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EXPERIMENTAL ESTIMATIONS OF GROWTH AND DEVELOPMENT COEFFICIENTS OF AN AUTUMNAL GENERATION OF CORYNONEURA LOBATA EDWARDS AND TVETENIA CALVESCENS (EDWARDS) (CHIRONOMIDAE; DIPTERA)

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Summary

(1) Experimental estimations of growth coefficients evaluated at a constant water temperature (6.8°C) of the larval instars II,III and IV of Corynoneura lobata Edwards and Tvetenia calvescens (Edwards) indicated significant declines in the daily larval length increment with increasing size. The instantaneous growth rate of C.lobata decreased from 0.044 mm for individuals of the second instar to 0.014mm for fourth instar larvae, while in T.calvescens from 0.035 mm to 0.020 mm for II and IV instar larvae respectively.
(2) A good fit between length and time course was represented for both species by the Gompertz growth model.
(3) The estimated duration of larval development, including II,III, and IV instar larvae, at a constant temperature of 6.8°C was between 33.7 and 69.9 days in C.lobata, whereas in T.calvescens from 72.0 to 113.6 days.
(4) The increments in dry weight, expressed as absolute growth, showed for both species an increase in weight of a factor between 10 and 20 from instar II to instar IV larvae. The power relationship between dry-weight and length exhibited for both species a marked increase in weight in the fourth instar larvae, regarding also the high variation within this instar stage.

Introduction

Larval chironomids are often the numerically dominant members of the rhithral macrobenthic biocoenosis (COFFMAN 1973; SCHMID 1987). A determination of the role which larval chironomids play within the structural resilience (BRUNS & MINSHALL 1983; MAY 1972,1974) of the temporal and spatial pattern of patch-dynamics depends upon detailed investigations on the ecology of species (TOWNSEND 1989). This present study is part of a long-term investigation of the evaluation of parameters towards questions regarding stochastic and partly deterministic predator-prey models (HASSEL 1978; MANGEL & CLARK 1988) which assume density-dependent factors to be major components within the elucidation of epigean and interstitial patch-dynamics.

The generated growth data of the most abundant chironomid species C.lobata and T.calvescens of the Ritrodat study site of the Oberer Seebach are used to estimate the developmental time of an autumnal generation of these multivoltine species (SCHMID 1987, SCHMID, in press).

Materials and methods

Five Surber samples with a mesh size of 30µm were taken randomly within the study area of Ritrodat from September to the end of November 1989 at biweekly intervals. The larval specimens of the detritivores C.lobata and T.calvescens of each sample (0.05m² of the upper 10cm of bedsediments) were immediately grouped into instars under a dissecting microscope. Single second instar larvae were placed in glass vials containing 1ml of brook water with an excess of food. Twice a week detritus (FPOM) was collected from Surber samples and given to the larvae in a size ranging between <60µm and 150µm. The determination of larval developmental rates was carried out in the laboratory at a constant temperature of 6.8°C (±0.2), which was equivalent to the mean water temperature of the Seebach while the experiment was conducted and it is the mean annual temperature in the Ritrodat area (BRETSCHKO 1987). Together with a change of water, daily measurements of the total larval length (excluding appendages) to the nearest 0.05mm were recorded. The initial average length at the start of the experiment was 0.60mm and 0.80 mm for C.lobata and T.calvescens respectively. During the experiments more individuals of the field population of both species were added to reduce laboratory specific artefacts (like specific food selection regarding particle size; no water current and constant temperature) within the estimation of developmental rates.

Another set of samples from the field population was collected between September and October 1989 to estimate absolute growth by means of dry weight increments between instar larvae. Length -dry weight relationships were obtained from individuals of both species preserved in formalin for a few days. Larval length was measured with an eyepiece micrometer to the nearest 0.05mm, while dry weight estimations were conducted by drying the larvae in an oven for 24h at 60°C and then weighing all individuals separately to the nearest 0.1 µg on a Mettler UM3 microbalance.

Data calculations on logarithmic transformed values were performed using the SPSS/PC package for ANOVA. Multiple Regression Analysis was carried out on raw data using the same computer package.

The algorithm based on the models for growth curves were used after RICKER (1979) and SCHNUTE (1981).

Results and discussion

Growth in length

The separation and determination of successive larval instars was carried out by measuring the head capsule width of all larval specimens, because of occasionally widely overlapping body lengths between instars (SCHMID 1987). Three estimates of growth parameters for both species were obtained: (a) from the linear relationship between larval length and time at each recorded instar level separately; (b) from the linear relationship between larval length and time for the whole generation under study and (c) from the Gompertz growth model, which was the estimated growth curve model for both species of chironomids. Both species showed a similar trend of higher daily increments in length of individuals of the second instar than in the successive instars (Fig.1,2; Table1a). The daily mean growth rates of second instar larvae of C.lobata were significantly higher ($P<0.0010$; Table 2) compared with the

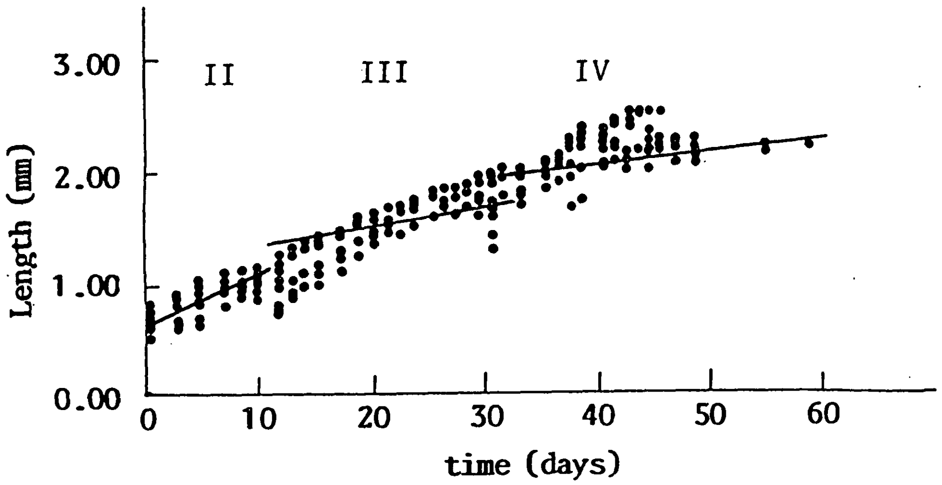

Fig.1 .The linear relationships between larval length.(mm) and time (days) for C.lobata at three instar levels separately, at a constant temperature of 6.8°C.

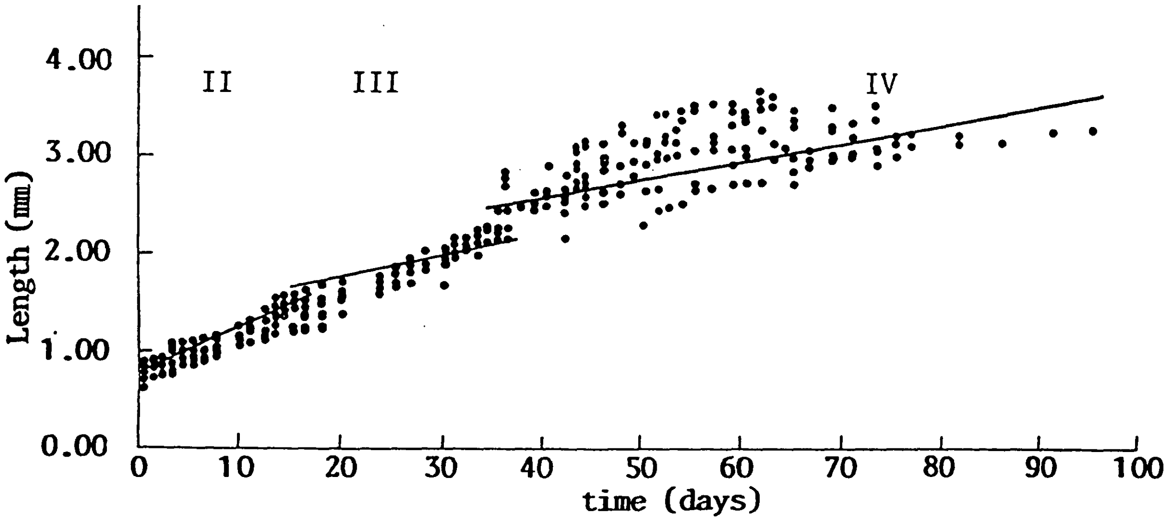

Fig.2.The linear relationships between larval length (mm) and time (days) for T.calvescens at three instar levels separately. Relationship at a constant temperature of 6.8°C.

following larval developmental stages. A distinct reduction of the daily length increment of third instar larvae shortly before moulting into the IV instar in C.lobata and T.calvescens is indicated in the decrease of significance of the estimated linear model for the length-time relationship of third instar larvae (Table 1a). This specific tendency of strong reductions of growth in length shortly before ecdysis, especially between the third and fourth instar of both species, might be partly caused by shrinkage of larvae (pers.observ.) and as it was suggested by McCAULEY 1974 (cited in LADLE et al.1985).

The instantaneous growth rate (RICKER 1979) in length for T.calvescens differed significantly between III instar and IV instar larvae ($P<0.0000$; Table 2, 1a). However, the overall mean growth rate (Table 1b) exhibited no clear difference between both populations and the linearized expression does not account both a higher growth in length at instar II and the smoother growth at the later instar level. On the other hand, growth curves based on the Gompertz model indicated distinct different instantaneous growth rates between both species (Fig.3;Table 1c).

Table 1a: Growth parameters of the linear relationship between larval length (mm) and time (days) for C.lobata and T.calvescens at each recorded instar level separately.

Instar	a	b	LL(95%CL	b)UL	DF	F	P
C.lobata (II)	0.6155	0.0438	0.0271	0.0607	19	29.81	0.0000
C.lobata (III)	1.2062	0.0153	0.0039	0.0266	23	7.79	0.0104
C.lobata (IV)	1.9312	0.0136	0.0053	0.0219	24	11.54	0.0024
T.calvescens(II)	0.8788	0.0348	0.0294	0.0401	8	226.56	0.0000
T.calvescens(III)	1.5423	0.0343	0.0033	0.0653	13	5.73	0.0325
T.calvescens(IV)	2.4095	0.0204	0.0121	0.0288	18	26.19	0.0001

Table 1b: Growth parameters of the linear relationship between larval length and time for all recorded instars of C.lobata and T.calvescens of the respective autumnal generation.

	a	b	LL(95%CL	b)UL	DF	F	P
C.lobata	1.1334	0.0377	0.0079	0.0535	74	22.56	0.0000
T.calvescens	0.9499	0.0357	0.0332	0.0382	57	818.82	0.0000

Table 1c: Parameters of the Gompertz growth model for fitting the growth curves to data represented in larval length of C.lobata and T.calvescens of the respective autumnal generation time.

Equation: $L(t)=L_{max}e^{-e^{-g(t-t_0)}}$ (after SCHNUTE 1981).

	Lmax	g	LL(95%CL	g)UL	t_0	$L(t_0)$
C.lobata	2.55	0.05265	0.0375	0.0678	5.2	0.88
T.calvescens	3.40	0.03322	0.0252	0.0412	15.0	1.35

Table 2: Analysis of Variance comparing the growth rates between all recorded instars of C.lobata and T.calvescens.

	SS	Error SS	DF	MS	Error MS	F	P
C.lobata	0.0059	0.0327	2	0.0030	0.0004	7.93	0.0010
T.calvescens	0.0026	0.0154	2	0.0013	0.0002	8.40	0.0000

Table 3a: Regression parameters for the power relationship of dry weight (mg) and length (mm) on all recorded instar larvae of C.lobata and T.calvescens of the respective autumnal generation.

	a	b	LL(95%CL	b)UL	DF	F	P
C.lobata	0.0020	2.8677	2.5595	3.1758	96	341.24	0.0000
T.calvescens	0.0020	2.1898	1.9781	2.4014	21	463.03	0.0000

Table 3b. Student T-test for testing the equality of two population regression coefficients of the curvilinear length-dry weight relation.

	b	±95%CL b	T	DF	P
C.lobata	2.8677	0.1552	7.2271	117	0.001
T.calvescens	2.1898	0.1018			

Table 3c. Student T-test for testing the equalities of the regression coefficients of the curvilinear length-dry weight relation between the recorded instar larvae of C.lobata and T.calvescens.

Instar	b	±95%CL b	T	DF	P
C.lobata (II)	0.4832	0.6719	5.7270	34	0.001
T.calvescens (II)	2.6254	0.4344			
C.lobata (III)	-0.0980	0.4501	3.1587	36	0.005
T.calvescens (III)	1.4741	0.2304			
C.lobata (IV)	0.6770	0.3280	17.3296	38	0.001
T.calvescens (IV)	4.3873	0.4737			

Table 4: Duration (D) of larval development in days at a constant water temperature (6.8°C) for each instar level separately of C.lobata and T.calvescens. Data represented as calculated mean with 95%CL.

	II-instar	III-instar	IV-instar	Total
C.lobata	9.6 (8.7 10.5)	18.2 (10.6 25.8)	24.0 (14.4 33.6)	51.8 (33.7 69.9)
T.calvesecens	18.8 (14.9 22.7)	22.6 (18.9 26.3)	51.4 (38.2 64.6)	92.8 (113.6 72.0)

The maximum length (Lmax) of C.lobata was achieved after a mean developmental time of 51.8 days (Table 4), whereas T.calvescens reached a maximum length after a developmental time of 92.8 days (Fig.3; Table 1c,4). The inflection point (t_0) in this growth model corresponds to the time where the rate of length increment begins to decrease. Thus, the population of C.lobata reached the calculated inflection point after 5.2 days shortly before moulting into the third instar, while T.calvescens exhibited a reduction of growth after 15 days at the beginning of the third larval development stage (Fig.3; Table 1c). The mean larval length at t_0, ($L(t_0)$), was 0.88 mm and 1.35 mm for C.lobata and T.calvescens respectively. Comparing both growth functions of C.lobata, it can be seen in table 1b and 1c that the estimated growth rate of the Gompertz model is similar to the upper limit value calculated after the linear model. In the case of the autumnal generation of T.calvescens, there is no distinct difference between both growth functions, which seems to be due to the modest scatter of measurements between instars (Fig.2). Nevertheless, there is evidence that growth rates are distinct functions of larval development stages rather than being constant over the life span, which is documented in literature (LADLE et al.1985; MACKEY 1977). Moreover, growth functions like the Gompertz model seem to be a reliable model from the actual data set of length increments.

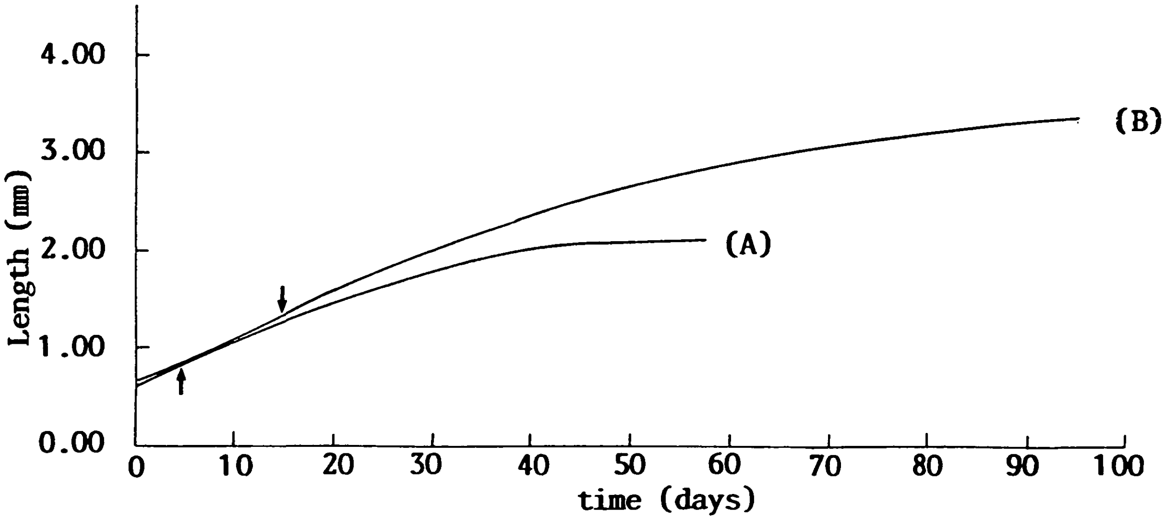

Fig.3. Growth curves of C.lobata (A) and T.calvescens (B) for their respective autumnal generation at a constant temperature of 6.8°C. Growth curves are fitted to all recorded instars. Arrows indicate the inflection-point (t_0) of the Gompertz growth curves.

Growth in weight

Despite the high variability in dry weight measurements (Fig.4, 5) specially in the fourth instar, absolute growth could be estimated as the difference between final and inital dry weight calculated (RICKER 1979). This estimate in successive instars in C.lobata ranged from 1.0 to 10.9µg, while in T.calvescens from 3.2 to 67.2µg in the autumnal generation. Therefore, it would mean that in the estimated generation dry weight was gained (from the second to the fourth instar larvae) by a factor of 10 for C.lobata and a factor of 20 for T.calvescens. In respect of dry weight measurements in both species two points should be mentioned in general: firstly, the fact that individuals showed different values of dry weight for a given length, and secondly there was a tendency of decreasing dry weight shortly before moulting into the next larval stage (Fig.4, 5).

Length-dry weight relationship

The relationship between weight and length is usually best described as: $W = aL^b$, where a and b are constants. Figure 4 and 5 shows the results obtained for C.lobata and T.calvescens, where can be seen a b-value of 2.86 and 2.19, respectively (Table 3a). Theoretical b-coefficients around 3.0 have been reported (KONSTANTINOV 1958), but it seems that is not generally the case in chironomids. On the other hand, MACKEY (1977) studied length-age growth rates and length-weight relationships at 3 different temperatures in larval chironomids and concluded that the larger the larval chironomids at maturation the greater the value of b. On the contrary to this observation, in the present study T.calvescens larvae larger than C.lobata at maturation exhibited a lower value of b. However, the two populations displayed a significant different slope for the curvilinear length-dry weight relationship of the estimated autumnal generations ($P < 0.001$; Table 3b). A different and more complex pattern was observable when comparing the growth for both species on each instar level separately (Table 3c). T.calvescens showed a distinctly steeper and significantly different

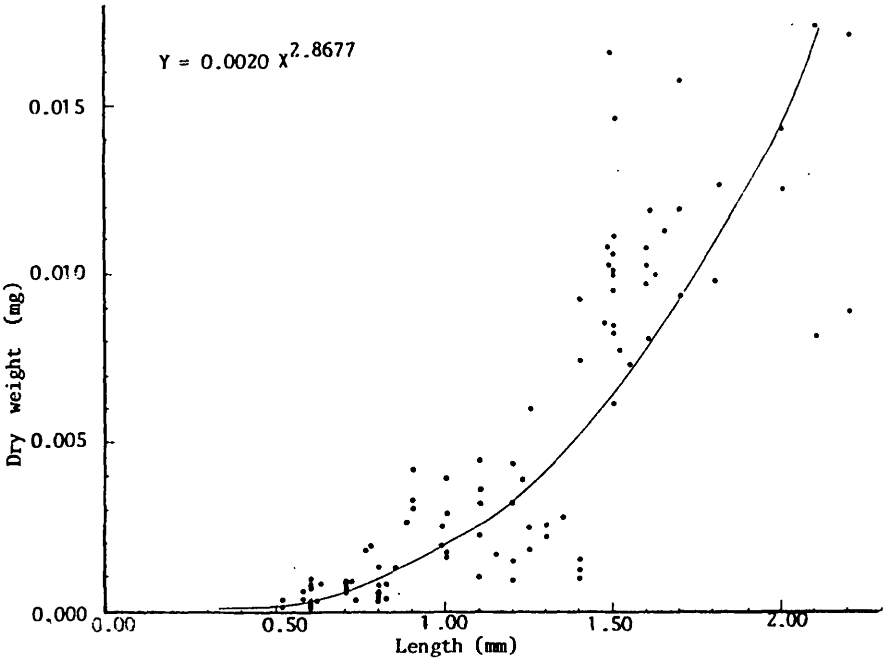

Fig.4.Larval dry weight (mg) plotted versus larval length (mm) for all recorded instars of C.lobata.

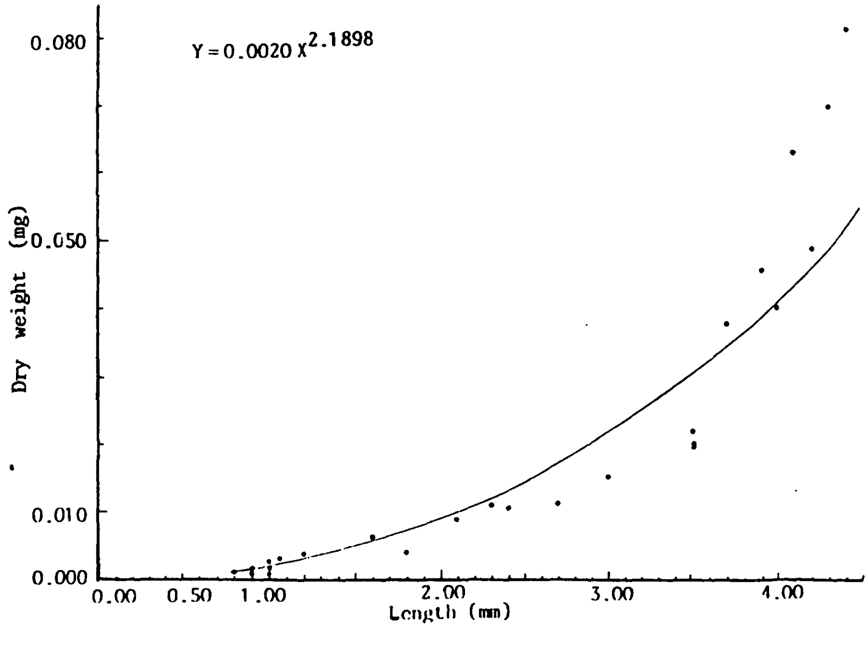

Fig.5.Larval dry weight (mg) plotted versus larval length (mm) for all recorded instars of T.calvescens.

increment of the relationship (b-values) compared to larvae of C.lobata in the fourth instar (Table 3c); this might reflect a feeding efficiency related to their preferred habitat (like epilithic mosses) in the former species. The same effect can be seen at second and third instar level and C.lobata was characterized by an obvious scattering of data points (Fig.4). Moreover, in the same species in the third instar larvae there was a tendency for a negative relation between dry weight and length (Table 3c). These results may indicate a clear pattern of different growth modes when both species are compared.

As a general conclusion, it can be stated that both populations of chironomid species exhibited a clearly different growth pattern, on instar level as well as a whole larval generation. Not having included first instar larvae due to high mortality rates under laboratory conditions, estimations for the larval development could be drawn. As expected, the developmental time increased distinctly from instar II to instar IV larvae for both species (Table 4). At this low water temperature (6.8°C) the larval development time for C.lobata was short, as it has been reported for other chironomid species of the same genus (MACKEY 1977). Highest growth rates in length were found in early instar larvae, whereas the absolute growth in dry weight indicated a steeper increase in fourth instar larvae, in particular in T.calvescens.

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