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Life history and production of *Deleatidium* (Ephemeroptera: Leptophlebiidae) in an unstable New Zealand river

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Abstract Life history and production of a *Deleatidium* species (*lilli* group) (Ephemeroptera: Leptophlebiidae) was studied for a 12-month period in a flood-prone river in the South Island, New Zealand in 1985–86. Mean larval density was highest (9170–18 580 m^{-2}) following a long period (> 5 months) of low stable flow (< 30 $m^3 s^{-1}$), but typically ranged from 3550 to 4310 m^{-2}. The annual cycle of *Deleatidium* was difficult to interpret but there appeared to be two overlapping, poorly synchronised generations each year. Production of the winter generation calculated using the Size-frequency method (51.40 g DW m^{-2}), was five times higher than that of the summer generation (9.17 g DW m^{-2}) and annual production was 60.57 g DW m^{-2}. Mean biomass of the winter generation (7.59 g DW m^{-2}) was higher than that of the summer generation (0.87 g DW m^{-2}) but the production to biomass ratio (P/B) of the summer generation (10.54) exceeded that of the winter generation (6.77). The ability to feed on low-biomass epilithic layers, behavioural responses that minimise population losses during floods, and flexible life history patterns enable this species to attain high annual production in a physically harsh environment.

Keywords *Deleatidium* spp.; Leptophlebiidae; life history; annual production; spates; disturbance; stream

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INTRODUCTION

Floods can have strong effects on epilithic, macroinvertebrate, and fish communities in streams by reducing invertebrate density, biomass, and species diversity; and affecting production of epilithon, grazers, collector-gatherers, and their predators (Fisher et al. 1982; Molles 1985; Mathews et al. 1988; Scrimgeour et al. 1988; Scrimgeour & Winterbourn 1989). Few studies have calculated secondary production in flood-prone rivers and streams. Secondary production of insect communities in a flood-prone Sonoran desert stream can be high (120.9 g DW m^{-2}) as a result of high water temperature, adequate food supply, and short invertebrate development times (Jackson & Fisher 1986). Indeed, in these systems production by individual mayfly species ranges from 0.6 to 19.5 g DW m^{-2} (Jackson & Fisher 1986).

Braided rivers on the east coast of the South Island of New Zealand are highly unstable, floods occur throughout the year, and frequently exceed 30 $m^3 s^{-1}$ — the threshold above which gravels and cobbles are mobilised (Scrimgeour & Winterbourn 1989). In these rivers, collector-gathering mayfly nymphs of *Deleatidium* species are numerically dominant and can comprise 50–83% of the macroinvertebrate fauna in any one month (Pierce 1986; Sagar 1986; Scrimgeour & Winterbourn 1989). Larvae of *Deleatidium* are an important group in trophic energetics and are preyed upon by aquatic insects (Winterbourn 1974; Devonport & Winterbourn 1976), fishes (Sagar & Eldon 1983; Scrimgeour & Winterbourn 1987), and birds (Pierce 1986).

Production estimates for *Deleatidium* exist for some streams on the West Coast of New Zealand (Collier 1988) and for a relatively stable, foothills-fed stream in Canterbury, South Island (Winterbourn 1974), and in the North Island of New Zealand (Hopkins1976), but no previous study has quantified production of *Deleatidium* in a moderately large, flood-prone, New Zealand river. Estimates of annual production of *Deleatidium* in smaller New Zealand streams range from 2.5 to 19.6 g DW m^{-2} (Hopkins

1976; Collier 1988) and annual production estimated for mayflies elsewhere are typically less than 15 g DW m^{-2} (Waters & Crawford 1973; Welton et al. 1982; Benke 1984).

In the present study, the life history and production were investigated and density, cohort growth, production (P), biomass (B), and turnover rates (P/B) of *Deleatidium* were calculated over 12 months in Ashley River, a flood-prone river in South Island, New Zealand. *Deleatidium* is a highly variable genus and the Ashley River population may consist of one or more species belonging to the informal *lilli* group (Winterbourn & Gregson 1989).

STUDY AREA

Field work was carried out in the Ashley River, an unstable, braided river (catchment area 1340 km^2) located 25 km north of Christchurch, New Zealand. Discharge is highly variable (1.4–462 $m^3 s^{-1}$: 1970–86) and large floods can occur at any time of the year. Mean annual discharge measured at Ashley Gorge (43°14′S, 172°13′E) 35 km up stream of the study area between 1970 and 1980 was 15.3 $m^3 s^{-1}$ (Bowden 1982).

The study site was located 26 km from the sea where the floodplain is 500 m wide, stream bed gradient was less than 5°, and the river comprised up to six braids. Substratum consisted mainly of gravels (maximum widths 8–65 mm), and small and large cobbles (65–90 mm). Water temperatures were measured on the day of mayfly collections (1300–1500 h NZST) with a hand-held thermometer, and ranged from 6.5°C in winter (July) to 21.5°C in summer (February). The riparian vegetation is primarily grasses (*Poa* spp.), and willows (*Salix* spp.), poplars (*Populus* spp.), and broom (*Cytisus scoparius* L.). Rooted macrophytes were absent from the major channels, but a thin film of diatoms (range of mean biomass = 0.03–0.15 mg C cm^{-2}) covered stone surfaces during most months (Scrimgeour & Winterbourn 1989).

METHODS

Sample collection, processing, and estimation of production

Benthic sampling was performed monthly from May 1985 to April 1986. A total of five benthic samples were taken from the entire range of riffle microhabitats (river margin: mean water depth = 4 cm, mean water velocity = 0.09 $m^3 s^{-1}$, centre of riffle: mean water depth = 36 cm, mean water velocity = 0.72 $m^3 s^{-1}$) with a 0.1 m^2 Surber sampler (0.25 mm mesh net). Stream bed materials were agitated to a maximum depth of 10 cm and all invertebrates collected were preserved in 70% ethanol for 1–2 weeks before identification and weighing.

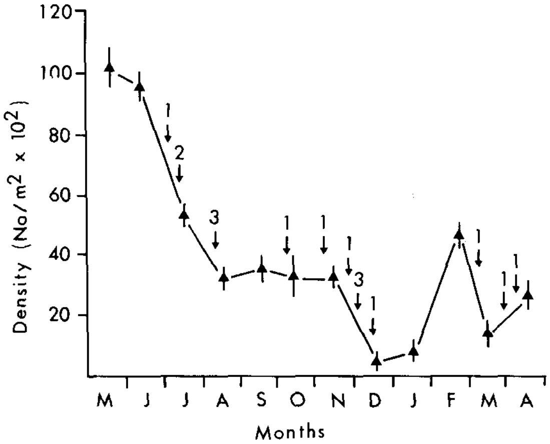

Fig. 1 Density of *Deleatidium* ($\bar{x}$ ± s.e) in benthic samples from the Ashley River, 31 May 1985–13 April 1986. Arrows indicate occurrence and size of floods during the study period: 1, < 50 $m^3 s^{-1}$; 2, 50–90 $m^3 s^{-1}$; 3, > 90 $m^3 s^{-1}$.

Size-frequency distributions of head capsule widths of *Deleatidium* larvae were obtained by measuring a random sub-sample of at least 100 individuals from each collection. Mayflies from monthly samples were pooled, placed into a Petri dish and larvae in at least ten 1 cm^2 fields were selected at random for measurement with a linear eyepiece micrometer at 40 × magnification. Following measurement, individual larvae were weighed so that a head capsule width to dry-weight body regression could be calculated. Individual larvae were dried to constant weight at 60°C and weighed to the nearest 0.1 mg on a Mettler H52 pan balance. Lastly, numbers of final-instar larvae and larvae about to emerge (dark wing pads) were recorded.

Annual production was calculated using the Size-frequency (Hynes) method (Hamilton 1969; Benke 1979). This method assumes that an average size-frequency distribution obtained from samples taken over a year will approximate the mean survivorship of a hypothetical average cohort (Benke 1984). Potentially more accurate methods could not be employed because of difficulties in identifying cohorts accurately and in determining patterns of growth.

The taxonomy of the genus *Deleatidium* is poorly known, and species cannot be identified below the

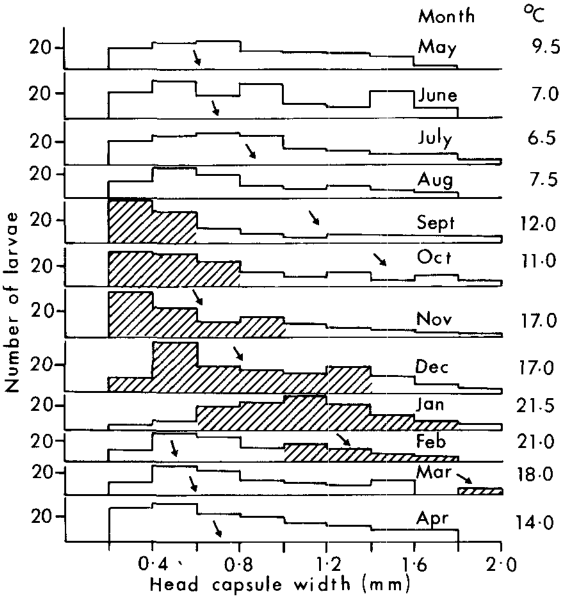

Fig. 2 Size-frequency distributions of *Deleatidium* larvae taken in benthic samples, Ashley River, 31 May 1985–13 April 1986. Arrows indicate probable growth of winter (open areas) and summer generations (hatched area).

informal groups of *lilli* and *myzobranchia* (Winterbourn & Gregson 1989). Thus, the Ashley River assemblage may consist of one or more undescribed species. Colour patterns on the thorax and abdominal terga appeared consistent among individuals of the same size throughout the year, and suggests that collections were composed predominantly of one undescribed species.

Statistical analyses

The hypotheses that: (1) mayfly density, and (2) numbers of final-instar larvae and larvae about to emerge (dark wing pads) showed no significant change throughout the study period were tested with a Model I, single-factor ANOVA. Before these tests, residuals were examined to test for homogeneity of variances. For all analyses alpha < 0.05 was used.

RESULTS

Mayfly density and life history

Density of *Deleatidium* larvae varied significantly ($F = 273, P < 0.001$) during the 12-month study period, was highest in May–July following a particularly long period (> 5 months) of low (< 30 m^3 s^{-1}) stable flow and lowest following several floods that occurred during December (Fig. 1).

Although the annual cycle and pattern of growth of *Deleatidium* were difficult to interpret, the data suggest two overlapping, poorly defined generations per year. The relatively high number of larvae about to emerge in January and February (Fig. 2), combined with the high numbers of small larvae in February, suggest the appearance of a winter generation that developed over autumn and winter with emergence beginning in August. The low numbers of late-instar larvae (> 1.6 mm head width) present in October–December probably belong to this poorly synchronised winter generation. A second, more defined summer generation appeared in September with most individuals emerging from January to March (Fig. 2).

Numbers of final-instar larvae and larvae about out to emerge (black wing pads) varied significantly ($F = 147, P < 0.001$) throughout the year. Although final-instar larvae were present throughout the year, larvae about to emerge were present only in August–March (Fig.3).

Production estimates

Size-frequency data indicate the presence of two overlapping generations each year. Annual production was estimated by summing production of each generation after correcting with a cohort production interval (CPI winter = 1.2, CPI summer = 1.7). Annual production was high (60.57 g DW m^{-2}) because of the high production of the winter generation (Table 1). This high production probably reflected the long period (> 5 months) of stable flow (< 30 m^3 s^{-1}) before July 1985. During this time mortality of mayflies would have been minimal and mayflies may have congregated within the reduced riffle areas. To quantify the effect of including the high mayfly densities of May–July, production was recalculated for the winter generation (Table 2). The recalculated production estimates of the winter generation (19.96 g DW m^{-2}) and annual production (29.13 g DW m^{-2}) were considerably lower. Turnover ratios (P/B) of the summer and winter generations ranged from 6.77 to 10.54; P/B was highest for the summer generation.

DISCUSSION

Errors in calculating production may result from the heterogenous distribution of larvae of different sizes, inadequate sampling of habitat (Winterbourn 1974;

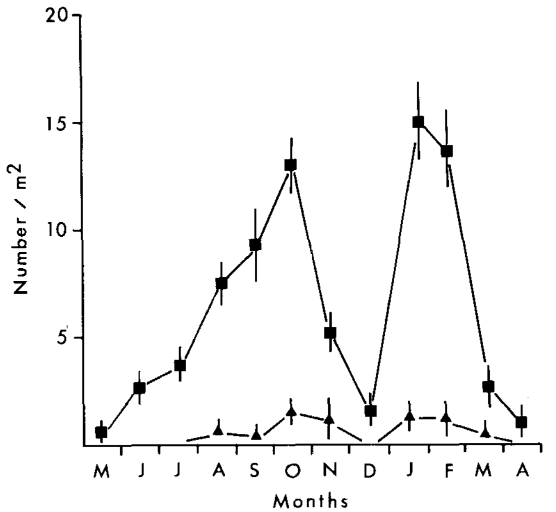

Fig. 3 Density (x̄ s.e.) of final instar *Deleatidium* larvae (■) and larvae about to emerge (▲) from the Ashley River, 31 May 1985–13 April 1986.

Hall et al. 1980), or inadequate sampling of small instars (Zelt & Clifford 1972); these errors may be substantial (Hall et al. 1980). In the present study, these errors were reduced since mayflies were collected with a small-mesh net (0.25 mm), and across a range of riffle microhabitats. This would ensure that any differences in microhabitat of larvae at different times of the year or of different-sized larvae would be incorporated into production estimation. As a result, it is unlikely that high production estimates for *Deleatidium* result from sampling errors. Rather, high annual production of *Deleatidium* may result from several factors including: the ability to feed on very low-biomass epilithic layers; behavioural responses that minimise population losses during floods; flexible life history patterns which maintain growth, production, and high biomasses at all times.

Annual production of *Deleatidium* (60.57 g DW m^{-2}) in the Ashley River is considerably higher than that reported for the genus in other New Zealand streams (2.5–19.6 g DW m^{-2}: Hopkins 1976; Collier 1988; Winterbourn et al. 1988; Collier & Winterbourn 1990) and mayflies elsewhere (Waters & Crawford 1973; Kruger & Martin 1980;Welton et al. 1982; Jackson & Fisher 1986; Rader & Ward 1989). Differences in annual production of *Deleatidium* in the Ashley River and other New Zealand rivers may partly reflect differences in invertebrate density and mean biomass. Densities of *Deleatidium* in the Ashley River are up to four times higher than in a smaller (mean annual discharge = 1 m^3 s^{-1}), more

Table 1 Calculation of production of the winter generation (February–November) of *Deleatidium* in the Ashley River using the size-frequency method (Benke 1979). CPI, cohort production interval.

Size group length (mm)	No. (m^2)	W (mg)	B ($g\ m^{-2}$)	ΔN	Weight at loss $\bar{W}$	Weight loss $\bar{W}\Delta N$	× 9 ($g\ m^{-2}$)
0.2–0.4	5541	0.015	0.083				
				−2249	0.022	0.050	−0.45
0.4–0.6	7790	0.029	0.226				
				975	0.041	0.040	0.36
0.6–0.8	6815	0.053	0.361				
				867	0.077	0.067	0.60
0.8–1.0	5948	0.100	0.601				
				1613	0.147	0.236	2.13
1.0–1.2	4335	0.192	0.832				
				1186	0.253	0.300	2.70
1.2–1.4	3149	0.314	0.989				
				−132	0.493	0.063	−0.59
1.4–1.6	3281	0.672	2.205				
				1768	0.888	1.569	14.12
1.6–1.8	1513	1.103	1.669				
				1211	1.587	1.921	17.29
1.8–2.0	302	2.070	0.625				
				302	2.070	0.625	5.63
			7.59				42.83

Total production = 42.83 × 1.2 (CPI correction) = 51.40 g m^{-2}; P/B = 6.77

stable Canterbury River (Winterbourn1974) where annual production of *Deleatidium* is 19.6 g DW m^{-2} (Collier 1988) and up to 10 times greater than in small west coast, South Island, streams (width = 0.5–5 m) where annual production of *Deleatidium* ranges from 1.2 to 10.4 g DW m^{-2} (Winterbourn & Collier 1987; Winterbourn et al. 1988; Collier & Winterbourn 1990). Production in such streams was highest in Hidden Creek, an alkaline spring-fed stream with a more stable discharge and temperature regime (Collier & Winterbourn 1990). Additionally, mean biomass was 2.5–5 times higher in the Ashley River compared to west coast streams (Collier & Winterbourn 1990).

High annual production of *Deleatidium* probably reflects the long period (> 5 months) of stable flow (< 30 $m^3 s^{-1}$) before July 1985. In fact, the 173-day spate-free period was the longest period of stable flow in 13 years. Mortality of mayfly larvae during low-flow conditions resulting from substrate movement would be minimal and larvae may have congregated within the reduced riffle areas. Nevertheless, the revised annual production estimate excluding the high mayfly densities found in May–July is still high (29.13 g DW m^{-2}) and suggests that environmental conditions in the Ashley River are conducive to high production.

High annual production may partly reflect the ability of larvae to feed on very low-biomass epilithic layers. Mayfly larvae of *Deleatidium* are collector-browsers, feeding on epilithon and associated particulate material. Although epilithic biomass was reduced by the occurrence of floods during the study period, a thin film (0.03–0.15 mg C cm^{-2}) of diatoms (predominantly *Gomphonema*) covered stones during most months (Scrimgeour & Winterbourn 1989). The ability of *Deleatidium* to feed effectively on low-biomass organic layers (5.1 mg Chl. *a* m^{-2}) has been documented (Rounick & Winterbourn 1983) and suggests that epilithic biomass would have to be extremely low or mayfly density high, before food availability would limit production. Similarly, the availability of particulate organic material in the benthos throughout the year suggests that spates may not cause an absolute shortage of food. Indeed, it is likely that spates result in an input of floodplain material which can be utilised by collector-gathering mayflies. Lastly, spates of moderate size and frequency may increase food availability for grazers by producing a low-biomass yet highly productive epilithic layer (Scrimgeour & Winterbourn 1989) such as created by moderate grazing (Lamberti & Resh 1983; Lamberti et al.1989). Thus, floods may ensure the presence of a high-quality epilithic food source by reducing competition of algae for space, light, and nutrients (Gregory 1983; Lamberti & Resh 1983) and is likely important in the Ashley River where nutrient availability is low (Biggs & Close 1989).

Table 2 Annual, winter, and summer production (P), mean biomass (B) and turnover rates (P/B) for larval *Deleatidium* collected from the Ashley River. Revised production estimates are those calculated for the winter generation (February–November) excluding the particularly high mayfly densities in May–July 1985.

Production period	P ($g\ m^{-2} yr^{-1}$)	B ($g\ m^{-2}$)	Turnover ratio (P/B)
Summer generation	9.17	0.87	10.54
Winter generation	51.40	7.59	6.77
Summer + winter generations	60.57	7.25	8.35
Revised winter generation	19.96	3.67	5.44
Revised annual production	29.12	5.34	5.45

The presence of reduced invertebrate densities following spates may not only represent mortality but also displacement of invertebrates. Indeed, invertebrate populations in frequently perturbed rivers may be constantly redistributing themselves via behavioural drift and crawling from refugia occupied during floods (i.e., hyporheos, stream margins, in-stream debris, backwaters) to riffle areas. The recolonisation ability of *Deleatidium* is high and enables them to quickly recolonise previously denuded areas (Sagar1983; Scrimgeour et al. 1988). Thus, rapid movement from refugia to riffle areas after subsidence of spates would reduce the cost (i.e., lost feeding opportunities or increased risk of predation) of occupying refugia.

In addition to feeding habits and behavioural responses, the flexible, poorly synchronised life history patterns contributed to the success of *Deleatidium* in maintaining high densities, biomass, and production in the Ashley River. Input by immigration of aerial adults and subsequent oviposition in addition to recolonisation from spatial refuges may be important mechanisms by which mayfly populations recolonise riffle areas. The predominance of poorly synchronised life cycles, and of cohorts with long flight periods, provides the opportunity for immediate growth and reproduction following spates (Winterbourn et al. 1981; Towns 1983; Bothroyd 1987; Scrimgeour & Winterbourn 1989). The relative importance of life history patterns, feeding habits, recolonisation abilities, and behavioural responses in contributing towards the high annual production is unclear. The relative importance of each of these mechanisms must be known before population dynamics in these physically harsh environments can be understood.

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