

Life Histories of Some Benthic Insects from the La Trobe River, Victoria

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Abstract

The life histories of the following species were studied over 2 years at various sites throughout the catchment of the La Trobe River: *Tasmanocoenis tonnoiri* and *Tasmanocoenis* sp. (Ephemeroptera: Caenidae), *Atalophlebioides* sp. and two *Atalonella* spp. (Ephemeroptera: Leptophlebiidae), two *Baetis* spp. (Ephemeroptera: Baetidae), *Leptoperla primitiva* and *L. nevoissi* (Plecoptera: Gripopterygidae), *Cyphon* sp. (Coleoptera: Helodidae), *Ecnomus* sp. (Trichoptera: Ecnomidae). The life cycles of these species varied from univoltine (four taxa) to bivoltine (Leptophlebiidae, Baetidae, *Ecnomus* sp.) or trivoltine (*T. tonnoiri*). Although the species displayed various degrees of synchrony of growth, distinct changes in the size distribution of the larvae or nymphs occurred with time and thus cohorts were evident.

Introduction

The life histories of the Plecoptera, Ephemeroptera and Trichoptera have been studied extensively in temperate rivers and streams of the Northern Hemisphere (Hynes 1976; Edington and Hildrew 1981; Brittain 1982). In temperate streams of (southern) Australia, the life histories of the Victorian Plecoptera (Hynes and Hynes 1975) and two species of Ephemeroptera from South Australia (Suter and Bishop 1980) only have been examined; there are additional unpublished data for Ephemeroptera and Plecoptera from Victoria and New South Wales (Yule 1982; Campbell 1983). Studies on a greater variety of benthic insects have been carried out in New Zealand (Winterbourn 1978, 1982 and references therein; Towns 1981, 1983), apparently the only other temperate region in the Southern Hemisphere for which such data exist. In New Zealand, poorly synchronized life cycles predominate; in temperate Australia, the life cycles published so far show better synchrony.

During surveys of the benthic invertebrate fauna of the upper and lower catchments of the La Trobe River in 1979-1981 (Marchant *et al.* 1984a; Metzeling *et al.* 1984), larvae and nymphs from various orders of benthic insect (Plecoptera, Ephemeroptera, Trichoptera, Coleoptera) were collected in sufficient numbers to enable interpretation of life histories; in this paper, 11 common species are examined. Although studies of life histories were a secondary aim of the surveys, knowledge of life histories will give such surveys greater predictive value.

Only three of the species in this study could be given specific names. Although we were able to identify consistently the remaining species, only one (a caenid mayfly) was associated with an (undescribed) adult. As so few published data exist on the life histories of these groups (except Plecoptera) in temperate Australia, it seems counterproductive for such data not to be presented until formal taxonomic studies have been completed.

Study Area and Methods

Detailed descriptions of the sampling sites (Fig. 1) in the upper and lower catchment of the La Trobe River ($38^{\circ}10'S$, $146^{\circ}30'E$.) are given by Metzeling *et al.* (1984) and Marchant *et al.* (1984a), respectively. In the upper catchment, which is mostly forested, the river width is 2–12 m, the water velocity is 0.3 – 0.5 m s^{-1} and the substratum varies from small cobbles (average size 4–5 cm) to sand. In the lower catchment (altitude <150 m), which is used for agriculture and industry, the river width is 15–20 m, the water velocity is 0.3 – 0.7 m s^{-1} and the substratum is almost entirely sand.

At each site in the upper catchment, 10 samples were taken every 3 months with a Surber sampler, which sampled an area of 0.05 m² and was fitted with a net of $150\text{-}\mu\text{m}$ mesh. In deeper water at each site in the lower catchment (generally >0.5 m deep), an air-lift sampler was used. This sampled an area of approximately 0.02 m² and its catching net was also of $150\text{-}\mu\text{m}$ mesh. Thirty samples were taken at each site every 2 months along this reach of the river, 15 from the main channel and 15 from within 1 m of the bank. All samples were preserved with formalin in the field and later in the laboratory specimens were floated from the inorganic fraction in a saturated solution of calcium chloride. Specimens were stored in 70% (v/v) ethanol and representatives deposited in the Department of Biological Survey, Museum of Victoria; nomenclature follows that used in this voucher collection. Head widths or body lengths were all measured under low power ($<26\times$).

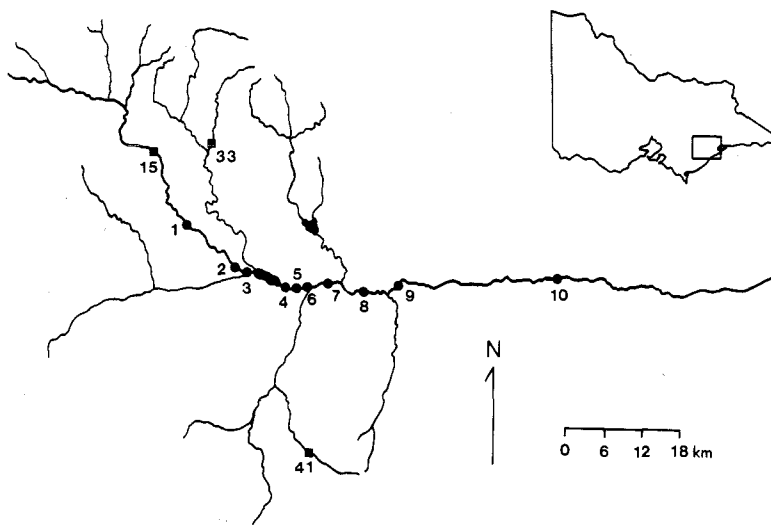


Fig. 1. Map of the La Trobe River, showing the position of the sampling sites in the upper (■) and lower (●) catchments.

The interpretation of the life history of a species was generally based on specimens collected from a single site. For a few species, which only occurred in low numbers at single sites, composite collections were produced by pooling specimens from a number of sites. In such cases, there were no obvious differences in the size-frequency distributions between sites on a particular occasion.

At sites in the lower catchment, the arithmetic mean densities and their standard errors, calculated from data transformed to $\log_{10}(x+1)$ (Elliott 1977), were determined for some species. The significance of differences in density between successive sampling occasions was tested using *t*-tests on the transformed data.

As taxa from the lower catchment usually occurred in both the main channel and at the banks, data on densities and size-frequencies from the two habitats were combined by assuming that the main channel represented 90% of the river bed and the banks 10%. This appeared reasonable because the river was generally 15–20 m wide here and the bank habitat, as previously defined, occupied 2 m (1 m on either bank) of this width. It was also assumed that drift was not responsible for changes in density observed between sampling trips, except during floods, i.e. drift into a site was assumed to equal drift out.

Spot readings of temperature were made when samples were taken. These were supplemented at some sites in the upper catchment by records from maximum–minimum thermometers. At certain places in the lower catchment, continuous records (readings every 3 h) of water temperature were available. Spot temperatures were regressed against readings made at about the same time on an appropriate continuous record; then monthly mean temperatures at a particular site could be estimated from the monthly mean temperatures from the continuous record. Estimated monthly mean temperatures were multiplied by the number of days in each month and the results summed to give the total annual degree days (above 0°C).

Results

Temperature

At the sites (15, 33, 41; Fig. 1) in the upper catchment, minimum spot temperatures were 7–8°C and maxima were 14–19°C. Records from maximum–minimum thermometers at sites 33 and 41 extended the temperature range by 2°C at the lower end and by 6°C at the upper end. In the lower catchment, temperatures were higher (Table 1). Monthly mean temperatures for sites 1, 5 and 6 were based on regressions of spot temperatures against continuous records taken at sites 12 km downstream in the case of site 1, and 1–3 km downstream in the case of sites 5 and 6. For these three sites, the amount of variance in the spot readings explained by the regressions was greater than 90% (i.e. $r^2 > 0.9$). Continuous records were available at site 10.

Table 1. Range of monthly mean water temperatures and the total annual degree days (>0°C) at selected sites in the lower catchment of the La Trobe River

Total annual degree days were calculated by averaging data from two full consecutive years

Site	Monthly mean water temperature (°C)		Total annual degree days
	Min.	Max.	
1	8	21	4810
5	15	23	6708
6	14	24	6720
10	10	24	6072

Heated water enters the river 100 m upstream of site 5 (Fig. 1). The temperature of this water never exceeded 25°C during our study and never exceeded ambient temperature by >4°C; if ambient temperature exceeded 25°C, water was not released. Thus, its influence was to increase minimum monthly mean temperatures at sites 5 and 6, but it had little effect on maximum monthly mean temperatures (Table 1).

Life Histories of Insects

Caenidae (Ephemeroptera)

Nymphs of *Tasmanocoenis tonnoiri* Lestage were most abundant at site 10 in the lower catchment, but were found at all sites in this region, particularly the most disturbed sites (4–10) (Marchant *et al.* 1984a). Nymphs occurred both at the banks and in the main channel.

Little or no growth of nymphs occurred during winter in the single cohort present at site 10 (May–September 1979; Fig. 2) but density decreased significantly ($t = 2.8$, $P < 0.01$). Mature nymphs (with dark wingpads) were first recorded in November 1979; the presence of nymphs in the smallest size-class indicates that hatching of the next generation had already started, either from eggs laid by the overwintering cohort or from eggs laid in late autumn. By January 1980, density had increased significantly ($t = 4.7$, $P < 0.001$) and the population was composed of two cohorts. Density had increased

($t = 7.9$, $P < 0.001$) again by March 1980 with the hatching of a large cohort that overwintered. Mature nymphs in March were considered to be members of the younger cohort in January, and it was presumably eggs from this generation that produced the overwintering cohort.

Much the same sequence of events occurred between May 1980 and March 1981. However, density between July and November 1980 was much lower, perhaps as a result of flooding during July. Densities had recovered by the next summer and were at about the same level as in May 1979. Adults arising from the mature nymphs present in January probably gave rise to the younger cohort present in March.

Thus, *T. tonnoiri* at site 10 was at least trivoltine with one overwintering cohort with a duration of about 8 months and two successive summer cohorts with a duration of about 2 months each. As monthly mean summer (November–March) water temperatures at site 10 were usually $> 20^{\circ}\text{C}$ (and reached 24°C in March 1981), it is possible that growth of nymphs was more rapid than indicated during this season, and that samples taken only every 2 months missed this. However, between November and March in both years the density of the proposed summer cohorts generally decreased with time, as would be expected. Thus, in the absence of additional summer data, the simplest interpretation is of two successive cohorts of nymphs that grow rapidly, the first cohort giving rise to the second.

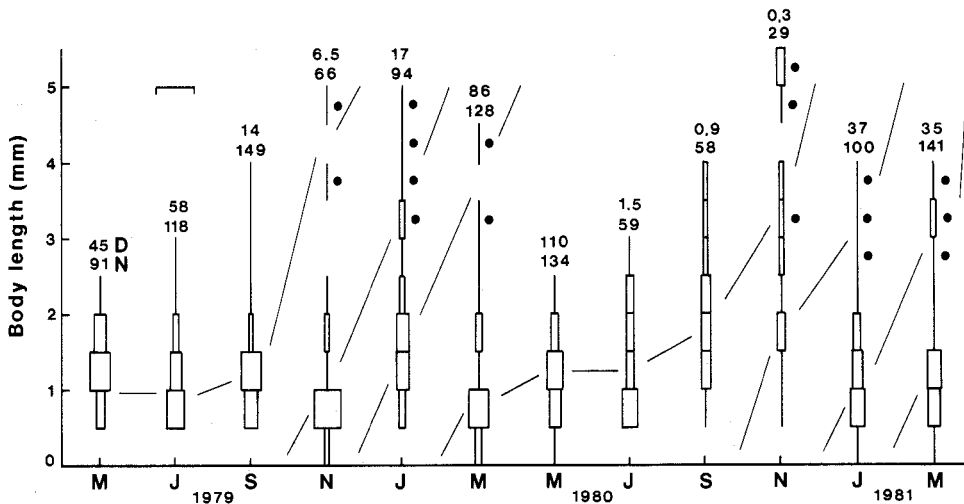


Fig. 2. Size-frequency (%) distributions of *T. tonnoiri* at site 10. Scale bar indicates 100%. ● Size-classes with nymphs with dark wingpads. Lines indicate approximately the progression of the modal size-classes. N, number of nymphs measured; D, mean density (No. 0.02 m^{-2}).

At site 8 (Fig. 1), *T. tonnoiri* also appeared to be trivoltine, although the total annual degree days would have been somewhat higher at this site (but less than that at site 6, Table 1). *T. tonnoiri* also occurred at two lowland sites on the Thomson River, the catchment of which is adjacent (north-east) to that of the La Trobe River. Here again the species appeared to be trivoltine, even though annual degree days were only 5662 (for March 1980–March 1981). Not enough nymphs were caught at other sites (1–7, 9) to enable life-history patterns to be interpreted. However, density of *T. tonnoiri* varied in much the same way at sites 1 (4810 degree days) and 6 (6720 degree days) as at site 10, suggesting the life history was similar. Thus, *T. tonnoiri* may be trivoltine over a range of temperature regimes.

Nymphs of *Tasmanocoenis* sp. 2 were found only in the upper catchment where they were most abundant on cobbles (Metzeling *et al.* 1984). This species was clearly univoltine at the three sites (15, 33, 41) from which nymphs were measured (Fig. 3). Hatching occurred in summer and the nymphs grew until the onset of winter (May). There was little growth during winter, but substantial growth in spring, after which emergence began. Although temperature probably exceeded 20°C during summer at each of these sites, there was no evidence (e.g. in February) of a summer generation. The number of nymphs measured on each occasion (Fig. 3) equalled 10% of the total number caught in 1.5 m² (3 sites × 10 samples × 0.05 m²); a 10% subsample was taken from each sample from the upper catchment to facilitate sorting and counting (Metzeling *et al.* 1984). These values show that density generally decreased during the life of each generation, as expected.

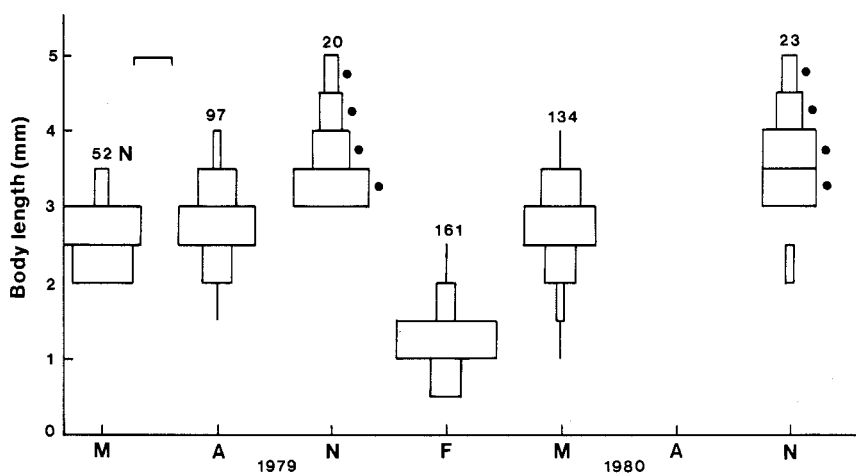


Fig. 3. Size-frequency (%) distributions of *Tasmanocoenis* sp. 2 at sites 15, 33 and 41. Scale bar indicates 25%. Symbols as in Fig. 2.

Leptophlebiidae (Ephemeroptera)

In the lower catchment, *Atalonella* spp. 2 and 4 were confined to the least disturbed sites (sites 1–3; Marchant *et al.* 1984a), whereas in the upper catchment *Atalonella* sp. 2 was found at all sites and *Atalonella* sp. 4 at 60% of these sites (Metzeling *et al.* 1984).

Atalonella sp. 2 was bivoltine in both years of the study at site 1 (Fig. 4a). The summer generation of 1979–1980 first appeared in November 1979 after the winter generation had begun emerging in September 1979. In January 1980, the summer generation was close to emergence and the overwintering generation had started to hatch. Density steadily increased until May 1980, indicating continual recruitment to this generation between January and May. Density declined during winter and by September fast-growing individuals had started to emerge. The following summer generation (1980–1981) was again distinct, but in both summers these generations were of low density compared with that of the overwintering generation. The overwintering generation that had started to hatch in January 1981 was not nearly as strong as that in the previous year.

Atalonella sp. 4 was also bivoltine at site 1 (Fig. 4b). In September 1979, the density of the overwintering cohort was two orders of magnitude lower than in July and only relatively large individuals were present. By November, density had increased by one order of magnitude and small individuals were again present. Thus, for unknown reasons small nymphs were not sampled in September. The overwintering generation did not finally emerge until summer (January 1980). The summer generation had hatched by January 1980 as shown by the increase in density and was close to emergence in March by which time the overwintering generation had also hatched. Recruitment to this latter generation

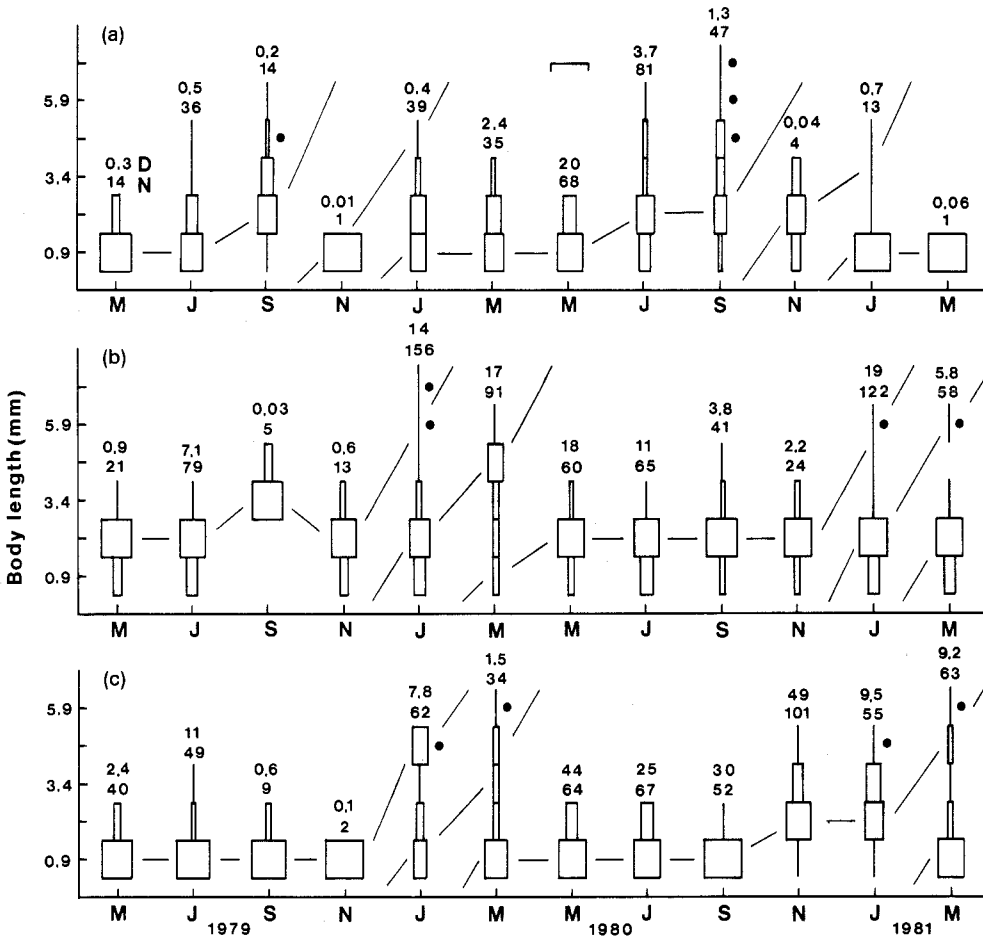


Fig. 4. Size-frequency (%) distributions of *Atalonella* sp. 2 (a), *Atalonella* sp. 4 (b) and *Atalophlebioides* sp. 4 (c). Scale bar indicates 100%. Symbols and lines as in Fig. 2.

occurred until at least May, as indicated by rising densities, and probably also until July (as in the previous year) as shown by the presence of very small nymphs. This overwintering generation also did not start emerging before summer. The subsequent summer cohort had again hatched by January (1981) and grew quickly over summer to emerge by March 1981.

Both species of *Atalonella*, although they had broadly overlapping size-classes of nymphs for most of the year, consistently showed a sequential pattern of emergence. In both years, the main period of emergence of *Atalonella* sp. 2 (from the overwintering cohort) began

in spring (September) and was complete by November, whereas *Atalonella* sp. 4 did not begin emerging (from its overwintering cohort) until summer (January). *Atalonella* sp. 2 also emerged to some extent during summer, but the strength of its summer cohorts was always less than its overwintering cohorts and less than the overwintering cohorts of *Atalonella* sp. 4.

Spatial segregation of nymphs of these two species also occurred for part of the year. Between July and November in both years, *Atalonella* sp. 2 was either absent from the main channel or occurred there in very low densities. On the other hand, *Atalonella* sp. 4 occurred in both habitats but had higher densities in the main channel. Between January and May, both species occupied both habitats. Overall, 97% of the *Atalonella* sp. 4 population occurred in the main channel at site 1 (as opposed to an expected 90%) while only 75% of *Atalonella* sp. 2 occurred in this habitat.

Atalophlebioides sp. 4 was also bivoltine at site 1 (Fig. 4c). This species occurred at only a few sites in the upper catchment (Metzeling *et al.* 1984) and, like the previous two species of *Atalonella*, was confined to the least disturbed sites in the lower catchment. At site 1, 99% of the population of *Atalophlebioides* sp. 4 occurred in the main channel; on only three occasions was more than one specimen found at the bank.

The overwintering generation in 1979 increased in density from May to July and then decreased until November. This cohort did not emerge until summer (January), but the densities of the largest size-classes in January were higher than those of the size-classes present in November, indicating that there had been recruitment between the two months. Also, the predominance of the smallest size-class in September suggests that recruitment occurred between July and September even though density decreased markedly between these months. Thus, it seems that recruitment to the overwintering generation in 1979 was more or less continual but varied in intensity. The summer generation in early 1980 was reasonably distinct and the subsequent overwintering generation, which had hatched by March 1980, was much stronger than that in 1979. The predominance of the smallest size-class in September 1980 indicates that recruitment to the overwintering cohort occurred again during spring. No summer cohort had hatched by January 1981, although emergence from the overwintering cohort had begun. The cohort that had hatched by March 1981 was presumably the start of the next overwintering generation. *Atalophlebioides* sp. 4 thus differed from the two species of *Atalonella* in that recruitment to the overwintering generation appeared to continue over a longer period and the summer generation was not always evident.

Very small leptophlebiid nymphs, which could not be identified definitely to any of the above three species or any of the other 11 species of leptophlebiid at site 1 (Marchant *et al.* 1984b), were most abundant, as expected, during recruitment in summer and autumn. Their presence indicates that the densities of the three species probably have been underestimated.

Baetidae (Ephemeroptera)

Two species of baetid occurred commonly in the lower catchment of the La Trobe River: *Baetis* sp. 4 was abundant only at the least disturbed sites (sites 1-3; Marchant *et al.* 1984a) and was rare at other sites, and *Baetis* sp. 5 was most abundant at site 10 but present at most sites. Both species occurred sporadically at sites in the upper catchment with *Baetis* sp. 5 being the commoner of the two (Metzeling *et al.* 1984).

At site 1, *Baetis* sp. 4 appeared to be at least bivoltine (Fig. 5a) and probably multivoltine during both years of the study. In 1979, densities were very low. The overwintering cohort was present in July and September but had emerged by November by which time a summer generation had hatched. Density had increased an order of magnitude by January 1980, indicating continued recruitment to the summer generation, some individuals of which

had started to emerge. A further increase in density by March indicated that another cohort (the overwintering generation) had hatched and that there had been more recruitment to the summer generation. Thus, during the summer there was continual recruitment and those individuals that emerged between January and May probably belonged to a number of overlapping cohorts.

The overwintering generation in 1980 was stronger and lasted longer than that in 1979; it decreased in density continually between March and November 1980 when emergence began. Density increased markedly from November 1980 to January 1981 and fast-growing individuals that hatched in this period probably merged with the remnants of the overwintering generation in the largest size-classes. Individuals from the bulk of the summer generation had started to emerge by March, but there was no indication of hatching of the overwintering generation as had occurred by this time in 1980.

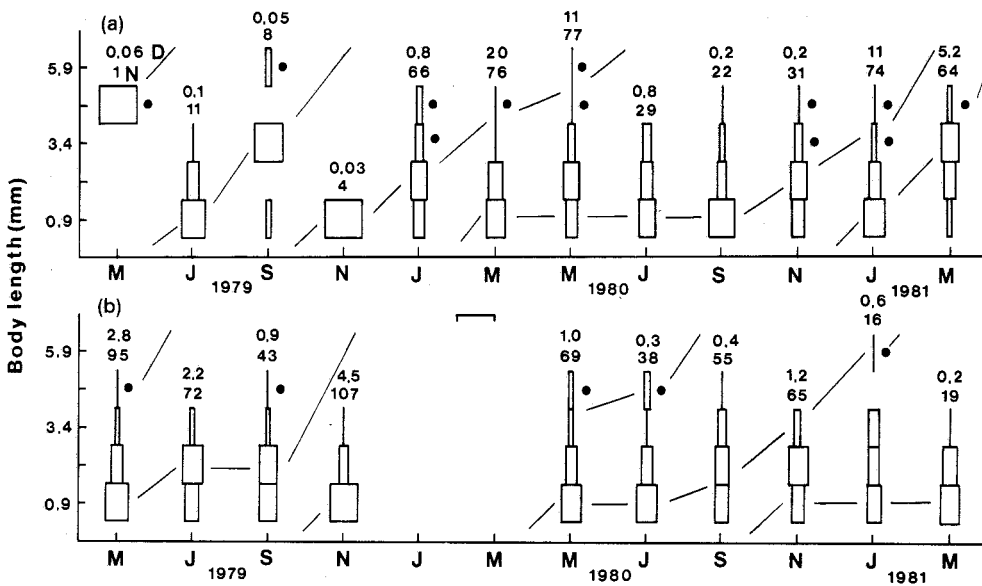


Fig. 5. Size-frequency (%) distributions of *Baetis* sp. 4 (a) and *Baetis* sp. 5 (b). Scale bar indicates 100%. Symbols and lines as in Fig. 2.

Baetis sp. 5 at site 10 was bivoltine (Fig. 5b). The overwintering generations in both years were of comparable strength and in both years the density of overwintering nymphs decreased continually. Emergence from the overwintering generations began in September and probably continued to January. No nymphs of the summer generation were caught in January and March 1980, and in these months in 1981 densities of this generation were very low. Their absence in 1980 has no obvious cause, but assuming their rate of growth was similar to that in 1981 then they reappeared in May 1980 in the largest size-classes and had started to emerge. This species was present at sites upstream during these months, indicating that their disappearance at site 10 was not a general phenomenon.

Baetis spp. 4 and 5 not only had largely disjunct distributions but to some extent also occupied different habitats. At site 10, 76% of the population of *Baetis* sp. 5 occurred at the bank, which occupied only 10% of the river bed; this was the only species of *Baetis* that occurred at the site. *Baetis* sp. 4 occupied both habitats at site 1, but for about 6 months between July and January was recorded only at the bank; two other species of

Baetis occurred occasionally at this site in both habitats. In addition, *Baetis* sp. 4 maintained high densities throughout summer (January–March) while *Baetis* sp. 5 had low densities during this period.

Gripopterygidae (Plecoptera)

Leptoperla neboissi McLellan and *Leptoperla primitiva* McLellan occurred occasionally in the upper catchment but were commonest in the lower catchment. Nymphs of *L. primitiva* were found at all sites in the lower catchment but were common only at three (2, 8, 10); nymphs of *L. neboissi* were found only at six of the ten sites (1, 2, 7–10). More than 95% of the nymphs of both species were found at the banks and for the purposes of estimating their size-frequency distributions and densities (see below) both species were considered to be restricted to the bank.

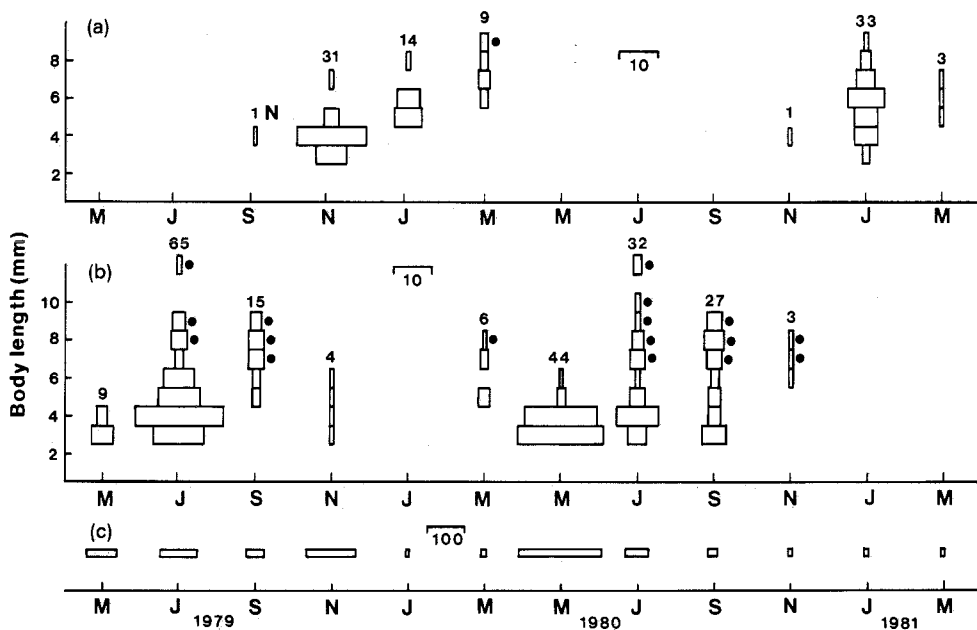


Fig. 6. Size-frequency distributions of *L. neboissi* (a) and *L. primitiva* (b) at sites 1–10; the number of immature Gripopterygidae (<3 mm in length) is also given (c). ● Final instar nymphs. Number of specimens in each size-class is indicated by the scale bars. Symbols as in Fig. 2.

All nymphs of both species caught at each site in the lower catchment were measured. The combined data (Fig. 6) show that each species was univoltine and that the nymphs of the two species developed sequentially. *L. primitiva* hatched in the autumn and grew through winter to emerge in spring, whereas *L. neboissi* hatched in spring and emerged the following summer or early autumn. An adult *L. primitiva* was caught in September 1980 and an adult *L. neboissi* was caught in January 1981.

The total number of nymphs caught on each occasion (Fig. 6) represents the density of nymphs in 3 m² (150 × 0.02 m²). The changes in density of the two species thus corresponded with the pattern of hatching and emergence described above. In addition, the changes in abundance of immature gripopterygids (Fig. 6) generally followed the pattern of hatching of the two species. As other species of gripopterygids were much less common

and occurred at only a few sites, it seems legitimate to consider the density of these immatures, the different species of which could not be distinguished, as representing the density of immature *Leptoperla*. About 90% of the immatures were found at the bank.

A few juvenile specimens of *L. primitiva* were present in November 1979 and a last instar nymph of this species was present in March 1980. These may represent a small summer generation, but no specimens were caught in January 1980 and a similar cohort was not present the following year. Misidentification was not the cause of these irregularities.

Helodidae (Coleoptera)

Cyphon sp. 1 was common at all sites in the upper catchment, but in the lower catchment it only occurred at the least disturbed sites (sites 1–3). It was most abundant at site 1 and here 90% of the population was found in the main channel. At site 1, *Cyphon* sp. 1 had a clear univoltine life cycle (Fig. 7). Hatching occurred in summer and the larvae grew strongly through autumn and into winter to reach maximum larval size by late winter or early spring. Densities declined during the life of each cohort, as expected.

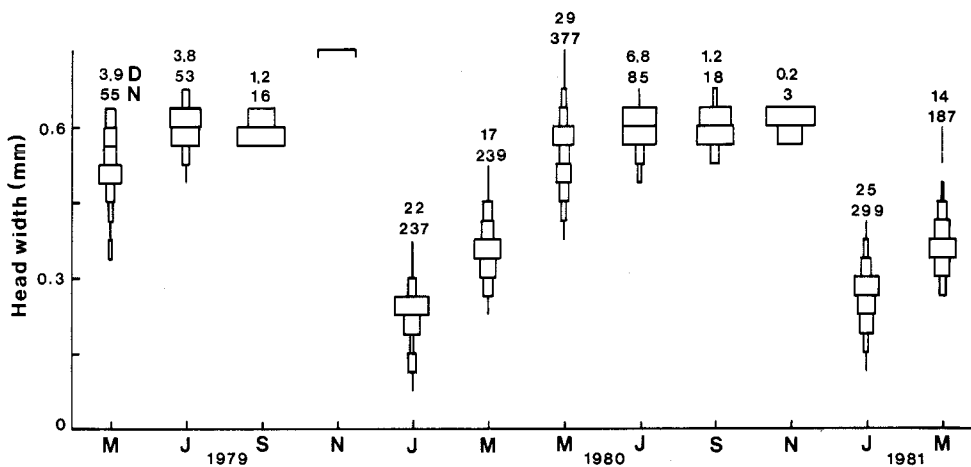


Fig. 7. Size-frequency (%) distributions of *Cyphon* sp. 1 at site 1. Scale bar indicates 50%. Symbols as in Fig. 2.

Ecnomidae (Trichoptera)

Ecnomus spp. occurred in both the upper and lower catchments but were abundant only in the latter region at disturbed sites (4–10). At sites 5 and 6 in the lower catchment, where larval density was highest, density was almost always higher in the main channel and 98% of the population occupied this habitat. The *Ecnomus* larvae possibly comprised more than one species in the La Trobe River but were assumed to be a single species at sites 5 and 6. From measurements of head widths five instars could be distinguished: instar 1, 0.15–0.20 mm; instar 2, 0.26–0.30 mm; instar 3, 0.35–0.45 mm; instar 4, 0.59–0.73 mm; instar 5, 0.83–1.30 mm.

At sites 5 and 6, *Ecnomus* appeared to be bivoltine (Fig. 8) with a fast-growing summer generation and a slow-growing overwintering generation. Larvae that hatched in September or November, probably from eggs laid by the preceding overwintering generation, grew to the fifth instar and began pupation by January. The overwintering generation hatched, presumably from eggs laid by the summer generation, between January and March and grew through the winter to pupate the following spring. Adult *Ecnomus* were caught at

light traps at sites 5 and 6 and at a number of sites in the upper catchment between November and February. At both sites, the summer generation appeared to be less numerous than the overwintering generation.

At site 5 (Fig. 8a), significant increases in density occurred between November 1979 and January 1980 ($t = 7.3$, $P < 0.001$) and between January and March 1980 ($t = 2.5$, $P < 0.05$). Thus, recruitment to the summer generation continued after November 1979, but by January 1980 larvae had grown to the fifth instar, and by March 1980 only the fifth instar larvae of this cohort remained. Between January and March 1980, the overwintering cohort hatched and probably continued to do so into the autumn. By January 1981, the next summer generation was almost finished and the overwintering generation had hatched. Temperatures were slightly warmer between November 1980 and January 1981 (1958 degree days) than between November 1979 and January 1980 (1861 degree days). This may well explain the more rapid development of the summer generation in 1980–1981 compared with 1979–1980 and the earlier hatching of the overwintering generation in 1981.

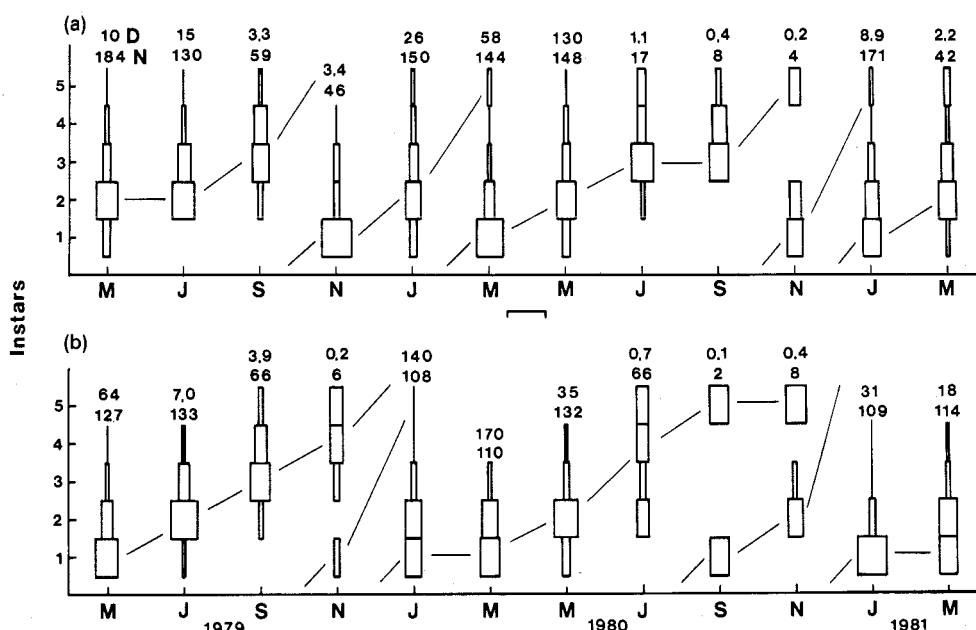


Fig. 8. Instar frequency (%) distributions of *Ecnomus* sp. at sites 5 (a) and 6 (b). Scale bar indicates 100%. Symbols and lines as in Fig. 2.

The summer generations at site 6 appeared to grow more rapidly or hatch earlier than those at site 5 and in both years the overwintering generation was established by January (Fig. 8b). This more rapid development may be attributable to the somewhat higher summer temperatures at site 6 than at site 5: 1926 degree days between November 1979 and January 1980, and 2047 degree days between November 1980 and January 1981.

Discussion

Although the samples in this study were taken every 2 or 3 months instead of monthly as in many other studies in temperate streams, the life histories were generally distinct, especially when the size-frequency distributions were interpreted in conjunction with data on densities. These data do not indicate irregular or unexpected increases in density due to recruitment either from deep in the sediment of the river or from small size-classes

not caught quantitatively in the 150- μ m mesh of the nets. Four species were clearly univoltine with synchronous growth, but few data on emergence were obtained. The other species were either bivoltine or trivoltine and displayed various degrees of synchrony of growth. The Ephemeroptera (especially the Baetidae) with such voltinism generally appeared to emerge over at least 5 months and probably somewhat longer. All the species had seasonal life cycles (*sensu* Hynes 1970) in which distinct changes in the size distribution of the larvae of nymphs occur with time as opposed to non-seasonal cycles in which all size-classes are present more or less continuously and cohorts are absent.

Some information about the synchrony of larval or nymphal growth is available from other studies on aquatic insects in temperate Australia. Studies on Ephemeroptera (Suter 1980; Suter and Bishop 1980; Campbell 1983) have generally shown less synchronous growth than was observed in this study and usually the presence of multiple cohorts of nymphs at a given site, each with a different rate of development. Emergence periods of 5 months or more were common and were much longer than usually found in the Northern Hemisphere (Macan 1979; Vannote and Sweeney 1980). For most species, however, nymphal growth was complete within 1 year. Hynes and Hynes (1975) obtained detailed data on nymphal growth for 27 species of Plecoptera in Victoria. Many had discernible life cycles with synchronous growth; only one showed more or less continual recruitment and emergence with all sizes of nymphs present at all times. However, growth and emergence lacked seasonal rigidity and emergence periods often extended over many months. Only one pair of coexisting closely related species that grew and emerged sequentially was recorded; in similar studies in the Northern Hemisphere, several such pairs have usually been recorded. It was suggested this degree of flexibility was an adaptation to an uncertain climate, a conclusion that probably can be applied also to the Ephemeroptera on the basis of present data.

It is not clear, however, what environmental features of rivers in temperate Australia are uncertain or unpredictable. Seven years of continuous water-temperature records were available for a site in the lower catchment of the La Trobe River (just below site 3, Fig. 1) above the input of heated water. The temporal predictability of these data can be gauged by calculating Colwell's (1974) predictability index, which varies from 0 (no predictability) to 1. In this case the index was 0.59 and was significantly ($P < 0.05$) different from zero using Colwell's G statistic. In addition, the total annual degree days for sites in the lower catchment uninfluenced by heated effluent (sites 1 and 10, Table 1) fell close to the regression lines calculated by Vannote and Sweeney (1980) that relate total annual degree days to latitude for various rivers in the central and eastern United States. Thus, the temperature regime in the lower catchment of the La Trobe River could not be described as unpredictable and in fact is what would be expected at a similar latitude in North America.

If temperatures in other permanent temperate rivers and streams in Australia are equally predictable, some other factor must be sought. Smith and Williams (1983) have suggested that the absence in Australia of a predictable (autumnal) input of leaves to streams could influence life cycles of stream invertebrates. However, there is no evidence so far that such an influence occurs and, in fact, many streams probably do receive a seasonally varying input of leaves because leaf-fall in Australian forests reaches a distinct peak in summer (Lake 1982). It seems more likely that unpredictable discharge, particularly in summer when rainfall decreases in much of southern Australia (Beadle 1981), could account for most of the uncertain nature of the habitat. Winterbourn *et al.* (1981) believe much the same occurs in New Zealand where streams are subject to heavy but temporally unpredictable rainfall.

Possibly on account of its predictability, temperature has been shown to play a vital role in the Northern Hemisphere in controlling the rate of development of aquatic insects (Vannote and Sweeney 1980). Evidence from this study and from those of Hynes and Hynes (1975) and Suter and Bishop (1980) indicates that it is also important in temperate

Australia. Hynes and Hynes (1975) recorded *L. primitiva* as clearly univoltine with emergence in autumn at a site where temperature varied annually from 7 to 15°C. They also found that *L. primitiva* coexisted with *Leptoperla bifida* McLellan, which was also univoltine but emerged in spring and early summer; this was their only pair of coexisting closely related species that displayed sequential emergence. In the lower catchment of the La Trobe River, temperatures were higher than at the site sampled by Hynes and Hynes and summer temperatures exceeded 20°C (Table 1). Here *L. primitiva* was again univoltine but emerged earlier, in spring, and apparently avoided high summer temperatures by not hatching until autumn. *L. bifida* appeared to have been replaced at this locality by *L. neboissi*, which occurred only during the summer.

Similarly, variations in the life cycle of *Ecnomus* sp., which have already been discussed, and the contrast between the trivoltine life history of *T. tonnoiri* in the lowlands and univoltine cycle of *Tasmanocoenis* sp. 2 in the upper catchment probably can be explained by differences in water temperature. Suter and Bishop (1980) found that *Tasmanocoenis tillyardi* (Lestage) was bivoltine but with two parallel generations: one hatched in spring and emerged the following spring, the other hatched in autumn and emerged the following autumn. They did not record short summer generations for this species, as we did for *T. tonnoiri*, possibly because mean summer water temperatures never exceeded 20°C (estimated approximately from data on maximum and minimum temperatures given by Suter 1980), whereas this occurred at all sites in the lower catchment of the La Trobe River.

Brittain (1982) concluded that ephemeropteran life cycles show a distinct latitudinal trend with multivoltine life cycles and non-discernible cohorts present in the tropics where water temperature is high and well-synchronized cycles with discernible cohorts at the lower temperatures of the temperate zone. This pattern appears to hold within Australia at least for certain families of Ephemeroptera. Marchant (1982) showed that species of *Tasmanocoenis* (Caenidae) and *Cloeon* (Baetidae) in the tropical Northern Territory had short nymphal life spans of about 1 month and lacked discernible cohorts; in the La Trobe River both these families had species with slower, more synchronous life histories.

In New Zealand streams, poorly synchronized life cycles apparently predominate among the benthic insects (Towns 1981) and cohorts are generally absent. For instance, leptophlebiid nymphs in a New Zealand stream at a similar latitude (36°S.) to the La Trobe River generally displayed poorly synchronized growth (Towns 1983) and six sympatric species showed little evidence of serial development or emergence. Such temporal segregation occurs to some extent in the La Trobe River, e.g. with *L. primitiva* and *L. neboissi*, and is commonly observed among closely allied species of mayfly and stonefly in the Northern Hemisphere (Hynes 1970, 1976; Vannote and Sweeney 1980; Brittain 1982). Competition among nymphs for a scarce resource, e.g. food, is usually invoked to explain such differences. However, as noted by others (e.g. Towns 1983) there is little experimental evidence to support this assumption and it is possible that such consistent differences in life histories result more from consistent and predictable changes in abiotic factors such as temperature. If each member of a group of congeneric species has a different preferred temperature range for growth, as a result of physiological differences, and if these ranges occur in a consistent sequence each year, as a result of the predictability of temperature change (as shown previously), then a consistent sequence of development or emergence could result.

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