

Life Histories of some Australian Siphlonurid and Oligoneuriid Mayflies (Insecta : Ephemeroptera)

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Abstract

The life histories of nine populations of mayflies were investigated through monthly field collections over a 3-year period. Seven species were studied, one each from the genera *Tasmanophlebia*, *Ameletoides* and *Mirawara* (Siphlonuridae) and four from *Coloburiscoides* (Oligoneuriidae). Nymphs were sorted and measured and life histories inferred from size frequency diagrams, and cohorts were separated using a technique for distinguishing multiple overlapping normal distributions. The life histories were all relatively poorly synchronized with adult emergence extended over 5 months or more in every case. A wide size range of nymphs was present in most populations for most of the year and these often formed multiple overlapping cohorts. The time required for development by different cohorts of a single population was quite varied.

Marked differences in the length and timing of the adult emergence period, and of the importance of particular cohorts, were apparent in different years. It was concluded that more than a single year's data from one site was necessary to interpret the life histories of Australian mayflies adequately.

The four *Coloburiscoides* species investigated displayed a wide range of development times and patterns, the shortest being displayed by *C. haleuticus*. This species had some cohorts that seemed to complete their development in about 6 months, whereas *C. giganteus* had some cohorts that required up to 3 years and also appeared to have a nymphal or early-instar diapause of between 9 and 11 months.

The life-history patterns found in this study did not readily fit into the classification schemes proposed by Northern Hemisphere workers. The general asynchrony found in this and previous Australian studies makes it doubtful that a useful classificatory system for Australian mayfly life histories can be developed.

Introduction

There have been few studies of the life histories of Australian mayflies. The first were those of Duncan (1972), who described the life histories of six species in Victoria, of which two were oligoneuriids and one a siphlonurid. All were studied for a single year and each at only a single site. Suter (1980) and Suter and Bishop (1980) investigated a further four species over a single year in South Australia, two of the species *Tasmanocoenis tillyardi* (Tillyard) and *Baetis soror* Ulmer, at two sites. None of the species was a siphlonurid or oligoneuriid. Marchant (1982) investigated the life histories of two species, *Cloeon fluviatile* Ulmer and *Tasmanocoenis* sp., for a year at one site in a tropical billabong in the Northern Territory, and Campbell and Holt (1984) that of the leptophlebiid *Kirrara procera* Harker over 2 years at two localities in south-eastern Australia. Finally, Marchant *et al.* (1984) reported data on seven species of mayflies (two baetids, two caenids and three leptophlebiids) from a study of the life histories of aquatic insects from the La Trobe River in Victoria.

In this paper, the life histories of a further seven species of mayflies from south-eastern Australia are described. These include *Mirawara aapta* Harker, *Tasmanophlebia* sp. and *Ameletoides* sp. (Siphlonuridae) and *Coloburiscoides giganteus* Tillyard, *C. munionga* Tillyard,

C. haleuticus Eaton and an unnamed species of *Coloburiscoides* (Oligoneuriidae). All of the species were investigated for at least 2 years and most for 3. In addition, *Ameletoides* sp. and *Coloburiscoides haleuticus* were each studied at two sites.

Methods

Study Sites

Nine study sites were selected (Fig. 1), with a single population studied at each. Physical characteristics of the sites are summarised in Table 1.

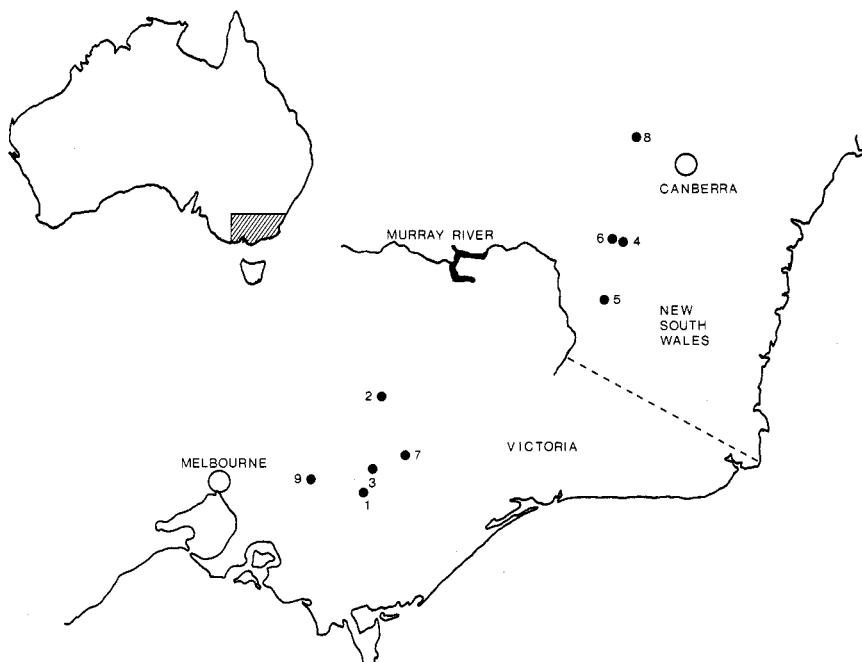


Fig. 1. Map of south-eastern Australia, showing the location of the study sites. The localities are as follows: 1, Tanjil River; 2, Chalet Creek; 3, Aberfeldy River; 4, Alpine Creek; 5, Diggers Creek; 6, Eucumbene River; 7, Wellington River; 8, Goodradigbee River; 9, Big Pat's Creek.

Collection Techniques

Serial collections of nymphs were taken at approximately monthly intervals between May 1977 and March 1980 using a Freshwater Biological Association-type rectangular frame pond net fitted with nylon mesh with an aperture size of 300 µm. From October 1979, an outer net, 1 m long with an aperture size of 50 µm, was also used at some sites in an attempt to collect first-instar nymphs, which are missed by the coarser mesh. Since full sorting of 50-µm mesh samples is very slow, these samples were not sorted completely in this study but only checked for the presence of early instars to establish the time of egg hatching.

Because of differences in the habitats of the insects, the net was used differently depending on the species being collected. For nymphs of all species of *Coloburiscoides*, which live in rapidly flowing water, the net was held with the opening facing upstream. Rocks immediately upstream of the opening were turned over and any nymphs visible were brushed by hand into the net. The same technique was used for *Ameletoides* sp. but the net was also swirled through pools where these nymphs are also abundant. *Mirawara aapta* and *Tasmanophlebia* sp. both live in relatively still water and they were collected by swirling the net through the water just above the substrate.

Table 1. A list of the study sites with some of their physical features

Site No.	Species studied	Site name	Location	Altitude (m)	Annual accumulated degree days	Gradient	Current speed of stream (m s^{-1}) ^A	Comments
1	<i>Ameteoides</i> sp.	Tanjil R., east Branch	146°16'E., 37°50'S.	1450	2440	1 : 63	<0.3	Narrow (<2 m) shallow (<0.5 m) stream, silty pools separated by short stony riffles
2	<i>Ameteoides</i> sp.	Chalet Ck	146°27'E., 37°08'S.	1120	2520	1 : 6	1.2	Narrow (<2 m) shallow (<0.5 m) stream, gravel pools separated by stony riffles and logs
3	<i>Mirawara aapta</i>	Aberfeldy R.	146°26'E., 37°51'S.	320	4700	1 : 125	0.5	Broad (~20 m) shallow (<0.5 m) stream with cobble bed
4	<i>Tasmanophlebia</i> sp.	Tributary of Alpine Ck	148°35'E., 35°55'S.	1280	2870	1 : 150	0.5	Narrow (<1 m) shallow (<0.3 m) stream with sand and silt substrate
5	<i>Coloburisoides giganteus</i>	Diggers Ck	148°29'E., 36°20'S.	1390	3260	1 : 26	1.1	Narrow (<4 m) shallow (<0.5 m) stream with bed of boulders, cobbles and bedrock
6	<i>Coloburisoides munionga</i>	Eucumbene R.	148°31'E., 35°53'S.	1340	3620	1 : 135	1.6	Broad (~20 m) shallow (<1 m) stream with a bed of cobbles and boulders
7	<i>Coloburisoides haleuticus</i>	Wellington R.	146°37'E., 37°32'S.	300	4700	1 : 145	1.0	Broad (~20 m) shallow (<0.5 m) forest stream with a bed of cobbles and small boulders
8	<i>Coloburisoides haleuticus</i>	Goodradigbee R.	148°32'E., 35°10'S.	380	4300	1 : 210	1.3	Broad (~30 m) shallow (<1 m) stream with a bed of cobbles and boulders
9	<i>Coloburisoides</i> sp.	Big Pat's Ck	145°46'E., 37°46'S.	210	3870	1 : 60	1.4	Narrow (<3 m) shallow (<1 m) forest stream with a bed of sand and gravel, banks lined with <i>Medaleuca</i> sp. roots

^A Maximum current speed for each site except site 1.

Samples were preserved in the field using Kahle's solution (Norris and Upton 1974). Upon return to the laboratory, each sample was hand-sorted at approximately 10 \times magnification.

Nymphal Measurements

In determining the life histories of insects, usually either size or degree of physiological development is used as an indicator of age (Clifford 1970a). In the present study, size was used as the primary indicator, with the presence of black wing pads being the only physiological stage distinguished. Mayfly wing pads darken just before emergence and the presence of such nymphs can be taken as an indicator that emergence is occurring (Needham *et al.* 1935).

The character measured to indicate size in the genera *Coloburiscoides*, *Ameletoides* and *Mirawara* was the length of the combined pronotum and mesonotum, which are fused to form a type of carapace that is large, rigid and easily measured. The measurement was made between the anterior edge of the pronotum and a line linking the posterior edge of the mesothoracic wing pads. In nymphs of *Tasmanophlebia*, the pronotum and mesonotum are not fused, and, since in the first few instars these structures are broader than they are long, the width of the mesonotum was measured.

All specimens in each sample were measured to the nearest 0.05 mm using a measuring eyepiece calibrated with a 200 by 0.01-mm stage graticule. Sex has been indicated in the results where it could be determined for the last few instars.

Analysis of Size Data

Because of the large number of nymphal instars, the frequent wide overlap in size between different instars, and the heterogeneous development patterns within the order (cf. Fink 1980, 1982), no attempt was made to ascertain the number of nymphal instars. Instead, life-history patterns were derived from the size frequency histograms for each sample. Because of the wide size range of nymphs present on most occasions, the graphical method developed by Cassie (1954) was used to distinguish the cohorts present and to determine their relative contributions to the sample (Fink 1980; Towns 1983). This technique distinguishes, and determines the means of, overlapping normal distributions. Lines have been drawn in the figures, connecting what are presumed to be the means of one particular cohort in successive monthly samples. Two major criteria were used for deciding which means should be linked: it was assumed that the means will usually increase in size from one sample to the next, and that the percentage contribution of a cohort to a sample is likely to be similar from one sample to the next.

Fecundity

The numbers of eggs produced by females of one species in each genus were either counted or estimated. For *Ameletoides* sp., *Tasmanophlebia* sp. and *Mirawara aapta*, mature female nymphs or female subimagoes were dissected and all the eggs present were counted. Female imagoes were not used since there is a possibility that they may already have oviposited some eggs.

Extruded egg masses were taken from female imagoes of *Coloburiscoides munionga* collected from the Eucumbene River at Kiandra and from Spencer's Creek near Mt Kosciusko. The total volume of several extruded egg masses from each population was determined using a Weld pycnometer (Salzberg *et al.* 1966). The volume of 10 single eggs was also determined using the formula

$$V = \frac{1}{6}\pi gs^2,$$

where g is the greatest diameter and s the smallest diameter of the egg. This formula has previously been used by Green (1956) to calculate the volume of ovoid cladoceran eggs and by Clifford (1970b) to calculate the volume of eggs of the mayfly *Leptophlebia cupida* (Say). The number of eggs per mass was then calculated by division of the mean volume of the egg masses by the mean volume of the 10 eggs.

Physicochemical Data

On each sampling occasion, water and air temperatures were recorded with a mercury thermometer. During the final year of the study, current speed was also measured with a stopwatch and an orange attached to a 2 m long string. Conductivity and in some cases total solids concentrations were determined at each site but only once. Conductivity was determined in the field with a Yellow Springs Instrument Company model 33 conductivity meter. Total solids was determined by evaporating 200-ml aliquots of water samples (Anon. 1976).

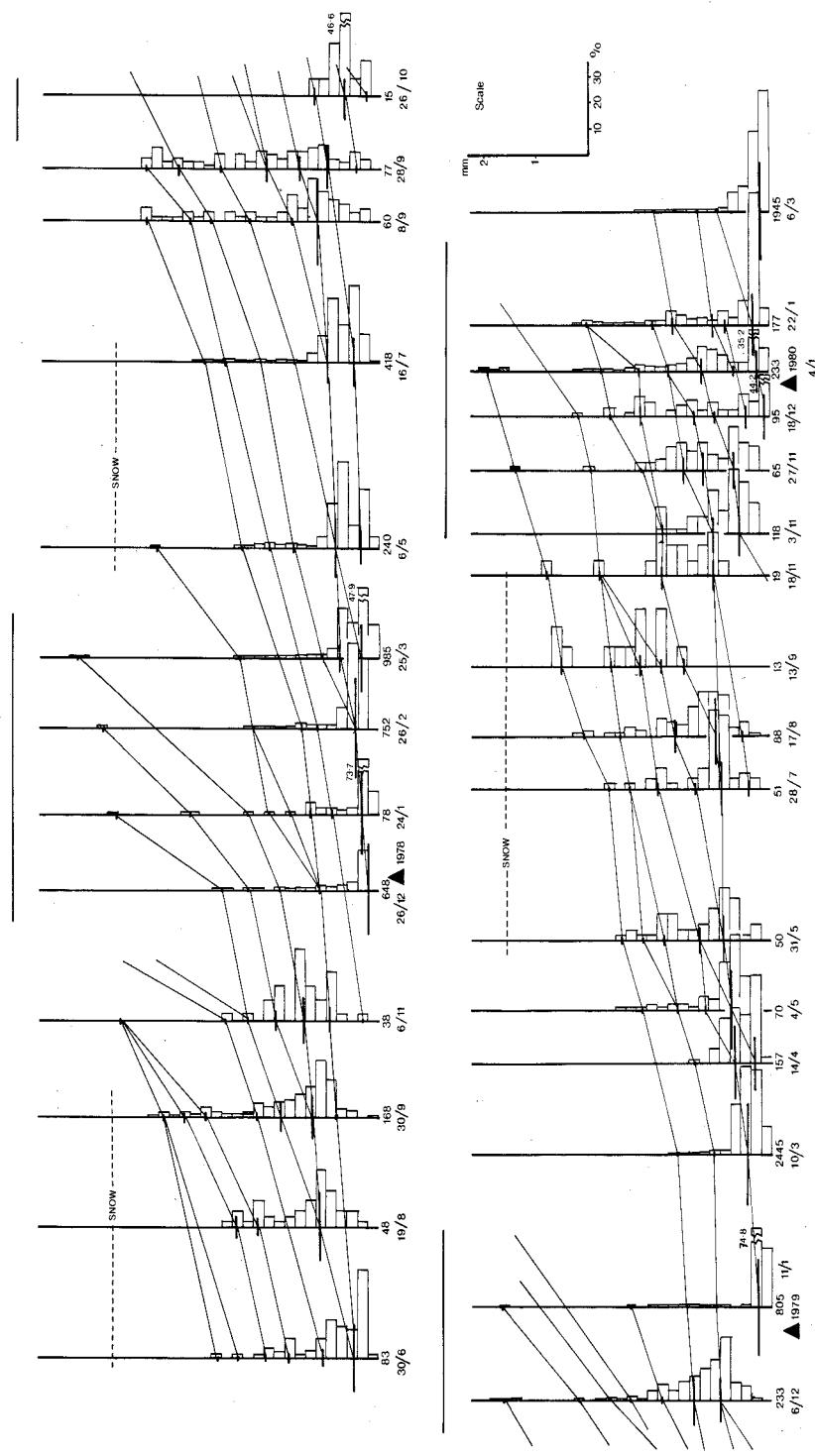


Fig. 2. Life-history data for *Ameloides* sp. at Mt Baw Baw. Size frequency histograms indicate the percentage of nymphs in each sample present in 0.2-mm size classes. The dimension measured was combined pronotum and mesonotum length. Scale lines are provided for the size frequency histograms, and the presence of female and male nymphs is indicated by the solid and shaded areas, respectively. The distance between the histograms is proportional to the time elapsed between the samples. Numbers along the baseline indicate the number of nymphs in each sample and the day and month the sample was collected. Arrowheads indicate the beginning of each year. Superimposed on the histograms are thick horizontal lines indicating the means of cohorts determined by the method of Cassie (1954). The length of these lines indicates the relative size of each cohort, and the thinner lines connecting them indicate presumed growth. The period of emergence is also indicated by the solid line above the figure.

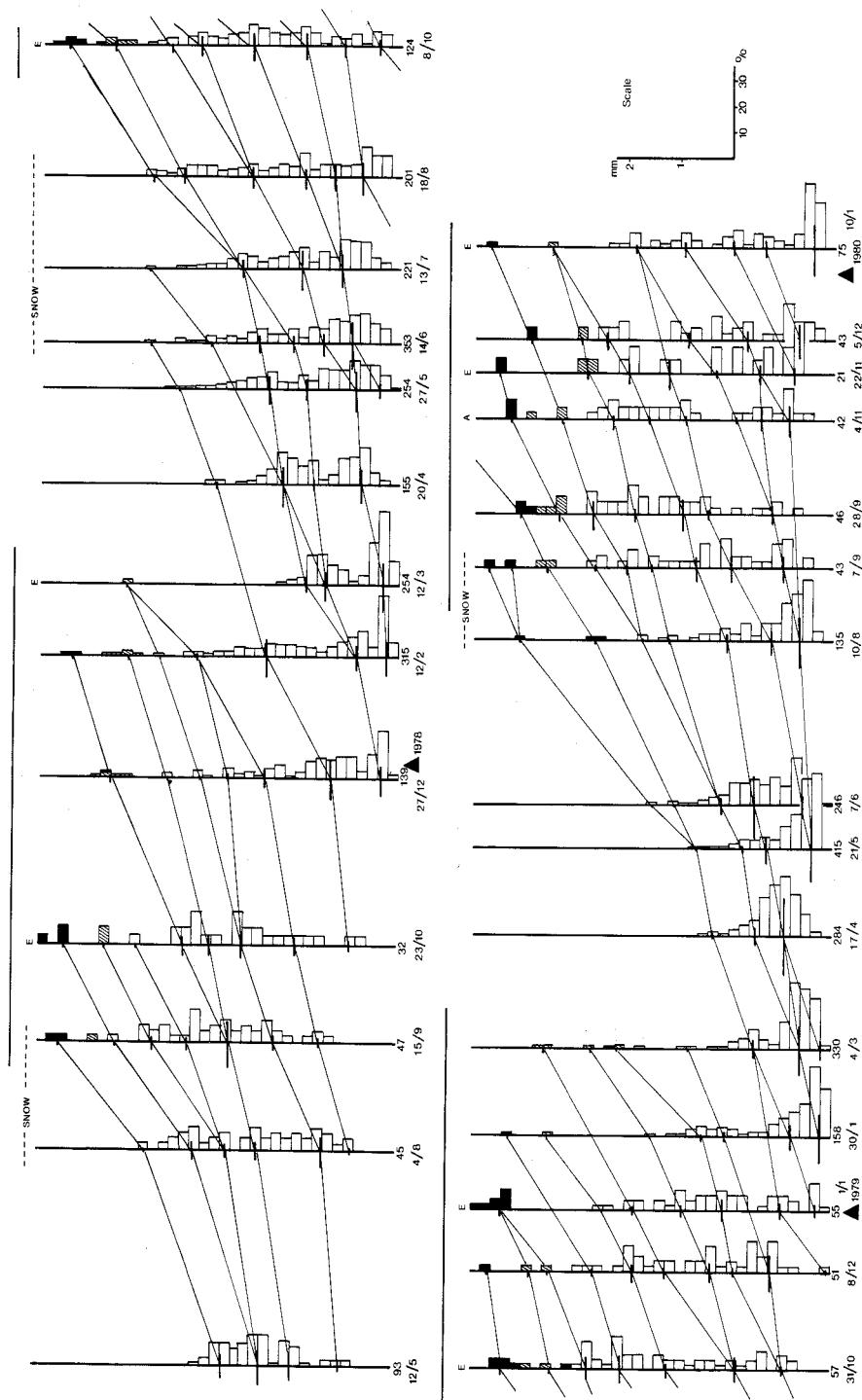


Fig. 3. Life-history data for *Ameloides* sp. at Mt Buller. Labelling as for Fig. 2. E, exuviae collected. A, imagoes or subimagoes.

Results

The results for each population are presented in Figs 2–10. Water temperature data for each site are plotted in Fig. 11. Data on egg numbers are presented in Table 2.

Table 2. Egg numbers determined for several populations of Australian Siphlonuridae and Oligoneuriidae

Species site	n	Egg number Range	Mean
<i>Ameletoides</i> sp.			
Mt Baw Baw	3	8700–13 560	10 720
<i>Mirawara aapta</i>			
Aberfeldy River	3	6400–10 120	8020
<i>Tasmanophlebia</i>			
Alpine Creek	3	1260–1840	1570
<i>Coloburiscoides munionga</i>			
Spencer's Creek	5	5680–12 300	7540
Eucumbene River	5	2030–4300	2620

Ameletoides sp.

A wide size range of nymphs of *Ameletoides* sp. was present for much of the year, and development was relatively asynchronous at both Mt Baw Baw (site 1) and Mt Buller (site 2).

At Mt Baw Baw, most nymphs appeared to take 2 years to complete their development (Fig. 2) with a few taking only 1 year. The disappearance of most of the large nymphs between September and November in both 1977 and 1978 indicates that emergence began as early as October. A few early-instar nymphs were collected later in the winter, indicating delayed hatching of some eggs. After hatching, the nymphs grew relatively slowly through two winters and a summer and emerged in their second summer. Temperatures in the stream were quite low (Fig. 11a), falling below 2°C in winter and barely reaching 15°C in summer, which may account for the slow growth rates.

The population of *Ameletoides* sp. at Mt Buller completed its nymphal life in a year or less (Fig. 3). The adult emergence period for this population was apparently even longer than for that at Mt Baw Baw. Mature nymphs occurred as early as August in 1979 although there was still some light snow on the stream banks until mid-September of that year. In 1977, mature nymphs were present in September, and in 1978 in October. Emergence continued until March in both 1978 and 1979, giving an emergence period of 7–8 months. Small nymphs were numerous in the samples collected between December and March each year, indicating a relatively short development period for the eggs. Small nymphs continued to occur throughout the year, but whether this was due to some eggs taking longer to develop, or whether it was simply a reflection of the long adult emergence period cannot be determined from the data available. The nymphs appearing in the summer samples apparently grew through winter to emerge the following spring. In 1979, a second large recruitment appeared in the May sample. These nymphs, apparently arising from eggs of adults emerging in March and April, would presumably have completed their development in about March 1980. A similar cohort was also present in 1978, but was relatively much smaller. The reason for its large size in 1979 was presumably a larger-than-usual March–April emergence that year. This in turn was related to more nymphs than usual hatching in the second half of 1978 and completing their development over the summer.

Both the population at Mt Buller and that at Mt Baw Baw are notable for their multiple overlapping cohorts. The reason for the shorter life history in the Mt Buller population is

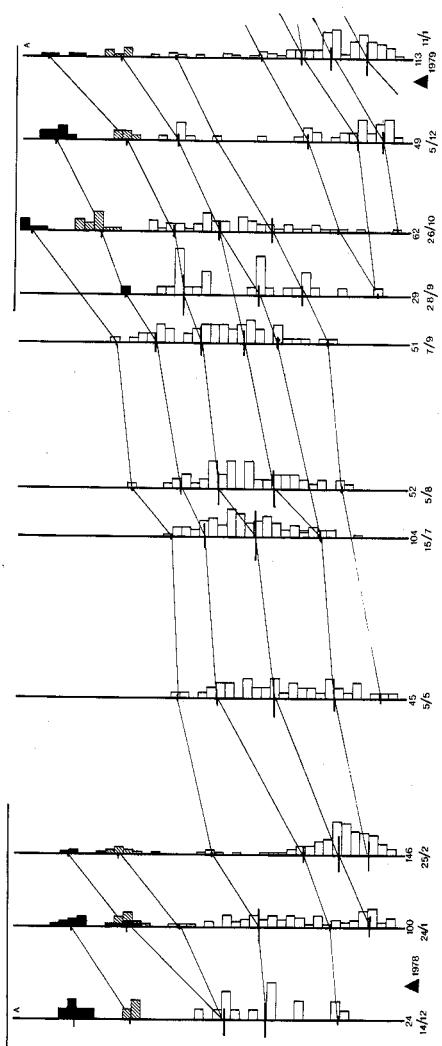
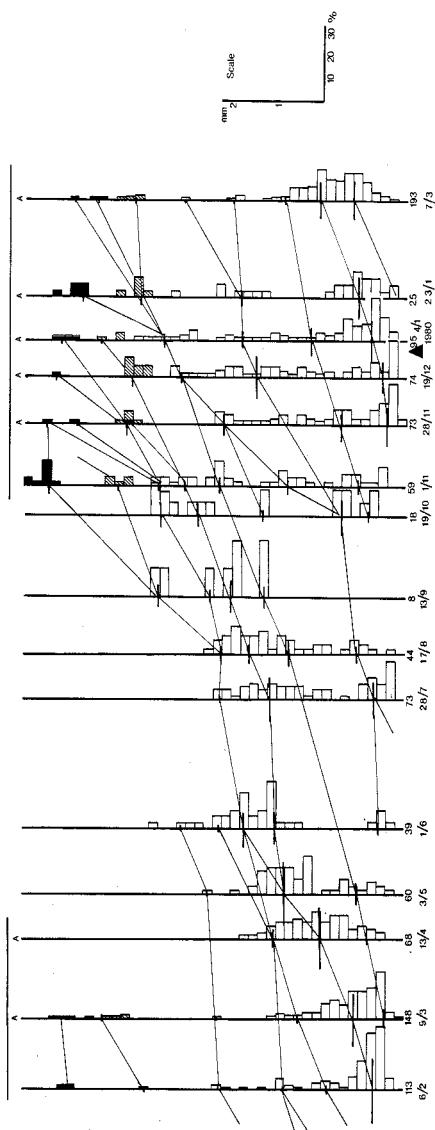


Fig. 4. Life-history data for *Mirawara apta*. Labelling as for Fig. 2.



not clear. Water temperatures were lower in summer but higher in winter at the Mt Buller site, compared with those at Mt Baw Baw (Fig. 11b), but the total number of degree days was similar—an average of 2516 per year for Chalet Creek compared with 2442 per year for the Tanjil River. The difference may also be due to differences in food, although gut content analyses (Campbell 1985) indicated that these were not large either.

Specimens of *Ameletoides* sp. were observed emerging both in the field and in the laboratory. Between mid afternoon and evening, emerging nymphs crawled from the water up a rock face until they were 10–15 cm clear of the water in the head-up position. The emergence took several minutes with the subimago then flying rapidly directly upwards and disappearing from sight. Most of the nymphs emerged around dusk.

Mirawara aapta

At site 3 (Aberfeldy River), *M. aapta* had an extended emergence period with adults flying between late October and early April (Fig. 4). Most eggs probably hatched quite rapidly since small nymphs were always in the collection following the first appearance of mature nymphs. The presence of small nymphs in the July and August samples of 1979 suggests some delayed hatching as well.

Most nymphs completed their development in about a year. Several cohorts appeared to take less than a year, one in the summer of 1978–9 taking only 10 months and part of another in 1979–80 taking only 9. In contrast, two cohorts that were already quite large animals when sampling began took a further 13 months to complete their development and must have taken 15–18 months at a minimum for their entire nymphal growth.

This species, like *Ameletoides* sp., had both a long adult emergence and a wide size range of nymphs present throughout the year. Like the Mt Baw Baw population of *Ameletoides*, the nymphal development time was quite variable. The Aberfeldy River is a comparatively warm stream (Fig. 11c), and the high water temperatures coupled with the carnivorous diet of *M. aapta* enable a short life history even in such a large species.

M. aapta nymphs swam to the water surface where ecdysis occurred rapidly. Within seconds the subimago took off and flew rapidly straight upwards. Emergence always began as light was fading and subimagos could be collected at a light on the stream bank for several hours after dusk, which suggests that emergence may continue for that period.

Subimagos transformed on the evening after their emergence. Along the Murrumbidgee River at Bolaro, subimagos were collected resting near the bases of the stems of *Juncus* sp., whereas elsewhere subimagos were only collected emerging or at lights. The subimagos probably normally rest near the tops of overhanging trees, and only at sites like Bolaro, where there are no trees for some considerable distance from the river, do they rest so close to the ground. Female imagos oviposited on quiet pools from 0900 h (E.S.T.) to 1600 (E.S.T.). They flew singly 10 cm or less above the surface of pools, touching the tip of the abdomen to the water at regular intervals. Evidently, the eggs are released singly or in small groups.

Tasmanophlebia sp.

Size frequency data for *Tasmanophlebia* sp. are only available from March 1978 (Fig. 5) and, because the species was not abundant, numbers of individuals in some samples were fairly small. The life history may include one or two generations per year. Eggs of the main generation hatched in January and February, and the nymphs grew through winter emerging as adults from September right through to December and January. Those adults that emerged apparently produced an additional summer generation, which hatched in about September, grew rapidly through the summer and emerged in late February or March. In both years, there was also a quite large cohort that appeared in July or August and emerged in January or February. Presumably this cohort arose from the delayed hatching of eggs laid during summer and autumn. A few small nymphs were present in almost every sample, a further indication of some delayed hatching.

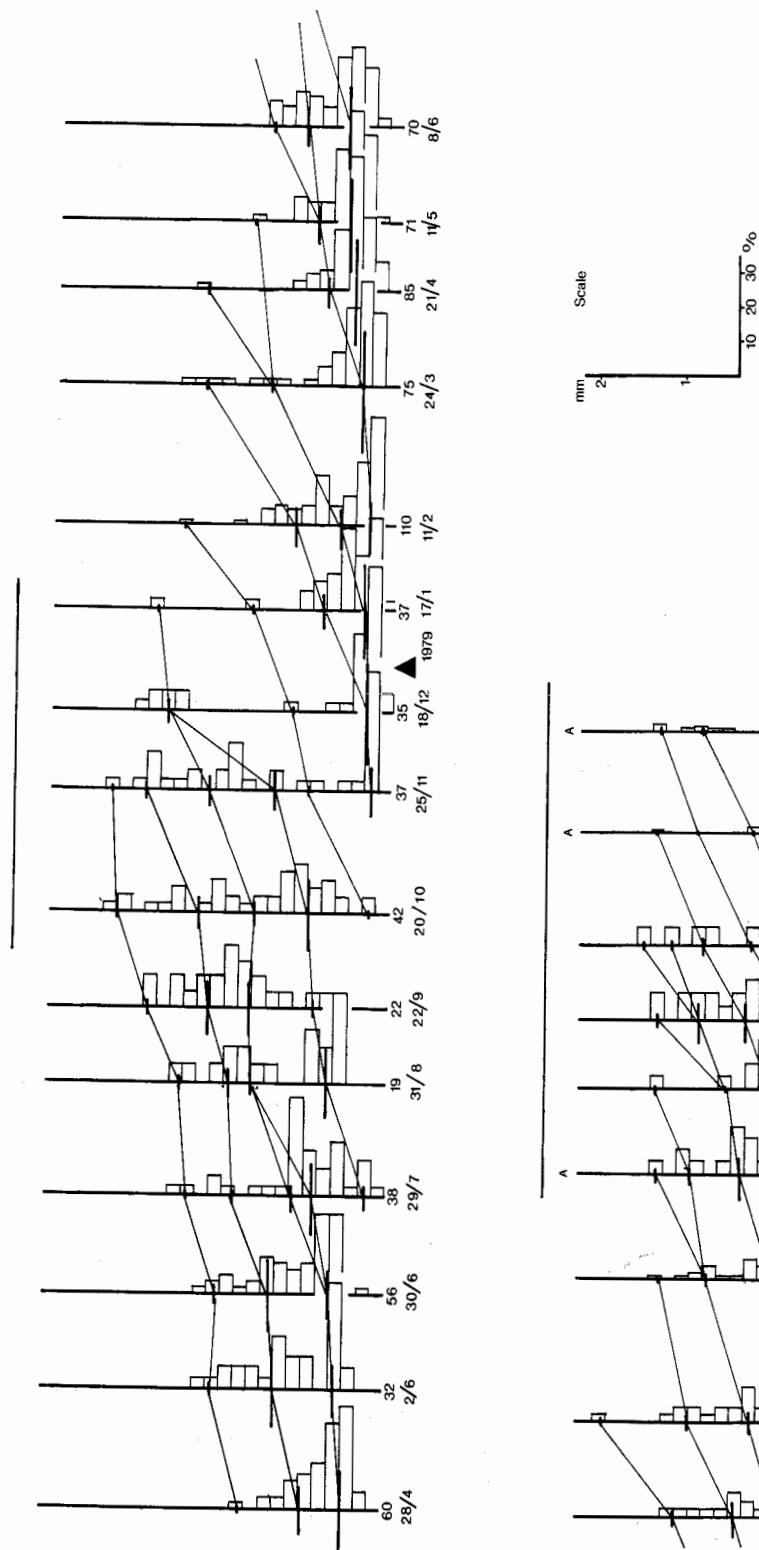
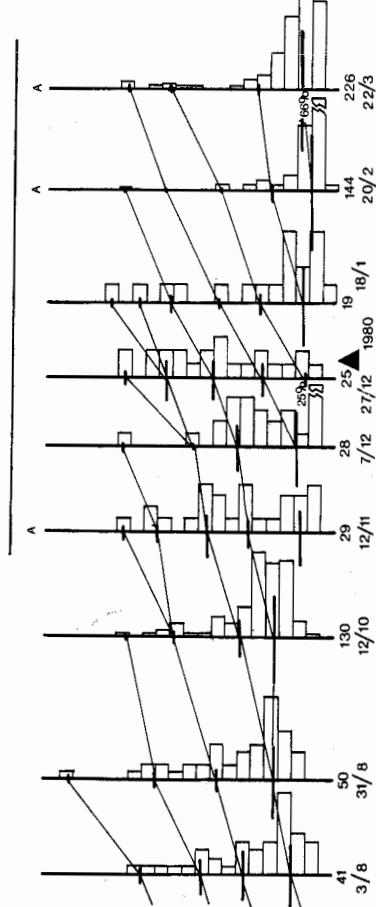


Fig. 5. Life-history data for *Tasmanophlebia* sp. The dimension measured was mesonotum width, otherwise labelling as for Fig. 2.



Alpine Creek is a comparatively cool stream with a maximal summer temperature of only 15°C (Fig. 11d). The seasonal temperature range was also small, only 12·3°C, which was smaller than for any other stream studied, except Big Pat's Creek.

Tillyard (1921, 1933) has described emergence for *Tasmanophlebia lacustris* Tillyard, *T. nigrescens* Tillyard and *T. lacuscoerulei* Tillyard. In all three species, the nymph crawls from the water before ecdysis. The same is also true for *Tasmanophlebia* sp., which, in the laboratory, was observed leaving the water at dusk.

Coloburiscoides giganteus

Although the numbers of *C. giganteus* nymphs were small in many of the samples, the life history was still clear (Fig. 6). In Diggers Creek (site 5), eggs hatched in October and early November. The nymphs grew through the summer and the following winter. Most emerged between November and February of their second summer. However, some had not completed their development and grew for a further year before emergence. The proportion of nymphs requiring the extra year of nymphal growth varied from year to year, being quite large in the cohort that hatched in the spring of 1976, and smaller in the cohorts that hatched in the springs of 1977 and 1978.

The emergence period for the species appears to be quite well defined, occurring between mid-November and March each year. Mature nymphs emerging early in the hatch were somewhat larger than those emerging later, and there is probably a similar variation in adult size. Female nymphs were larger than male, and this difference was reflected in the adults.

The smallest nymphs collected were always found for the first time at about the same time as the emergence begins, but were only collected in November and December, even though most of the mature nymphs were collected in January and February. An examination of the 50 µm mesh net samples indicated that smaller nymphs were present in the October and November samples only. This indicates that the species has an egg or early-instar diapause of between 7 and 11 months. Eggs laid in one spring-summer emergence either do not hatch until the following October, or hatch and the first-instar or second-instar nymphs descend into the hyporheic habitat of the stream where they remain for the same period.

Diggers Creek is quite cool for most of the year (Fig. 11e) but water temperatures may exceed 20°C briefly during the summer months.

C. giganteus subimagoes were never collected at a light until complete darkness had fallen. Both Tillyard (1933) and I have collected subimagoes from rocks in mid-stream at first light although exuviae were never found. It would appear that subimagoes emerge during the night, directly from the water and, on cold nights at least, fly to the nearest rock until temperatures are warmer the following morning.

Coloburiscoides munionga

C. munionga was quite abundant in the Eucumbene River (site 6) and consequently most of the samples used for the life-history study contained more than 100 specimens (Fig. 7). In addition, because the females of this species carry the egg mass externally before oviposition, several were collected and returned to the laboratory for observation of the hatching time.

Two egg masses were collected from females at site 6 and a third from a female taken at Spencer's Creek on the Mt Kosciusko summit road, all in January 1982. Each egg mass was maintained in the laboratory in a Petri dish half filled with water taken from the stream at which the female was caught. The laboratory temperatures varied between 22 and 25°C, which was similar to water temperature in the two streams at the time (Fig. 11f). One of the two batches of eggs from the Eucumbene River had shown no sign of development after 5 months and was abandoned; of the other, 95% of the eggs hatched within 24 h 14 days after they were collected. The eggs collected from the Spencer's Creek specimen also hatched

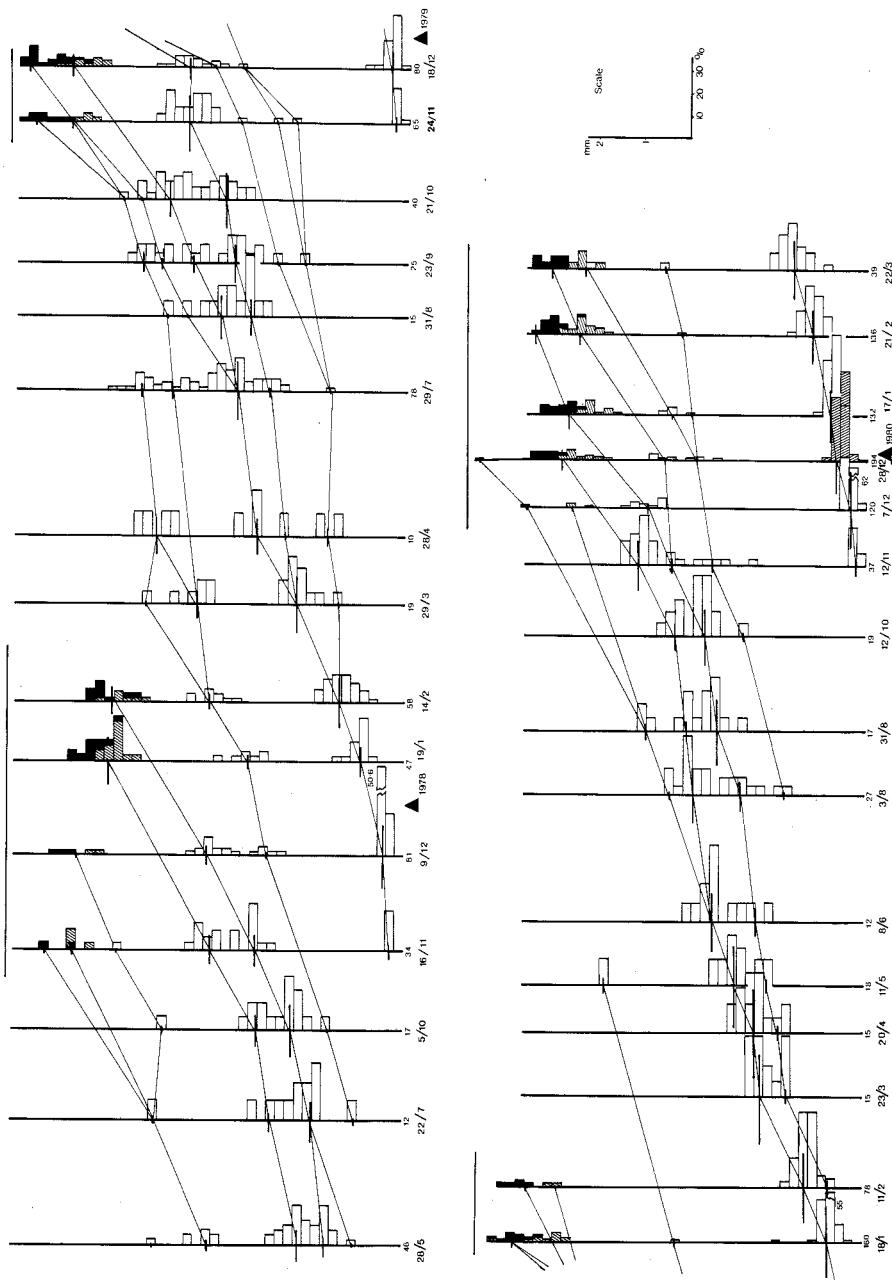
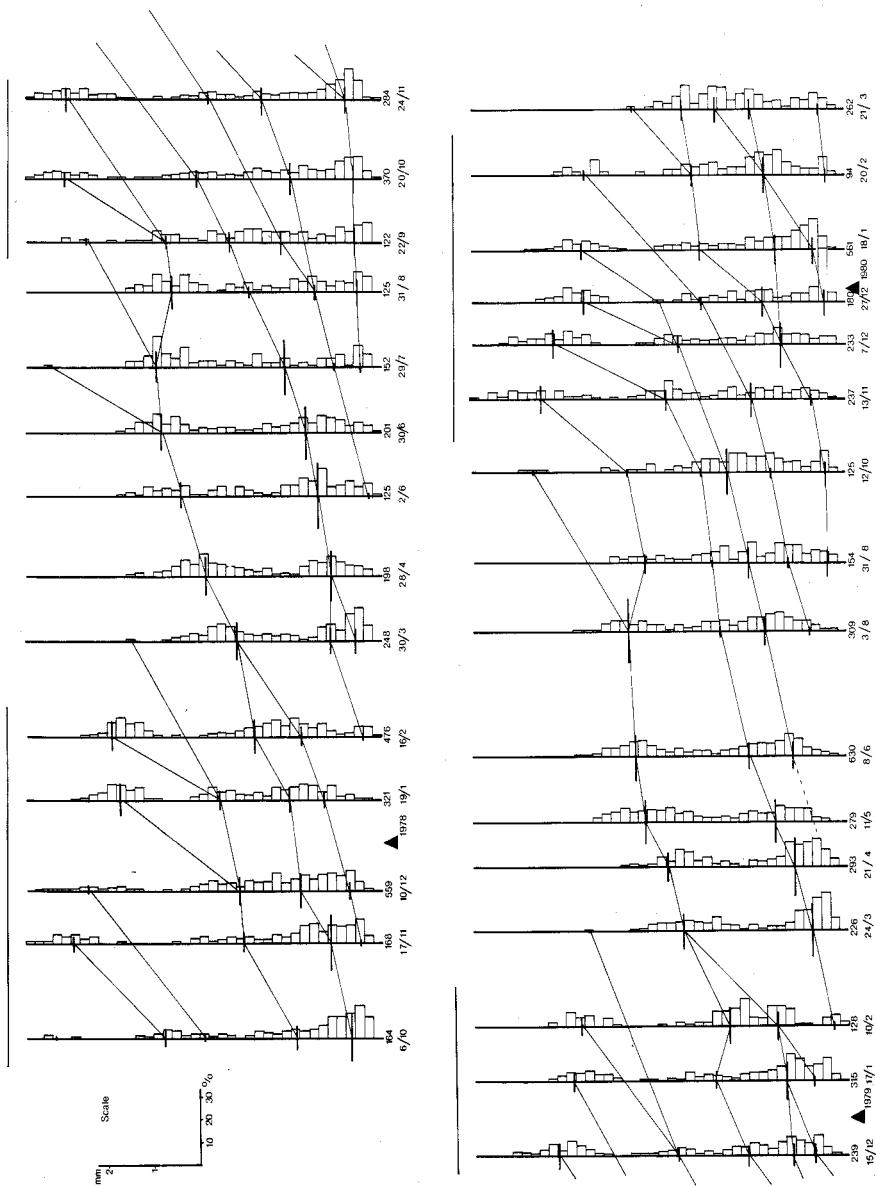


Fig. 6. Life-history data for *Coloburiscoides giganteus*. Labelling as for Fig. 2.

Fig. 7. Life-history data for *Coloburiscoides munonga*. Labelling as for Fig. 2.



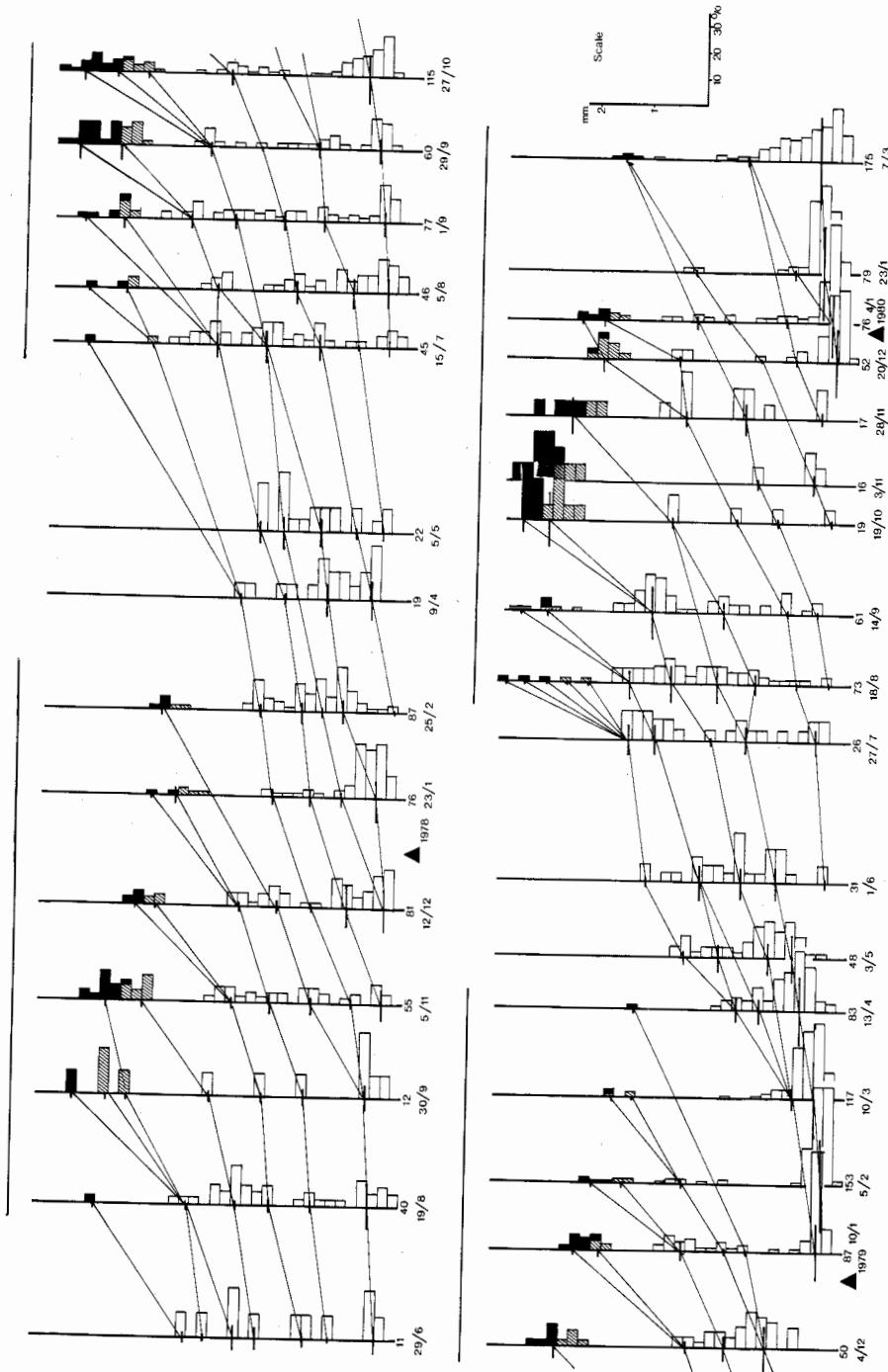


Fig. 8. Life-history data for *Coloburisoides haluticus* at the Wellington River. Labelling as for Fig. 2.

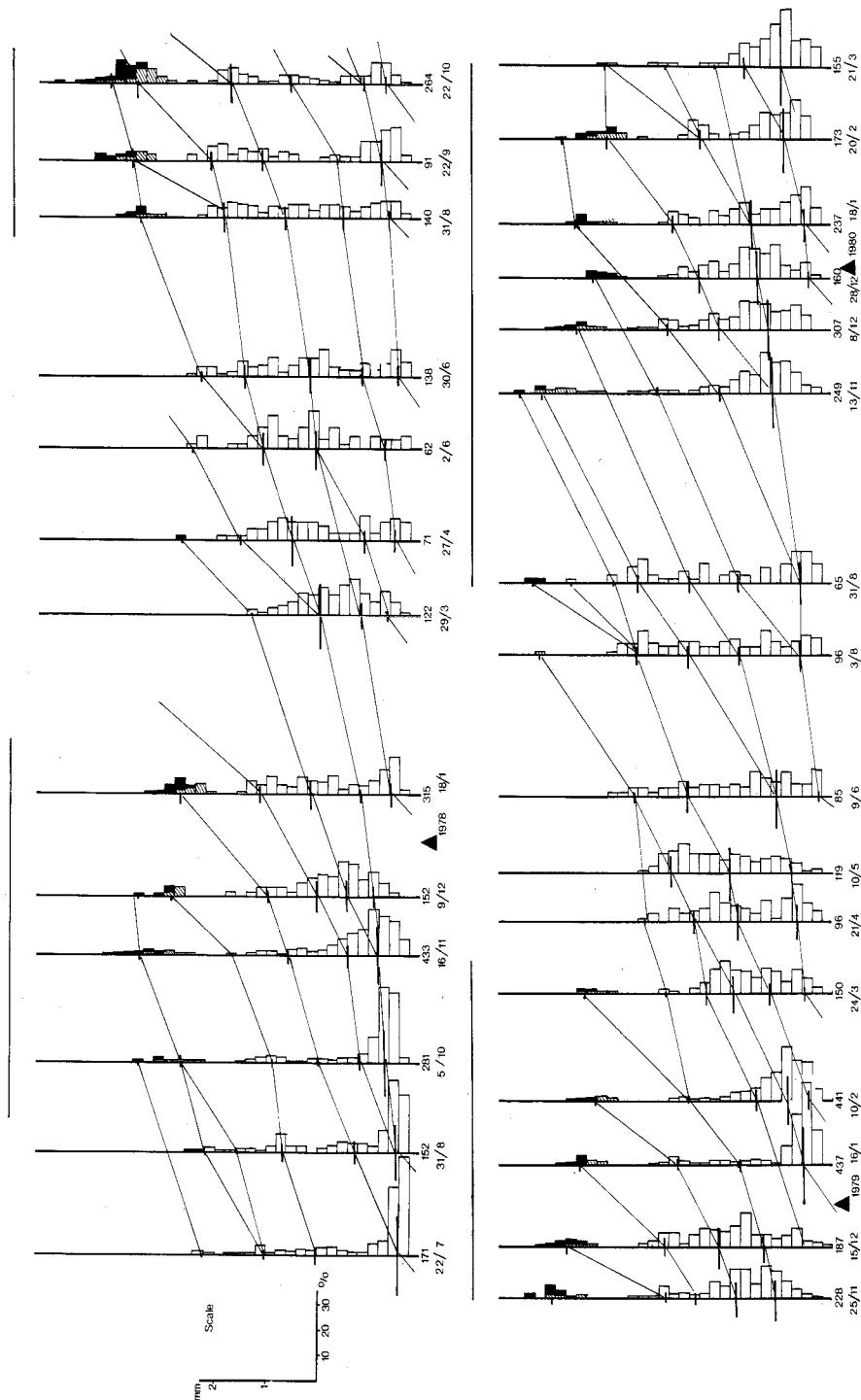


Fig. 9. Life-history data for *Coloburiscoides haleniticus* at the Goodradigbee River. Labelling as for Fig. 2.

14 days after collection. Once again, most hatched in 24 h and 2 days later (16 days after collection) 98% of the eggs had hatched. None of the few eggs remaining hatched in the ensuing 5 months.

Nymphs of *C. munionga* emerged between September and March. Adults were most abundant, however, between about late October and late February. There seemed to be two peak hatching periods for the eggs, one in late spring and the other in late summer. In 1977, the spring hatching occurred between the November and December sampling times, a little later than in the following two years. In 1978, the spring hatch occurred between September and October, and in 1979 between October and November. In each case, the influence of the hatch may be seen in both the increase in sample size and the increase in numbers of small-size-class nymphs. A second peak hatching period occurred in summer. In 1978-79 and 1979-80, it occurred between December and January and in 1977-78 between January and February. The nymphs from these two hatches grew through the autumn and winter to emerge in the following spring and summer, respectively. The size frequency distributions in autumn and winter appear bimodal as a result. Both cohorts took a year to complete their development. A third, smaller cohort appears to hatch in winter. It was quite small in the winter of 1978 but considerably larger in 1979. In view of the data on egg hatching, these small cohorts must have arisen from a small number of early emerging adults. They completed their development in 8 months.

Subimagos of *C. munionga* and *C. haleuticus* always emerged directly from the water surface and transformed on the following evening. Swarms of male imagos of *C. munionga* began to appear at 2-5 m above the stream just as the last light faded. Imagos could be collected at lights for some hours, so swarming may continue for some time after dark.

Egg numbers were quite different between the populations at Spencer's Creek and the Eucumbene River, where the life history was determined (Table 2). On average the eggs were smaller in the Eucumbene River population (4.6×10^{-6} cm³ compared with 8.2×10^{-6} cm³ and the volume of the egg masses was about one-fifth (1.2×10^{-2} cm³ compared with 6.2×10^{-2} cm³). Even within a population, it is clear that fecundity in this species is quite variable.

Coloburiscoides haleuticus

The life history of *C. haleuticus* was studied at two sites (site 7, the Wellington River and site 8, the Goodradigbee River) approximately 370 km apart. Even so, the life histories of the two populations appear quite similar (Figs 8 and 9). Both populations are notable for the long emergence times. At site 7, mature nymphs were present in collections in August each year (and in July in 1978) and were still present in March or April, indicating an emergence period of 8-9 months. At site 8, emergence appeared to take place from August to March in 1978-79 and 1979-80 but to be restricted to between October and January in 1977-78.

In the Wellington River, the largest numbers of mature nymphs were collected in spring. Although there was some variation between years, mature nymphs were always relatively abundant in October. The newly hatched nymphs became most abundant in late December and early January, indicating that the eggs hatched about a month after oviposition. Smaller numbers of newly hatched nymphs continued to appear throughout the year. This may be due to delayed hatching but is more likely to be simply a reflection of the long emergence period. The development time for the nymphs was variable. The largest cohorts took about 11 months to develop, giving a 12-month generation time. There was considerable variation amongst the cohorts, however, with a range of 6-15 months for nymphal development. Size of emerging nymphs decreased markedly during each emergence period.

At the Goodradigbee River (site 8), the nymphal development time varied between about 6 and about 15 months. In 1978-79 and 1979-80, large hatches of small nymphs occurred in December-January. However, the hatch of nymphs in the summer of 1977-78 appeared to be relatively much smaller. Unlike the Wellington population, at Goodradigbee River additional large hatches of nymphs occurred in winter. This was especially noticeable in

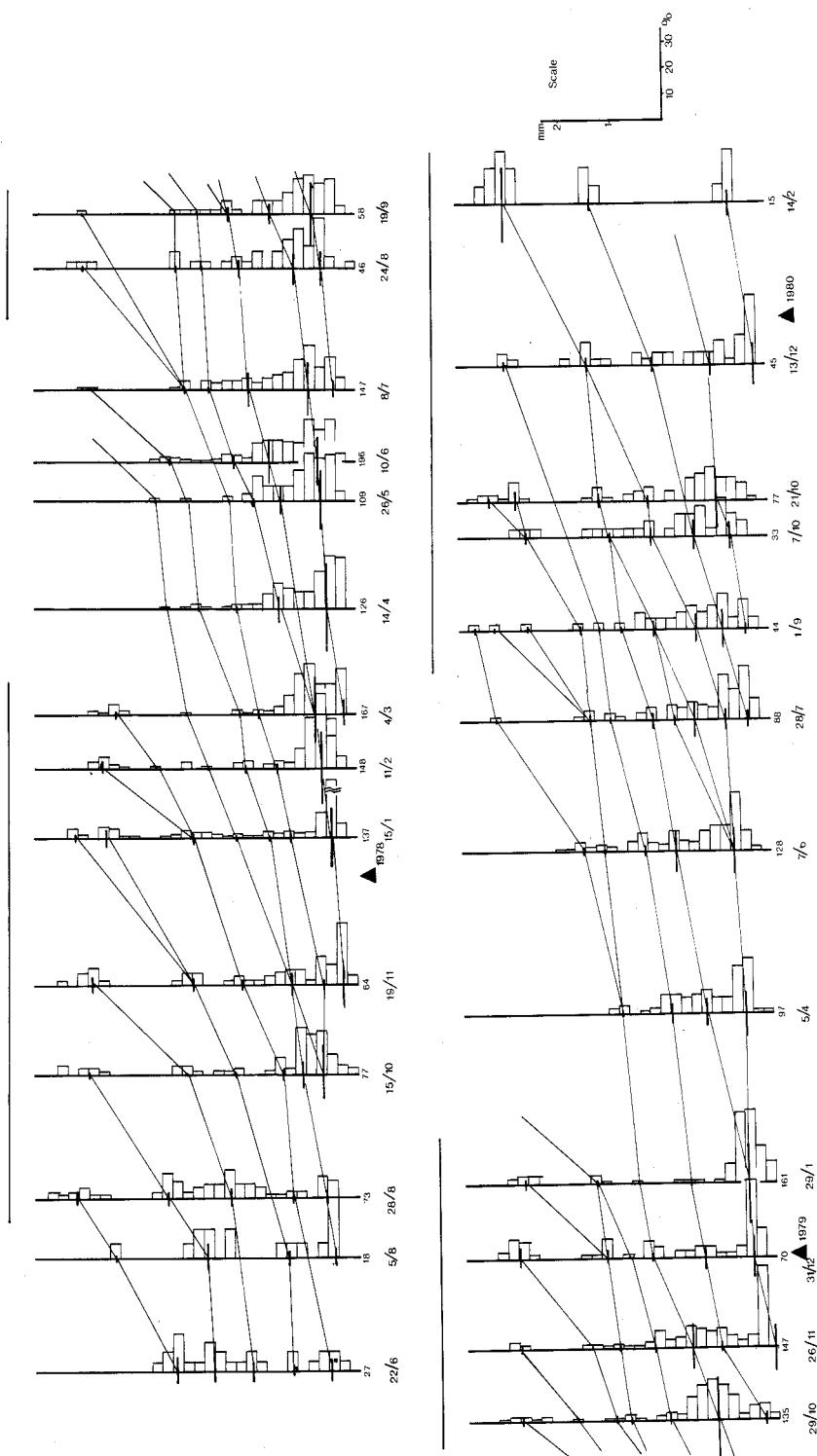


Fig. 10. Life-history data for *Coloburiscoides* sp. Labelling as for Fig. 2.

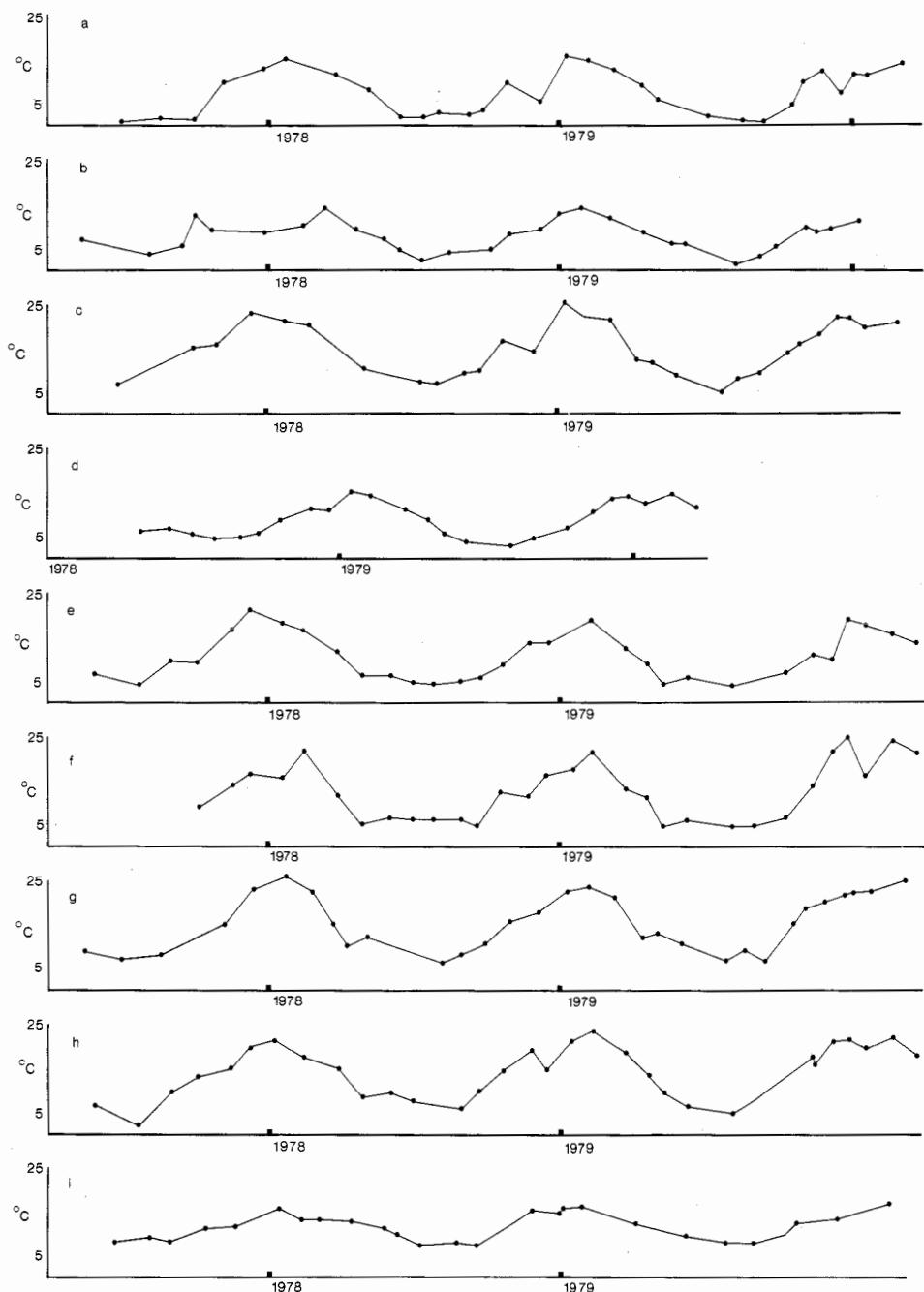


Fig. 11. Stream temperatures recorded at each of the study sites during the course of the study. The localities are as follows: (a) site 1, Tanjil River; (b) site 2, Chalet Creek; (c) site 3, Aberfeldy River; (d) site 4, Alpine Creek; (e) site 5, Diggers Creek; (f) site 6, Eucumbene River; (g) site 7, Wellington River; (h) site 8, Goodradigbee River; (i) site 9, Big Pat's Creek.

1977 and 1979. Water temperatures were somewhat lower in the Goodradigbee than in the Wellington River (Figs 11g, 11h) and, perhaps, the development time for eggs laid in late summer and in autumn was longer as a result. A considerable number of the winter hatching nymphs appeared to be unable to complete their development by the end of the following autumn and to continue to grow until the spring, taking 15–16 months to complete their development.

In *C. haleuticus*, male imagos swarmed at dusk over the centre of the stream. Swarming in this species seemed to be a fairly precisely timed event, occurring for about 20 min and ceasing before the light had completely faded. The swarms were initially at about 20–25 m above the stream but as the light faded they descended to about 10 m. Two populations, at the Wellington and Wonnangatta Rivers, always swarmed above bridges and it is likely that the bridges were used as visual location markers by the species. Use of markers by swarming mayflies has previously been noted in the literature (Savolainen 1978). In both populations, the swarms consisted of up to several hundred males only. Females apparently fly into the swarm, select a male and the pair then mate while descending towards the water. Females were never collected in net sweeps through the swarm, but pairs *in copula* were collected as they descended from the swarm. The egg mass is extruded and touched to the water surface to release the eggs, with the female often flopping into the water shortly afterwards.

Coloburiscoides sp.

Like *C. haleuticus*, *Coloburiscoides* sp. (Fig. 10) had an extremely long emergence period, from July to March. There was a similarly long period of recruitment of small nymphs with a peak from November to February. Since some small nymphs were still being collected between April and July, it is likely that hatching was delayed for some of the eggs.

Nymphal development seemed to take about a year for most of the nymphs. As for *C. haleuticus*, however, some cohorts departed quite markedly from this pattern and development periods ranged from about 7 to around 19 months. The stream had the smallest annual range of water temperature (Fig. 11i) and was warmer in winter and cooler in summer than any other investigated, and this may have influenced the variability of the life history.

The size of the emerging nymphs was less variable than for the other species of *Coloburiscoides* investigated. Early in the emergence, the nymphal size increased, reached a peak and then decreased as the emergence season progressed.

Discussion

In general, the life cycles could be related to either intrinsic factors such as the size to which the species grows and its dietary habits, or to environmental factors such as the abundance of food, water temperature and current speed.

Mirawara aapta was the largest species studied and the nymphs completed their development in a year or less. The Aberfeldy River is a warm stream (about 4700 degree days per year) and the nymphs are carnivorous, a diet that has a higher energy content per unit weight than any other available to stream invertebrates (Anderson and Cummins 1979).

Tasmanophlebia sp. were the smallest nymphs studied and completed their development in 6–12 months. As detritus feeders, their diet is not as energy-rich as that of *M. aapta* (Anderson and Cummins 1979) and they also live in a cooler habitat.

Ameletoides sp. may take 10–24 months to complete its life history. There was a considerable difference in the length of the life history of Mt Baw Baw and Mt Buller populations. Most of the Mt Baw Baw population took 2 years to complete the life cycle, whereas at Mt Buller the life cycle was completed in a year or less. In both populations, the patterns of nymphal development varied between years.

Within *Coloburiscoides*, *C. giganteus* has the longest life cycle, taking 1 or 2 years as growing nymphs after almost a year of nymphal or egg diapause. This species is the largest within the genus, and was living at the coolest site. *C. munionga* was studied at a higher-altitude

site than the previous species, but the Eucumbene River is warmer than Diggers Creek (3620 compared with 3260 degree days per year) and the species does not grow as large. In addition, *C. munionga* consumes more algae than *C. giganteus* (Campbell 1985) and thus has a richer diet. These factors would be sufficient to account for the far shorter life history of this species. *C. haleuticus* was investigated in lower-altitude warmer streams. It displayed a basic 1-year life cycle, similar to that of *C. munionga*, at both sites at which it was studied. Variation in length of the life cycle shown by the differed cohorts of *C. haleuticus* was greater than for *C. munionga*. There was little difference in the length of the life histories between the Wellington River and Goodradigbee River population of *C. haleuticus*. *Coloburiscoides* sp. occurred at the lowest altitude and the stream had the most even temperature throughout the year. The period of nymphal development was a year for most nymphs as it was for *C. haleuticus*, but the range of variation was less in the former species.

Synchronism and Variability of Life Cycles

One of the major features of the life histories of the Australian Siphlonuridae and Oligoneuriidae is the apparent lack of synchrony. This manifests itself in a number of ways. The most obvious is in the extended emergence period of most species. Of eight species whose life histories are now known, only two have emergence periods of less than 6 months. The longest emergence period is 9 months and was found in two species, *C. haleuticus* and *Coloburiscoides* sp. The second manifestation of asynchronism is in the large size range of nymphs present in the stream at any time. Three factors probably combine to produce this effect. The long emergence periods mean that oviposition and consequently egg hatching would also occur over a long time. Additionally, in some species, eggs apparently continue to hatch for several months after the end of the emergence period, a phenomenon well known in mayflies (e.g. Macan 1957; Illies 1959, 1968; Clifford 1969). Finally, several species have a number of overlapping cohorts and often more than one generation present at a time, either because all or part of a cohort takes more than a year to complete its growth.

The life histories of all of the species investigated varied between years. Variation was apparent in emergence, egg hatching and nymphal development pattern.

Timing of the emergence period of two species, *Tasmanophlebia* sp. and *Ameletoides* sp. at Mt Baw Baw, varied markedly from year to year. *Tasmanophlebia* sp. appeared to complete its emergence by the end of November in the summer of 1978-79; however, in the following summer emergence appeared not to commence until November and to continue to March. At Mt Baw Baw, mature *Ameletoides* sp. nymphs were only present from January to March in the 1977-78 summer but were present from December to January and November to January in 1978-79 and 1979-80, respectively. In two other species the emergence period was markedly shorter in 1977-78 than in the other two years. In the Aberfeldy River, *M. aapta* only emerged between December and February in 1977-78 although in the two following years it emerged from September to March. In the Goodradigbee River, *C. haleuticus* emerged between October and January in 1977-78 but emerged between August and March in the two following years.

For several species, the timing and degree of synchrony of the main egg hatch differed between years. This was most noticeable in the populations of *Tasmanophlebia* sp. and *M. aapta*. *Tasmanophlebia* sp. appeared to have a major egg hatch between October and December 1978-79 but between December and February in 1979-80. *Mirawara aapta* had its main egg hatch between January and February in the 1978-79 summer, but between November and January the following year. In *Coloburiscoides* sp., hatching occurred over a much more extended period in 1978-79 than in the other two summers. *C. haleuticus*, on the other hand, seems to have been far more synchronous in its main egg hatch in 1978-79 and 1979-80 than it was in 1977-78. Finally, between June and August 1977, eggs of *C. haleuticus* hatched in the Goodradigbee River; there was not a hatch of anything like similar proportions at a similar time in either of the two subsequent years.

Several nymphal cohorts each with a different development time were present for every species each year, but the relative proportion of the population present in a given cohort was often quite different from year to year. *C. giganteus* nymphs recruited into the population in November–December 1976 appeared in the November and December 1977 samples as three cohorts. Two of these emerged in January–February 1978 but a third continued to grow through to emerge in late spring. The third cohort formed a conspicuous and significant part of the population in the stream in the winter of 1978. On the data for 1977–78, therefore, the life history of the species would be interpreted as most nymphs taking 16 months to develop but with a significant proportion of the population taking an extra 9 months. However, virtually all of the nymphs recruited to the population in November–December 1977 appeared to emerge in the summer of 1978–79, taking 12–16 months to complete their development, with only a very few nymphs requiring the extra 9 months. The interpretation of these data would be that the nymphal development time is 12–16 months, although the occasional straggler requires longer. Similar differences between years were also apparent with other species. For *Ameletoides* sp. at Mt Buller, there was apparently a large nymphal recruitment in May–June 1979. The same recruitment occurred in 1978, but was not so large, and in 1977 it was barely detectable. The size of the summer cohorts of *Tasmanophlebia* also varied between the two years.

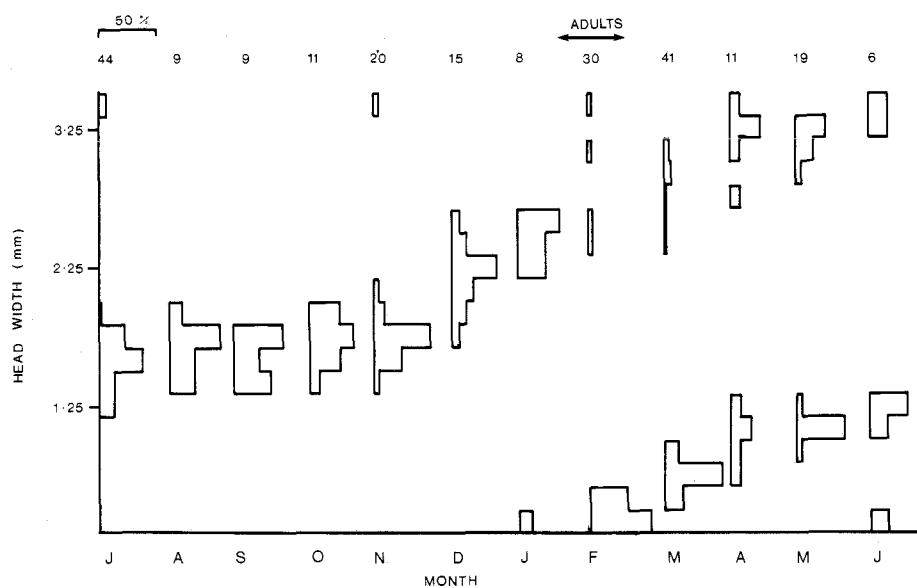


Fig. 12. Size frequency diagram for *Coloburiscoides* sp. nymphs collected from Chalet Creek between July 1971 and June 1972. The number of specimens in each sample is indicated at the top. The horizontal arrow indicates the months in which adults were taken in the field or in which nymphs with black wing pads were present in the sample. Data are expressed as percentage of nymphs in 0·16-mm head width size classes. Figure after Duncan (1972).

Previous Studies on Australian Mayfly Life Histories

The only previous study on the life histories of siphlonurid or oligoneuriid mayflies in Australia was that of Duncan (1972), who studied a species of *Coloburiscoides* and *Ameletoides* sp. in Chalet Creek and *Coloburiscoides* sp. in Wilks Creek near Marysville. The species of *Coloburiscoides* from Chalet Creek she called *Coloburiscoides giganteus*; however, it appears to be an undescribed species referred to here as *Coloburiscoides* sp. 1. The study was carried

Table 3. Life histories of temperate Australian mayflies other than Siphlonurids and Oligoneuriids

Species	Location	Nymphal development No. of generations	Emergence season (length, in months)	Egg development time	Reference
Leptophlebiidae					
<i>Atalophlebia australasica</i>	Deep Creek, S.A.	2	5 and 10	Spring-autumn (5-5)	No diapause
	Chalet Creek, Vic.	1	12	Summer (4-5)	No diapause
	Chalet Creek, Vic.	1	12	Summer (5-6)	6 weeks
<i>Atalophlebioides</i> sp. A	La Trobe River, Vic.	1	12	Summer-autumn (3-4)	No diapause
<i>Atalophlebioides</i> sp. B	Goodradigbee River, N.S.W.	1	12	Summer (3-5)	No diapause
<i>Kirrara procerata</i>	Wellington River, Vic.	1	12	Autumn-spring (10)	No diapause
	Spring Creek, S.A.	1	10-12	Autumn-spring (10)	Suter (1980)
	La Trobe River, Vic.	1	12	Spring (3)	Marchant <i>et al.</i> (1984)
	La Trobe River, Vic.	2	12 and 4	Summer-autumn (3)	Marchant <i>et al.</i> (1984)
<i>Nousia inconstipata</i>	Deep Creek, S.A.	1-2	8-13	Winter-autumn (7)	6 month winter diapause
<i>Nousia</i> sp. 2	Spring Creek, S.A.	1	12	Summer (5)	Suter and Bishop (1980)
<i>Nousia</i> sp. 4	Chalet Creek, Vic.				Duncan (1972)
Baetidae					
<i>Baetis soror</i>	La Trobe River, Vic.	2	9 and 5	Spring-autumn (7)	No diapause
<i>Baetis</i> sp.	La Trobe River, Vic.	1	7-10	Spring-summer (8)	No diapause
<i>Baetis</i> sp. 4	Deep Creek, S.A.	1-2	8-12	Spring-summer (6)	Delayed hatching
<i>Baetis</i> sp. 5	Spring Creek, S.A.				Marchant <i>et al.</i> (1984)
Caenidae					
<i>Tasmanocoenis tillyardi</i>	La Trobe River, Vic.	2	5 and 9	Spring-summer (5)	No diapause
	La Trobe River, Vic.	1	12	Spring-summer (2)	No diapause
<i>Tasmanocoenis tonnoiri</i>	La Trobe River, Vic.				Suter and Bishop (1980)
<i>Tasmanocoenis</i> sp. 2	La Trobe River, Vic.				Marchant <i>et al.</i> (1984)
					Marchant <i>et al.</i> (1984)

out for 1 year only and generally on much smaller sample sizes than those available in the present study.

For *Ameletoides* sp. (which she referred to as *Ameletoides lacus-albinae*) Duncan (1972) described a 1-year life history with an emergence period of 6 months. An analysis of the life history by morphological stages proved difficult to interpret, but she did find that, in October, March and May, two cohorts of stage II nymphs were present, which is consistent with the multiple cohorts apparent in the present study.

Coloburiscoides sp. 1 was not a species whose life history was investigated in the present study. However, it is a very similar species to *Coloburiscoides giganteus* both in size and general form as well as in habitat. Duncan believed that *Coloburiscoides* sp. 1 was univoltine with an emergence period in January and February. Her size frequency diagrams (Fig. 12) show large nymphs present consistently from February to July and I believe that the emergence period was in reality from February through to at least March or April. Full-grown nymphs not yet emerged by about April probably did not emerge until late the following spring.

The smallest nymphs of *Coloburiscoides* sp. 1 occurred in Duncan's collection in January and February. She used a coarser net than used here (23 strands per centimetre or approximately 430 µm) so that these nymphs must have been larger than the smallest collected in the present study. The presence of these small nymphs coincident with the first of the mature nymphs was explained by suggesting that emergence may have started earlier than the presence of mature nymphs had indicated, and that the period of embryonic development was very short. Since her December and January samples were very small, this was possible. In the light of the life history of *Coloburiscoides giganteus*, however, I consider it far more likely that *Coloburiscoides* sp. 1 also had a diapause in the egg as an early instar.

The second species of oligoneuriid whose life history Duncan described was *Coloburiscoides* sp., a species also investigated in the present study. Duncan studied the species at a site on Wilks Creek, about 26 km north of the Big Pat's Creek site, and at an altitude of 470 m compared with 210 m at Big Pat's Creek. Duncan suggested that the life history was completed in less than a year, which would be consistent with the results from the present study.

There are four published and two unpublished previous accounts on Australian mayfly life histories. Marchant (1982) studied the life histories of *Cloeon fluviatile* and a species of *Tasmanocoenis* in tropical billabongs in Northern Territory. He found that the species bred continually throughout the year, and estimated that the life cycle took about 1 month. Life histories of this type are common in tropical mayflies (Brittain 1982). The other five studies all investigated temperate mayfly populations. I have already discussed Duncan's (1972) results for the Siphlonuridae and Oligoneuriidae. Her results for other species together with those of Suter (1980), Suter and Bishop (1980), Campbell and Holt (1984), and Marchant *et al.* (1984) are summarized in Table 3.

The shortest nymphal development period recorded for a temperate Australian mayfly before the present study was 7 months, for *Atalophlebia australasica* (Pictet) by Suter (1980). Most species have a nymphal growth period of about 12 months, with 13 months the longest record (Suter 1980). Relatively long emergence periods are also common, with three of the seven other temperate species studied having adults emerging for 6 months of the year or more. Both delayed hatching of eggs and winter egg diapause have been recorded previously, although the diapause was considerably shorter than that found in *Coloburiscoides giganteus*.

Most of the other Australian life-history studies have revealed a relatively poor degree of synchrony in all of the species studied. This was particularly evident in the data on Duncan's (1972) *Atalophlebioides* sp. B and in Suter's (1980) data. Campbell and Holt (1984) found that *Kirrara procera* had a reasonably well-synchronized life history for much of the year, but only one of the seven species of mayfly investigated by Marchant *et al.* (1984) shows a well-synchronized life history. It has already been noted that only one species in the present study had a well-synchronized life history.

Like the present study, Suter (1980) and Suter and Bishop (1980) found that a number of populations had more than one cohort present at a time and these cohorts were referred to as 'generations'. I believe this terminology is inappropriate and confusing. The problem can be illustrated using the life history of *Coloburiscoides munionga* from the present study, which is represented in Fig. 13. In the present study, these overlapping cohorts, C1, C2 and C3, are recognized, which are considered to constitute a single generation. I would classify the species as univoltine since each cohort requires a year to complete its development whereas Suter (1980) would have classified the three cohorts as three 'generations' and considered the species trivoltine. Whatever the terminology, the phenomenon of a species having multiple cohorts present at a site at any given time is apparently common in Australian mayflies. Furthermore, each cohort follows a development pattern different from that of the other cohorts present at the site. Nine species from four families are known to have such life histories in Australia: *Tasmanocoenis tillyardi* (Caenidae), *Baetis soror* (Baetidae), *Atalophlebia inconspicua* (Eaton) and *Atalophlebia australasica* (Leptophlebiidae), *Coloburiscoides munionga* and *C. haleuticus* (Oligoneuriidae), and *Ameletooides* sp., *Mirawara aapta* and *Tasmanophlebia* sp. (Siphlonuridae).

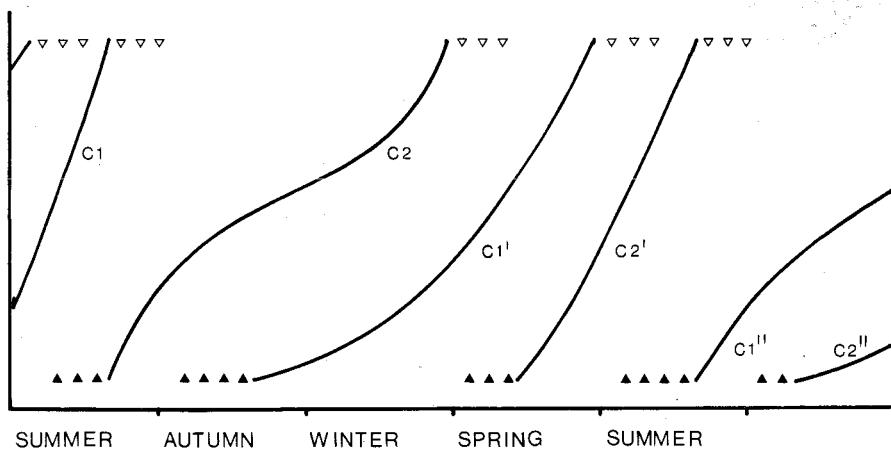


Fig. 13. Diagrammatic representation of the life-history of *Coloburiscoides munionga*. ▲ Nymphal recruitment. △ Presence of adults. — Nymphal growth. Cohorts are numbered C1, C2, etc. Cohort C1 gives rise to C1', which gives rise to cohort C1'', and so on.

The two previous studies that have investigated Australian mayfly life histories over more than 1 year both showed some differences between years. Campbell and Holt (1984) found that *Kirrara procera* (Leptophlebiidae) commenced emergence from the Wellington River 2 months earlier in 1979–80 than it had in 1977–78. In fact, in 1979–80 emergence appeared to be substantially complete by the beginning of January, whereas in 1977–78 it did not commence until the end of February. Marchant *et al.* (1984) found differences in the life histories between two successive years for one species of *Baetis* in the La Trobe River but found little evidence of between-year differences in the other six mayfly species they investigated. However, the samples were only taken bimonthly and sample sizes were often small, reducing the degree of resolution of the study.

Suter (1980) studied the life histories of two species (*Baetis soror* and *Tasmanocoenis tillyardi*) at two sites. He found marked differences in the life cycles between the sites, with a shorter development time for some of the cohorts at one site. This he attributed to higher prevailing water temperatures. If this is the case, it is likely that these two species also display flexibility in their life histories from year to year.

From this evidence, and that of the present study, it would appear that life histories of temperate Australian mayflies are generally variable both geographically and between years, and not strongly seasonal. Their major features may be summarized as follows:

1. long emergence periods, usually 5 months or more;
2. poor synchronization of development, so that a large size range of nymphs is present at any time;
3. multiple cohorts common at a given site, each with a different development pattern;
4. variability in length of life cycle and in patterns of growth, both geographically and from year to year.

Comparison of Australian and Northern Hemisphere Mayfly Life Histories

Most life-history studies of Northern Hemisphere mayflies have been conducted at relatively high latitudes, and the life histories have been quite synchronous and strongly seasonal. Perhaps the best indication of this is the brevity of their emergence periods. In Europe, for example, Illies (1968) notes that species of *Baetis* may have emergence periods of up to 6 months but that in most other species the period is shorter. He cites four species with emergence periods of only 1 month. Macan (1979) gives data on emergence periods for 13 British species plus the genus *Leptophlebia*. In 9 of the 14, these were 3 months or less, and *Baetis rhodani* (Pictet), with an emergence period of 8 months, was the only species with an emergence period longer than 5 months. A similar situation exists in the higher latitudes in North America. Coleman and Hynes (1970), for example, found an emergence period of $4\frac{1}{2}$ months for *Stenonema vicarium* (Walker), while five other species in the same Ontario stream all had emergence periods of less than 3 months. A number of other authors have also recorded short emergence periods for species living in northern United States and Canada (e.g. Leonard and Leonard 1962; Harper and Magnin 1971; Clifford *et al.* 1973; Boerger and Clifford 1975; Hall *et al.* 1975).

Another reflection of the high degree of seasonality in high-latitude, Northern Hemisphere mayflies is the degree of synchrony of development of the nymphs. The synchrony may be sufficient to allow two, or in some cases three, species in the same genus to exist sympatrically by having their development in different phases. This phenomenon is widespread in Europe. Landa (1968), for example, cites five examples of such species pairs and one of a species trio from central Europe. Macan (1981) also describes a number of such species pairs from Britain. The same phenomenon has been recorded on a number of occasions from northern United States and Canada (e.g. Ide 1935; Coleman and Hynes 1970; Hynes 1970; Boerger and Clifford 1975; Sweeney and Vannote 1981).

These highly seasonal and synchronous life histories are in marked contrast to those of Australian mayflies. Almost all the Australian species studied have had long emergence periods. The Australian mayfly fauna is poorly known taxonomically and ecologically but, even so, there is as yet no evidence of any species pairs of the type discussed above.

Berner (1950) noted that there are clear latitudinal tendencies in the life histories of the North American mayfly fauna. He pointed out, in all of the species that occur both in Florida and in Canada, the Canadian populations have brief emergence periods whereas the Florida populations emerge year round. According to Berner (1950), few of the Florida mayflies have seasonal life histories even though quite a number of them have seasonal life histories in more northern parts of their geographic ranges. He attributed these differences to the climatic differences between the cooler higher-altitude areas and the warmer lower latitudes of Florida. The principal factor, he suggested, was higher stream temperatures. Clifford and co-workers have developed Berner's (1950) observation further (Clifford *et al.* 1973; Clifford, cited in Brittain 1982). Clifford *et al.* (1973) suggest a trend in mayfly life histories from the equator to the arctic as follows:

Tropics	Multivoltine species
Moderate temperate	Univoltine with growth throughout the year
Cold temperate	Univoltine with most growth restricted to one part of the year
Arctic	Univoltine with life cycle completed in a very short part of the year

The Australian fauna seems to fit the 'moderate temperate' category relatively well. Clifford *et al.* (1973) did not comment on the reduction in life-cycle synchrony that also seems to occur from the arctic to the tropics.

Multiple cohorts such as those found in this study and by Suter (1980) do not appear to have been recorded for high-latitude Northern Hemisphere mayflies. They have, however, been recorded several times in mayflies in more temperate parts of North America (e.g. McCafferty and Huff 1978; Grant and Stewart 1980), and in New Zealand by Towns (1983).

Several classification systems have been proposed for the life histories of cold-temperate mayflies (Landa 1968; Hynes 1970; Sowa 1975), however, it could not be expected that the life histories of the moderate-temperate species would fit easily into such schemes, and indeed they do not. Suter (1980) concluded that the life history of only one of the six populations that he studied could be fitted into Landa's (1968) classification. One difficulty is that none of the classifications so far proposed allows for a species to have more than one type of life history at once. Yet species with two or more cohorts may in fact do this. *Coloburiscoides munionga*, for example, has both of Landa's (1968) A1 and A3 life histories concurrently at a single site. Most proponents of classifications have noted only that one species may have different life-history types in different localities or in different years (e.g. Landa 1968; Hynes 1970).

Of the nine populations investigated in the present study, none fits comfortably into the classificatory systems previously mentioned. *Mirawara aapta* and *Tasmanophlebia* sp. would probably fit into Landa's (1968) A category (univoltine) but would require a new sub-category for species with long emergence periods and continuous growth. They would also fit into Sowa's (1975) univoltine category but they would not fit into either the seasonal or the aseasonal categories of Hynes (1970). Suter (1980) suggested that too little was known as yet about the life histories of Australian mayflies to propose a classification for them. This is still the case and, in view of the variability of the life histories in time and space, such a classification may well be of limited use.

Variation in the life histories of the Northern Hemisphere Ephemeroptera has been found a number of times. The most commonly documented differences are those between different locations and there are now numerous examples of this (e.g. Ide 1935; Brown 1961; Minshall 1967; Newell and Minshall 1978; Macan 1981; Brittain 1982), however, since most of the variation noted has been attributed to temperature differences, it is likely that differences between years also occur. The variability in life histories noted in the Australian fauna are not, therefore, qualitatively different from those in the Northern Hemisphere. Whether or not the variations are different in frequency or intensity, it is not possible to tell on the data available.

Acknowledgments

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