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REPRODUCTION CYCLES IN SOME FRESHWATER AMPHIPODS IN SOUTHERN AUSTRALIA

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SUMMARY

Reproduction patterns in three populations of southern Australian amphipods were examined to investigate the suggestion that a basic difference exists in reproduction patterns between northern hemisphere and southern hemisphere stream invertebrates. The species considered were *Pseudomoera gabrieli,* sampled in Sassafras Creek, Victoria, and *Austrochiltonia australis,* sampled at Dandenong Creek, Victoria, and Aldgate Creek, South Australia. The former species showed continuous breeding, the latter, seasonal. These results, together with a review of published studies, indicated that for Amphipoda no such basic reproductive difference exists.

INTRODUCTION

The study of stonefly life cycles on the mainland of south-eastern Australia by Hynes and Hynes (1975) is of considerable interest for they found that, unlike most stoneflies of the northern hemisphere, the stoneflies investigated by them had life cycles which lacked precise seasonal timing. A similar finding was obtained for a wide variety of benthic invertebrates, including a species of amphipod, in New Zealand streams (Towns, 1976; Winterbourn, 1978). Hynes and Hynes concluded that although some of the flexibility in the life-cycle patterns was a response to temperature, an important determinant was the uncertain Australian climate. In the New Zealand aquatic studies, on the other hand, the flexibility in life cycles has been attributed to New Zealand's mild climate (Devenport and Winterbourn, 1976; Towns, 1976).

A further explanation unrelated to climate may be advanced for both studies. It is that the pattern of invertebrate life cycles in streams, if not rivers, is linked to the seasonal pattern of allochthonous organic input in the form of leaf-fall. Such input is known to be an important source of energy for maintaining stream ecosystems. In contrast to the situation in the northern hemisphere, the input in Australia and New Zealand mostly occurs over a long and imprecisely timed period: both countries lack native trees deciduous in the northern sense of that word. In the northern hemisphere, leaf-fall from deciduous trees provides massive and precisely timed allochthonous inputs to streams in autumn.

Drawing on the (then) unpublished work of Hynes and Hynes on Australian stoneflies, Williams and Wan (1972) hypothesised that the lack of a precisely timed autumnal leaf-fall would be reflected in poorly synchronised life cycles for Australian stream invertebrates (and in lowered species diversities) but this hypothesis was not taken up by Hynes and Hynes (1975) in their explanations of stonefly life-cycle flexibility.

Against this background, it is of interest to consider the life-cycle patterns of two species of amphipod known from Australian streams. One, *Pseudomoera gabrieli* Sayce (Eusiridae), is known thus far only from upland streams in Victoria. The other, *Austrochiltonia australis* (Sayce) (Ceinidae), with its congener *A. subtenuis* (Sayce), is widespread in south-eastern Australia (Williams, 1962) and occurs in many freshwater habitats, both lotic and lentic. The two known species of *Austrochiltonia* are by far the most common freshwater amphipods of temperate Australia. Amphipods from fresh waters in the northern hemisphere are claimed to exhibit seasonality in life-cycle patterns, as do stoneflies there.

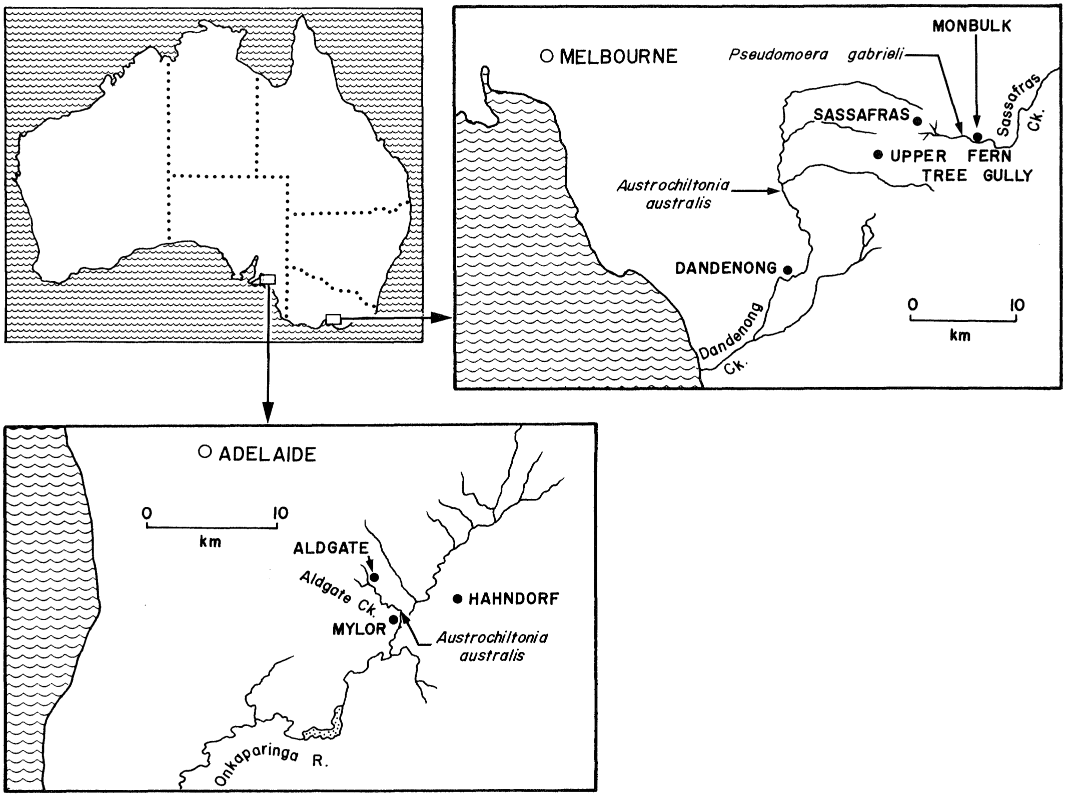

Fig. 1. Location of the three sampling sites.

LOCALITIES

Pseudomoera gabrieli was collected from Sassafras Creek, near The Patch, east of Melbourne, Victoria. *Austrochiltonia australis* was collected from Dandenong Creek, at Wellington Road, south-east of Melbourne, Victoria, and from Aldgate Creek, Mylor, south-east of Adelaide, South Australia (Fig. 1).

Sassafras Creek, at an altitude of 300 m above sea-level, is a typical stream of the Dandenong Hills, and maintains more or less constant flows throughout the year. Four to 5 m wide, it comprises pools with substrate of gritty silt and plant detritus and riffle areas with substrate of silt, stones and cobbles. The water is often turbid and rarely clear. Temperatures recorded during the study period were 9 to 15.5°C. Total dissolved solids were about 60 mg l^{-1}. Whilst *P. gabrieli* was the most abundant amphipod species in the creek, another species, *Neoniphargus* sp., also occurred at a low frequency in most samples. Only *P. gabrieli* provided sufficient animals for analysis. Collections were made at monthly intervals over an 18-month period from September 1961 to February 1963.

Dandenong Creek at the sampling point is 50 m above sea-level and about 6 m wide, a moderately large coastal lowland stream. Its flow is strongly seasonal with maximum discharge values recorded in early spring (September) and minimal ones in late summer/early autumn (February, March) (State Rivers and Water Supply Commission, 1965); minimal discharge values are only about 5 per cent of maximal values, and at times of low flow little water movement downstream is visible. The substratum is mud and there is much submerged and emergent macrophytic growth. The water is almost always turbid. Total dissolved solids were about 400 mg l^{-1}, and temperature during the study period was from 9 to 20°C. As in samples from Sassafras Creek, a species of *Neoniphargus* was also present, but at densities too low for adequate analysis. Samples were obtained at monthly intervals over a 16-month period from September 1961 to December 1962.

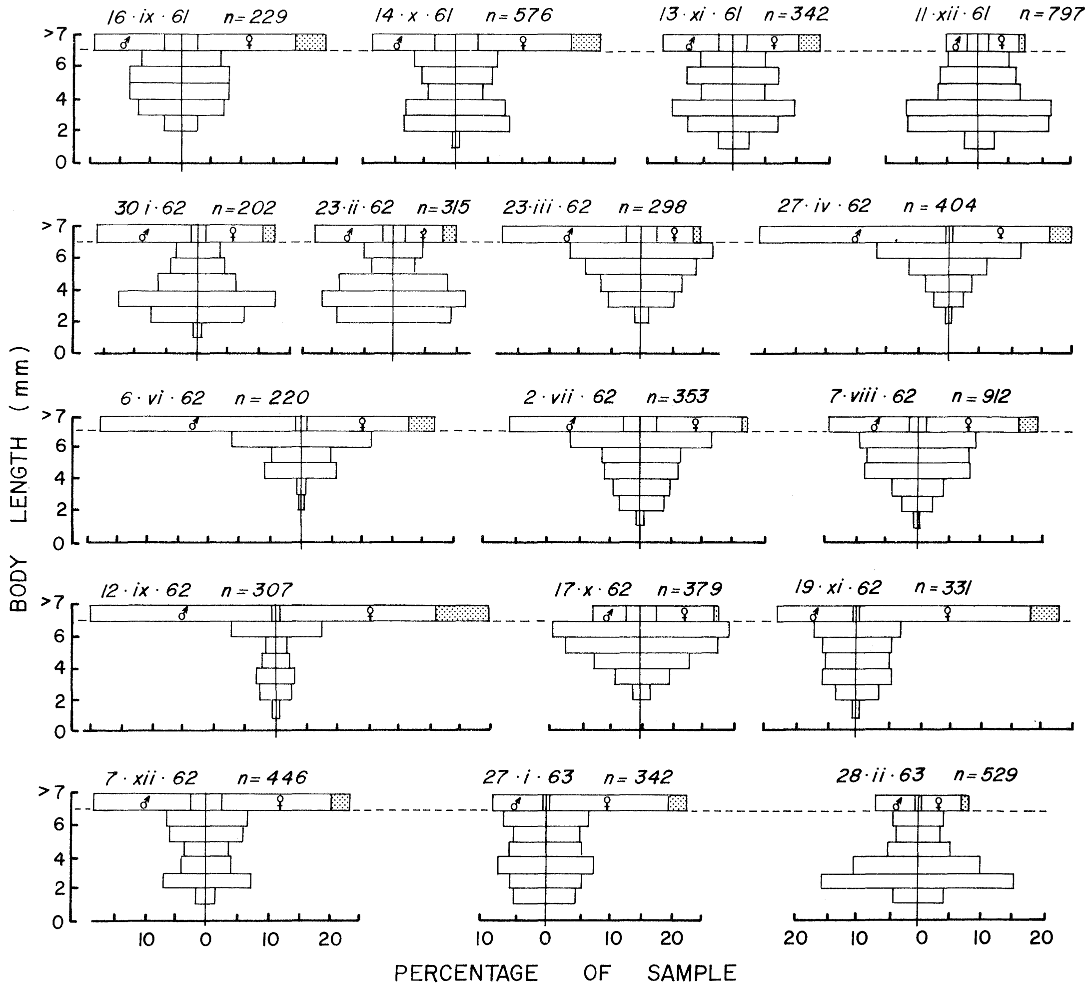

Fig. 2. Size and sex distribution of *Pseudomoera gabrieli* samples from Sassafras Creek, Victoria. The lengths of the specimens are given by the vertical scale and the length of each horizontal size-group block represents the percentage of the total in that size group. The horizontal dashed line shows the lower limit of sex distinction; below this line the blocks are centred; above it, males are shown on the left, females on the right. Females shown by the stippled areas are ovigerous.

Aldgate Creek, at 300 m above sea-level, is a small upland stream in the Mount Lofty Ranges. As in Dandenong Creek, flow shows a strong seasonality with minimal flows in late summer, and maximal ones in spring. Relatively deep pools with sandy substrata are connected by shallow riffle regions of approximate width 3 m. The water is moderately clear and during the study period temperatures varied from 7 to 17°C. Total dissolved solids were about 190-260 mg l^{-1}. Whilst *A. australis* was the abundant amphipod, a few individuals of *Neoniphargus* sp. were found in most samples. Samples were obtained monthly over a 15-month period, from October 1977 to December 1978.

METHODS

The collecting technique in all sampling was the same. A stramin hand-net was vigorously moved amongst bottom detritus, stones and other material in the stream for a few minutes. Net contents were transferred to containers at intervals. Preservation was in the field in 70 per cent ethanol. Temperature was measured with a mercury in glass thermometer at the time of sampling.

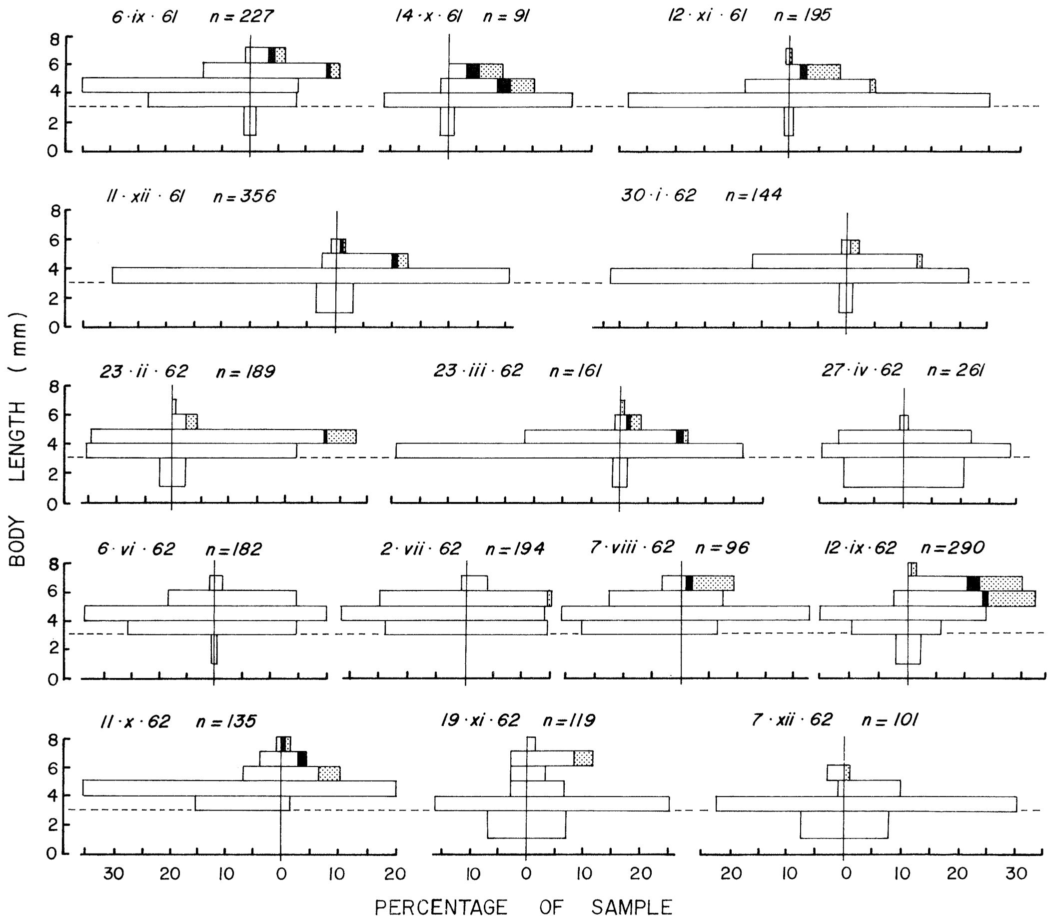

Fig. 3. Size and sex distribution of *Austrochiltonia australis* from Dandenong Creek, Victoria. The arrangement is as in Fig. 2, and the solid blocks represent pouched females.

In the laboratory, specimens were removed from field samples by hand and arranged into 1 mm size groups by comparison with a series of measured specimens. Ovigerous or pouched females of *A. australis* were directly measured with an eyepiece graticule. Adults were sorted into three main categories: males, non-breeding females (without brood pouch or eggs), reproductive females (with empty brood pouch or eggs). Eggs in brood pouches were counted except when pouches were damaged or partly empty, indicating egg loss during preservation or storage.

Pseudomoera gabrieli was distinguished from the other Australian eusirid, *Paramoera fontana* (Sayce), by the presence of 5 or fewer setae on the inner plate of maxilla 1. The sex of individuals of this species was very difficult or impossible to tell in specimens less than 7 mm long, and even in some longer neither oostegites nor male genital papillae could be distinguished without dissection. No female less than 7 mm long was found to be ovigerous. Hence, specimens of *P. gabrieli* over 7 mm long were classed as adults, those smaller as immatures. The largest specimens found were over 12.0 mm long.

Austrochiltonia australis was distinguished from *A. subtenuis* by examination of the third uropod, which is 2-segmented in *A. australis* and 1-segmented in *A. subtenuis.* Because both species may occur together, care was taken to ascertain that mixed populations did not occur at Dandenong Creek and Aldgate Creek. All specimens examined from both localities had 2-segmented third uropods. The sex of individuals over 3 mm long could be determined by examination of second gnathopods, which are enlarged in males. The largest specimens found did not exceed 8.00 mm in length.

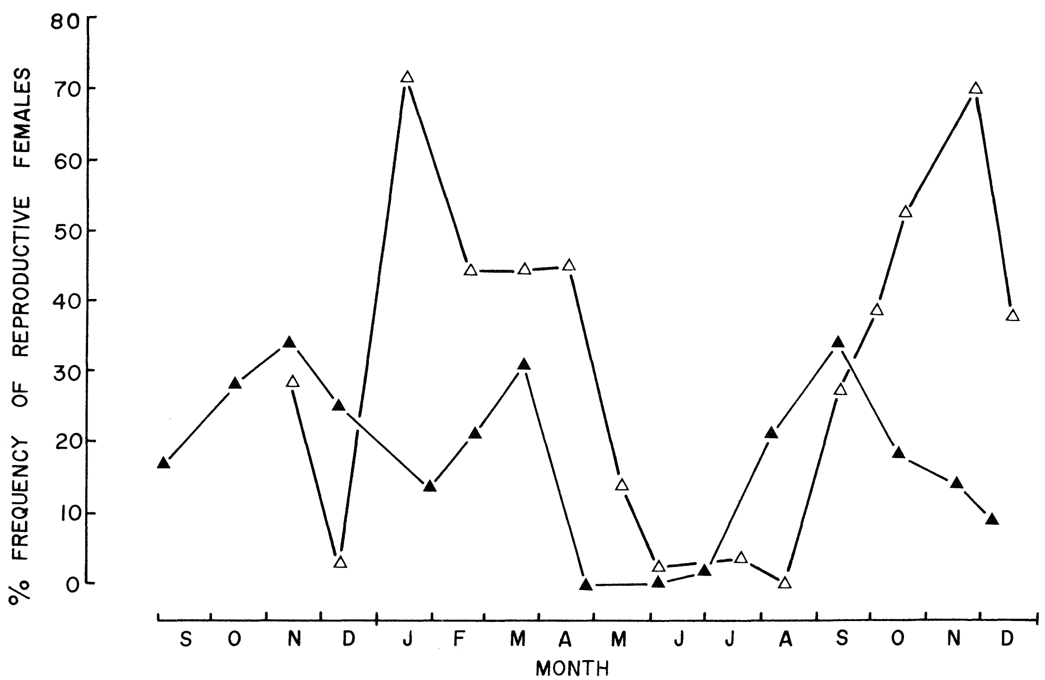

Fig. 4. Annual variation in breeding intensity of *Austrochiltonia australis* from Dandenong Creek (▲) and from Aldgate Creek (△). The symbols represent reproductive females (ovigerous or with empty brood pouch) expressed as a percentage of all females > 4.0 mm.

Representative specimens from each locality are lodged in the South Australian Museum, with register numbers C3871 to C3873.

RESULTS

(a) *Pseudomoera gabrieli*

Ovigerous females were present in all samples, their frequency varying from a low in July 1961 of 1.6% of total adults to a maximum in September 1962 of 14.6% (Table 1). In no sample did ovigerous females exceed 30% of total females. The continuous presence of ovigerous females was reflected in the relatively small changes in size-structure of the population throughout the year (Fig. 2). Small specimens, less than 3 mm long, composed less than 10% of the population in autumn and winter, but were more abundant in summer (Table 1).

Brood size varied between 19 and 62 eggs, the larger broods being carried by the larger females.

The ratio of males to females varied from 2.95 in March 1962 to 0.36 in January 1963. The fluctuations in sex ratio could not be related to other changes in population structure or to season.

(b) *Austrochiltonia australis* in Dandenong Creek

Changes in the size-frequency of the population and in the proportions of pouched and ovigerous females indicate a seasonal cycle (Fig. 3, Table 2). No females were ovigerous or pouched between April and June 1962, and only one was ovigerous in July 1962. In August 1962 and during the spring and summer months and in March 1962 reproductive females made up 20% or more of adult females in most samples (Fig. 4). The halt in breeding activity came abruptly. Juveniles reached their greatest relative abundance in April 1962 and were absent from the population in July and August 1962. Immatures also reached their greatest abundance in April, but the immature size class was never absent (Fig. 3).

Adults composed a large proportion of the population in winter and early spring, their frequency reaching a maximum of 83% in early November 1962. Many specimens that reached adult size by autumn survived the winter and were represented in the 6.0–7.0 mm and 7.0–8.0 mm size classes in the following

Table 1. Details of regular samples of *Pseudomoera gabrieli* from Sassafras Creek, Victoria.

	1961				1962											1963	
Date of sampling	6 Sept	14 Oct	13 Nov	11 Dec	30 Jan	23 Feb	23 Mar	27 Apr	6 June	2 July	7 Aug	12 Sept	17 Oct	19 Nov	7 Dec	27 Jan	28 Feb
Total specimens	229	576	342	797	202	315	298	404	220	353	912	307	379	331	466	342	529
Immatures	148	390	265	695	144	242	203	200	100	227	604	102	302	179	271	239	451
Males	26	59	31	27	31	34	59	121	70	65	121	93	21	41	76	27	35
Nonovigerous ♀♀	37	73	29	41	19	20	17	64	36	49	141	78	37	91	82	64	35
Ovigerous ♀♀	10	12	12	6	4	6	3	12	10	2	25	30	2	16	13	10	5
Spec. <3 mm as % total	5.7	18.3	19.0	28.0	16.3	18.7	2.0	0.7	0.5	7.9	5.1	5.5	2.4	6.9	17.8	19.6	39.1
Immatures as % total	64.6	67.7	77.5	87.2	71.3	76.8	68.1	49.5	45.5	64.3	66.2	33.2	79.7	54.1	58.2	69.9	85.3
Ovigerous ♀♀ as % adults	12.3	6.5	13.8	5.9	6.9	8.2	3.2	5.9	8.3	1.6	8.1	14.6	2.6	10.5	6.7	9.7	6.4
Ovigerous ♀♀ as % total females	21.3	14.1	29.3	12.8	17.4	23.1	15.0	15.8	21.7	3.9	15.1	27.8	5.13	15.0	13.7	13.5	12.5
Males/females	0.55	0.69	0.76	0.57	1.35	1.31	2.95	1.59	1.52	1.27	0.73	0.86	0.54	0.38	0.80	0.36	0.88

Table 2. Details of regular samples of *Austrochiltonia australis* from Dandenong Creek, Victoria.

		1961						1962							
Date of sampling	6 Sept	14 Oct	12 Nov	11 Dec	30 Jan	23 Feb	23 Mar	27 Apr	6 June	2 July	7 Aug	12 Sept	11 Oct	19 Nov	7 Dec
Total specimens	227	91	195	356	144	189	161	261	182	194	96	290	135	119	101
Juveniles	9	4	6	44	6	18	7	111	1	0	0	25	0	33	32
Immatures	60	33	124	251	91	71	98	86	56	56	23	46	23	49	54
Males	87	11	15	9	25	29	30	31	59	72	35	52	63	9	4
Nonovigerous ♀♀	59	31	32	39	19	57	18	33	66	65	30	110	40	24	10
Ovigerous ♀♀	8	6	15	8	3	14	5	0	0	1	7	49	6	4	1
Pouched ♀♀	4	6	2	5	0	1	3	0	0	0	1	8	3	0	0
Juveniles as % total	4.0	4.4	3.1	12.4	4.2	9.5	4.4	42.5	0.5	0	0	8.6	0	27.7	31.7
Immatures as % total	26.5	36.3	63.6	70.5	63.2	37.6	60.9	77.5	30.8	28.9	24.0	15.9	17.0	41.2	53.5
Ovigerous ♀♀ as % adults	5.1	11.1	23.1	13.1	6.4	14.0	8.9	0	0	0.7	9.5	22.4	5.4	10.8	6.7
Ovigerous ♀♀ as % adult females	11.3	14.0	30.0	15.4	13.6	19.7	19.2	0	0	1.5	18.4	29.3	12.2	14.3	9.1
Males/females, adult	1.22	0.26	0.30	0.17	1.14	0.41	1.15	0.94	0.89	1.09	0.92	0.31	1.28	0.32	0.36
Av. length ovig. ♀♀ (mm)	6.1	6.1	4.9	4.7	5.2	4.9	5.0			6.07	6.1	5.1	4.6	4.5	4.0
Av. length pouched ♀♀ (mm)	6.4	5.8	5.1	4.7		4.7	4.5				6.4	5.2	6.7		
Av. no. eggs/ovig. ♀	39(7)*	26(4)	35(13)	24(5)	—	27(9)	22(2)			—		48(48)	43(6)	39(3)	18(1)

*Figure in parentheses is the number of broods in which eggs were counted.

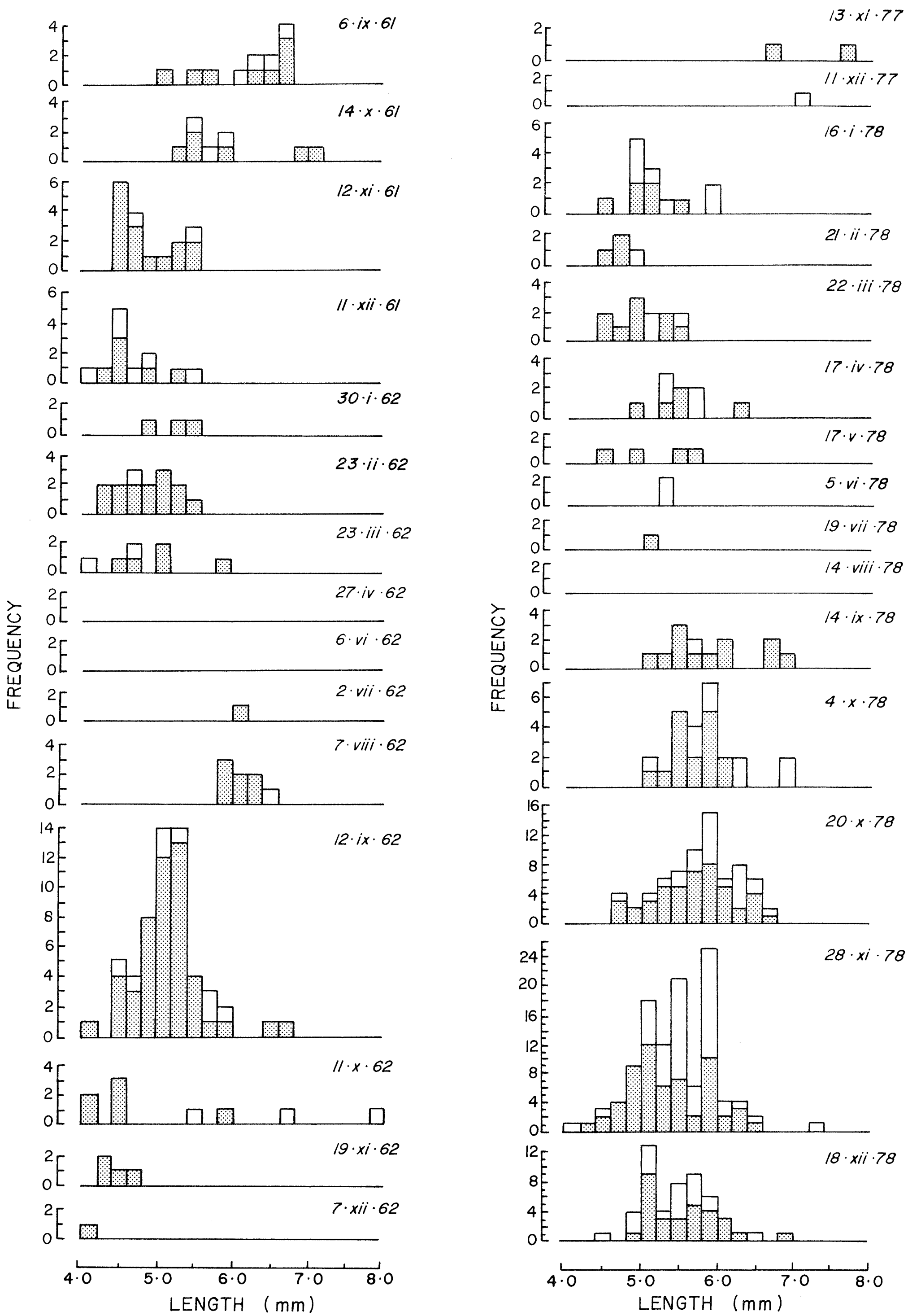

Fig. 5. Size distribution of ovigerous females of *Austrochiltonia australis* in each sample from Dandenong Creek (left) and from Aldgate Creek (right). Stippled blocks, ovigerous females; open blocks, pouched females.

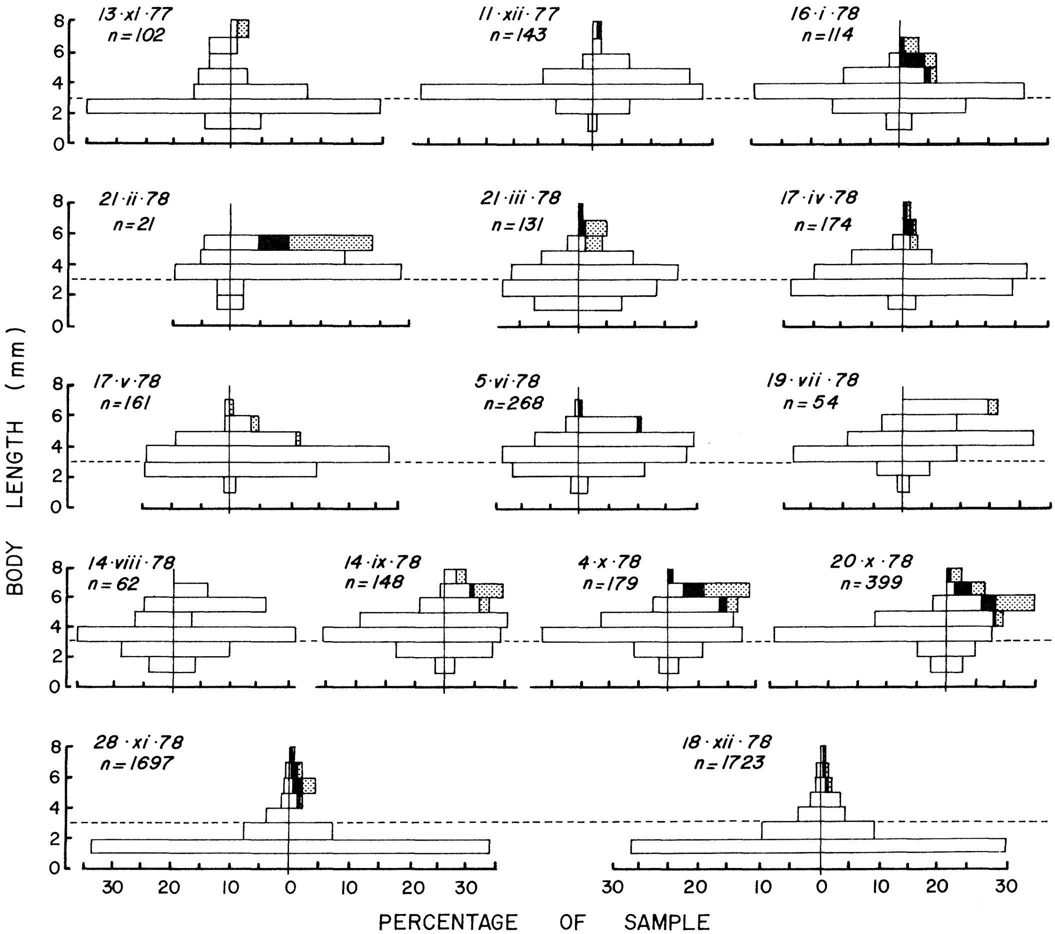

Fig. 6. Size and sex distribution of *Austrochiltonia australis* from Aldgate Creek, South Australia. The arrangement is as in Fig. 3.

spring. They apparently did not survive beyond November, and by December the largest animals were in the 5.0–6.0 mm size class. Females grew to larger size than males, the largest observed female being 7.9 mm, the largest male 6.5 mm. Also, fewer males than females reached the 6.0–7.0 mm size class. The females that became ovigerous in August and early spring were large, and the average size of reproductive females declined during the breeding season (Fig. 5). The small females breeding in December 1961 and 1962 probably were born in August-September of the same years. However, the average size of ovigerous females began to fall as early as September in 1962, and this must have resulted from slower ovarian development in females reproducing for the first time. The number of eggs per brood was so variable that although there was a trend towards larger females carrying more eggs, the average brood size varied erratically throughout the breeding season. The range in brood size was from 10 to 76.

(c) *Austrochiltonia australis* in Aldgate Creek

There was a seasonal cycle, with an almost complete absence of reproductive females in June, July and August 1978 (Fig. 6). Ovigerous females became abundant in September and their frequency increased during spring (Table 3). In January and November 1978 more than 70% of adult females were ovigerous or pouched (Fig. 4). Hence the non-breeding season occurred one month later than at Dandenong Creek, and the maximum frequency of reproductive females was much higher. In other respects the annual

Table 3. Details of regular samples of *Austrochiltonia australis* from Aldgate Creek, South Australia.

Date of sampling	10 Oct	1977 13 Nov	11 Dec	16 Jan	21 Feb	22 Mar	17 Apr	17 May	5 June	1978 19 July	14 Aug	14 Sept	4 Oct	20 Oct	28 Nov	18 Dec
Water temp °C	13	13	17	16	16	15	13	10	12	10	7.5	9	9.1	10.1	7	15
Total specimens	6	102	143	114	21	131	174	161	268	54	62	148	179	399	1697	1723
Juveniles	0	61	20	31	2	56	74	50	71	6	16	29	27	61	1405	1427
Immatures	1	20	72	52	8	38	63	66	86	15	23	44	61	148	100	132
Males, adult	4	14	14	13	2	10	17	17	28	7	7	28	24	56	34	29
Nonovigerous ♀♀	1	5	36	5	5	15	11	24	81	25	16	34	41	64	47	84
Ovigerous ♀♀	0	2	0	6	3	9	5	4	0	1	0	12	17	45	59	30
Pouched ♀♀	0	0	1	7	1	3	4	0	2	0	0	1	9	25	52	21
Juveniles as % total	0	59.8	14.0	27.2	9.5	42.7	42.5	31.1	26.5	11.1	25.8	19.6	15.1	15.3	82.8	82.8
Immatures as % total	16.7	19.6	50.3	45.6	38.1	29.0	36.2	41.0	32.1	27.8	37.1	29.7	34.1	37.1	5.9	7.7
Ovigerous ♀♀ as % adults	0	9.5	0	19.4	27.3	24.3	13.5	8.9	0	3.0	0	16.0	18.7	23.7	30.7	18.3
Ovigerous ♀♀ as % adult females	0	28.6	0	33.3	33.3	33.3	25.0	14.3	0	3.8	0	25.5	25.4	33.6	37.3	22.2
Males/females, adult	4.0	2.0	0.38	0.72	0.22	0.37	0.85	0.61	0.34	0.27	0.44	0.60	0.36	0.42	0.22	0.21
Av. length ovig. ♀♀ (mm)		7.3		5.0	4.7	4.92	5.5	5.1		5.2		5.9	5.7	5.7	5.3	5.6
Av. length pouched ♀♀ (mm)			7.1	5.2	4.8	5.2	5.5		5.3			5.7	6.0	5.9	5.6	5.4
Av. no. eggs/ ovig. ♀		76(2)*		26(3)	18(3)	30(9)	16(5)	15(4)		25(1)		54(11)	44(16)	48(37)	35(32)	35(27)

*Figure in parentheses is the number of broods in which eggs were counted.

cycle of *A. australis* at Mylor was similar to that of the Dandenong Creek population. The largest female was 7.8 mm long and the largest male 6.6 mm. The range in brood size was from 8 to 91 eggs.

DISCUSSION

A review of freshwater amphipod life cycles in the northern hemisphere showed that while in many localities stream amphipods display marked seasonality in reproduction, breeding is continuous in others (Hynes, 1955). Strictly seasonal breeding is shown by *Gammarus lacustris lacustris* in Wales and *G. pseudolimnaeus* in Ontario, both species having a simple annual cycle, with young being released in late spring and early summer, overwintering as immatures and breeding in the following spring (Hynes and Harper, 1972). Variations on this pattern are the two-year life cycle of *G.l. limnaeus* in Ontario, and, on the other hand, the rapid development to maturity before overwintering shown by *G. fasciatus* in England. Non-seasonal breeding is exemplified by *Crangonyx gracilis* (Hynes, 1955). Different populations of the same species may even have different reproductive patterns, this being shown by *G. pulex* which has a resting period in November in Cheshire, whilst in Dorset and on the Isle of Man, reproduction continues throughout the year (Hynes, 1955; Welton, 1979).

The lack of seasonality in the life cycles of *P. gabrieli* agrees with the findings on the life-cycle patterns of Australian mainland stoneflies (Hynes and Hynes, 1975) and of the amphipod *Paracalliope fluviatilis* in New Zealand (Towns, 1976). However, the agreement contributes no useful evidence for the hypothesis that the absence in Australia of a precisely timed autumnal leaf fall results in more flexible life cycles. It seems likely that the reproductive strategy adopted by *P. gabrieli* in Sassafras Creek is similar to that of those northern hemisphere amphipods which breed continuously, and is basically a response to the absence of marked seasonal variations in temperature and flow rates. There is no evidence to suggest that the strategy is a response either to the absence of an autumnal leaf fall or to the uncertainty of the Australian climate.

On the other hand, seasonality in the life cycle of *A. australis* in both upland and lowland streams is scarcely evidence against the hypothesis. Both localities where *A. australis* was studied displayed marked seasonal changes in flow regime and it seems likely that these would affect the life-cycle patterns of stream inhabitants. In other words, even if the lack of a precisely timed autumnal leaf fall represents the absence of a condition which induced life cycle seasonality, another condition, marked seasonal changes in flow regime, operates to induce it. The marked seasonality in the intensity of reproduction of *A. subtenuis* in Lake Modewarre (Lim and Williams, 1971) might be a reflection of recent derivation from a stream-dwelling population or frequent genetic interchange with a stream population.

Whilst our findings provide no direct information on the relationships between the patterns of life cycle and leaf fall, they do contribute in a general sense to our limited knowledge of invertebrate life cycles in Australian streams. When such knowledge is more taxonomically and geographically comprehensive, more insight into the factors controlling life cycle patterns may then be possible.

ACKNOWLEDGEMENTS

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