Life Histories of some Benthic Invertebrates from Streams of the Northern Jarrah Forest, Western Australia

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Abstract

Life history patterns of thirteen species of invertebrates from streams of the northern jarrah forest were examined over a 1-year period. Five species had univoltine cycles with a single cohort and demonstrated a high degree of synchrony of larval development and a restricted period of adult emergence. Two species of Leptophlebiidae also had univoltine cycles but showed the more typical pattern of Australian mayflies, with extended recruitment, multiple overlapping cohorts and a long period of adult emergence. *Uroctena* sp., a small gammarid, had a generation time of 1 year but showed considerable spatial variation in the degree of synchrony of development. This appeared to be a result of differences in the constancy of stream discharge and was not attributable to differences in the temperature regime of the streams.

At least three species demonstrated cohort splitting which resulted in an apparently bivoltine cycle. A life-history pattern of alternating long and short development times is described which, on average, would produce two generations every 3 years. This is considered to be a highly adaptive strategy for Australian stream insects with slow life cycles and can explain the extended periods of recruitment and adult emergence so often observed.

Streams of the northern jarrah forest are depauperate compared with other Australian streams, despite predictable temperature and discharge regimes. The insular nature of the south-west Bassian region and its long period of isolation may be the principle cause of this reduced diversity. The invertebrate community of these streams is simple in structure and has a high degree of seasonality that is atypical of the temperate streams of Australia and New Zealand.

Introduction

Life histories of stream insects from the temperate latitudes of the Southern Hemisphere are poorly documented, particularly when compared with those of their Northern Hemisphere counterparts. Early studies on the southern fauna suggested a high degree of flexibility in life cycles, with loosely synchronized larval development and extended periods of hatching and adult emergence (Winterbourn 1966, 1974, 1978; Froehlich 1969; Hynes and Hynes 1975; Towns 1981, 1983). While this certainly holds true for many New Zealand stream invertebrates and Australian mayflies (Suter and Bishop 1980; Campbell 1986), some groups of Australian stream insects show a higher degree of synchrony (Marchant *et al.* 1984; Yule 1985; Dean and Cartwright 1987).

Temperature is known to play a critical role in shaping the life-history patterns of aquatic insects and a predictable temperature regime is thought to be conducive to the formation of highly structured stream communities (Vannote and Sweeney 1980). Marchant *et al.* (1984) found that the temperature regime of a river system in south-eastern Australia was as predictable as would be expected at a similar latitude in North America and suggest that

temperature alone cannot account for the observed flexibility in the life cycles of Australian stream insects. They, together with Lake *et al.* (1985), suggest that the life history strategies shown by Australian lotic invertebrates may be influenced more by the highly variable pattern of stream and river discharge. Similarly, Winterbourn *et al.* (1981) argue that the unpredictable, and occasionally torrential, discharge pattern of New Zealand streams and rivers is largely responsible for the asynchronous life cycles of lotic invertebrates.

The south-west of Western Australia experiences a mediterranean climate with hot, dry summers and mild, wet winters. Bunn *et al.* (1986) found major temporal changes in the community structure of small forested streams in this region which they attributed largely to the predictable seasonal changes in stream discharge. These seasonal differences were not merely shifts in relative abundances but the result of temporal replacement of species, and distinctive summer and winter assemblages were observed. The present study was conducted to examine more closely these temporal changes and describes the life cycles of some of the common species of benthic invertebrates. An effort was made to select species from a broad range of higher taxa and representatives of the Amphipoda, Ephemeroptera, Odonata, Plecoptera and Trichoptera were studied. The Chironomidae have not been included in this paper, even though they represent the most diverse taxon in streams of the northern jarrah forest (Bunn *et al.* 1986). The life-history patterns of this important group will be published separately when some of the taxonomic problems have been resolved.

Study Area

A detailed description of the study area was given by Bunn *et al.* (1986). Briefly, the region supports a dry sclerophyll forest dominated by jarrah (*Eucalyptus marginata* Donn. ex Sm.) and, to a lesser extent, marri (*E. calophylla* R. Br.). The climate is typically mediterranean with an annual rainfall of approximately 125 cm, of which about 85% falls between May and October (Gardner 1942; Water Authority of Western Australia, unpublished data).

Four of the sites examined by Bunn *et al.* (1986) were sampled in this study. Waterfall Gully (Site 3) is a small stream in the northern half of the Wungong Catchment, approximately 50 km south of Perth, Western Australia. Wungong Brook (Site 6) and Seldom Seen Brook (Site 7) are two streams draining the southern half of this catchment and are both downstream of current strip-mining operations for bauxite (see Bunn *et al.* 1986, fig. 1). Both of these sites show signs of sedimentation, particularly during summer. Foster Brook (Site 11) is a perennial tributary of the North Dandalup River, approximately 20 km south of Wungong. All streams had a substratum consisting predominantly of gravel and sand with some larger rocks of concreted laterite.

Materials and Methods

Physical and Chemical Parameters

Rainfall data from stations near each of the sites in Wungong and North Dandalup catchments were obtained from the Water Authority of Western Australia. Streamflow records during this period were also obtained from Waterfall Gully (Site 3), Wungong Brook (downstream of Site 6) and Seldom Seen Brook (above Site 7). Records were not available for Foster Brook but data for the North Dandalup River, downstream of Site 11, were used.

A mercury-bulb thermometer was used to measure spot water temperatures at each site. Maximum-minimum thermometers also were anchored in the streams and were read and reset on each sampling occasion. The midpoint of these readings was used as an approximate measure of mean stream temperature from which the number of accumulated degree-days was calculated for each sampling interval. Long-term (1967–84) data on spot water temperatures, measured between 0900 and 1700 h, were available for Sites 3 and 7 and for Wungong Brook (downstream of Site 6) and the North Dandalup River (downstream of Site 11). These records were used to calculate predictability (P), constancy (C) and contingency (M) of stream temperatures using Colwell's (1974) method.

Stream depth was measured midstream at each site on each sampling occasion. Dissolved oxygen concentration was measured with a portable meter (Delta Scientific Model 1010). Two water samples

were taken at each site for analyses of pH and major cations and kept on ice until returned to the laboratory. Na^+, K^+, Mg^{2+} and Ca^{2+} were measured by atomic absorption spectrophotometry (Varian AA475) and pH with a Chemtrix type 40 meter.

Samples of Invertebrates

The four sites were sampled for benthic invertebrates on twelve occasions from March 1983 to February 1984 inclusive at 4- to 6-week intervals. Wungong Brook was not sampled in September 1983 because of exceptionally high stream flows. Three samples of benthic invertebrates were taken at each site between 0900 and 1500 h using a Surber sampler ($0 \cdot 1$ m^2; 250 μm mesh net). Samples were washed in the field, and the material retained on a sieve (250 μm) was subsequently fixed in 4% formaldehyde.

Adult stream insects were collected at the four sites using general-purpose survey traps (Ellisco Model 110103) each with a 15 Watt Blacklight tube. The traps were operated from dusk to dawn within 1 day of sampling the benthic fauna. Adult caddisflies, mayflies, and stoneflies were also collected from the riparian vegetation with a sweep net.

Benthic samples were washed through two sieves in the laboratory ($3 \cdot 35$ mm and 250 μm) and the material retained on the coarse sieve was hand-sorted from a white tray. The fine fraction was sorted at $\times 12$ magnification with a Wild Stereomicroscope. Invertebrates were stored in 70% ethyl alcohol for subsequent identification and measurement. Adult stream insects were sorted from the light-trap samples, identified and counted.

Analysis of Life-history Data

Thirteen common species of benthic invertebrates were chosen for size-frequency analysis. These were; one species of amphipod, *Uroctena* sp. (Gammaridae); five species of mayflies, *Baetis soror* Ulmer (Baetidae), *Tasmanocoenis tillyardi* (Lestage) (Caenidae), *Neboissophlebia occidentalis* Dean, *Bibulmena kadjina* Dean and *Nyungara bunni* Dean (Leptophlebiidae); one species of dragonfly, *Austroaeschna anacantha* Tillyard (Aeshnidae); two species of stoneflies, *Leptoperla australica* (Enderlein) and *Newmanoperla exigua* (Kimmins) (Gripopterygidae); and four species of caddisflies, *Taschorema pallescens* (Banks) (Hydrobiosidae), *Smicrophylax australis* (Ulmer) (Hydropsychidae), *Notoperata tenax* Neboiss and *Lectrides parilis* Neboiss (Leptoceridae).
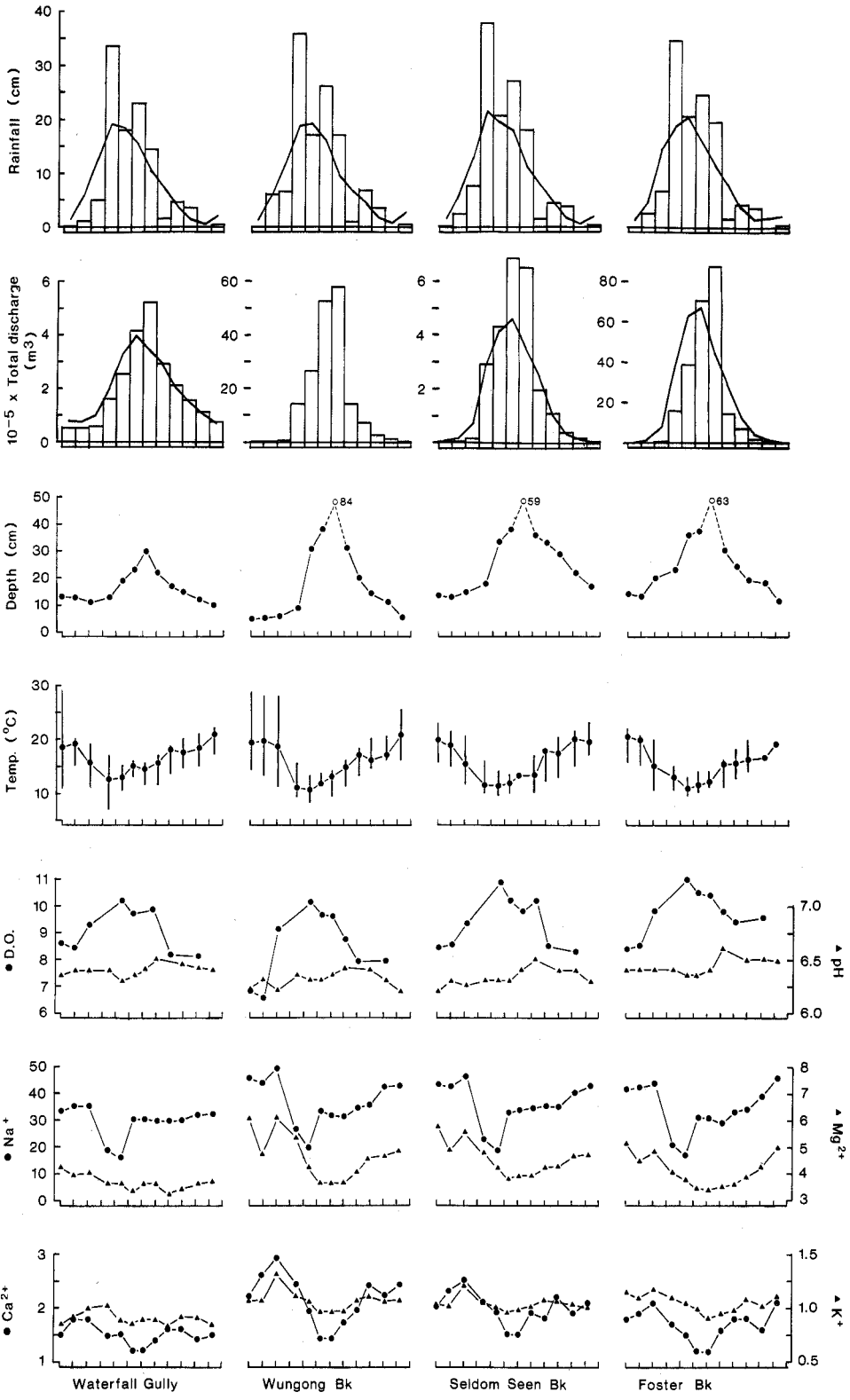
The maximum head width of insect nymphs and larvae was measured with a graticule eyepiece, in most cases at $\times 50$ magnification to the nearest $0 \cdot 02$ mm. The larger specimens of *A. anacantha* were measured at lower magnifications. The head length of *Uroctena*, from the base of the antennule to the second thoracic segment, was measured instead of head width. The size-frequency distributions of the total collections of each species were plotted to determine size groups or, in the case of caddisflies, larval instars. Size groups were assigned subjectively, taking into account peaks in the distribution and an increase in size interval with increasing age. No attempt was made to ascertain the number of nymphal instars, although some of the assigned size groups obviously represented a single instar.

Size-frequency distributions of each species were calculated for each sampling occasion. Data for most species are based on specimens collected from single sites; however, specimens from all sites were pooled for the less common species. The proportion of the total number of each species of adult insect in blacklight samples was calculated for each sampling occasion.

Results

Physical and Chemical Data

The monthly rainfall at each site during 1983–84 showed the same seasonal pattern as the long-term data and annual totals were only slightly less than the long-term means (Fig. 1). With the exception of Waterfall Gully, total discharge closely followed the rainfall pattern, with most of the flow occurring between June and November. On average, 92% and 93% of the annual flow at Seldom Seen Brook and North Dandalup River, respectively, occurs during this period. Long-term discharge data were not available for Wungong Brook near Site 6. However, discharge of this stream between June and November into Wungong Dam accounts for 91% of the average annual total. In contrast, elevated summer flows at Waterfall Gully account for 25% of the annual total. All of the streams were small (2–3 m wide) and, with the exception of the September samples, generally shallow (5–40 cm). Waterfall Gully showed very little seasonal variation in depth, even at this time.

Waterfall Gully   Wungong Bk   Seldom Seen Bk   Foster Bk

March 1983 − February 1984

The streams were generally warm, with winter temperatures rarely dropping below 10°C (Fig. 1). Foster Brook was slightly cooler than the three more northern sites, accumulating 5074 degree-days during the 343-day study period compared with 5283, 5431 and 5279 degree-days for Waterfall Gully, Wungong Brook, and Seldom Seen Brook, respectively. The highest temperatures and greatest range were recorded in Wungong Brook, the shallowest site, during summer and autumn (Fig. 1). The predictability (P) of stream temperatures at each of the sites was high with a low constancy and high contingency (Table 1). Despite a far greater constancy of stream discharge (Fig. 1), Waterfall Gully had only a slightly more constant temperature regime than the other three sites.

Table 1. **Predictability (P), constancy (C) and contingency (M), after Colwell (1974), of water temperatures in the four streams from 1967 to 1984**

Stream	P	C	M	C/P (%)	M/P (%)
Waterfall Gully	0·52	0·15	0·37	29	71
Wungong Brook	0·42	0·10	0·32	24	76
Seldom Seen Brook	0·41	0·09	0·32	22	78
North Dandalup River	0·44	0·10	0·34	23	77

Dissolved oxygen concentrations were at or near saturation only during the winter months when flows were high (Fig. 1). The water was slightly acidic and pH ranged from 6·2 to 6·6 throughout the year. Concentrations of major cations were similar and low at all sites, particularly during winter (Fig. 1).

Life Cycles

Amphipoda

Uroctena sp., a small, blind gammarid, was the second most abundant invertebrate in streams of the Wungong catchment but rarely occurred in the North Dandalup catchment. Nine size groups, each representing a 60 μm increment in head length, were assigned for the analysis of monthly size-frequency distributions. Juveniles appeared in the populations at Wungong and Seldom Seen Brooks during late autumn–early winter and presumably were from the previous year's brood (Fig. 2). Females reached maturity at the end of their first year (size group 5, head length >0·41 mm) and began brooding in early winter. Larger females, most of which carried broods, were present in the population as late as mid summer (January). In contrast with the populations at Wungong and Seldom Seen Brooks, brooding females were present at all times of the year at Waterfall Gully (Fig. 2). As a consequence, juveniles were released throughout the year and there were no obvious seasonal changes in the size-frequency distribution.

Ephemeroptera

Baetis soror was the most common baetid mayfly in streams of the northern jarrah forest. Seven size groups were chosen from the total size frequency distribution, the last of which was comprised predominantly of males. The life cycle of this species was difficult to interpret because, although cohorts were evident at some times of the year, the development of nymphs was poorly synchronized. Several overlapping cohorts were evident at Waterfall

Fig. 1. Physical and chemical characteristics of the four study sites from March 1983 to February 1984. Monthly rainfall and total discharge for Waterfall Gully (8·7 km^2), Wungong Brook (80·3 km^2), Seldom Seen Brook (7·5 km^2) and North Dandalup River (153 km^2) are given (open bars). Mean values for monthly rainfall and discharge also are presented (solid line). Water temperatures are plotted with maxima and minima for each sampling interval and all concentrations are in g m^{-3}.
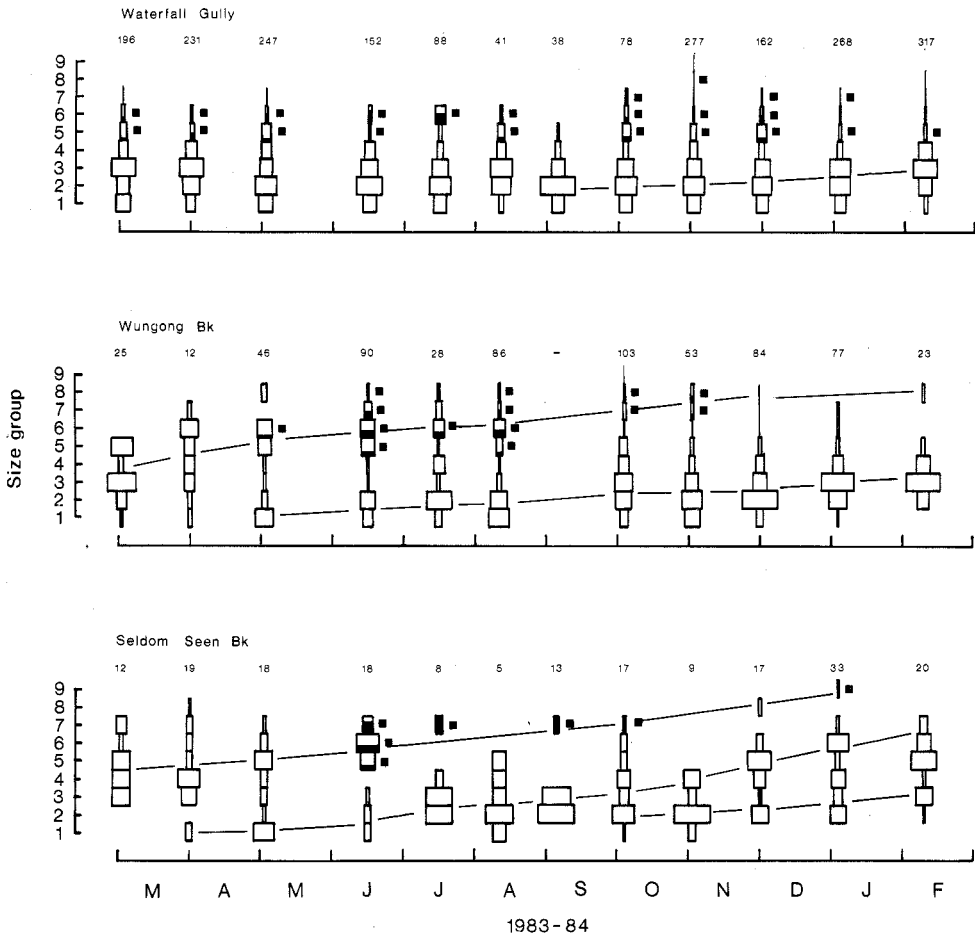
Fig. 2. Size-frequency (%) distributions of *Uroctena* sp. at Waterfall Gully, Wungong and Seldom Seen Brooks. The number of individuals measured is given at the top of each figure. Square symbols indicate the presence of ovigerous females and their proportion in each size group is shaded. Head lengths (μm) of each size group are: **1**, 171–230; **2**, 231–290; **3**, 291–350; **4**, 351–410; **5**, 411–470; **6**, 471–530; **7**, 531–590; **8**, 591–650; **9**, 651–710.

Gully and Foster Brook where adults and, particularly, mature nymphs were present at most times of the year (Fig. 3). Few small individuals were recorded and, as a result, it is not possible to determine whether the species is bivoltine or merely univoltine with overlapping cohorts.

Tasmanocoenis tillyardi (Caenidae) was present only at Wungong and Seldom Seen Brooks, the sites influenced by bauxite mining. Seven size groups were chosen though no attempt was made to distinguish between male and female nymphs. The life cycle of this species was clearly univoltine with small nymphs first appearing in late summer (Fig. 4). Adults were not recorded from either site though adult emergence and egg laying must occur during early summer.

Three species of leptophlebiid mayflies were common in these small streams. The life cycle of *Bibulmena kadjina* was clearly univoltine with juvenile nymphs appearing in late spring (Fig. 5). Nymphs grew rapidly during summer and autumn but had almost disappeared from the sites by July. Mature nymphs were collected from deep pools downstream in Wungong Brook and North Dandalup River during August but were not recorded from any
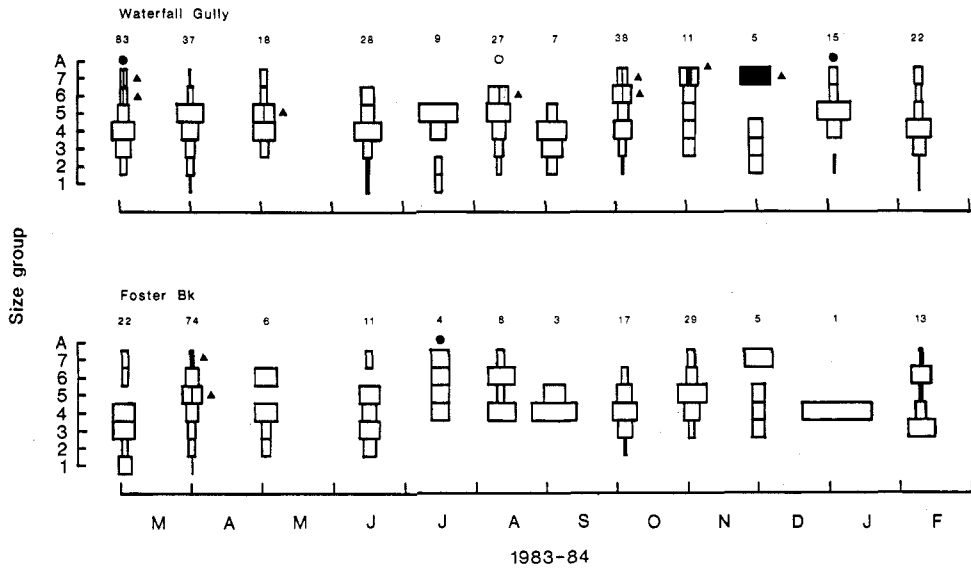
Fig. 3. Size-frequency (%) distributions of *Baetis soror* at Waterfall Gully and Foster Brook. No. individuals measured is given at the top of each figure; ●, collections of adults (A) in 1983–84; ○, collections of adults from previous years; ▲, nymphs with blackened wing-pads, their proportion in each size group being shaded. Head widths (μm) of each size group are: **1**, 171–230; **2**, 231–290; **3**, 291–370; **4**, 371–490; **5**, 491–630; **6**, 631–790; **7**, 791+.

Fig. 4. Size-frequency (%) distributions of *Tasmanocoenis tillyardi* at Wungong and Seldom Seen Brooks. No. individuals measured is given at the top of each figure. Head widths (μm) of each size group are: **1**, 171–210; **2**, 211–270; **3**, 271–350; **4**, 351–450; **5**, 451–570; **6**, 571–790; **7**, 791+.
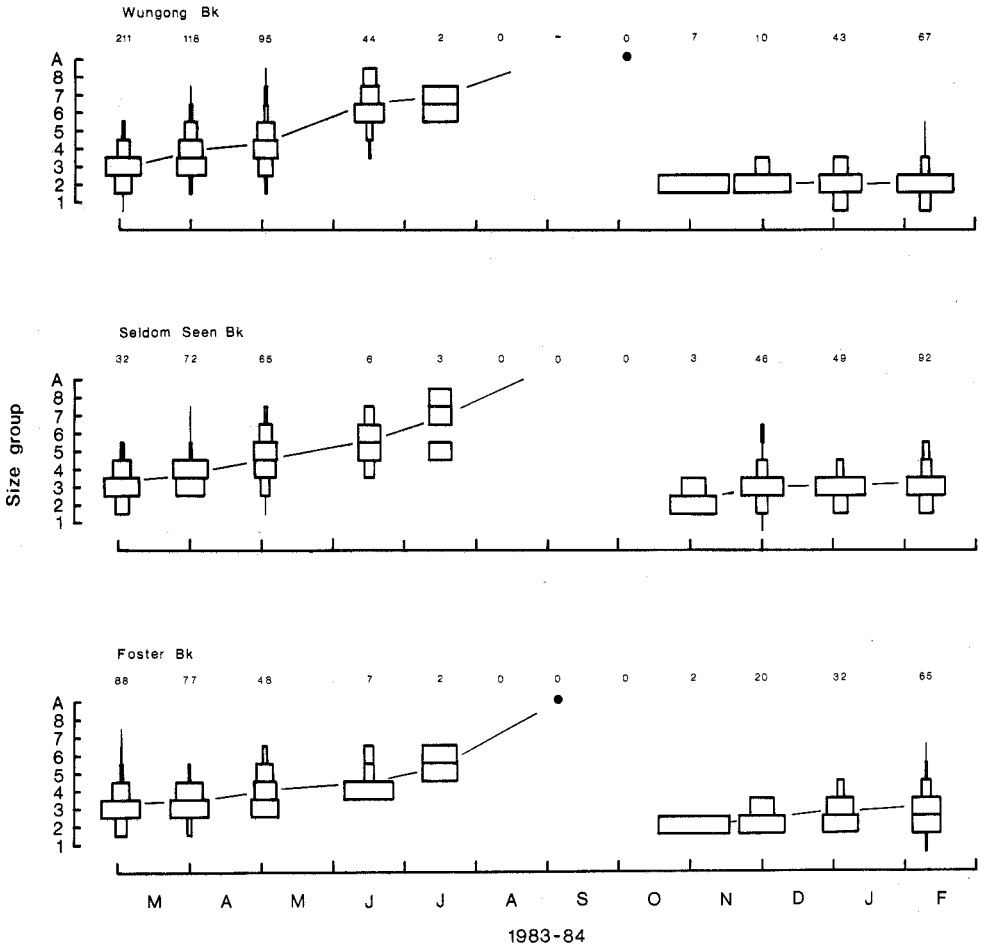
Fig. 5. Size-frequency (%) distributions of *Bibulmena kadjina* at Wungong, Seldom Seen and Foster Brooks. Labels as for Fig. 3. Head widths (μm) of each size group are: **1**, 161–230; **2**, 231–330; **3**, 331–450; **4**, 451–610; **5**, 611–770; **6**, 771–970; **7**, 971–1210; **8**, 1211+.

of the study sites. Adults emerged for a brief period during spring (Fig. 5). *Neboissophlebia occidentalis* and *Nyungara bunni* also had univoltine life cycles but with several apparently overlapping cohorts (Figs 6, 7). During autumn, the populations of *Neboissophlebia* were comprised predominantly of juveniles and this major cohort grew through winter with adult emergence in early summer. Hatching continued at intervals during winter, in most cases producing several apparent cohorts. This was particularly evident at Foster Brook (Fig. 6). Nymphs in these later cohorts appeared to grow faster than those in the first winter cohort with the result that ripe nymphs and adults were recorded only during summer and autumn.

Nyungara bunni had a life cycle very similar to that of *Neboissophlebia*, though the first major cohort grew more rapidly during winter, and emergence occurred in late winter to early spring (Fig. 7). Hatching again continued at intervals during winter, producing at least three additional cohorts, and ripe nymphs and adults from these were recorded throughout spring and summer. As a result, adult emergence extended from late winter to late summer, earlier than that of *Neboissophlebia*, though still with considerable overlap.
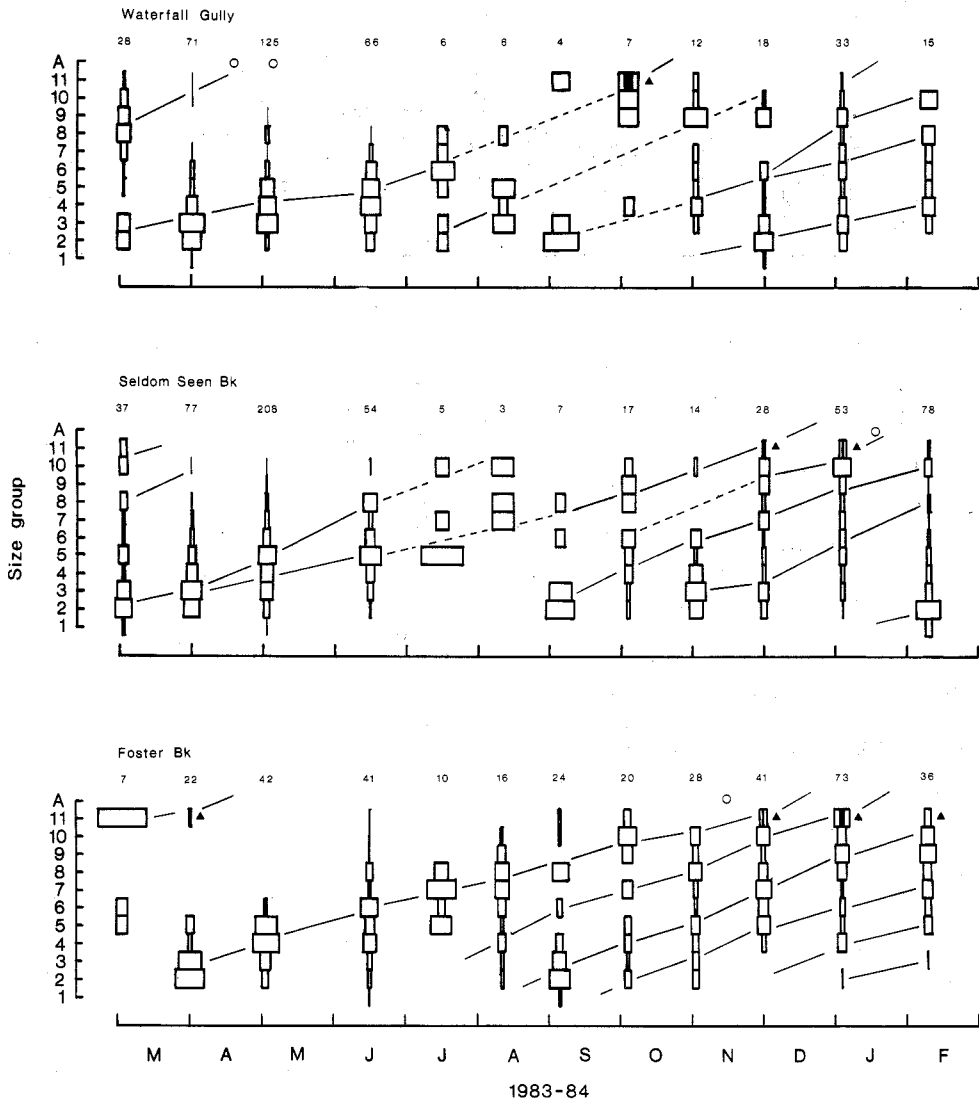
Fig. 6. Size-frequency (%) distributions of *Neboissophlebia occidentalis* at Waterfall Gully, Seldom Seen and Foster Brooks. Labels as for Fig. 3. Head widths (μm) of each size group are: **1**, 181–230; **2**, 231–310; **3**, 311–390; **4**, 391–490; **5**, 491–610; **6**, 611–730; **7**, 731–850; **8**, 851–1010; **9**, 1011–1210; **10**, 1211–1470; **11**, 1471+.

Odonata

Austroaeschna anacantha was the most common dragonfly in streams of the northern jarrah forest. Most hatching occurred throughout the winter months (June to August inclusive) and this cohort grew rapidly during spring and summer (Fig. 8). The cohort appeared to split in late summer and it is possible that some of these individuals would emerge in the following autumn. Two cohorts also were evident in late summer and nymphs that did not emerge in autumn continued to grow through a second winter and emerged during the following summer.
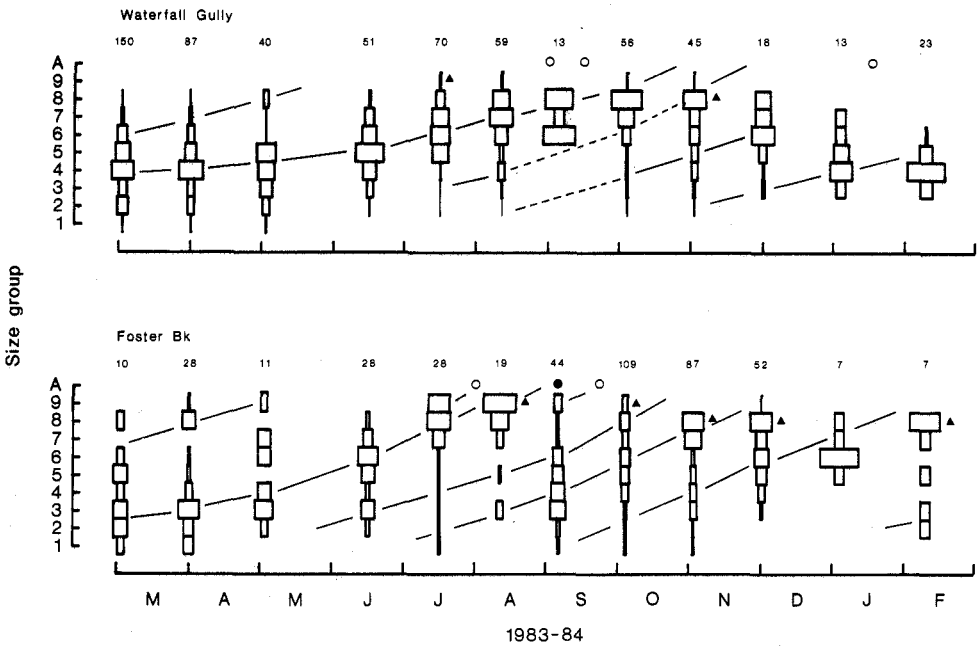
Fig. 7. Size-frequency (%) distributions of *Nyungara bunni* at Waterfall Gully and Foster Brook. Labels as for Fig. 3. Head widths (μm) of each size group are: **1**, 261–310; **2**, 311–390; **3**, 391–490; **4**, 491–630; **5**, 631–790; **6**, 791–990; **7**, 991–1190; **8**, 1191–1410; **9**, 1411+.
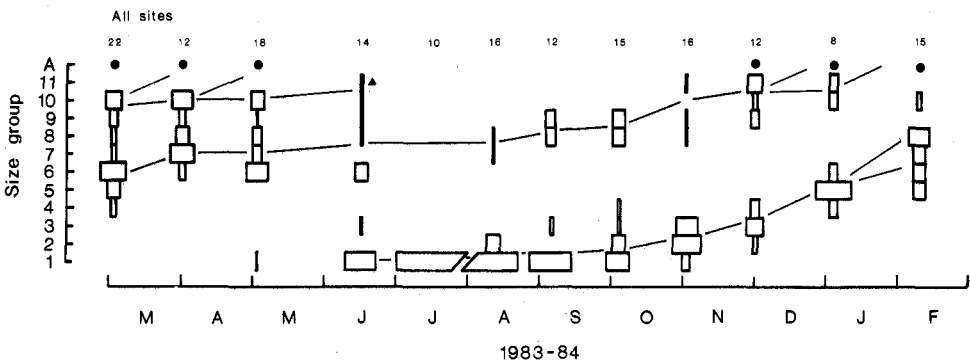

Fig. 8. Size-frequency (%) distribution of *Austroaeschna anacantha* at all sites. Labels as for Fig. 3. Head widths (mm) of each size group are: **1**, 0·84–0·96; **2**, 1·08–1·16; **3**, 1·30–1·42; **4**, 1·54–1·72; **5**, 1·78–2·00; **6**, 2·06–2·40; **7**, 2·48–2·84; **8**, 2·94–3·56; **9**, 3·68–4·40; **10**, 4·64–5·36; **11**, 6·22–7·84.

Plecoptera

The total size-frequency distribution of *Leptoperla australica* revealed obvious instars, and seven size groups were chosen to correspond with these (Fig. 9a). This species had a very fast, univoltine life cycle with recruitment during late autumn (Fig. 10). Nymphs developed rapidly during winter and adults emerged for a brief period in early spring.

Newmanoperla exigua is a smaller stonefly than *Leptoperla* and, correspondingly, had a smaller range of head capsule widths (Fig. 9b). Seven size groups were again chosen though there were no obvious instars. Hatching began at the same time as *Leptoperla* but continued
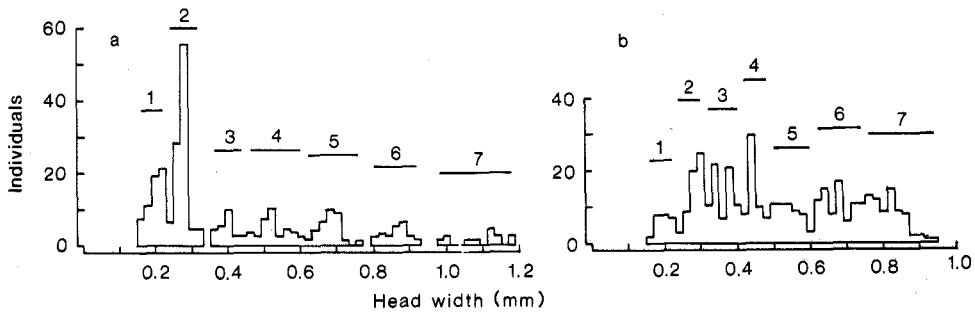
Fig. 9. Size-frequency distributions of (a) *Leptoperla australica* and (b) *Newmanoperla exigua*. (Size groups are indicated by horizontal bars.)
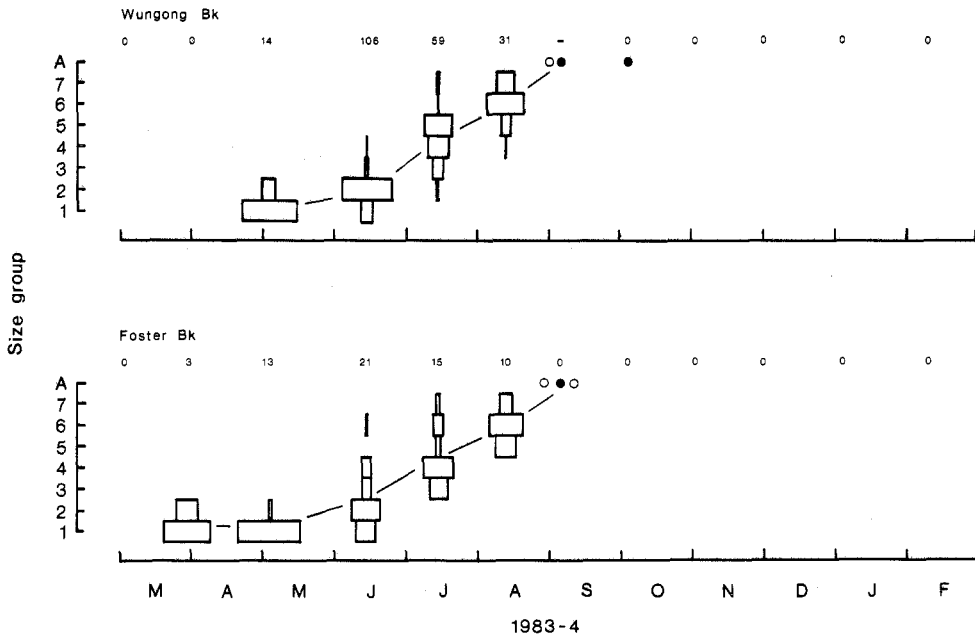

Fig. 10. Size-frequency (%) distributions of *Leptoperla australica* at Wungong and Foster Brooks. Labels as for Fig. 3.

at intervals throughout winter (Fig. 11). As a result, the life cycle of this species was not as tightly synchronized as that of *Leptoperla* and a wide range of size classes was present throughout winter. Adult emergence occurred slightly after that of *Leptoperla* and continued until the end of spring (Fig. 11).

Trichoptera

The size-frequency distributions of *Smicrophylax australis*, *Lectrides parilis* and *Notoperata tenax* each revealed five larval instars (Figs 12a, 12c and 12d, respectively). However, there were seven distinct peaks in the size-frequency distribution of *Taschorema pallescens* (Fig. 12b). Female pupae and adults of this species are conspicuously larger than those of males and this sexual dimorphism is thought to have given rise to a bimodal distribution of fourth and fifth instar larvae.
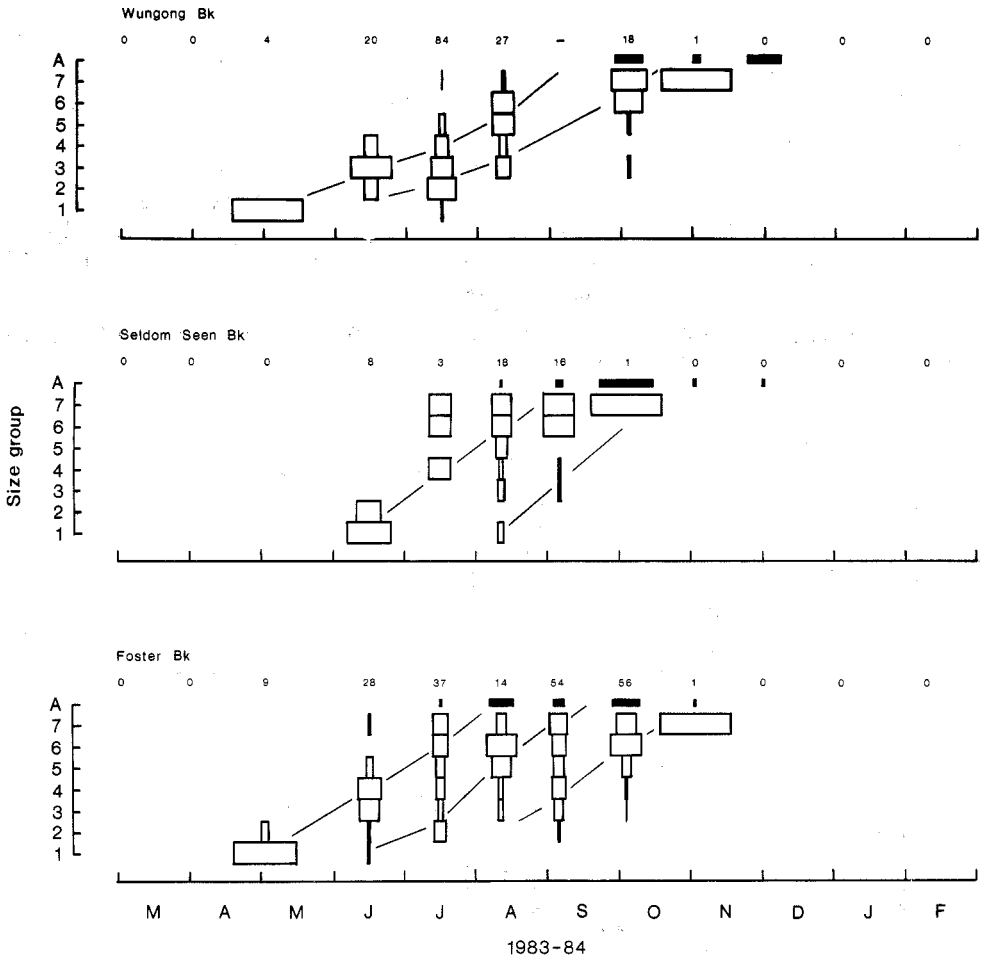
Fig. 11. Size-frequency (%) distributions of *Newmanoperla exigua* at Wungong, Seldom Seen and Foster Brooks. Labels as for Fig. 3, except that the horizontal bars indicate the relative abundance of adults ($n = 19$, 22, and 39 respectively).

Most hatching of *Smicrophylax australis* at Wungong Brook presumably occurred during autumn and winter, following the spring–summer emergence of adults; however, few first instar larvae were collected (Fig. 13). Larvae grew rapidly through spring (September to November) with some emergence during late summer. This, together with the recruitment of first instar larvae, explains the decrease in mean size of larvae in the population throughout the summer months. Most larvae from the previous year appeared to grow slowly through late summer and autumn and emerged in late winter and spring (Fig. 13). No first instar and few second instar larvae were recorded from Foster Brook. Unlike the population at Wungong Brook, none of the larvae that hatched in 1984 grew fast enough to emerge in late summer. Larvae from the previous year's recruitment grew slowly and emerged during spring and early summer of their second year. As a result, adult emergence was confined to a shorter period than that observed at Wungong Brook (Fig. 13).

First instar larvae and adults of *Taschorema pallescens* were present throughout most of the year, though larval development followed two loosely synchronized cohorts (Fig. 14). Larvae that appeared in late winter grew rapidly, resulting in a peak of adult emergence
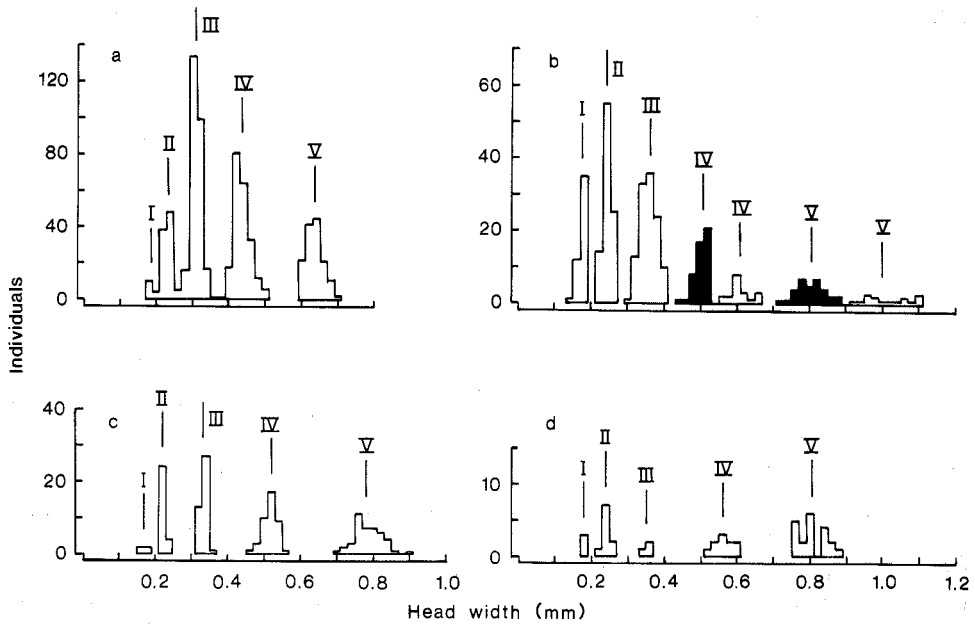
Fig. 12. Size-frequency distributions of (*a*) *Smicrophylax australis*, (*b*) *Taschorema pallescens*, (*c*) *Lectrides parilis* and (*d*) *Notoperata tenax*. Vertical lines represent the mean head-capsule width of each instar. Fourth and fifth instars of *T. pallescens* have been separated into what are thought to be males (shaded) and females.
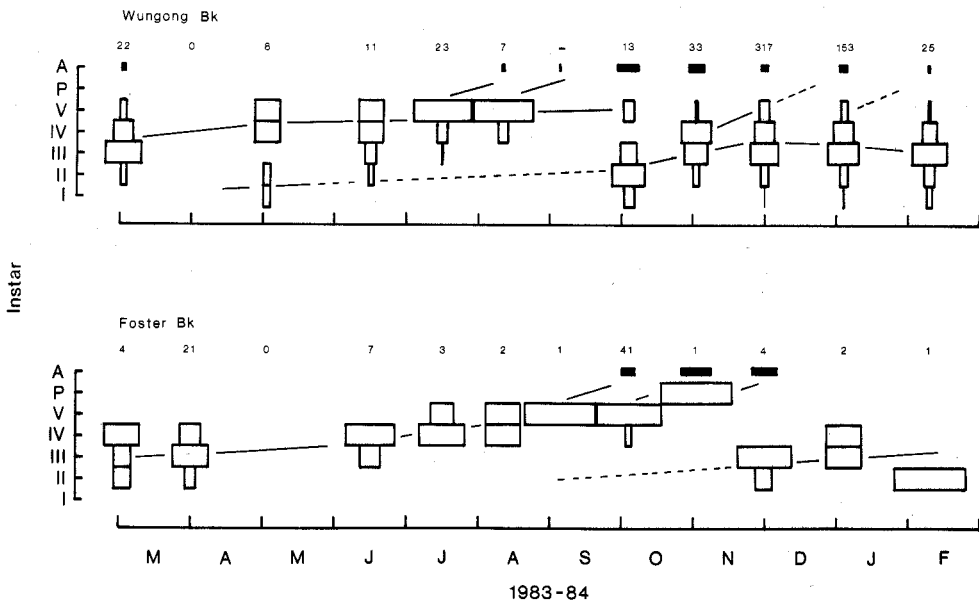

Fig. 13. Size-frequency (%) distributions of *Smicrophylax australis* at Wungong and Foster Brooks. Labels as for Fig. 3, except that the horizontal bars indicate the relative abundance of adults (*n* = 31 and 11, respectively). P, pupae and pharate stages.

during the following summer (January). A second cohort of larvae appeared during summer and grew slowly through autumn and winter, with emergence in spring (Fig. 14).
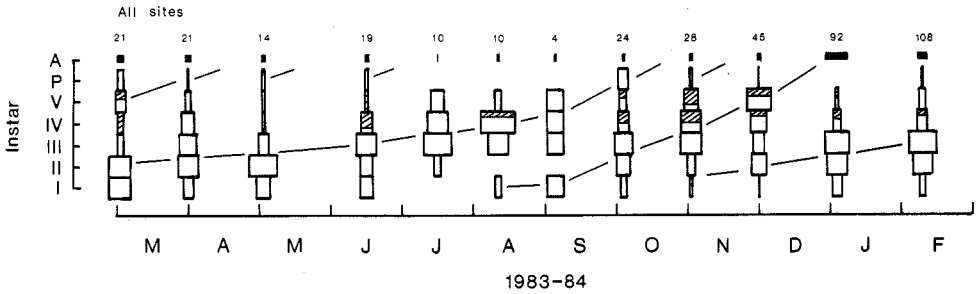

Fig. 14. Size-frequency (%) distributions of *Taschorema pallescens* at all sites. Labels as for Fig. 13 (number of adults, $n = 260$). Fourth and fifth instars are separated into what are thought to be males (shaded) and females.

Few larvae of *Lectrides parilis* were collected during the winter months and most of these were fourth and fifth instars (Fig. 15). Emergence of adults from this cohort occurred in spring and early summer. Hatching presumably occurred during autumn and winter, though few first instar larvae were collected. The 1984 cohort appeared to split in February resulting
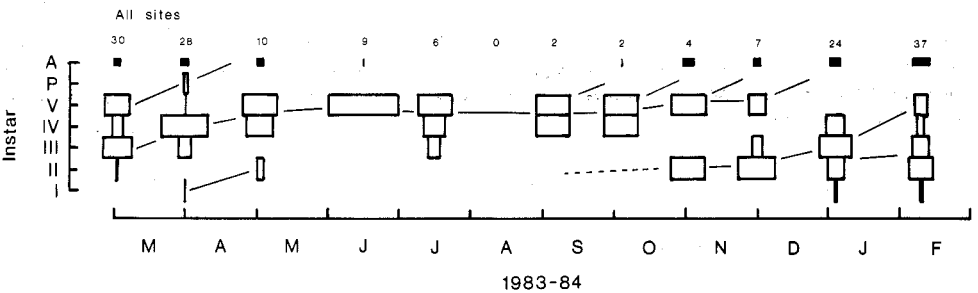

Fig. 15. Size-frequency (%) distributions of *Lectrides parilis* at all sites. Labels as for Fig. 13 (number of adults, $n = 70$).

in a bimodal distribution of size classes. This also was evident in the larvae collected in March and April and it is likely that some individuals were able to pupate and emerge during autumn. Those that did not emerge at this time remained as fourth or fifth instar larvae until spring (Fig. 15).
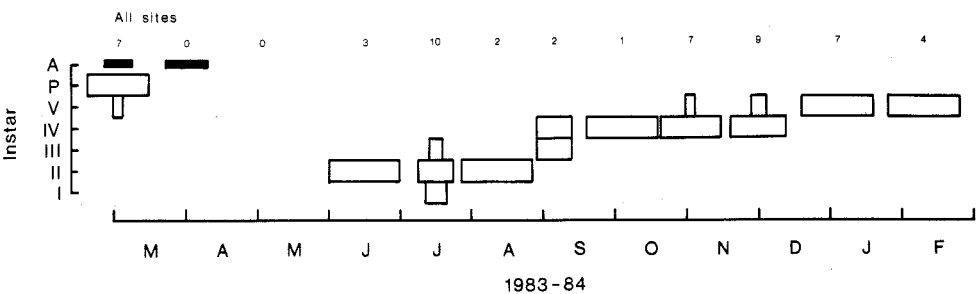

Fig. 16. Size-frequency (%) distributions of *Notoperata tenax* at all sites. Labels as for Fig. 13 (number of adults, $n = 18$).

Notoperata tenax had a clearly defined univoltine life cycle, with synchronized larval development (Fig. 16). Hatching occurred in early winter and larvae grew slowly throughout the year. Pupation and adult emergence were restricted to early autumn (March–April).

Discussion

The mediterranean climate of the northern jarrah forest gives rise not only to predictable stream flows (see Bunn *et al.* 1986) but also to predictable stream temperature regimes. The high predictability of both temperature and discharge is the result of high contingency (*sensu* Colwell 1974) and provides well defined seasonal cues for the stream biota. That is, a predictable change in environmental conditions which may trigger adult emergence and/ or hatching. In light of this, the high incidence of synchronous larval development shown by the stream invertebrates of the northern jarrah forest is not surprising.

Five of the thirteen species examined in this study had univoltine cycles with single cohorts and either fast or slow larval development (*sensu* Hynes 1970). *Leptoperla australica* had a fast winter cycle with highly synchronized larval development and a restricted period of adult emergence. The life cycle of *Newmanoperla exigua* was less synchronized because of extended hatching during winter and, as a consequence, featured an extended period of adult emergence, slightly later than that of *Leptoperla*. The more loosely defined life cycle of *N. exigua* is very similar to that of its south-eastern congenor, *N. thoreyi* (Hynes and Hynes 1975). The third species of gripopterygid stonefly in these streams, *Riekoperla occidentalis*, has a similar winter cycle to the other two and adults of this species have been collected only between late July and early October (Hynes and Bunn 1984). Synchronized seasonal life cycles appear to be the rule rather than the exception in the gripopterygid stoneflies of temperate southern Australia, particularly in the warmer streams (Hynes and Hynes 1975; Yule 1985).

Bibulmena kadjina (Leptophlebiidae) also showed a highly synchronized univoltine cycle which is atypical of mayfly life histories in Australia (Campbell 1986). The nymphs hatch in early summer and grow rapidly through autumn and winter, at which time they appear to move downstream into deeper, quieter pools. Nymphs of this species have broad, lamellate gills (see Dean 1987, figs 32, 35) and presumably move downstream to escape the high water velocities experienced in these small streams during winter. Adults emerge for a brief period in spring and must return to the headwaters to lay their eggs. High densities of young nymphs are present in headwater streams during summer and the species forms a dominant component of the invertebrate fauna at this time (Bunn 1985; Bunn *et al.* 1986; *B. kadjina* = Leptophlebiidae sp. B).

Tasmanocoenis tillyardi showed a similar life-history strategy to that of *Bibulmena*, though recruitment occurred later in the summer. The species also appears to move downstream in response to high winter flows and was virtually absent from the small streams in the latter half of the year. The life cycle differs from the 'bivoltine' cycle recorded for this species in a South Australian stream (Suter and Bishop 1980). The period of recruitment of the populations in Wungong and Seldom Seen Brooks was much shorter than that of the population sampled in the above study and there was no evidence of a second cohort. The life cycle of *T. tillyardi* in Wungong and Seldom Seen Brooks is identical though, to the 'G1' generation described by Suter and Bishop (1980).

Notoperata tenax, also, had a slow univoltine cycle and featured tightly synchronized larval development and a limited period of adult emergence, even when samples from all sites were pooled. Several species from a wide range ot taxa, including *Aphroteniella filicornis* (Chironomidae), *Hydrobiosella michaelseni* (Philopotamidae) and *Sternopriscus browni* (Dytiscidae), are also known to have univoltine larval cycles but were not measured in this study. It is apparent that a single cohort, univoltine cycle with synchronized larval development is a common life-history strategy of stream invertebrates of the northern jarrah forest.

Uroctena sp. had a generation time of 1 year, though it showed considerable variation in the degree of synchrony of development between sites, even over such a small spatial scale. Ovigerous females were present at Wungong and Seldom Seen Brooks throughout the winter months and most of the recruitment occurred at this time. The population at Waterfall Gully behaved rather differently in that ovigerous females were present all year. The three streams are in the same small catchment and have very similar water chemistries and, particularly, temperature regimes (Table 1, Fig. 1). However, Waterfall Gully has an unusual discharge pattern compared with the other two streams. A headwater spring source produces elevated flows during summer and reduces the seasonal range. Perhaps the low summer flows *per se*, or abiotic/biotic factors associated with low summer flows, prevent summer brooding at Seldom Seen and Wungong Brooks.

Smith and Williams (1983) suggested that the temporal pattern of stream flow was a major factor influencing the life cycles of two species of amphipods in streams in south-eastern Australia. *Austrochiltonia australis* (Ceinidae) had a seasonal life cycle at two localities with a markedly seasonal flow regime. In contrast, *Pseudomoera gabriela* (Eusiridae) bred continuously throughout the year at a site noted for its lack of seasonal variation in flow and temperature. Data presented here, demonstrate that temporal variations in flow regime can also influence the reproductive cycles of different populations of the same species of stream amphipod.

Life cycles of the other two leptophlebiids, *Nyungara bunni* and *Neboissophlebia occidentalis*, are more typical of those recorded previously in Australia and New Zealand with extended hatching and multiple overlapping cohorts (Towns 1983; Campbell 1986). Recruitment of *Nyungara* began early in the summer and adults from this first cohort grew rapidly and emerged as adults in late winter. Nymphs of *Nyungara* remain in the small streams and morphologically are more suited than the other two leptophlebiids to the swifter winter flows (see Dean 1987, fig. 12). Recruitment of *Neboissophlebia* in summer also results in a major cohort that grows through winter, though adults first appear much later than those of *Nyungara*. Although recruitment in both species occurs throughout the winter months, several cohorts are apparent, particularly at Foster Brook. These must be the result of synchronized hatching, though it is difficult to say what may trigger such events.

Suter and Bishop (1980) described the life cycle of *Baetis soror* in a South Australian stream as having three distinct cohorts in a single year. The life cycle of this species at Waterfall Gully and Foster Brook cannot be established from the data presented, though cohorts are present on some occasions. This species shows the least degree of synchronous development of those examined in this paper.

Of the remaining four species, *Smicrophylax australis*, *Lectrides parilis* and *Taschorema pallescens* all show, to some extent, two cohorts in a single year; this results in an extended period of adult emergence from spring to the end of autumn. The most tenable explanation of this apparent 'bivoltinism' is cohort splitting, and these species demonstrate it to varying degrees. By way of explanation, three life-history strategies are illustrated in Fig. 17. The first of these describes a simple univoltine cycle, e.g. *Notoperata tenax*, with winter recruitment and a limited period of adult emergence during the following summer. Three generations would be completed during a 3-year period (A, A1 and A2). The second strategy describes a semivoltine life cycle with overlapping cohorts (A and B). During the same 3-year period, slow-growing species such as this would produce two generations of A and one of B. The third strategy describes those slow-growing species that display cohort splitting. Larvae that hatch early and/or grow fast enough in winter may emerge in a single year but not until late summer or autumn (e.g. B, A1). Eggs from this cohort presumably would hatch late in the following winter and may not develop sufficiently to be able to emerge in the same summer. These individuals would continue to grow through a second winter and emerge early in the following summer (e.g. B1, A2). Eggs from slow-growing cohorts that have emerged early in summer (e.g. C) would hatch early and give rise to adults in late summer or autumn of the same year (e.g. C1). On average, three cohorts (A, B, C)

each would complete two generations every 3 years (Fig. 17c). Adults do not appear during
the winter months, and avoid the cold and wet conditions experienced in the terrestrial
environment at this time.

Pritchard (1978) demonstrated split cohorts in *Tipula* and proposed that most aquatic
insects in temperate climates display cohort splitting to some extent. Other examples include
a baetid mayfly (Murphy 1922), a pitcher-plant chironomid (Paterson and Cameron 1982),
and three species of hydropsychid caddisflies (Rutherford and Mackay 1986). The life cycle
of *Taschorema pallescens* recorded here is very similar to that described for the sponge-
feeding leptocerid, *Ceraclea transversa*, in a Kentucky stream (Resh 1976). *Smicrophylax
australis* at Wungong Brook and *Lectrides parilis* both show cohort splitting during summer
following an extended period of recruitment. Some of these larvae are able to pupate and
emerge in late summer (*Smicrophylax*) or autumn (*Lectrides*) and the remainder presumably
continue through a second year of development before emerging early in the following
summer. None of the larvae of *Smicrophylax* at Foster Brook appeared to emerge in their
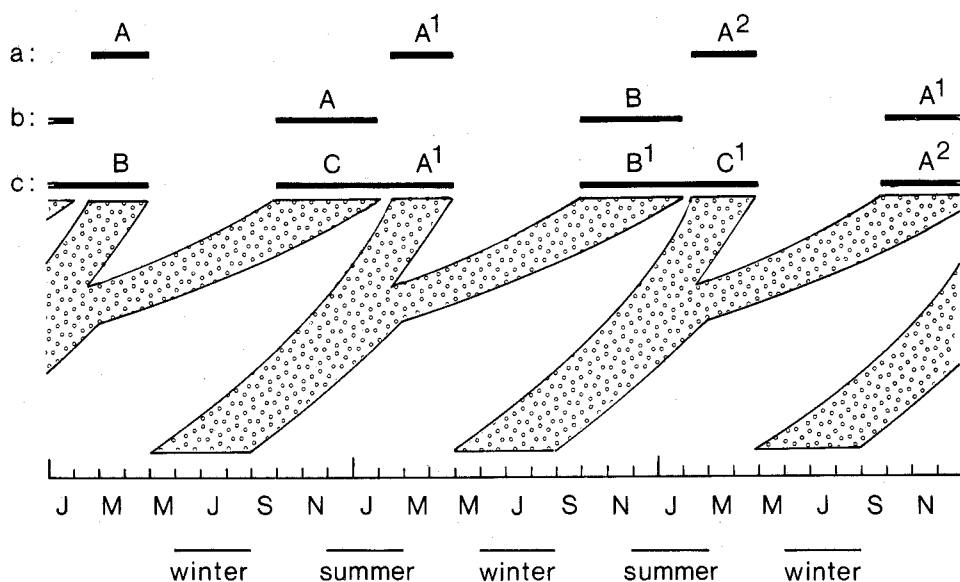

Fig. 17. Summary of life-history strategies of stream invertebrates of the northern jarrah forest over
a 3-year period: (*a*) univoltine cycle producing three generations of a single cohort; (*b*) semivoltine
cycle with two overlapping cohorts producing two generations of one and one of the other; and (*c*)
alternating fast and slow cycle with three overlapping cohorts, each producing two generations.

first year and, apparently as a result, no adults or pupae were recorded during late summer
at this site. The only period of adult emergence at Foster Brook corresponds to the slow-
growing cohort of the previous year. Most nymphs of *Austroaeschna anacantha* appear to
take 2 years to develop; however, the broad range of cohorts observed in late summer and
autumn suggest that, like the above three species, some nymphs may reach maturity after
their first year.

Gene mixing between 1-year and 2-year cohorts of these species of insects can occur in
two ways. Firstly, at the peak of adult emergence, adults from both cohorts are present and
interbreeding would be possible. Secondly, the growth rates are influenced by factors such
as temperature and food quality, and individuals from a late-hatched cohort, for example,
may grow fast enough to emerge in a single year. Environmental conditions, also, will
influence the relative proportions of each type of adult present from year to year. A short
winter would result in a brief period of recruitment and lead to the emergence of most of

the population in late summer/autumn. Individuals that recruit later than this fast-growing cohort would not be able to emerge at this time and might have to endure the extremes of drought conditions that may ensue. Summer conditions may be more moderate following a long winter, and individuals that have recruited late in the year will be able to survive and emerge early in the following summer. Individuals that recruit late and grow slowly through summer are at risk of perishing if conditions during summer are extreme. However, this may be outweighed by increased body size and increased fecundity of these slow-growers (Vannote and Sweeney 1980). In essence, this is a plastic life-history strategy in that, depending on local conditions, the population may vary from largely univoltine to largely semivoltine cycles.

The strategy of alternating short and long generation times of cohorts (sesquivoltinism?) would be highly advantageous for aquatic insects in an unpredictable climate. Species with life cycles that are strictly semivoltine would be faced with extinction in unusually dry years. I suggest that cohort splitting, such as that described here, is a highly adaptive strategy for Australian stream insects with 'slow' life cycles and that the incidence of this is probably widespread. The life cycles of *Tasmanocoenis tillyardi* (Suter and Bishop 1980, fig. 8), *Ecnomus* sp. (Marchant *et al.* 1984, fig. 8) and *Coloburiscoides giganteus* (Campbell 1986, fig. 6), for example, can be interpreted in this way. This strategy can explain the extended periods of both recruitment and adult emergence, so often observed in the life histories of Australian aquatic insects. The latter may simply represent the overlap of cohorts that have recruited from two different years (Fig. 17c). To test this, life-history studies of at least 2, and preferably 3, years' duration will be required.

The mediterranean climate of south-western Australia results in predictable stream-temperature and discharge regimes, yet these streams are depauperate compared with other Australian streams. Conditions of climatic predictability should be conducive to the formation of highly structured, diverse stream communities but this has not occurred. Most genera and in fact most families, with the notable exception of the Chironomidae, Simuliidae, Leptoceridae and Dytiscidae, are represented by only one or two species (Bunn *et al.* 1986). This apparent anomaly is probably a result of a number of factors. Most important is that perennial streams in the south-west of Western Australia flow through an island of vegetation surrounded by the Indian Ocean and desert, and are effectively isolated from permanent streams elsewhere in the continent. The reduced faunal diversity may be due, in part, to the insular character of this region. Many of the stream insects in south-western Australia have Gondwanic origins, and subsequent invasions from the north through Asia have reached south-eastern Australia through Queensland but have not reached the west. The absence of other south-eastern groups that have semivoltine or longer larval cycles also suggests that the south-west has been drier than it is at present. This may have led to the extinction of groups with longer life cycles. The remaining species are those with fast and slow univoltine cycles and those that are capable of cohort splitting. The result is a simple community structure with a high degree of seasonality that is atypical of the temperate streams of Australia and New Zealand.

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