1984 as a result of emergence of large individuals. It is notable that a drop in mean individual dry weight of males occurred between July and August because some fast-growing, larger males of the 1982 year-class reached maturity and emerged, completing their nymphal life in just over a year. This was also evident in the size–frequency distributions, which indicate that males of more than 15 mm in length had disappeared by September 1983.

Maximum likelihood estimate of degree-days required to complete nymphal growth

Variation in the coefficient of determination (r^2) of the regression between body length and cumulative degree days, for different values of minimum temperature threshold, is shown in Fig. 4. The coefficient of determination peaked at a minimum threshold temperature MT of $2 \cdot 6 \,°C$ for males and $3 \cdot 1 \,°C$ for females, both having values of $0 \cdot 9798$. Thus, approximately 98% of nymphal growth, in terms of body length, can be accounted for by accumulated degree-days above $2 \cdot 6 \,°C$ for males and above $3 \cdot 1 \,°C$ for females.

The regressions for males at $MT = 2 \cdot 6 \,°C$ and for females at $MT = 3 \cdot 1 \,°C$ are illustrated in Fig. 5. The slope of the regression for females was significantly greater ($P < 0 \cdot 01$) than that for males.

These regression lines have been used to estimate the number of degree-days required from hatching to attain a given body length. The line was extrapolated back to a point equivalent to a body length of $0 \cdot 6$ mm; the size at hatching recorded in the laboratory. The
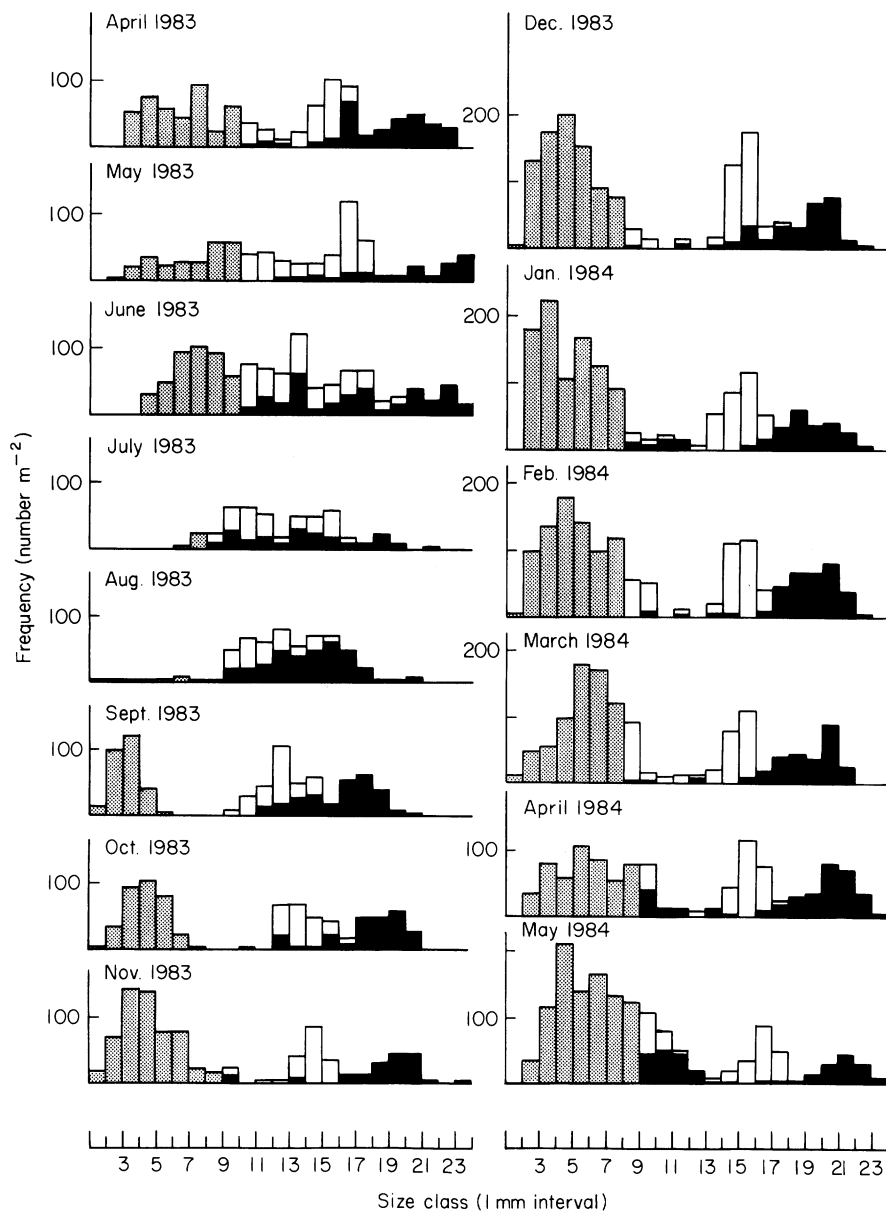
FIG 2. Size class-frequency histograms of nymphs of *E. danica* taken at monthly intervals: (■), females; (□), males; (▨), unsexed small individuals.

total degree days required to attain a body length of y is given by $(y - 0.6)/b$, where b is the regression coefficient in $BL = a + b \times DD$.

Table 1 provides estimates of degree-days ($\pm 95\%$ C.L.) required to complete nymphal growth and reach maturity for a range of body lengths of both males and females. These values can be considered alongside monthly degree-days over 2·6 °C for males and over 3·1 °C for females (Table 2).
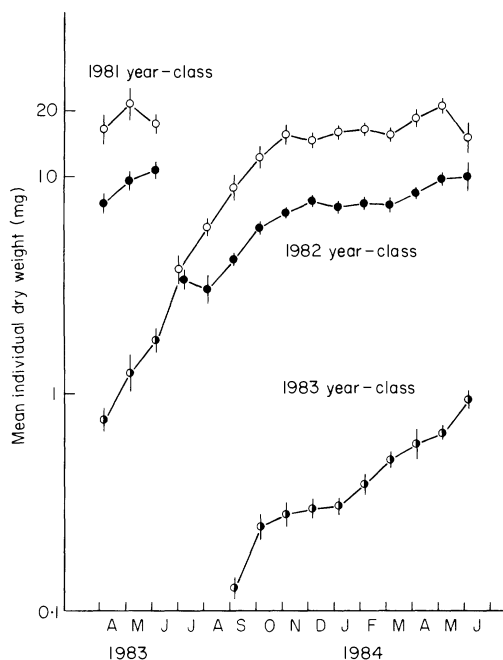
FIG. 3. Animal pattern of increase in geometric mean individual dry weight ($\pm 95\%$ C.L.): ($\bullet$), males; ($\bigcirc$), females; ($\mathbb{O}$), both sexes combined, for each of three year-classes.
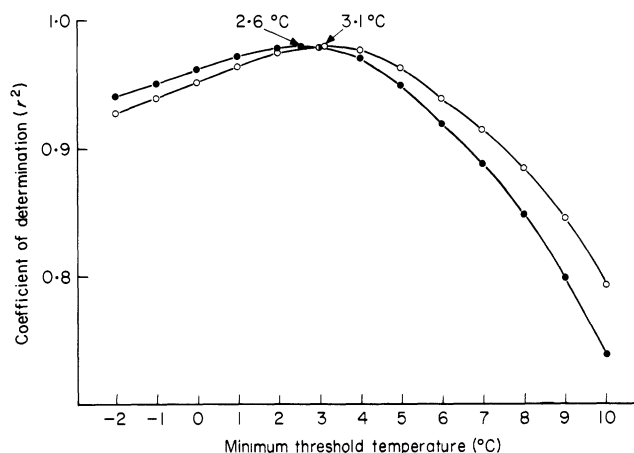
FIG. 4. Relationship between coefficient of determination (r^2) of body length–degree-days regression and minimum threshold temperatures: ($\bullet$), males; ($\bigcirc$), females.

For a nymphal life of approximately 2 years (egg laid year n, adult emerges year $n + 2$), the longest conceivable period from hatching to emergence is from the beginning of July in year n to the end of August in year $n + 2$. Eggs collected from females in early June hatched after 25 days at a constant temperature of 14 °C under natural day-length conditions in the laboratory—thus, the very first batch of eggs could give rise to nymphs by the beginning of July in the field. The number of degree-days available for growth of

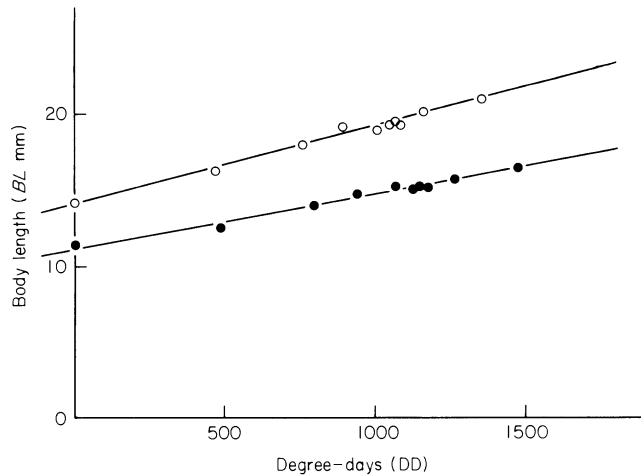FIG. 5. Maximum likelihood regressions of body length (BL) against degree-days (DD) for males (●) and females (○). Regression equations with 95% C.L. for parameter values are: $BL = (11·285 \pm 0·390) + (3·531 \pm 0·413) \times 10^{-3}$ DD (male); $BL = (14·139 \pm 0·519) + (5·030 \pm 0·588) \times 10^{-3}$ DD (females).

TABLE 1. Estimate of degree-days required to reach maturity for males and females of various body lengths. The ranges of sizes illustrated are for individuals actually observed in the field with fully developed wing pads

	Body length (mm)	Degree-days (95% C.L.)
Male		
(MT = 2·6 °C)	17·5	4786 (5420–4285)
	16·0	4361 (4939–3905)
	14·0	3795 (4298–3398)
Female		
(MT = 3·1 °C)	24·0	4652 (5268–4165)
	22·5	4354 (4930–3898)
	21·0	4056 (4593–3631)

TABLE 2. Monthly accumulated degree-days above the threshold temperature of 2·6 °C (applicable to males) and 3·1 °C (females)

Threshold temperature	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	March	April	May
2·6 °C	349·2	445·7	487·6	305·3	145·4	126	57·8	20·6	30·5	87·8	210·2	221·4
3·1 °C	334·2	430·1	470·1	289·8	132·4	112·3	46·2	12·4	22·4	74·8	194·7	205·9

males during this period is estimated as 5908·3 and for females 5551·1. The shortest conceivable period from hatching (of eggs laid in year n) to adult emergence (in year $n + 2$) is from the beginning of May in year $n + 1$ to the beginning of June in year $n + 2$. The number of degree-days available in this period is 2708·9 for males and 2531·3 for females. All of the estimated degree-days requirements to complete growth, for both males and females (Table 1) lay between these lower and upper limits. It is concluded that the majority of the population should emerge as adults in the second summer after oviposition.

The possibility of a 1-year life cycle (egg laid year n, adult emerges year $n + 1$) can also be investigated. The maximum conceivable period from hatching to adult emergence is

from the beginning of July in year n to the end of August in year $n + 1$. The number of degree-days available in this period is 3420·8 for males and 3225·7 for females. The 95% confidence limits of estimated degree-days required by females to reach maturity do not include the value 3225·7. Thus, it is unlikely that any female will complete development by the first summer after oviposition. However, for males of less than 14·5 mm body length, the confidence limits include the value of 3420·8 degree-days and some males may complete development during the year after oviposition, given the temperature conditions prevailing at the study site.

These conclusions are in agreement with the earlier interpretation of changes through the year in size–frequency distribution and mean individual weight of *E. danica* nymphs.

Population biomass and production

Variation in population biomass throughout the study period is illustrated in Fig. 6a. Females contributed on average about twice as much biomass as males. Of the two year-classes present at any one time, the older generation comprised the bulk of the overall population biomass.

Figure 6b gives separate monthly production estimates for each year-class and, where possible, for each sex. The older year-class was consistently more productive than the younger and females were more productive than males. Production in winter was much lower than in summer. Annual production was calculated for the period from July 1983 to June 1984, inclusive (Table 3). The 1982 year-class contributed 85% of the total annual production of 5·58 g dry weight m^{-2} year^{-1}, and the females were three times as productive as the males. The ratio of annual production to annual mean population biomass ($P/\bar{B}$) was higher for the small individuals that made up the 1983 year-class than for the 1982 year-class. Females had a higher $P/\bar{B}$ ratio than males.

DISCUSSION

The relationship between insect growth and thermal unit accumulation has been widely used in terrestrial studies, especially those involving predictions about time of emergence of pest species (e.g. Aliniazee 1975; Reissig *et al.* 1979). In freshwater studies too, the influence of temperature on growth is recognized but the degree-days approach has had only limited application (e.g. Humpesch & Elliott 1980; Wright, Mattice & Beauchamp 1982). The conventional approach is to grow animals in the laboratory at a range of constant temperatures and to extrapolate linearly from the data to determine the minimum threshold temperature at which growth rate is zero. One probable reason that the degree-days approach has not been widely used in freshwater studies is the great difficulty of rearing aquatic insects through their whole larval life in the laboratory, and this is particularly true for insects from lotic habitats. A further drawback with laboratory studies at constant temperatures is the question of applicability of results to natural field conditions where temperatures fluctuate daily and seasonally. Several authors have paid attention to the effect of fluctuating temperatures (Fahy 1973; Sweeney 1978; Humpesch 1982).

The method described in this paper suffers from the disadvantage that the data are not gathered under controlled conditions, but, in its favour, it is free from the restrictions mentioned above. In fact, it is applicable to both field and laboratory data. Note that the use of log transformation or curvilinear regression is required if weight is used instead of length. Accuracy of the degree-days estimate depends on the closeness of data points to the fitted regression line. In this study, variance about the regression line is remarkably low,
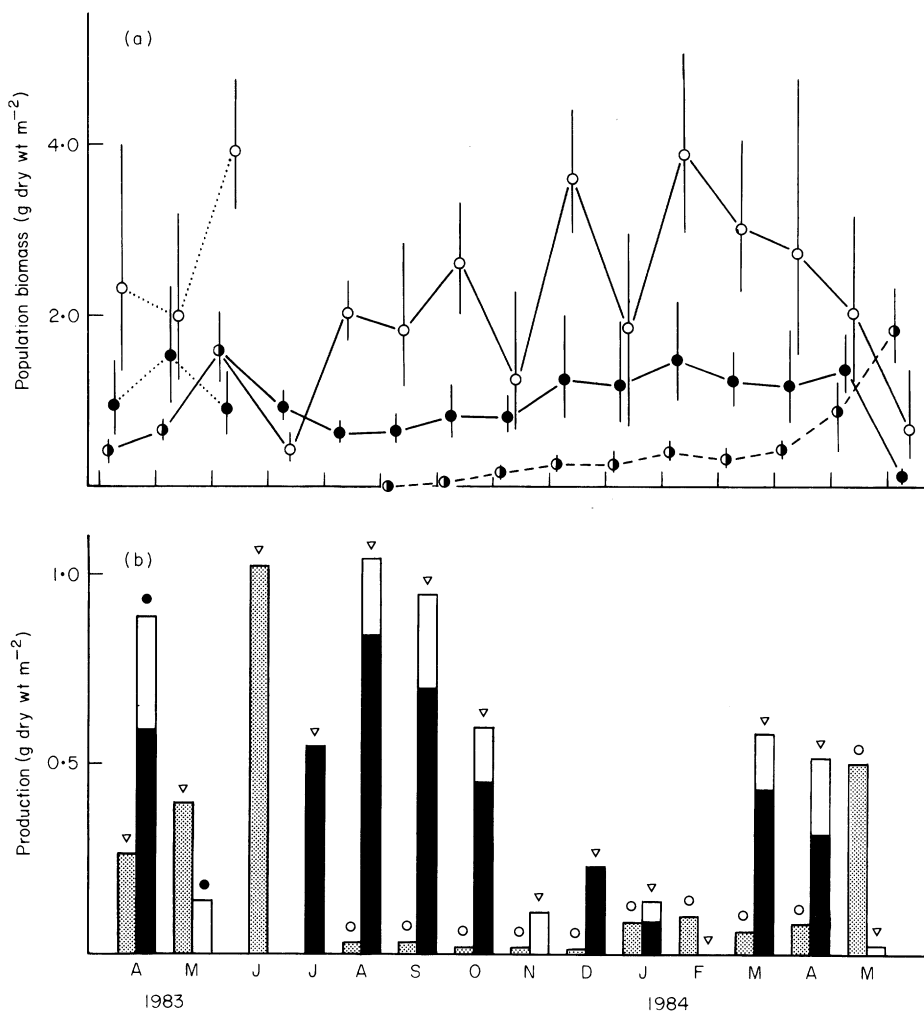
FIG. 6. (a) Annual pattern in population biomass (g dry wt. m^{-2} ± 95% C.L.) for the 1981 year-class (· · · · ·), the 1982 year-class (——) and the 1983 year-class (– – –). (●), Males (O), females; (◐), both sexes combined. (b) Monthly estimates of production. (●) Indicates the 1981 year-class, (▽) the 1982 year-class and (O) the 1983 year-class. (■), Females; (□), males; (▨), unsexed small individuals.

TABLE 3. Annual population production (P), mean biomass ($\bar{B}$) and $P/\bar{B}$ ratios of the *E. danica* population in the River Tud, Norfolk from July 1983 to June 1984, inclusive

		P (g dry wt m^{-2} year^{-1})	$\bar{B}$ (g dry wt m^{-2})	$P/\bar{B}$
1982 Year-class	total	4·74	3·16	1·50
	male	1·14	0·99	1·15
	female	3·60	2·17	1·66
1983 Year-class	total	0·84	0·41	2·08
	total	5·58	3·57	1·57

indicating that factors other than temperature, such as variations in food supply or predation, have had little effect on the pattern of increase in body length through the year. The high values of coefficient of determination obtained in this study for both sexes of *E. danica* justify the subsequent estimation of degree-days required to complete nymphal growth. It is encouraging that the conclusion from this analysis, that all females and most males should take 2 years from oviposition to adult emergence is in good agreement with the interpretation of changes in size–frequency distribution through the year.

The use of linear regression in the method was not based on any a priori assumption about the relationship between body length and degree-days nor does its successful application necessarily mean that this relationship is intrinsically linear. The point to note is that predictions based on linear regression are valid as long as the regression line fits the data reasonably well. In fact, it may be tempting to assume that the increase in body length against degree-days will be exponential. However, data presented by Clifford, Hamilton & Killins (1979) showed no significant deviation from linearity in the relationship between body length and time at a constant temperature for almost the entire period of growth, except close to hatching, of another mayfly *Leptophlebia cupida* (Say). Similarly, a logistic growth pattern in *Hexagenia bilineata* (Say) became apparent only at a low constant temperature and by taking measurements near the dates of hatching and adult emergence (Wright, Mattice & Beauchamp 1982). If curvilinearity becomes evident only when measurements very close to hatching and emergence are taken into account, then for the purpose of prediction it is probably better to use linear regression. In most situations these measurements are not available and a curvilinear regression would be likely to result in a larger bias in degree-days estimation.

It is possible to carry out similar analyses, based on minimum threshold temperature derived in the present study, and to produce predictions about time to emergence of each sex of *E. danica* in three contrasting locations in Europe (Table 4). Some inaccuracy is bound to be introduced because only monthly mean temperatures were reported (instead of daily mean temperatures as in the present case). Nevertheless, the predictions fit

TABLE 4. Predictions of the life cycle of *E. danica*, based on the degree-days available in three different localities, as compared with the life cycles actually observed

Locality		Degree-days available from hatching (taken as July 1st, year 0) until the end of August			Life cycle		
		Year 1	Year 2	Year 3	Prediction	Observation	Reference
Lissuraga, Atlantic Pyrenees	♂ ♀	4840 4626	8756 8360	12672 12094	About half of both male and female populations in 1 year, the other half in 2 years.	1 or 2 years*	Thibault (1971a,b)
Lambourn, Southern England	♂ ♀	3893 3679	7004 6608	10115 9537	Small proportion of males and very small proportion of females in 1 year; mostly in 2 years.	Mostly 2 years*	Wright, Hiley & Berrie (1981) Ham, Wright & Berrie (1981)
Stampen, Southern Sweden	♂ ♀	2666 2514	4477 4172	6288 5830	Proportion of males and small proportion of females in 2 years; the rest in 3 years.	Partly 2 years* Mostly 3 years	Svensson (1977)

* The original papers make no distinction between lengths of life cycles of males and females.

remarkably well with the observations made by the original investigators, indicating that patterns in the life cycle of *E. danica* in a given locality are predictable with reasonable accuracy from information presented in this study.

The partial difference in length of life cycle of male and female nymphs, with a fraction of males but not females maturing a year early, has not been reported previously for an ephemeropteran species. However, differences between sexes in growth have been noted for *Isonychia bicolor* (Walker) (Sweeney 1978), for *Dolania americana* Edmunds and Traver (Harvey, Vannote & Sweeney 1980), for *Hexagenia bilineata* (Say) (Wright, Mattice & Beauchamp 1982) as well as for *Ephemera danica* (Svensson 1977; Wright, Hiley & Berrie 1981).

Estimates of annual production of ephemeropteran species include $1 \cdot 40$ g dry weight m^{-2} year^{-1} for *Beatis bicaudatus* McDunnough (Pearson & Kramer 1972), $1 \cdot 8$–$2 \cdot 5$ g dry weight m^{-2} year^{-1} for *B. vagans* McDunnough (Waters 1966), $5 \cdot 6$ g dry weight m^{-2} year^{-1} for *B. rhodani* (Pictet) (Welton, Ladle & Bass 1982), $5 \cdot 3$–$6 \cdot 7$ g dry weight m^{-2} year^{-1} for *Ephemerella subvaria* McDunnough (Waters & Crawford 1973) and $4 \cdot 4$ g dry weight m^{-2} year^{-1} for *Ephemerella ignita* (Poda) (Welton, Ladle & Bass 1982). The value derived for *Ephemera danica* in the present study ($5 \cdot 6$ g dry weight m^{-2} year^{-1}) lies within the same range, though all the above species are either univoltine or multivoltine whereas *E. danica* is basically semi-voltine at the study site. In terms of the annual $P/\bar{B}$ ratio, *E. danica* contrasts with other ephemeropterans. Zelinka (1979) documented $P/\bar{B}$ ratios ranging between $8 \cdot 0$ and $9 \cdot 1$ for *B. rhodani* and Welton, Ladle & Bass (1982) reported a value of $7 \cdot 4$ for *B. rhodani* and $4 \cdot 1$ for *Ephemerella ignita*, whereas the values for *Ephemera danica* in the present study were all less than $2 \cdot 1$. This result adds some weight to the view that species populations with a 2-year life cycle exhibit lower $P/\bar{B}$ ratios than those with a 1-year or shorter life cycle (Waters 1977).

ACKNOWLEDGMENTS

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