

A method for estimating larval life spans of aseasonal aquatic insects from streams on Bougainville Island, Papua New Guinea

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SUMMARY

1. The larval life spans of twelve species of aseasonal aquatic insects (eight Trichoptera, three Ephemeroptera, one Odonata) were investigated in two tropical streams with near constant water temperatures.
2. Life spans were estimated from equations relating larval life span to the ratio between cohort production (estimated from the size–frequency technique) and annual production (estimated from regressions in the literature).
3. Life spans varied from 40 to 250 days and were positively correlated with maximum larval dry weight ($r = 0.73$, $P < 0.001$). Ephemeroptera had the shortest larval life spans (40–110 days), Trichoptera intermediate (95–185 days) and Odonata the longest (250 days).

Introduction

In a recent study of the seasonality of benthic invertebrates of Konaiano Creek, a mountain rainforest stream on the tropical island of Bougainville (Yule & Pearson, in press), Papua New Guinea, the life cycles of fifteen species of aquatic insect were examined. All taxa showed asynchronous, aseasonal life cycles with continuous hatching and larval growth throughout the 22 months of the study. Such life cycles seemed to result from a lack of environmental cues for synchronization of hatching, growth and emergence. The climate of Bougainville is remarkably equable with little variation in air temperature, rainfall and humidity at the creek.

Although monthly size–frequency data were available for each species, Yule & Pearson were unable to determine the larval life span of any of the species because it was impossible to distinguish and follow cohorts. In this paper we propose a method which uses size–frequency data to produce estimates of larval life span. Such estimates are particularly scant for tropical streams, especially those in the aseasonal humid tropics. This is a result not only of the small

number of studies conducted in such habitats, but also a result of the difficulties in following the course of rapidly growing species simply from field collections of specimens. Most information currently available is for single species or small groups of species (e.g. Bishop, 1973; Hynes, 1975; Marchant, 1982; Dudgeon, 1989, 1995). A study of larval development times for thirty-five species of aquatic insects (including Plecoptera, Ephemeroptera, Trichoptera and Chironomidae) from three mountain streams in Costa Rica (Jackson & Sweeney, 1995) is the only attempt to cover a diverse range of taxa from a single tropical location.

Materials and methods

Konaiano Creek (6°18'S, 155°30'E) is a small stream, 1.2 km long, flowing through rainforest at an altitude of 720 m. The reach studied was 50 m long and 0.6–3.5 m wide with an average depth of 20 cm. The stream bed consisted largely of cobbles with patches of fine sediment; riffles, runs, backwaters and small waterfalls

(1–2 m high) were present. As the stream is close to the equator there is a yearly variation in daylight of only 36 min. Water temperature is consistently high, and varied from a mean minimum of 19.3 °C (over 22 months) to a mean maximum of 22.2 °C (read every few days from a maximum–minimum thermometer). Rainfall is high (at least 200 mm month⁻¹) and fairly uniform throughout the year resulting in regular spates which rise and fall rapidly. Further details of conditions at the study site are given by Yule & Pearson (in press) and Yule (1993, 1995b).

The study reach was sampled monthly from July 1987 to April 1989 using a Surber sampler (400 cm²) with a net of 300-µm mesh. On each sampling occasion twelve samples were taken. Samples were preserved in 70% alcohol and head capsule widths of specimens were measured using an ocular micrometer at × 64. Eleven of the fifteen species studied by Yule & Pearson (in press) were used in the current study: Hydropsychidae spp. 1 and 2; *Chimarra* sp., Philopotamidae sp. (Philopotamidae); *Nyctiophylax* sp. (Polycentropodidae); *Anisocentropus* sp. (Calamoceratidae); nr *Triaenodes* sp. (Leptoceridae); *Apsilochorema* sp. (Hyrobiosidae); *Barba* sp. (Leptophlebiidae); *Pseudocloeon* sp. (Baetidae); *Lieftinckia kimminsi* Kimmins (Megapodagrionidae).

Additional samples were taken from the Bovo River, which arises near Konaiano Creek. The study reach on the Bovo was, however, at an altitude of 20 m, and close to the coastal town of Arawa. Here samples were taken monthly from May 1988 to April 1989. As the stream bed consisted of sand, some cobbles and many large boulders and as the flow was usually fast (> 0.7 m s⁻¹) a Surber sampler could not be used easily; instead, a 5-min kick sample was taken with an FBA net (175-µm mesh, bag 50 cm long). Spot water temperatures varied from 24 to 26 °C over a year; further environmental details are given by Yule (1995a). The head capsule widths of the mayfly *Caenodes* sp. (Caenidae), the only taxon examined at this site, were measured as described above.

Head widths were converted to dry weights using general regression equations for the relevant orders of insects (Table 1) from Smock (1980), Meyer (1989) and Towers, Henderson & Veltman (1994). Although equations were available from these sources for individual species, it was not possible to match the current taxa confidently with any of these. Thus we relied on ordinal level equations. Separate calculations (see below) were carried out for each set of dry weights

Table 1 Regression equations relating head width (HW, mm) to dry weight (W, mg) from Smock (1980) (1), Meyer (1989) (2) and Towers *et al.* (1994) (3)

Order		Source
Ephemeroptera	ln W = 0.795 + 3.57 ln HW	1
	ln W = -0.365 + 3.47 ln HW	2
	ln W = -0.289 + 2.84 ln HW	3
Trichoptera	ln W = 0.999 + 2.77 ln HW	1
	ln W = 0.401 + 2.73 ln HW	2
	ln W = 0.361 + 2.52 ln HW	3
Odonata	ln W = -0.460 + 2.51 ln HW	1

in order to provide a range of estimates of larval life span.

Calculation of larval life spans

For each species an average size–frequency distribution was constructed using data from all available samples (Table 2). For simplicity, only dry weights from Smock's (1980) equations are shown in this table, although calculations were also made using the other two sets of dry weights. From such data it is possible to estimate production of an average cohort (CP) using the size–frequency technique (Benke, 1984), which assumes that the average size–frequency distribution approximates the survivorship of the average cohort. This assumption is most likely to be met by taxa that show continuous hatching and larval growth throughout the period of sampling, such as those in this study. To obtain an estimate of annual production (P), values for cohort production have to be corrected for the fraction of the year each taxon takes to complete development. This is known as the cohort production interval (CPI; Benke, 1984) and for aquatic insects is equivalent to the larval life span. CPI (measured in days) is related to P and CP thus:

$$P = (CP \times 365)/CPI \quad (1)$$

In this study it is the CPIs which we wish to estimate rather than the levels of annual production. This can be done if annual production can be estimated by other means. Recently two regression studies have been published which enable production to be predicted from knowledge of a taxon's dry weight and water temperature. Benke (1993) reviewed over 1500 estimates of production (P in mg dry weight m⁻² year⁻¹) from stream studies and regressed annual P/B (B = mean annual biomass, mg dry weight m⁻²)

Table 2 Average size–frequency distributions for eleven taxa from Konaiano Greek and *one from Bovo River. Mean densities (D, number 0.48 m⁻²) were based on Surber samples taken monthly for 21 months (†mean number per kick sample taken monthly for 11 months). Mean dry weights (W, mg) were calculated from head widths of instars or size classes using regressions given by Smock (1980). Mean biomasses (B, mg 0.48 m⁻²) for each instar or size class were calculated as D × W; totals are equivalent to the mean biomass for each taxon

	Instar	D	W	B		Instar	D	W	B
Trichoptera					Hydropsychidae sp.2				
<i>Chimarra</i> sp.	1	5.14	0.020	0.103		1	17.2	0.064	1.10
	2	7.05	0.060	0.423		2	33.2	0.176	5.84
	3	6.48	0.119	0.771		3	28.1	0.569	16.0
	4	7.52	0.341	2.56		4	27.5	1.69	46.5
	5	8.90	0.929	8.27		5	2.30	3.50	8.02
				Total = 12.1					Total = 77.4
					Head width (mm)				
Philopotamidae sp.					Ephemeroptera				
	1	1.38	0.015	0.021	<i>Barba</i> sp.	<0.2	0.36	0.003	0.001
	2	1.67	0.105	0.175		0.3	5.01	0.018	0.09
	3	1.57	0.267	0.419		0.4	11.0	0.055	0.60
	4	3.76	0.774	2.91		0.5	9.18	0.130	1.19
	5	3.19	2.18	6.94		0.6	9.23	0.260	2.40
				Total = 10.5		0.7	8.90	0.470	4.18
						0.8	8.13	0.780	6.34
Nyctiophylax sp.						0.9	4.72	1.21	5.71
	1	2.14	0.014	0.030		1.0	5.95	1.80	10.7
	2	2.48	0.052	0.129		1.1	4.57	2.57	11.7
	3	3.38	0.121	0.409		1.2	4.24	3.55	15.1
	4	2.81	0.339	0.953		1.3	3.24	4.77	15.5
	5	2.05	0.832	1.71		1.4	1.57	6.28	9.86
				Total = 3.23		>1.4	0.05	7.10	0.36
									Total = 83.7
Apsilochorema sp.					Pseudocloeon sp.				
	1	0.95	0.031	0.029		<0.2	5.56	0.003	0.019
	2	2.67	0.107	0.286		0.3	26.1	0.018	0.470
	3	1.33	0.334	0.444		0.4	31.5	0.055	1.73
	4	1.62	0.818	1.33		0.5	17.7	0.130	2.30
	5	2.52	2.51	6.34		0.6	14.2	0.260	3.68
				Total = 8.42		0.7	12.2	0.470	5.71
						0.8	5.05	0.780	3.94
Anisocentropus sp.						0.9	2.48	1.21	3.00
	1	1.95	0.015	0.029					Total = 20.9
	2	2.00	0.047	0.094	Caenodes sp.*				
	3	3.19	0.138	0.440		<0.2	61.4†	0.003	0.210
	4	2.24	0.453	1.02		0.3	99.4	0.018	1.79
	5	1.29	1.38	1.78		0.4	78.3	0.055	4.31
				Total = 3.36		0.5	42.4	0.130	5.51
						0.6	44.3	0.260	11.5
nr. <i>Trienodes</i> sp.						0.7	39.2	0.470	18.4
	1	3.48	0.006	0.021		0.8	13.4	0.780	10.5
	2	4.48	0.011	0.049					Total = 52.2
	3	4.48	0.023	0.103	Odonata				
	4	5.62	0.048	0.270	<i>Lieftinckia kimminsi</i>				
	5	5.57	0.166	0.920		<0.5	2.19	0.055	0.120
				Total = 1.37		1.0	2.81	0.37	1.04
						1.5	2.76	1.19	3.28
Hydropsychidae sp.1						2.0	1.90	2.68	5.09
	1	53.2	0.084	4.47		2.5	2.24	4.95	11.1
	2	90.4	0.260	23.5		3.0	2.29	8.13	18.6
	3	76.1	0.967	73.6		3.5	1.00	12.3	12.3
	4	43.3	3.591	155.5		4.0	1.33	17.6	23.4
	5	31.0	9.90	307					Total = 74.9
				Total = 564					

Table 3 Regression equations used to relate P/B or g to water temperature (T, °C) and dry weight (W, mg) or maximum dry weight (Wm, mg)

From Benke (1993)	
Ephemeroptera	$\log_{10}P/B = 0.716 + 0.030T - 0.382\log_{10}Wm$
Trichoptera	$\log_{10}P/B = 0.447 + 0.026T - 0.025\log_{10}Wm$
Odonata	$\log_{10}P/B = -0.220 + 0.039T + 0.048\log_{10}Wm$
From Morin & Dumont (1994)	
Ephemeroptera	$\log_{10}g = -2.07 + 0.038T - 0.14\log_{10}W$
Trichoptera	$\log_{10}g = -2.29 + 0.032T - 0.21\log_{10}W$
Combined	$\log_{10}g = -2.09 + 0.025T - 0.27\log_{10}W$

against mean annual water temperature (T, °C) and maximum individual dry weight (Wm, mg). He produced separate equations for Trichoptera, Ephemeroptera and Odonata (Table 3), as well as for a number of other groups, including a general equation based on all 1500 estimates. In a second study, Morin & Dumont (1994) regressed daily growth rates (g, day⁻¹) against individual dry weight (W, mg) and water temperature (T, °C) based on 579 estimates from the literature. They calculated an equation for the combined data as well as individual equations for Ephemeroptera and Trichoptera (Table 3).

We used Benke's equations to estimate P/B ratios for the twelve taxa in this study. Maximum individual dry weights (Wm) were assumed to equal the mean dry weights of the largest instar or size class; three estimates were available for each taxon (except the odonatan), one from each of the regressions relating head width to dry weight (Table 1). Mean water temperatures for Konaiano Creek and the Bovo River were 20.7 and 25.1 °C, respectively. Estimates of B were calculated (Table 2) as the sum of the mean biomasses for each size class or instar. CP for each taxon was estimated using the size–frequency procedure. Larval life span or CPI (days) was then calculated as:

$$CPI = (365 \times CP) / [(P/B) \times B] \quad (2)$$

which is equivalent to eqn (1) rearranged.

Morin & Dumont's equations (Table 3) were used to estimate daily growth rate (g) for each size class or instar for a given taxon; again three sets of dry weights were available. The values were then multiplied by mean biomass for each size class or instar (Table 2) and the products summed to give total daily production for a taxon. Daily production was converted to annual

Table 4 Larval life spans (days) calculated from Benke's (1993) regression (upper line for each taxon) and Morin & Dumont's (1994) regression (lower line). Estimates are shown for each of the three separate regressions relating head width to dry weight: Smock (1980), Towers *et al.* (1994), Meyer (1989). *Based on a regression for combined data rather than on one specifically for Odonata

	Smock	Towers <i>et al.</i>	Meyer	Mean (%CV)
<i>Chimmara</i> sp.	111	113	109	107
	110	100	97	(6.1)
Philopotamidae sp.	122	112	118	122
	143	117	122	(8.8)
<i>Nyctiophylax</i> sp.	128	117	125	116
	120	99	104	(10.0)
<i>Apsilochorema</i> sp.	111	104	102	110
	136	112	97	(12.5)
<i>Anisocentropus</i> sp.	160	148	157	149
	158	132	140	(7.6)
nr. <i>Trianaodes</i> sp.	116	108	111	93
	83	71	71	(22.2)
Hydropsychidae sp.1	166	155	162	185
	239	191	195	(16.9)
Hydropsychidae sp.2	186	169	184	183
	208	168	182	(8.0)
<i>Barba</i> sp.	178	100	113	110
	106	76	85	(33.0)
<i>Pseudocloeon</i> sp.	86	52	56	66
	78	60	66	(20.0)
<i>Caenodes</i> sp.	48	30	31	39
	47	36	40	(20.0)
<i>Lieftinckia kimminsi</i>	277	—	—	248
	218*	—	—	(16.9)

production (P) by multiplying by 365. CP was calculated as before. Larval life span or CPI (days) was calculated as:

$$CPI = (365 \times CP) / P \quad (3)$$

which is also a rearranged version of eqn (1).

Results

From eqns (2) and (3) and the three regression equations relating head width to dry weight it is possible to calculate six estimates of larval life span for most taxa (Table 4). The six estimates for each taxon agree well, with coefficients of variation ranging from 6 to 30%. Estimates of dry weight from Smock's equations were usually about twice as large as those from the other two equations, both of which gave quite similar values. Such estimates of dry weight appear in both the numerators and denominators of eqns (2) and (3)

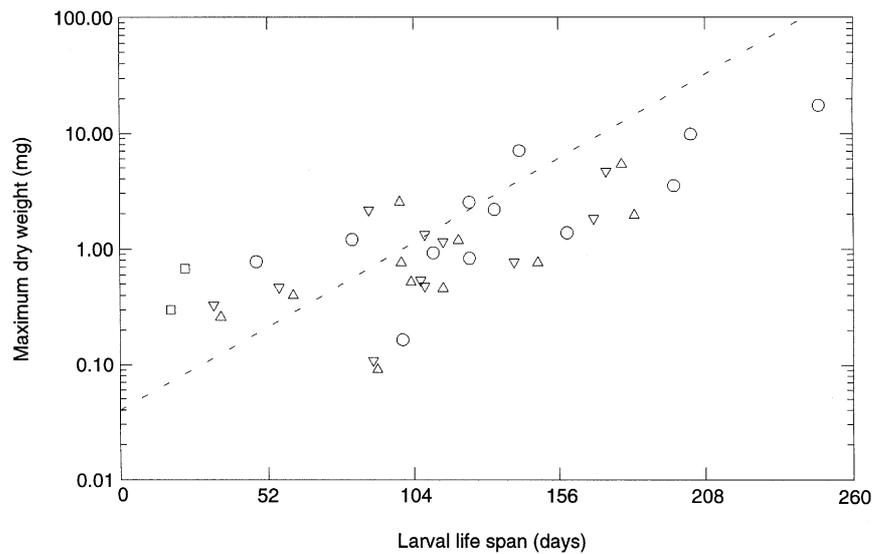


Fig. 1 Relation between larval life span and log maximum larval dry weight for the twelve taxa in the current study. The data are divided into three groups depending on which dry weight regression was used: \circ Smock (1980); \triangle Meyer (1989); ∇ Towers *et al.* (1994). The dashed line represents the results of Jackson & Sweeney (1995) for various aquatic insects from streams in Costa Rica. The \square indicate data for the two Ephemeroptera from the Northern Territory (Marchant, 1982).

but in somewhat different forms, i.e. in calculations of CP, B or P. Thus their effects to some extent cancel out in the final calculation of larval development time. The Ephemeroptera had somewhat higher coefficients of variation than the Trichoptera. This occurred because the coefficient in Benke's equations for Wm (maximum dry weight) was larger, by an order of magnitude, for the Ephemeroptera than for the Trichoptera (Table 3), thus imposing more variation on the calculation of P/B when Wm is altered.

The larval life span calculated for *L. kimminsi* from eqn (3) is less soundly based because it is calculated from a combined regression for growth rate based on data from Ephemeroptera, Plecoptera, Trichoptera and Diptera; a separate regression for Odonata was not available. Also only one dry weight regression was available for this taxon. Thus only two estimates of larval life span could be calculated.

Separate mean values for larval life span were calculated from the two estimates for each dry weight regression (Table 4) and are plotted against the appropriate log Wm (Fig. 1). Larval life spans were positively correlated with log maximum size of larvae ($r = 0.73$, $P < 0.001$), with data from each set of dry weights showing the same linear trend.

We have included on this plot larval life span estimates for two species of tropical mayfly (*Cloeon fluviatile* Ulmer (Baetidae) and *Tasmanocoenis arcuata* Alba-Tercedor and Suter (Caenidae)) studied by Marchant (1982) in billabongs in the Northern Territory (NT, Australia). These estimates were recalculated from the original data after converting body length to

dry weight using Smock's equation for Ephemeroptera; the equations given by Meyer (1989) and Towers *et al.* (1994) relating body length to dry weight for Ephemeroptera were very similar to Smock's and thus the calculations were only carried out for one set of dry weights. The recalculated larval life spans for *C. fluviatile* were 24 and 22 days using eqns (2) and (3), respectively, and for *T. arcuata* they were 16 and 19 days. These values are somewhat shorter than Marchant's original estimate of 1 month for both species. The new estimates fit the same linear trend as the rest of the data (Fig. 1).

Discussion

As far as we know the approach outlined above for calculating larval life spans has not been used before. A somewhat similar procedure was used by Marchant (1982) to elucidate the life cycles of two species of tropical mayfly, but a less comprehensive regression between P/B and body mass (Banse & Mosher, 1980) was used, as it was the only one available. This regression incorporated data from terrestrial and marine (as well as freshwater) invertebrates and did not include water temperature as an independent variable. Thus, its predictions for freshwater taxa were probably not as accurate as those from the regressions used above; furthermore, separate regressions for individual orders of aquatic insect were not available.

Despite improvements in the type and robustness of the regressions linking growth or turnover ratio (P/B) to body size and water temperature, predictions

from these equations must still be used cautiously. Benke (1993) strongly argued that his regressions should not be used to estimate P/B (and thus annual production) because the r^2 values were fairly low: 0.20–0.54 for the three orders of insects considered here. He also suggested that the production data on which the regressions were based were themselves limited in their accuracy. Morin & Dumont (1994) made the same points for their growth regressions ($r^2 = 0.34$ – 0.36 for Ephemeroptera and Trichoptera) but contended that the remaining variability was largely sampling error resulting from a generally small sampling effort in the original studies. In spite of these potential inaccuracies Morin & Dumont's equations produced unbiased estimates of annual production when compared with observed values.

The ability of both Morin & Dumont's equations and Benke's to produce similar estimates of larval life span indicates that the assumptions behind the calculations are fairly robust. Actual measurements of dry weight for the various instars or size classes would remove some uncertainty from the calculations. However, as pointed out above, variations in dry weight do not have a marked impact on the results. And given the unexplained variation that remains in both Benke's and Morin & Dumont's equations, actual measurements of dry weight would not greatly improve the accuracy of the life span estimates. We have tried to overcome these difficulties by calculating a range of life spans from the various regressions. The resulting variation is not great (most CVs are from 10 to 20%) and the clear linear trend shown by the results (Fig. 1) when plotted against maximum dry weight indicates consistency in the data.

Ideally, larval life spans of aquatic insects from tropical streams should be determined directly. However, this usually requires cages in the stream or laboratory rearing facilities. Jackson & Sweeney (1995) circumvented this problem by transporting thirty-five species (five Ephemeroptera, two Plecoptera, ten Trichoptera, eighteen Chironomidae) collected live in mountain streams in tropical Costa Rica to laboratory growth chambers in the United States. As water temperatures at their collecting sites were almost constant (20–23 °C), the rearing temperature (constant 20 °C) was probably less artificial than might be supposed and generally the chambers seemed to impose few obvious impediments to larval development. Jackson & Sweeney plotted larval (plus pupal, if present)

development time against log adult biomass for their thirty-five species and obtained a positive correlation ($r = 0.81$). This is similar to our correlation using maximum larval dry weight rather than adult biomass. Indeed, the regression line derived from Jackson & Sweeney's data is close to the linear trend of our data (Fig. 1). There is thus similarity in the estimates of larval life span for aquatic insects from three separate tropical regions (NT, Papua New Guinea and Costa Rica), derived using two quite different methods.

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