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INFLUENCE OF DAM OPERATION ON MAYFLY ASSEMBLAGE STRUCTURE AND LIFE HISTORIES IN TWO SOUTH-EASTERN AUSTRALIAN STREAMS

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ABSTRACT

The mayfly fauna, and in particular the life histories of two mayflies, *Coloburiscoides* sp. and *Baetis* sp. 3, was studied in two nearby streams located in the headwaters of the River Murray, SE Australia. The Mitta Mitta River is regulated by the Dartmouth Dam which releases cold water in summer for irrigation. Snowy Creek is a tributary of the Mitta Mitta River with natural flow and temperature regimes. The structure of the mayfly assemblage differs in the two streams. In the regulated Mitta Mitta there are 11 species, of which, caenids (*Tasmanocaenis tonnoiri* and River Murray sp. C), *Coloburiscoides* sp. and *Baetis* sp. 3 dominate. Snowy Creek, with a richer assemblage of 17 species, was dominated by *Coloburiscoides* sp., *Baetis* sp. 3 and two *Austrophlebioides* species. Monthly collections of mayfly nymphs and adults between September 1987 and August 1988, in both streams, allowed evaluation of possible life history changes in relation to dam operation. *Coloburiscoides* sp. and *Baetis* sp. 3 had synchronous life histories at both regulated and unregulated sites. *Coloburiscoides* appeared to be univoltine, and *Baetis* polyvoltine. At the regulated site, nymphal abundance in both *Coloburiscoides* and *Baetis* declined during the summer release, which coincided with the beginning of nymphal recruitment and appeared to delay nymphal hatching in *Coloburiscoides*.
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KEY WORDS: mayflies; stream regulation; assemblage structure; life histories; Australia

INTRODUCTION

Downstream effects of dams on stream communities are a consequence of changes in flow patterns, temperature regime, altered habitat, and variation in food type and availability (Ward, 1976; Ward and Stanford, 1979). Following river regulation, benthic organisms inhabiting downstream reaches have to cope with new imposed environmental conditions. Some species are eliminated or reduced in abundance while others increase.

One major potential environmental change which may result from river regulation is a change in downstream water temperature, an impact particularly associated with bottom release reservoirs. Changes induced through these impacts are the basis of the serial discontinuity concept of river regulation impact proposed by Ward and Stanford (1983). In much of south-eastern Australia, large reservoirs are used to supply water for irrigation during summer. River channels are used as major water delivery systems, which leads to a reversal of the natural flow regime. Whereas the pre-regulation rivers had minimal discharge and high water temperatures in summer, they now flow bankful and at temperatures substantially lower than those which occurred naturally. These patterns have been documented for the Goulburn and Tumut Rivers, and are also a feature of the Mitta Mitta River below Dartmouth Dam (Gippel and Finlayson, 1993; Finlayson *et al*., 1994).

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The change in annual pattern of temperature and discharge may be expected to impact particularly on the life histories of many of the aquatic invertebrates downstream of the reservoir. Water temperature is known to play a critical role in the growth and development of stream insects (Lehmkuhl, 1972; Perry *et al.*, 1985; Brittain and Campbell, 1991; Brittain, 1995) so reductions in water temperature of the order of 10°C, not uncommon in south-eastern Australian regulated rivers in summer, could be expected to have a major impact on the life cycles of the insects present.

Temperate aquatic insects display a range of life cycle patterns and development times. Amongst the mayflies of south-eastern Australia, Campbell and co-workers have documented life cycles ranging from several months up to 3 years (e.g. Campbell, 1986; Campbell *et al.*, 1990). In predicting the impacts of river regulation on invertebrate assemblages it was predicted that aquatic insects with longer life cycles would be more severely affected by river regulation than those with shorter development times. Insects which develop more slowly would take longer for their populations to recover through local population growth (although not necessarily from immigration), than those with a rapid turnover time. In addition insects with annual or longer life histories may be more sensitive to the effective loss of summer than polyvoltine species which can complete their growth under a range of temperature regimes. In addition, species with short life histories may be able to complete their life cycle during those parts of the year when the impact of regulation is less significant, operating somewhat like refugee species (Brittain and Saltveit, 1989).

This study constitutes part of an investigation of the environmental effects of the operation of Dartmouth Dam in north-eastern Victoria, Australia, where regulation involved summer releases of cold water to provide irrigation water for agricultural use in contrast with low water levels and absence of fluctuations the rest of the year (Doeg, 1984). Mayfly assemblage composition and structure were compared, and life cycles of some of the dominant species in a reach downstream of the reservoir, to those in unregulated conditions in an adjacent stream. Previous studies of the same system carried out shortly after the dam was established had already demonstrated that dam construction had a significant impact on the riverine invertebrate fauna (Blyth *et al.*, 1984; Doeg, 1984).

MATERIAL AND METHODS

Study sites

The study was carried out in the upper catchment of the River Murray, north-eastern Victoria, Australia. Two sites were selected, one on the unregulated Snowy Creek 200 m upstream of the junction with the Mitta Mitta River above the Mitta Mitta township (Station 102), and the other in the Mitta Mitta River 200 m upstream of the same junction (Station 103). Both sites are at an elevation of about 270 m.a.s.l. (Figure 1). Gradient is higher in Snowy Creek, consisting of the reach bed of riffles with cobble, stone and gravel substrates, while the Mitta Mitta River bed is composed of stones and gravel, with a thick layer of sediment and filamentous algae in the pre-release period, which became reduced during release. A complete description of the physical environment of the study site in both streams, and their dynamics during Dartmouth Dam construction and operation (1980–1981 pre-release and release periods, involving discharge values and substrate related changes), is provided in Blyth *et al.* (1984) and Doeg (1984). Dartmouth Reservoir is located about 17 km upstream of the sampling site, and provides water for irrigation which is released mainly from the hypolimnion in summer (January–March). During the rest of the year the river water is artificially maintained at a constant level (Figure 2). In Snowy Creek water level was measured just above the sampling site (20 m), while in the Mitta Mitta it was measured on the bridge supports about 100 m downstream. The river channel was much wider at the sampling site on the Mitta Mitta and more or less impossible to gauge, thus the water level scale was on the bridge where the river channel was much narrower. Although the rise in water level at the bridge was very high (Figure 2), it was much less, although probably 1 m, due to the wider channel at the sampling site.

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Sampling methodology

Samples were collected monthly between September 1987 and August 1988. Each sample usually consisted of five surber replicates (area 0.09 m^2) and two kick samples of 30 s duration. However in Snowy Creek in October 1987 ten surber replicates were taken and in the Mitta Mitta from January to April, only kick samples were collected due to the extremely high flows. The two kick samples, one in fast, shallow running water and another in slow, deep areas were complemented with three more extensive kick sample surveys and stone picking, in order to cover all habitat types at Snowy Creek in September and October 1987, and at Mitta Mitta River in September 1987. Mesh size for both sampling techniques was 300 μm. Light trapping and sweep netting for adults was also undertaken monthly.

Macroinvertebrates were sorted and preserved in 70% ethanol, and ephemeropterans identified to genus and where possible to species using keys produced by Dean (1989) and Suter (1989). Several of the species encountered were undescribed.

Life history analysis

Larval size was used to indicate age and the presence of larvae with black wingpads as an indication that emergence was occurring (Needham *et al*., 1935). A graticule eyepiece mostly at 50 × magnification, was used to measure larvae. In *Coloburiscoides* sp. the pronotum and mesonotum are fused, and so their total length was measured from the anterior border of pronotum to the posterior edge of mesothoracic wingpads, following Campbell (1986). Head width between compound eyes was the criterion used for *Baetis* sp. 3. Life history patterns were analysed from size frequency histograms for each sample date and site using pooled total abundance from surber and kick samples. The large number of nymphal instars in *Ephemeroptera*, and their frequent size overlap precludes determination of instar number (Campbell, 1986).

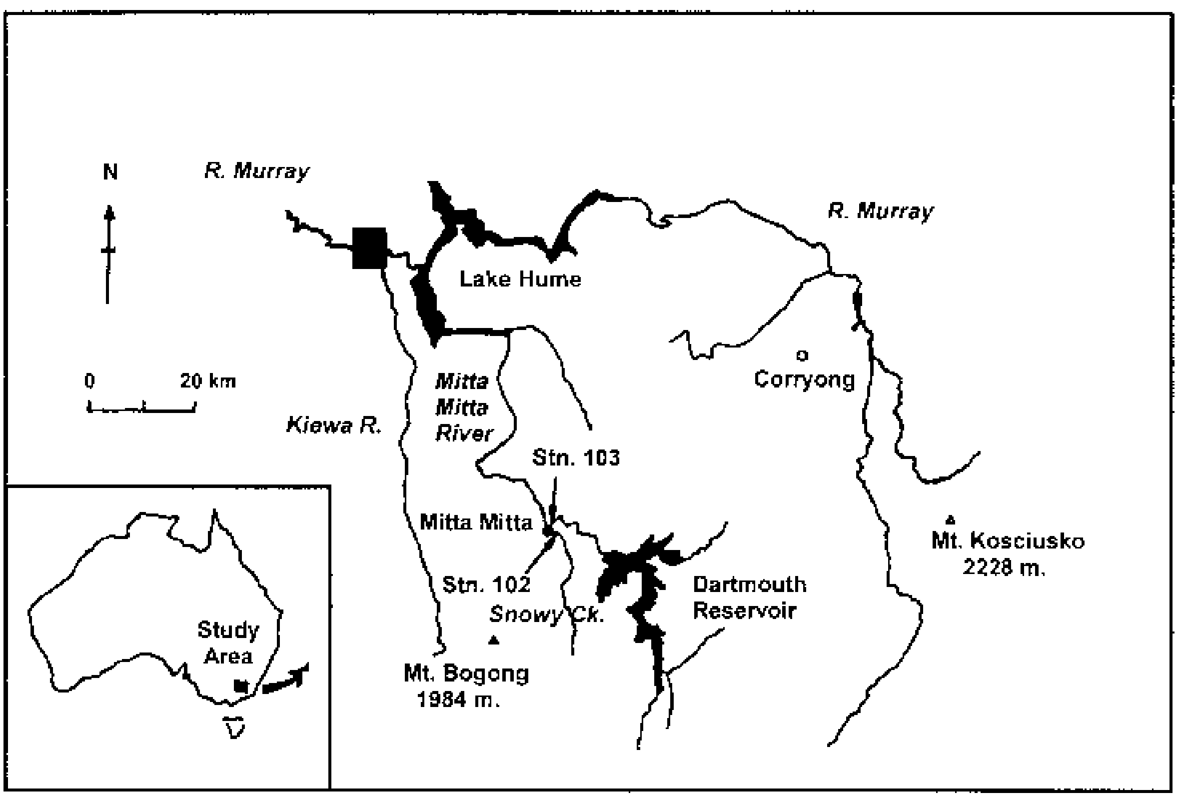

Figure 1. The study area

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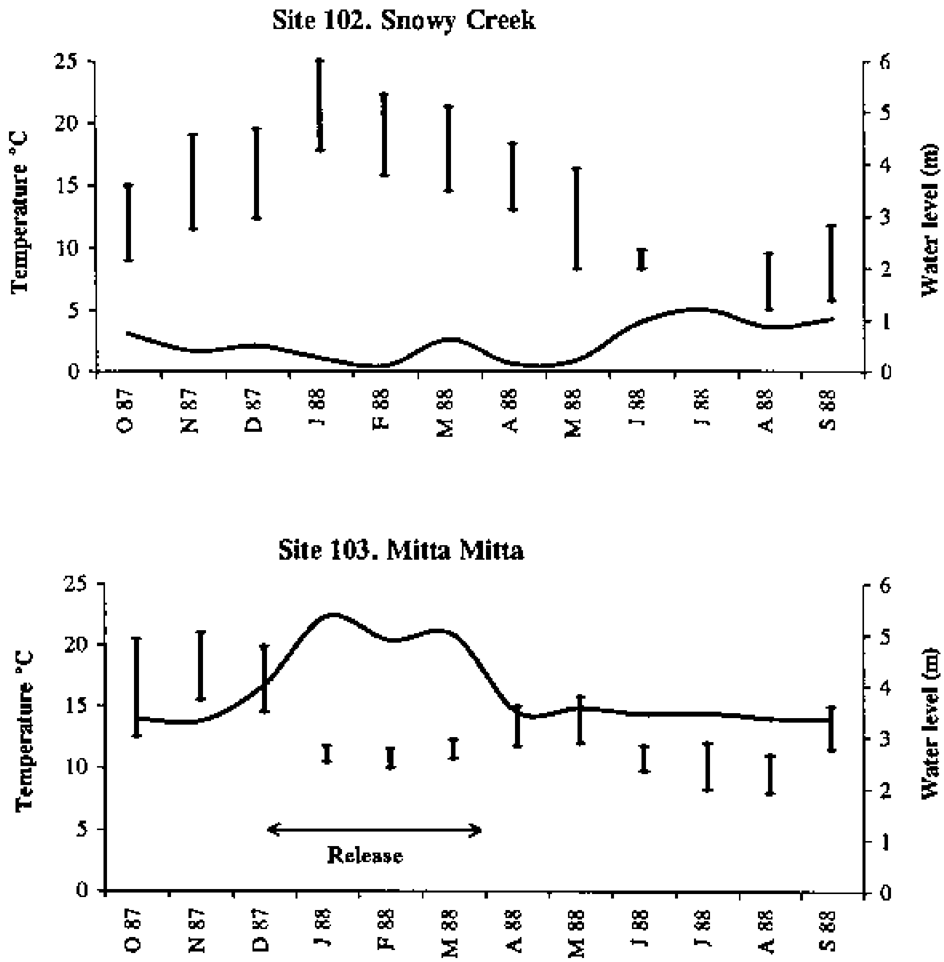

Figure 2. Monthly water temperature ranges and mean water levels in Snowy Creek and Mitta Mitta River, to compare a regulated versus unregulated patterns. Horizontal bar in the Mitta Mitta River represents release period

Community analysis

Assemblage composition data were analysed by classification and ordination performed with the NTSYS-pc package (version, 1.6, Applied Biostatistics Inc., 1990) on relative frequencies of individuals per site and sampling occasion. Clustering was done by unweighted pair group average linkage (UPGMA) based on the Bray–Curtis dissimilarity matrix. Detrended correspondence analysis (DCA) ordination (Hill, 1979) was executed with the program CANOCO (Version 3.12, 1991; Ter Braak, 1991) on its standard routine of detrending by segments.

RESULTS

Community composition

The mayfly material for both streams during the period studied, consisted of 13291 specimens belonging to 18 species. *Baetis* sp. 3, and a *Coloburiscoides* species similar to *C. haleuticus* (see Brittain and Campbell, 1991), were the dominant species with 5137 and 3102 specimens, respectively.

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Species composition differed between streams. In Snowy Creek the mayfly community included 17 species, ten of which were also in the Mitta Mitta (Table I). Differences in richness are mostly due to the absence from the Mitta Mitta of several rarer species present in Snowy Creek (less than 0.15% of total abundance). In both streams *Coloburiscoides* sp. and *Baetis* sp. 3 were abundant (Table I), as a percentage *Baetis* was much less abundant in the Mitta Mitta while *Coloburiscoides* was slightly less abundant in Snowy Creek. The *Caenidae* (*Tasmanocoenis tonnoiri*, River Murray caenid sp. C), were the most abundant mayfly family in the Mitta Mitta, while in Snowy Creek leptophlebiids (*Austrophlebioides marchanti* and *Austrophlebioides pusillus*) were the third most abundant family.

Classification and ordination

A matrix of 24 samples and the relative frequency per sample of 18 species, was analysed with similarity classification and ordination, to detect patterns within the communities. The classification separated two groups at a dissimilarity level of 70%, which comprised the samples from each river, indicating differences in species composition between the two. This result was confirmed by separation along axes I and II of the ordination analysis by DCA (Figure 3). Spring and winter samples from Snowy Creek differed with 45% and 35%, respectively, from the other samples. Within the Mitta Mitta samples, those corresponding

Table I. Species composition and relative frequencies of mayflies (abundance and percentage of dominant species are in bold) in Snowy Creek and Mitta Mitta River, SE Australia

Species	Abundance	Percentage
Station 102 Snowy Creek		
Baetis sp. 3	**4539**	**52.93**
Coloburiscoides sp.	**1821**	**21.23**
Austrophlebioides marchanti	**715**	**8.34**
Austrophlebioides pusillus	**650**	**7.58**
River Murray caenid sp. C	485	5.66
Nousia sp.	100	1.17
Caenid sp. D	96	1.12
Tasmanocoenis tonnoiri	62	0.72
Atalophlebia sp. 4	31	0.36
Garinjuga maryannae	12	0.14
Baetis sp. A	12	0.14
Baetis sp. B	10	0.12
Genus Y sp.	10	0.12
Centroptilum sp. 1	8	0.09
Tasmanophlebia lacuscoerulei	7	0.08
Atalophlebia sp. 3	3	0.03
Koorrnonga sp.	1	0.01
Total	8562	100.00
Station 103 Mitta Mitta		
Tasmanocoenis tonnoiri	**2294**	**48.51**
Coloburiscoides sp.	**1281**	**27.09**
Baetis sp. 3	**598**	**12.65**
River Murray caenid sp.	**508**	**10.74**
Austrophlebioides pusillus	23	0.49
Atalophlebia sp. 4	8	0.17
Caenid sp. D	5	0.11
Austrophlebioides marchanti	4	0.08
Nousia sp.	4	0.08
Baetis sp. A	3	0.06
Atalophlebia sp. 9	1	0.02
Total	4729	100.00

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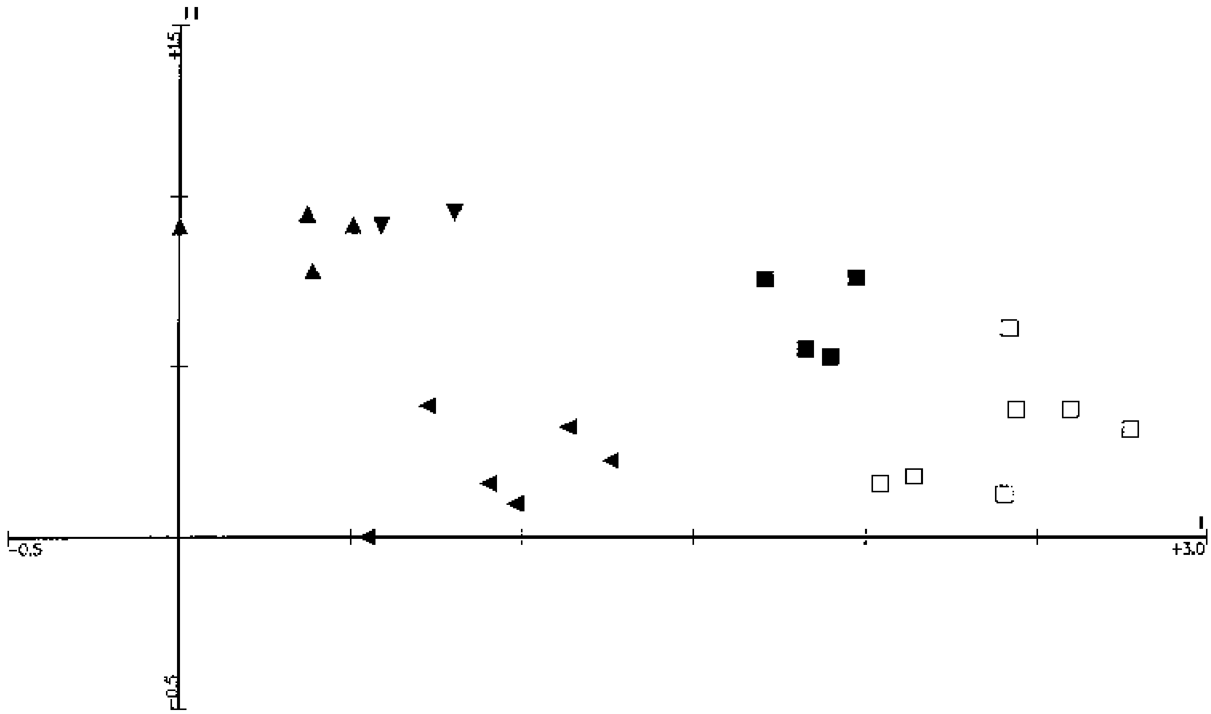

Figure 3. DCA ordination analysis of samples, with resulting groups from UPGMA classification on Bray–Curtis dissimilarity index. Snowy Creek sample groups: ▲, October, November, December 1987, August 1988; ▼, June, July 1988; ◄, September 1987, January, February, March, April, May 1988. Mitta Mitta sample groups: ■, April, May, June, July 1988; □, September, October, November, December 1987, January, February, March, April 1988

to autumn, after the summer water release, differentiate from the rest of the year. Distribution of samples on axes I and II of the DCA was consistent with the groupings in the classification (Figure 3). Axis scores of sites were related to the environmental variables: mean, maximum and minimum monthly temperature, and water level. Axis I (78.2% of the variance explained by the first four axes) site scores were related to water level ($r_S = 0.65$, $p = 0.001$) indicating higher values in the Mitta Mitta. Axis II (12.1% of the variance) was inversely related to minimum ($r_S = -0.47$, $p = 0.032$) and mean temperature ($r_S = -0.45$, $p = 0.036$), related to higher temperatures in summer and autumn samples from Snowy Creek. Mean and minimum temperatures were closely related ($r_S = 0.92$, $p = 0.0001$).

Life histories

Two mayfly species were chosen from the abundant species in the two streams for life history investigations. The criteria used to select the species were to consider first, which species showed representative numbers throughout the studied months in both streams, to accurately represent population dynamics and to relate it to annual environmental changes. Caenidae species contribute in a high percentage to the total mayfly community, but their densities and relative dominance, varied greatly with time and stream. *Tasmanocoenis tonnoiri* had very low densities in Snowy Creek, being absent from the benthos over 4 months. Similarly, River Murray caenid sp. C was absent from the reach studied in Snowy Creek for 6 of the 12 months studied, with 478 individuals collected in 4 months (from February to May). In the Mitta Mitta both species populations consisted of high numbers before release, and were reduced to minimal values afterwards, with a minimal recovery after release. The second aim was to select species with different life cycles, size and feeding strategies, to check some of the hypothesis indicated by Brittain and Saltveit (1989). *Coloburiscoides* sp. 1 is a large nymph requiring strong current for filter-feeding and cobbles or wood and tree roots for shelter (Brittain and Campbell, 1991; Peters and Campbell, 1991).

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Baetis sp. 3 nymphs are considered small collectors of detritus particles, but their habitat preferences have not been studied. In Australia, the genus *Baetis* has been recorded from temperate regions to the tropics, mostly from lotic habitats. The family is considered to be common and widespread (Williams and Campbell, 1987).

Coloburiscoides sp. 1. Populations of *Coloburiscoides* sp. from Snowy Creek have a similar life history to that of *C. haleuticus* Eaton (Campbell, 1986), with a long continuous emergence period from August to March, based on the presence of mature nymphs (Figure 4(a)). This is confirmed by adults collected in light traps (Brittain and Campbell, 1991). The newly hatched nymphs were more abundant from January onwards and continued to hatch during the summer months. In Snowy Creek this species was univoltine. In the Mitta Mitta River (Figure 4(b)) the life cycle pattern of *Coloburiscoides* sp. was more irregular and discontinuous. Mature nymphs were present from October to December, and after the irrigation release, from April to August 1988 being more abundant in May, when a peak in mature female nymphs occurred. Between January and March release of irrigation water from the reservoir drastically reduced *Coloburiscoides* sp. numbers, with only a few small nymphs being present. In March, when water levels fell again, there was an increase in the number of newly hatched nymphs (April–May 1988), with small numbers initially but then rapidly increasing. The period of recruitment is short, so that they overwinter synchronously at a smaller size than in Snowy Creek. The lower water temperatures during the release would also delay egg development (see Brittain and Campbell, 1991).

Baetis sp. 3. Mature nymphs of *Baetis* sp. 3 were present year round in Snowy Creek (Figure 5(a)), with a peak in January. Mature nymphs with black wingpads had smaller head width size in the summer generation (in February males 0.89 mm, $n = 14$; females 0.79 mm, $n = 4$) than the rest of the year (in June males 1.12 mm, $n = 12$; females 0.97 mm, $n = 8$), as previously reported for species with two or more generations per year (Clifford, 1982). Recruitment of young nymphs was continuous with the abundance of small instars greatest between January and March. *Baetis* sp. 3 was less abundant at Mitta Mitta than at Snowy Creek, with minimum numbers during summer release, and maximum before and after this event occurred (December 1987 and May 1988) (Figure 5(b)). Mature nymphs occurred throughout the year. During early summer, egg development and subsequent nymphal growth were rapid at the relatively high temperatures. However the increase in discharge and the fall in water temperatures arrested development. Many nymphs were also washed away by the irrigation release, catastrophic drift occurs when in the space of an hour there is major fall in temperature and a substantial increase in discharge (Brittain, unpublished data), but those remaining grew rapidly when discharge and temperatures returned to their normal levels. These gave rise to a new generation which grew and emerged during winter.

CONCLUSIONS

Species composition

Deep release dams alter mayfly assemblages, usually reducing species richness and densities (Brittain and Saltveit, 1989). In this study, several species present in the unregulated Snowy Creek were absent from the Mitta Mitta River, and the relative abundance of dominant species also differed between the two. Density differences were the results from physical changes induced by flow regulation, as reported for the whole community in this site close to the point of release (Doeg, 1984). Prolonged and constant flows increase fine particle sedimentation and filamentous algae on the stream bed (Doeg, 1984), while there is evidence that given long periods unregulated flows remove large quantities of surface sediment (Platts and Megahan, 1975). Silt sedimentation seems to improve channel conditions for burrowers, such as caenids, this being reflected in their high abundance in the regulated stream. Similarly, low discharge and/or reduced current velocity produces major changes in assemblage structure, with an increase in relative abundance of mayfly species typical of lentic habitats (Brittain and Saltveit, 1989). Simultaneously, rheophilous species are disadvantaged, and both *Austrophlebioides* species, well represented at Snowy Creek where they exhibited non-overlapping seasonal abundance, were almost absent from the Mitta

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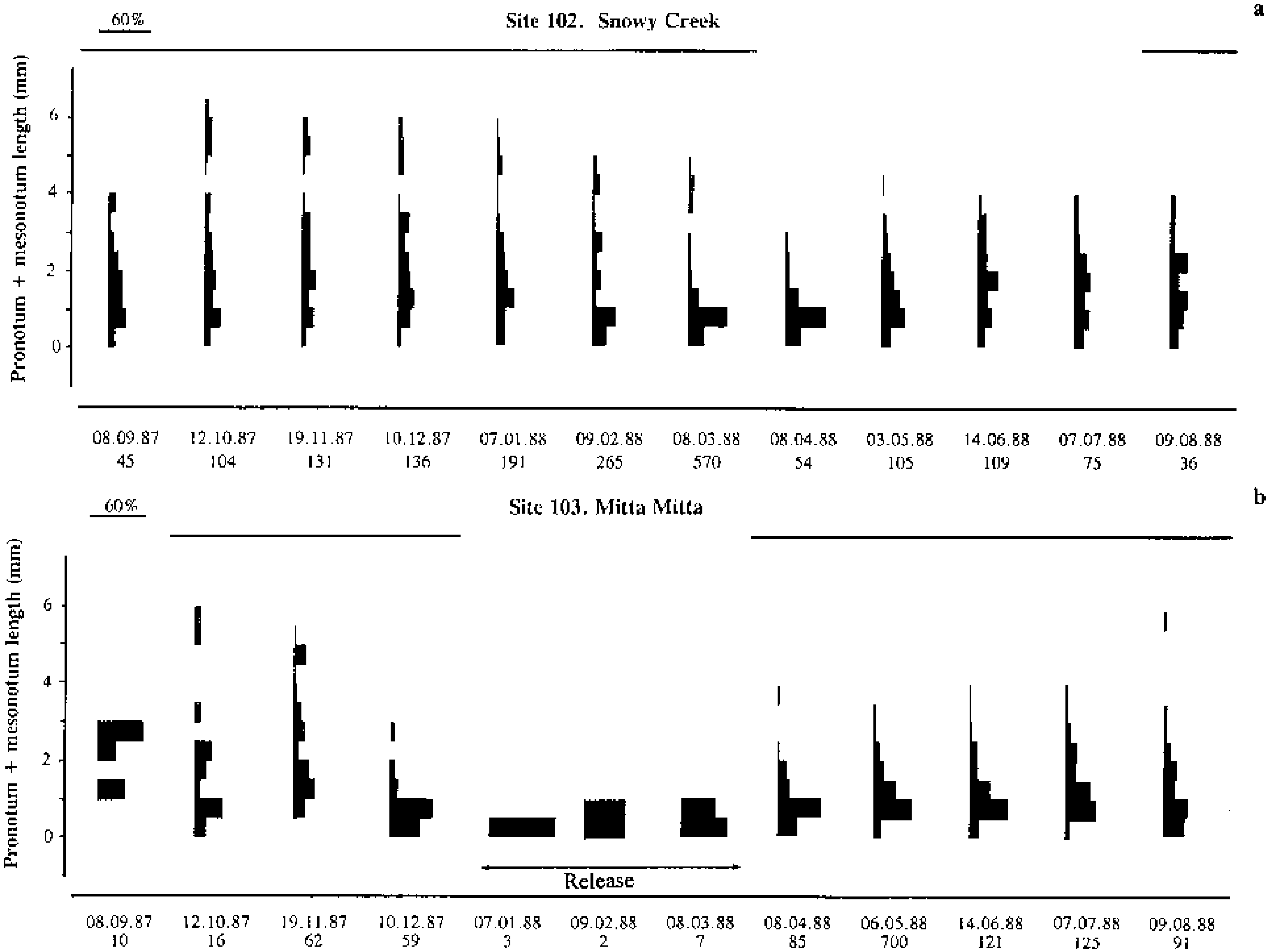

Figure 4. Size-frequency distributions of *Coloburiscoides* sp. at Snowy Creek and Mitta Mitta. Width of each bar represents the relative proportion of total animals found in each size class, the scale mark indicates 60%. Presence of mature nymphs is shown by a horizontal bar at the top of each graph. Collection dates and numbers of individuals used to calculate frequencies are shown below each bar

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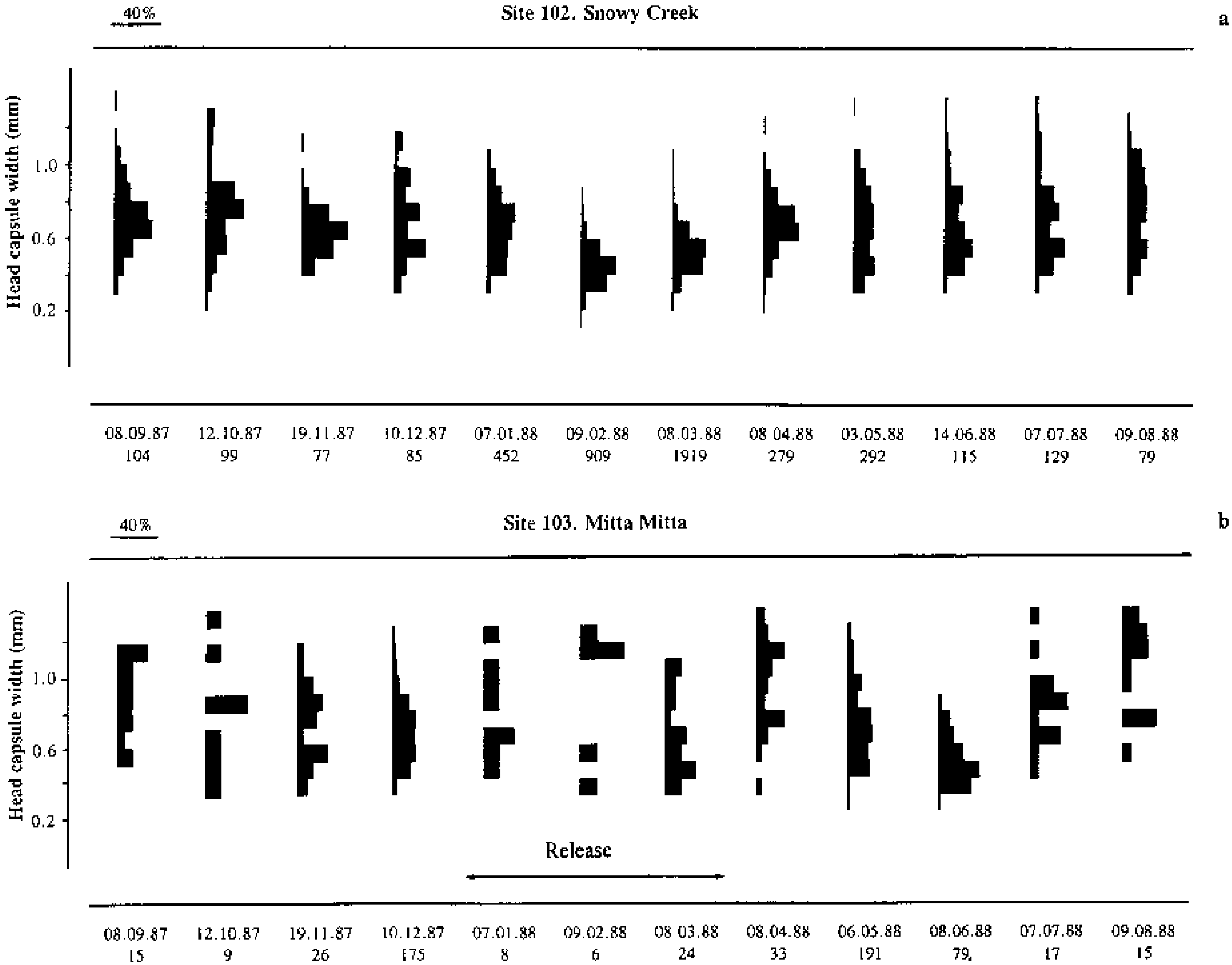

Figure 5. Size-frequency distributions of *Baetis* sp. 3 at Snowy Creek and Mitta Mitta. Width of each bar represents the relative proportion of total animals found in each size class, the scale mark indicates 40%. Presence of mature nymphs is shown by a horizontal bar at the top of each graph. Collection dates and numbers of individuals used to calculate frequencies are shown below each bar

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Mitta. The summer irrigation release can be concurrent with the egg stages of *A. pusillus* (Campbell *et al.*, 1990), and the early nymphal stages of *Austrophlebioides marchanti* (Parnong and Campbell, 1997). *Baetis* sp. 3, seems to find optimal conditions at Snowy Creek, while at the Mitta Mitta potential high summer densities are suppressed by sudden reservoir releases.

Life cycles

Temperature regulates insect life cycles decreasing developmental time and degree of synchrony. Univoltine species with an annual cohort can be more sensitive to water temperature changes than polyvoltine ones (Brittain and Saltveit, 1989). *Coloburiscoides* had a univoltine life cycle with a long emergence period, while *Baetis* sp. 3 a polyvoltine life cycle, with continuous emergence throughout the year. Irrigation releases occurred when recruitment for both species started, reducing the number of individuals and delaying egg hatching by low temperatures (Brittain and Campbell 1991; Brittain, 1995) and high water levels. Following the releases, in April and particularly May 1988, when water temperature rose, peaks in hatching occurred in both species. *Baetis* sp. 3 seemed able to complete a life cycle from May to August 1988, while *Coloburiscoides* sp. had a synchronous start of a new cohort from May 1988, completing the cycle within 8 months by December. *Coloburiscoides* is a warm adapted genus (Brittain and Campbell, 1991) so that hatching would be expected to be more successful at higher temperatures than during release. *Baetis* sp. 3 continued to emerge during release periods, and seems to be better adapted to such conditions than *Coloburiscoides*, even though its abundance was reduced in the Mitta Mitta River compared with Snowy Creek. According to Brittain (1995), *Baetis* sp. 3 is less warm adapted than the South Australian species *B. soror* (Suter and Bishop, 1990).

Baetis sp. 3 has a life cycle plasticity similar to *B. rhodani* and *B. tricaudatus* in the northern hemisphere (Clifford, 1982; Brittain and Saltveit 1989). Small size, short life cycles and continuous emergence appear advantageous under these environmental conditions, although even *Baetis* had reduced abundance. This may be due to changes in habitat or food availability, or by depletion of their usual maximum egg hatching peaks as a result of sudden release of cold water. *Coloburiscoides* sp. is expected to have disadvantageous life history attributes in relation to river regulation (Brittain and Saltveit, 1989) because of its larger size, univoltine life cycle, and warm adapted character. In spite of this its abundance in the Mitta Mitta remained high, and it seems able to adjust through synchronous hatching when temperatures rise after release, and by completing its life cycle in the 8 months until next summer release. However this species may be subject to year-to-year variations. Filter feeders are often favoured downstream of dams due to the increased levels of suspended algae, and this may favour *Coloburiscoides*.

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