

# Temperature-dependent growth and life cycle of *Deleatidium* (Ephemeroptera: Leptophlebiidae) in two high-country streams in New Zealand

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## SUMMARY

1. Measurements of larval growth rates were used to produce an empirical model for examining factors influencing patterns of size structure and emergence period for populations of the leptophlebiid mayfly *Deleatidium* (*lillii* group) in two high-country streams (South Island, New Zealand). Growth rates were measured *in situ* by enclosing groups of larvae and natural stream substrata in growth chambers.
2. Multiple regression analysis showed that temperature explained most variation among growth rates in both streams. Growth rates were also significantly related to larval size, although the effect was minor compared with temperature. A significant relationship between larval biomass per chamber and growth rate was shown at only one site.
3. Growth models based on multiple regression equations ( $R^2 = 0.70\text{--}0.84$ ) simulated the extended emergence period and complex size structure observed for populations of *Deleatidium* in the field. Larvae hatching from eggs deposited before mid-February (austral summer) probably emerge as adults before May (minimum cohort duration  $\approx 3$  months). Larvae hatching after mid-February probably do not emerge as adults until the following summer because of low growth rates during winter (maximum cohort duration  $\approx 11$  months).
4. On average, there are probably two generations of *Deleatidium* per year (bivoltine) at the study sites. The presence of numerous overlapping cohorts throughout summer, however, results in an extended emergence period and complex size structure.

## Introduction

Mayflies of the genus *Deleatidium* (Leptophlebiidae) are widespread and abundant in New Zealand streams (Winterbourn & Gregson, 1989; Scrimgeour 1991). Consequently the ecology of this taxon has received much attention (Winterbourn, 1974; Hopkins, 1976; Collier & Winterbourn, 1990; Scrimgeour, 1991; Marchant & Scrimgeour, 1991). There remain problems in identifying factors that underlie life cycle patterns, however. For example, the cohort and size structure of populations of *Deleatidium* are often complex with little recognizable synchronicity of growth and devel-

opment among individuals (Winterbourn, 1974, 1978; Collier & Winterbourn, 1990; Scrimgeour, 1991; but see Towns, 1983). Specific factors responsible for such complexity are unknown, but may involve the presence of several unresolved species, each with a different and perhaps synchronous life-cycle phenology (Towns, 1983; Collier & Winterbourn, 1990), and long emergence and oviposition periods (Winterbourn, 1974, 1978; Collier & Winterbourn, 1990). Since a range of developmental stages will be present at any given time, factors determining the complex life cycle may

underlie the ability of populations to quickly recover from the effects of flooding (Scrimgeour, Davidson & Davidson, 1988), and contribute to the numerical dominance of *Deleatidium* in many New Zealand streams.

In this paper, *in situ* measurements of larval growth rates are used to produce an empirical model for examining factors underlying the complex size structure and extended emergence period observed in populations of *Deleatidium* (*lillii* group) in two high-country streams of the South Island of New Zealand.

## Materials and methods

### Study sites

Sutton Stream (45°36'S, 169°54'E) and Stony Creek (45°35'S, 169°54'E) are tributaries of the Taieri River. Both streams are within the greater Sutton Stream catchment which lies between the Lammerlaw and Rock and Pillar mountain ranges in the south-eastern part of the South Island. The river valleys are incised and rugged with bedrock composed entirely of schist. Vegetation is largely exotic pasture grasses and native tussock grasses that are extensively grazed by livestock. The 400-m study reaches selected at each site have no canopy, although there are native shrubs along the stream margins; altitude ranges from 600 m a.s.l. at Sutton Stream to 820 m a.s.l. at Stony Creek. During 1991–92 mean discharge was  $175 \pm 62$  and  $306 \pm 89$  l s<sup>-1</sup>, mean concentration of PO<sub>4</sub><sup>-</sup> was  $8 \pm 1$  and  $9 \pm 2$  µg l<sup>-1</sup>, and mean concentration of NO<sub>3</sub><sup>-</sup> was  $30 \pm 21$  and  $13 \pm 4$  µg l<sup>-1</sup> in Sutton Stream and Stony Creek, respectively. Mean daily water temperature in Sutton Stream ranged from 0.0 to 17.4 °C (annual mean 5.6 °C). Mean daily temperature in Stony Creek ranged from 0.0 to 16.4 °C (annual mean 6.0 °C). Diel fluctuations in temperature may be as great as 10 °C during summer. Sutton Stream is inhabited by brown trout (*Salmo trutta* L.). Stony Creek is inhabited by the common river galaxias (*Galaxias* cf. *vulgaris* Stokell).

Collections of adult mayflies at Sutton Stream contained *Deleatidium lillii* Eaton, *D. myzobranchia* Phillips and *D. vernale* Phillips, while collections from Stony Creek yielded *D. lillii* and *D. myzobranchia*. Larvae of the *myzobranchia* group (Winterbourn & Gregson, 1989) are uncommon in Sutton Stream, but abundant in Stony Creek. Larvae of the *lillii* group are abundant in both streams. Hereafter, unless noted otherwise,

*Deleatidium* refers specifically to the *lillii* group (i.e. *D. lillii* and *D. vernale* in Sutton Stream, *D. lillii* in Stony Creek).

### Growth rates

Growth rates were measured *in situ* by enclosing groups of *Deleatidium* larvae in growth chambers. Growth chambers were constructed from 7.5-cm lengths of 10.2-cm (internal diameter) PVC pipe. The ends were capped with 250-µm nylon mesh held in place by PVC rings. Growth chambers were anchored with a stainless steel lead fastened to the chamber with a rivet, and to the stream bed with a metal stake. Chambers were placed in riffles with one of the ends facing up to allow entry of light. Before introducing larvae, five stones (maximum dimension ≤ 7 cm) from the stream bottom were placed in the chamber to provide biofilms for food. The mesh and the walls of the chamber provided additional surface for development of biofilms.

Larvae collected from the stream were measured with an ocular micrometer mounted in a dissecting microscope, and sorted into 1-mm length classes depending upon specimens available on a particular date. Lengths generally ranged from 2 to 9 mm. To account for size- and density-dependent factors, different numbers of individuals from each length class were introduced into different chambers. Food supply (as biofilm) was not manipulated and any food limitation of growth was assumed to be determined by larval density. During December 1992 and January 1993, algal biomass from chamber substrata and from twelve random locations in the streams at large were measured as chlorophyll *a* (Wetzel & Likens, 1979).

Once larvae were introduced to a growth chamber, the mesh was fastened over the top with a PVC ring and the chamber was anchored to the stream bottom for 2–6 weeks, depending on season. Longer incubation periods were selected during cold periods to ensure that measurable growth occurred. On completion of incubation, larvae were removed from the chambers and their lengths measured. Individual size, as ash-free dry mass (mg AFDM), was estimated from the following length–weight regression equation:

$$\text{mg AFDM} = 0.0011L^{3.3757} \quad (n = 57, R^2 = 0.91, P < 0.05)$$

where *L* is length in mm (Lester, 1992). Exponential growth was assumed (Elliott, Humpesch & Macan,

1988) and daily instantaneous growth rates (IGR =  $\text{mg mg}^{-1} \text{ day}^{-1}$ ) were estimated as the natural logarithm of the ratio of the final mean individual AFDM over the initial AFDM divided by the length of the incubation period (days) (Benke, 1984). Mean individual size (mg AFDM) during incubation was estimated as the geometric mean of initial and final mean individual size. Total biomass (mg AFDM per chamber) during incubation was estimated as the geometric mean of initial and final total biomass. Mean daily temperature ( $^{\circ}\text{C}$ ) was estimated as the average of hourly measurements obtained from submersible temperature recorders (Ryan Instruments, Redmund, Washington, DC, USA). Temperature data were not available from 31 October 1991 to 2 December 1991, and data from 31 October 1992 to 2 December 1992 were used for this time interval. Data were analysed by multiple regression with IGR as the dependent variable and temperature, mean individual size and total biomass per chamber as independent variables. Data were transformed ( $\ln(x)$  or  $\ln(x + 1)$ ) before analysis to enhance normality and linearity of relationship among variables.

#### *Size structure, abundance and biomass*

Information about size structure and abundance of *Deleatidium* was obtained from twelve to sixteen benthic samples taken from each study site on eleven dates between December 1991 and December 1992, with a 900-cm<sup>2</sup> Surber sampler fitted with a 230- $\mu\text{m}$  net. On 31 October 1992, however, only three samples were taken from Stony Creek because of weather conditions. Sample locations were randomly assigned within the 400-m study reaches using a grid system. In areas of unconsolidated substrata, the stream bed was sampled to a depth of about 10 cm. Over bedrock a roll of terry cloth was attached to the Surber frame which effectively sealed the sampler against the stream bottom. All samples were preserved in 6–8% formalin and stained with phloxine B. Larvae were removed from the samples by hand under  $\times 15$  magnification and their lengths measured ( $\pm 0.5$  mm). Benthic biomass (mg AFDM m<sup>-2</sup>) was calculated as the product of the estimated AFDM for larvae of a given length class (1 mm increments) and the abundance of individuals within that size class.

#### *Growth and life cycle*

Multiple regression equations allowed daily IGR to be estimated from size of *Deleatidium* larvae, water temperature and/or benthic biomass. Values obtained from these equations were used to construct plots of simulated larval growth trajectories. To construct a plot, growth was initiated at a larval length of 1 mm ( $\approx 0.001$  mg AFDM) on a specified date and allowed to progress iteratively in daily increments until a length of 10 mm ( $\approx 3$  mg AFDM) was achieved. Negative IGRs, which occurred when water temperature was  $\approx 0$   $^{\circ}\text{C}$ , were assumed to be statistical artefacts and were set to zero. A starting size of 1 mm was selected on the basis of the smallest larvae recovered from benthic samples and thus represented in the size–frequency data. Length at hatching was probably about 0.5 mm, however. Starting dates were selected on the basis of size–frequency histograms constructed from benthic samples. Mean daily temperature was obtained from submersible temperature recorders (see ‘Growth rates’ above). Benthic biomass (see ‘Size structure, abundance and biomass’ above) over consecutive sampling intervals was estimated as the mean of the biomass measured at the beginning and the end of the interval. Biomass m<sup>-2</sup> was converted to chamber equivalents on the basis of the planar area of the chambers (82 cm<sup>2</sup>). Plots of growth trajectories were layered upon size–frequency histograms to enhance interpretation of life-cycle patterns and to provide verification of potential cohort structure as indicated by modal peaks in size–frequency distribution.

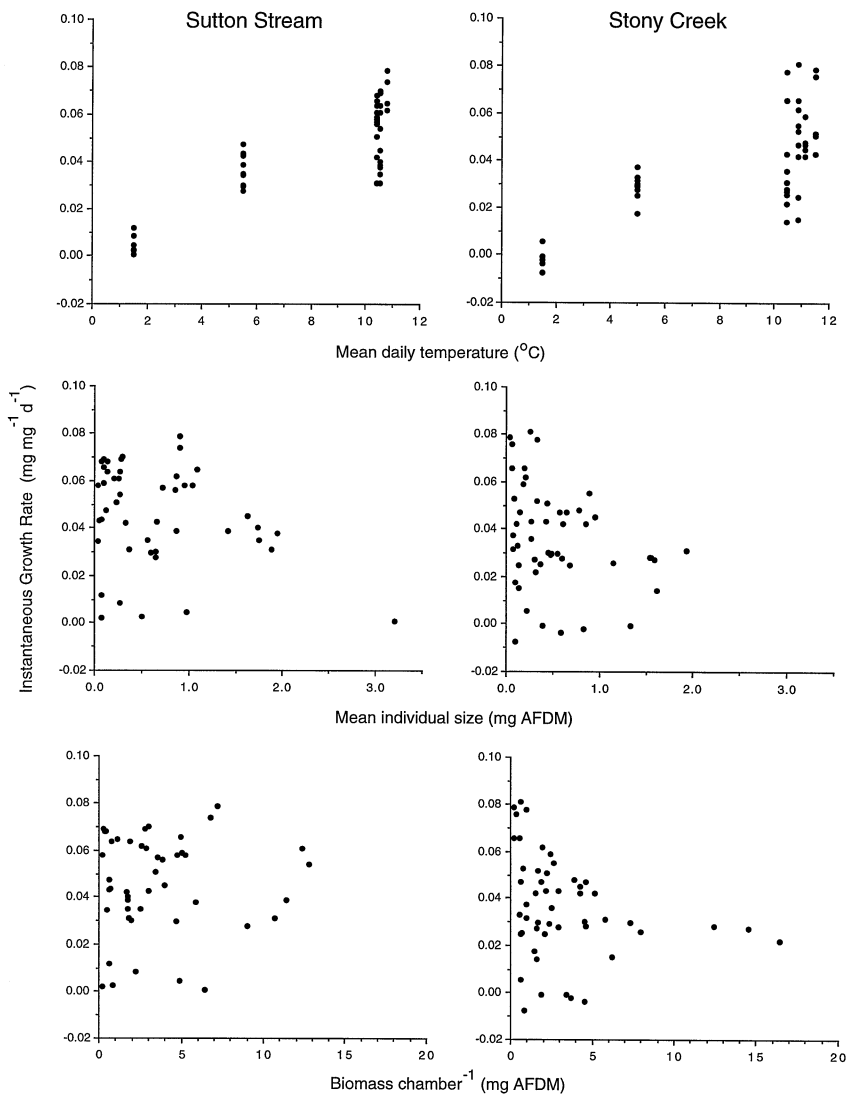
## Results

#### *Growth rates*

Growth rate was measured for forty-six groups of *Deleatidium* larvae over seven incubation intervals in Sutton Stream, and for fifty-two groups of larvae over six incubation intervals in Stony Creek (Appendix 1). A summary of multiple regression statistics is given in Table 1. Of all independent variables, temperature clearly explained the greatest amount of variation among growth rates in both streams (Fig. 1, Table 1). IGR was also significantly and negatively related to individual size (Table 1). In Sutton Stream, stepwise linear regression ( $F$  to remove = 3.99) indicated that total biomass per chamber had no significant effect

**Table 1** Summary of multiple regression statistics from an analysis of growth data for *Deleatidium lillii* group larvae in Sutton Stream and Stony Creek (South Island, New Zealand). Before analysis data from Sutton Stream were transformed by  $\ln(x)$ ; data from Stony Creek were transformed by  $\ln(x + 1)$

Variable	Coefficient	SE	F ratio	P	R <sup>2</sup>
<b>Sutton Stream</b>					
Intercept	-6.221				0.84
Temperature (°C)	1.344	0.093	210.7	0.0001	
Mean size (mg)	-0.212	0.067	10.0	0.0030	
Total biomass (mg)	0.043	0.072	0.4	0.5515	
<b>Stony Creek</b>					
Intercept	0.011				0.70
Temperature (°C)	0.029	0.003	92.1	0.0001	
Mean size (mg)	-0.014	0.007	4.4	0.0418	
Total biomass (mg)	-0.010	0.003	13.4	0.0006	



**Fig. 1** Scatter plots of mean instantaneous growth rate for *Deleatidium lillii* group larvae incubated in Sutton Stream and Stony Creek (South Island, New Zealand) under different conditions of mean daily water temperature, mean individual size and total larval biomass per chamber.

on IGR. In Stony Creek, stepwise linear regression indicated that total biomass had a significant and negative effect on IGR. Daily IGRs for *Deleatidium* in Sutton Stream and Stony Creek were described by the following equations:

$$\text{IGR}_{\text{Sutton}} = 0.002T^{1.356}S^{-0.186} \quad (P < 0.001, R^2 = 0.84)$$

$$\text{IGR}_{\text{Stony}} = (0.989T^{0.030}S^{-0.014}B^{-0.010}) - 1 \quad (P < 0.001, R^2 = 0.70)$$

where  $T$  is mean daily water temperature ( $^{\circ}\text{C}$ ),  $S$  is mean individual size (mg AFDM) and  $B$  is biomass per chamber (mg AFDM). Differences in the form of the equations resulted from different transformations. Data from Stony Creek were transformed to  $\ln(x + 1)$  because of negative IGRs on some dates (Appendix 1), whereas data from Sutton Stream were transformed to  $\ln(x)$ .

Mean ( $\pm$  SE) benthic biomass of *Deleatidium* in Sutton Stream was  $108 \pm 22$  mg AFDM  $\text{m}^{-2}$ ; mean benthic biomass in Stony Creek was  $53 \pm 8$  mg AFDM  $\text{m}^{-2}$ . The highest values of larval biomass in chambers were  $\approx 11$ – $15$  and  $23$ – $36$  times greater than the mean benthic biomass of *Deleatidium* observed in Sutton Stream and Stony Creek, respectively. The range for chambers in Sutton Stream (about  $1.2$ – $1.6$  g AFDM  $\text{m}^{-2}$ ) was similar to the average biomass of all browsing invertebrates in the stream at large (about  $1.4$  g AFDM  $\text{m}^{-2}$ ; Huryn, 1996). Although similar information is not presently available for Stony Creek, total invertebrate biomass is probably lower than that in Sutton Stream (unpublished).

Chlorophyll  $a$  was measured on substrata in chambers on 17 December 1992 and 3 January 1993, a period of maximum larval growth (Appendix 1). Chlorophyll  $a$  on 17 December was  $5.70 \pm 0.71$  mg  $\text{m}^{-2}$  in Sutton Stream (mean  $\pm$  SE,  $n = 4$ ) and  $5.01 \pm 0.93$  mg  $\text{m}^{-2}$  ( $n = 6$ ) in Stony Creek ( $P = 0.60$ , two-tailed  $t$ -test). On 3 January 1993, chlorophyll  $a$  was  $6.66 \pm 0.85$  mg  $\text{m}^{-2}$  ( $n = 4$ ) in Sutton Stream and  $6.58 \pm 0.95$  mg  $\text{m}^{-2}$  ( $n = 6$ ) in Stony Creek ( $P = 0.95$ , two-tailed  $t$ -test). There was no significant relationship between IGR and levels of chlorophyll  $a$  in either Sutton Stream or Stony Creek (simple linear regression,  $P > 0.05$ ).

Chlorophyll  $a$  was also measured on 3 December 1992 and 4 January 1993 from twelve random locations in each stream. On these dates, chlorophyll  $a$  was, respectively,  $19.51 \pm 3.30$  and  $20.13 \pm 3.84$  mg  $\text{m}^{-2}$  in

Sutton Stream, and  $6.01 \pm 1.66$  and  $7.70 \pm 0.79$  in Stony Creek. On both dates, chlorophyll  $a$  was significantly higher at Sutton Stream ( $P < 0.01$ , two-tailed  $t$ -test). On both dates, chlorophyll  $a$  was also significantly higher in random locations in Sutton Stream compared with chamber substrata ( $P < 0.01$ , two-tailed  $t$ -test). In contrast, chlorophyll  $a$  in the stream at large was not significantly different from chlorophyll  $a$  in chambers at Stony Creek ( $P = 0.45$ , two-tailed  $t$ -test). The outer surfaces of chambers were usually overgrown by algal turf in Sutton Stream. Chambers were never overgrown by algae in Stony Creek.

#### Temperature-dependent growth and life cycle of *Deleatidium*

Temporal changes in size structure indicated the presence of at least two cohorts of the *Deleatidium lillii* group in Sutton Stream: a summer cohort that hatched and completed development from October to mid-January, and a winter cohort that hatched in late January and completed growth by October or November (Fig. 2). Changes in size structure for populations in Stony Creek did not indicate synchronous development (Fig. 2).

Larvae with fully developed ('black') wing pads were present in both streams from November until March/April (Fig. 2), a period coinciding with the emergence of adults. Adults of *Deleatidium* collected near the study sites indicated that the minimum period of emergence for *D. lillii* extended from October to May, although adults were most numerous during December–January. Emergence of *D. vernale* from Sutton Stream extended from November until March. Iteration of the IGR equations indicated that a number of overlapping cohorts could simultaneously complete growth in 1 year and cause the complex pattern of size structure (Fig. 2). On average, however, only two complete generations will be produced each year. For example, in Stony Creek hypothetical cohorts initiated on 2 November 1991 show no overlap with the cohort initiated on 1 February 1992. In Sutton Stream a minor overlap is indicated between cohorts initiated on 31 October 1991 and 31 January 1992.

In general, growth predicted for each stream was similar. Larvae beginning growth in early November or December achieved maximum length by early February or March (3 months). Larvae beginning growth in early January achieved maximum length

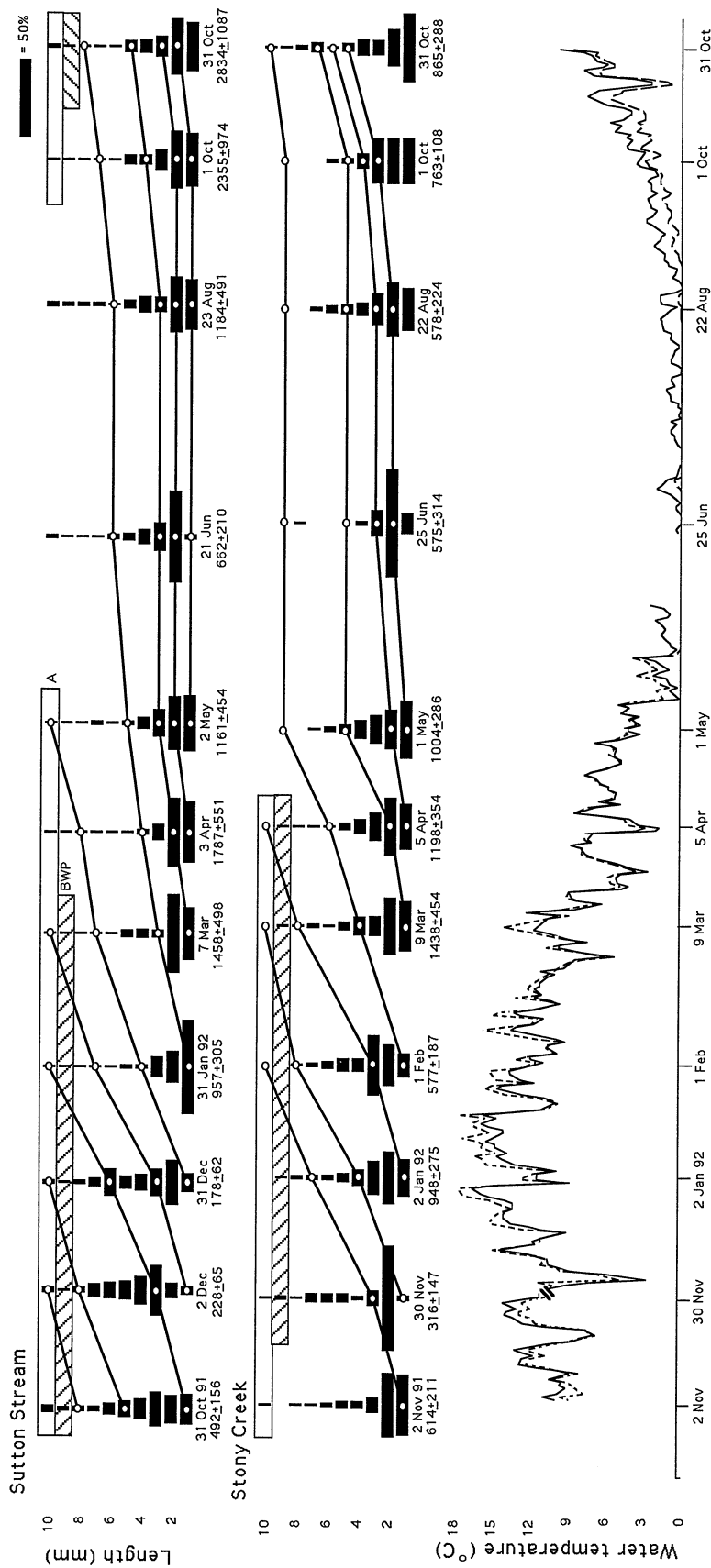


Fig. 2 Upper panels: temporal changes in size structure for populations of *Deletidium lillii* group in Sutton Stream and Stony Creek (South Island, New Zealand). Bar width shows proportional contribution of each length class to the population on a given date. Values below histograms are mean larval abundance (larvae m<sup>-2</sup> ± SE). Open circles and connecting lines are growth trajectories predicted for cohorts initiated on specified dates. Growth was terminated at 10 mm. Dates for cohort initiation were selected on the basis of presence of adults (A; open bar) or mature nymphs as indicated by 'black' wing pads (BWP; filled bar). Lower panel: mean daily temperature measured for Sutton Stream (solid line) and Stony Creek (broken line). Temperature for the 2 November to 2 December interval is from 1992. The remaining data are from 2 December 1991 to 31 October 1992.

by April or May (3–4 months). Larvae recruited after January achieved maximum length by late October or December (9–11 months), which is apparently the longest growth interval predicted by the equations, given conditions within the streams. These growth intervals are based on larvae achieving a length of 10 mm. Mature larvae, with black wing pads, are commonly smaller than 10 mm (e.g. 6–7 mm), and may complete growth earlier. Use of a starting length of 1 mm rather than the probable length at hatching, 0.5 mm, resulted in cohort durations that were about 10 days shorter. Mature larvae were only present when temperatures exceeded 6 °C (Fig. 2).

## Discussion

The IGR model satisfactorily accounted for temporal changes in size structure of *Deleatidium* in Sutton Stream (cf. cohorts initiated on 31 October 1991 and 7 March 1992; Fig. 2). The collective pattern of predicted growth trajectories also closely matched observed periods of larval maturation and adult emergence.

Although predicted differences in patterns of growth and cohort structure between Sutton Stream and Stony Creek were minor, analysis of growth data indicated significant density dependence only at Stony Creek. A comparison of chlorophyll *a* in chambers during December (when highest growth rates were recorded) indicated that conditions were almost identical among streams. However, this comparison is misleading. Measurements of primary production during December 1992 and January 1993 indicated that six to seven times more carbon was fixed per unit area in Sutton Stream compared with Stony Creek (unpublished). This disparity in primary production is reflected in amounts of chlorophyll *a* in the two streams.

Presumably because primary production is higher in Sutton Stream, mesh covering the chambers was quickly overgrown by algae, and may have been an important source of food for the enclosed larvae. In comparison, chambers in Stony Creek were never overgrown by algae, and the amount of chlorophyll *a* in the chambers was similar to that on the benthos. In any case, food available to grazing invertebrates in the stream at large was either similar to (Stony Creek) or much higher than (Sutton Stream) that in the chambers. Based on an ecosystem production budget for 1991–92, Huryn (1996) concluded that 80% of

annual primary production was not used by consumers in Sutton Stream. Therefore, growth of *Deleatidium* was probably not food limited and the IGR equation was a reasonable indicator of growth. Similar data are not available for Stony Creek, however, and the possible effect on larval growth of browser biomass other than *Deleatidium* is not known.

In Sutton Stream and Stony Creek, mayflies of the *Deleatidium lillii* group follow a seasonal, bivoltine, winter–summer cycle (Clifford, 1982) that is similar to life cycles reported for *Deleatidium* elsewhere on the South Island (Winterbourn, 1974; Collier & Winterbourn, 1990; Scrimgeour, 1991). This type of life cycle is characterized by an overwintering larval stage that completes development in the late spring, followed by a rapid summer generation (Clifford, 1982). It is important to distinguish generations and cohorts in this respect, however. For populations at Sutton Stream and Stony Creek, numerous overlapping cohorts are predicted to be present at any time. On average, however, only two complete generations will be produced each year. Such a life cycle could result from the co-occurrence of several species, each with a different life cycle pattern. This was apparently not the case at the study sites where *D. lillii* emerges continuously from October to May and *D. vernale* emerges from November to March. Unresolved species may be present, however. Although probably typical for the *Deleatidium lillii* group on the South Island of New Zealand (Winterbourn, 1974; Collier & Winterbourn, 1990; Scrimgeour, 1991), and for many mayfly species in Australia (Marchant *et al.*, 1984; Campbell, 1986), the complex life cycle observed at Sutton Stream and Stony Creek is unusual for mayflies occurring at similar latitudes (e.g. 45°) in the northern hemisphere (Clifford, 1982; Jacobi & Benke, 1991).

Temperature clearly plays an important role in governing mayfly life histories (Vannote & Sweeney, 1980; Newbold, Sweeney & Vannote, 1994), and it is apparent that temperature directly controls growth, development and emergence schedules of *D. lillii* in Sutton Stream and Stony Creek. Other than a period of cold torpor during winter, growth and development occur continuously. Larvae hatching from eggs deposited during spring and early summer probably emerge as adults during that summer. Larvae recruited during late summer will not emerge as adults until the following summer only because growth is slow during winter. The presence of multiple overlapping cohorts

throughout the summer appears to explain the extended emergence period observed for *D. lillii* and the resulting complex size structure at the study sites. A complex size structure combined with rapid growth and development may underlie the ability of populations of *Deleatidium* to quickly recover from losses due to flooding (Scrimgeour *et al.*, 1988). If temperature-dependent processes are of major importance, however, the rate of recovery should vary with season.

Towns (1983) described a seasonal univoltine winter cycle for a North Island population of *D. lillii* that was very different from the life cycle observed in Sutton Stream and Stony Creek. The life cycle of the North Island population was characterized by synchronous development and the presence of mature larvae from April to September (austral autumn–spring). Also, an apparent 2-month period of egg quiescence during October and November was indicated (see Fig. 4 of Towns (1983)). In contrast, the present study documented the continuous presence of mature larvae of the *D. lillii* group and emergence of *D. lillii* from October to May (austral spring–autumn) with no pause in development. The mean water temperature for a diverse group of streams near Towns' study site exceeds 15 °C from October to April (Mosley, 1982), whereas mean water temperatures in Sutton Stream and Stony Creek rarely reach 15 °C in any season. Perhaps the lower latitude of northern (36°S), compared with southern (45°S), populations resulted in thermal maxima during summer that caused developmental quiescence in the northern populations. Developmental quiescence caused by thermal maxima may lead to synchronized cohort structure of mayflies (as hypothesized by Newbold *et al.* (1994)). The absence of such maxima at higher latitudes may underlie the pattern of continuous and unsynchronized spring–autumn growth, development and emergence observed for southern populations of *D. lillii*.

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**Appendix 1** Summary of growth data for *Deleatidium lillii* group larvae in Sutton Stream and Stony Creek (South Island, New Zealand). *T* is mean daily temperature based on hourly measurements taken during incubation intervals. Incubation began on 'date in' and ended on 'date out.' *S* is the geometric mean of the mean individual biomass (mg AFDM) measured at the beginning and at the end of the incubation interval. *B* is the total larval biomass (mg AFDM per chamber) during the incubation. IGR is the instantaneous growth rate ( $\text{mg mg}^{-1} \text{day}^{-1}$ ) of larvae during the incubation interval. 'No. in' and 'No. out' refers to the number of original larvae and the number remaining at the end of the incubation period. *d* is the length of the incubation period in days

<i>T</i>	<i>S</i>	<i>B</i>	IGR	No. in	No. out	<i>d</i>	Date in	Date out
Sutton Stream								
10.4	0.14	1.87	0.064	15	12	28	6 Feb 92	5 Mar 92
10.4	0.86	3.83	0.056	5	4	28	6 Feb 92	5 Mar 92
10.4	0.95	4.77	0.058	5	5	28	6 Feb 92	5 Mar 92
10.4	0.23	3.43	0.051	15	16	28	6 Feb 92	5 Mar 92
10.4	0.21	2.88	0.061	15	13	28	6 Feb 92	5 Mar 92
10.4	1.04	5.22	0.058	5	5	28	6 Feb 92	5 Mar 92
5.5	0.05	0.64	0.043	15	10	32	31 Mar 92	2 May 92
5.5	0.56	2.52	0.035	5	4	32	31 Mar 92	2 May 92
5.5	0.65	9.02	0.028	15	13	32	31 Mar 92	2 May 92
5.5	0.61	4.69	0.030	10	6	32	31 Mar 92	2 May 92
5.5	0.04	0.46	0.034	15	11	32	31 Mar 92	2 May 92
5.5	0.65	1.95	0.030	3	3	32	31 Mar 92	2 May 92
5.5	0.07	0.69	0.044	14	7	32	31 Mar 92	2 May 92
5.5	0.67	2.97	0.043	5	4	32	31 Mar 92	2 May 92
5.5	0.12	0.61	0.048	5	5	32	31 Mar 92	2 May 92
5.5	0.87	1.74	0.039	2	2	32	31 Mar 92	2 May 92
1.5	0.27	2.27	0.009	10	7	41	20 Jun 92	31 Jul 92
1.5	0.50	0.87	0.003	3	1	41	20 Jun 92	31 Jul 92
1.5	0.08	0.60	0.012	10	6	41	20 Jun 92	31 Jul 92
1.5	0.97	4.87	0.005	5	5	41	20 Jun 92	31 Jul 92
1.5	0.08	0.23	0.002	3	3	41	20 Jun 92	31 Jul 92
1.5	3.21	6.42	0.001	2	2	41	20 Jun 92	31 Jul 92
10.5	0.30	2.98	0.070	10	10	27	3 Nov 92	30 Nov 92
10.5	0.26	12.39	0.061	52	44	27	3 Nov 92	30 Nov 92
10.5	1.75	1.75	0.035	1	1	27	3 Nov 92	30 Nov 92
10.5	1.42	11.36	0.039	8	8	27	3 Nov 92	30 Nov 92
10.5	0.10	0.25	0.069	3	2	27	3 Nov 92	30 Nov 92
10.5	0.27	12.78	0.054	52	42	27	3 Nov 92	30 Nov 92
10.5	1.95	5.85	0.038	3	3	27	3 Nov 92	30 Nov 92
10.5	1.89	10.67	0.031	8	4	27	3 Nov 92	30 Nov 92
10.5	0.28	2.76	0.069	10	10	27	3 Nov 92	30 Nov 92
10.5	0.27	0.80	0.064	3	3	27	3 Nov 92	30 Nov 92
10.5	1.74	1.74	0.040	1	1	27	3 Nov 92	30 Nov 92
10.5	1.63	3.99	0.045	3	2	27	3 Nov 92	30 Nov 92
10.8	1.09	1.09	0.065	1	1	15	2 Dec 92	17 Dec 92
10.8	0.90	7.20	0.079	8	8	15	2 Dec 92	17 Dec 92
10.8	0.86	2.59	0.062	3	3	15	2 Dec 92	17 Dec 92
10.8	0.91	6.78	0.074	8	7	15	2 Dec 92	17 Dec 92
10.4	0.10	5.01	0.059	50	47	28	2 Dec 92	30 Dec 92
10.4	0.13	0.39	0.068	3	3	28	2 Dec 92	30 Dec 92
10.4	0.10	4.96	0.066	50	47	28	2 Dec 92	30 Dec 92
10.4	0.04	0.19	0.058	5	5	17	17 Dec 92	3 Jan 93
10.4	0.07	0.37	0.068	5	5	17	17 Dec 92	3 Jan 93
10.4	0.34	1.68	0.042	5	5	17	17 Dec 92	3 Jan 93
10.4	0.37	1.84	0.031	5	5	17	17 Dec 92	3 Jan 93
10.4	0.72	3.59	0.057	5	5	17	17 Dec 92	3 Jan 93

## Appendix 1 Continued

<i>T</i>	<i>S</i>	<i>B</i>	IGR	No. in	No. out	<i>d</i>	Date in	Date out
Stony Creek								
11.1	0.11	1.55	0.042	15	14	32	6 Feb 92	9 Mar 92
11.1	0.14	1.90	0.047	15	12	32	6 Feb 92	9 Mar 92
11.1	0.18	2.43	0.059	16	12	32	6 Feb 92	9 Mar 92
11.1	0.96	4.28	0.045	5	4	32	6 Feb 92	9 Mar 92
11.1	0.86	4.30	0.042	5	5	32	6 Feb 92	9 Mar 92
11.1	0.79	3.92	0.048	5	5	32	6 Feb 92	9 Mar 92
5.0	0.07	0.98	0.037	15	12	35	1 Apr 92	6 May 92
5.0	0.59	2.97	0.027	5	5	35	1 Apr 92	6 May 92
5.0	0.07	0.99	0.031	15	14	35	1 Apr 92	6 May 92
5.0	0.47	2.36	0.029	5	5	35	1 Apr 92	6 May 92
5.0	0.12	0.55	0.033	5	4	35	1 Apr 92	6 May 92
5.0	0.49	7.36	0.029	15	15	35	1 Apr 92	6 May 92
5.0	0.37	0.73	0.025	2	2	35	1 Apr 92	6 May 92
5.0	0.45	4.52	0.03	10	10	35	1 Apr 92	6 May 92
5.0	0.10	1.46	0.018	15	14	35	1 Apr 92	6 May 92
5.0	0.55	1.65	0.03	3	3	35	1 Apr 92	6 May 92
1.5	0.39	3.46	-0.001	10	8	41	20 Jun 92	31 Jul 92
1.5	0.83	3.72	-0.002	5	4	41	20 Jun 92	31 Jul 92
1.5	0.10	0.81	-0.007	9	8	41	20 Jun 92	31 Jul 92
1.5	1.34	1.89	-0.001	2	1	41	20 Jun 92	31 Jul 92
1.5	0.58	4.52	-0.004	10	6	41	20 Jun 92	31 Jul 92
1.5	0.22	0.66	0.006	3	3	41	20 Jun 92	31 Jul 92
10.5	0.27	2.96	0.043	11	11	28	2 Nov 92	30 Nov 92
10.5	0.32	16.42	0.022	52	52	28	2 Nov 92	30 Nov 92
10.5	1.59	1.59	0.027	1	1	28	2 Nov 92	30 Nov 92
10.5	1.15	7.96	0.026	8	6	28	2 Nov 92	30 Nov 92
10.5	0.33	1.00	0.078	3	3	28	2 Nov 92	30 Nov 92
10.5	0.31	14.55	0.027	52	43	28	2 Nov 92	30 Nov 92
10.5	1.54	4.63	0.028	3	3	28	2 Nov 92	30 Nov 92
10.5	1.55	12.44	0.028	8	8	28	2 Nov 92	30 Nov 92
10.5	0.27	2.54	0.036	10	9	28	2 Nov 92	30 Nov 92
10.5	0.19	0.58	0.066	3	3	28	2 Nov 92	30 Nov 92
10.5	1.61	1.61	0.014	1	1	28	2 Nov 92	30 Nov 92
10.5	1.94	5.81	0.031	3	3	28	2 Nov 92	30 Nov 92
10.8	0.08	0.76	0.053	10	9	16	1 Dec 92	17 Dec 92
10.8	0.13	6.24	0.015	52	44	16	1 Dec 92	17 Dec 92
10.9	0.65	0.65	0.047	1	1	16	1 Dec 92	17 Dec 92
10.9	0.58	4.65	0.047	8	8	16	1 Dec 92	17 Dec 92
10.8	0.26	0.64	0.081	3	2	16	1 Dec 92	17 Dec 92
10.8	0.14	0.63	0.025	52	39	16	1 Dec 92	17 Dec 92
10.9	0.69	2.07	0.025	3	2	16	1 Dec 92	17 Dec 92
10.9	0.61	5.20	0.042	8	9	16	1 Dec 92	17 Dec 92
10.8	0.20	1.93	0.062	10	9	16	1 Dec 92	17 Dec 92
10.8	0.06	0.18	0.066	3	3	16	1 Dec 92	17 Dec 92
10.9	0.65	0.65	0.047	1	1	16	1 Dec 92	17 Dec 92
10.9	0.89	2.68	0.055	3	3	16	1 Dec 92	17 Dec 92
11.5	0.06	0.32	0.076	5	5	17	17 Dec 92	3 Jan 93
11.5	0.44	2.21	0.051	5	4	17	17 Dec 92	3 Jan 93
11.5	0.04	0.19	0.079	5	5	17	17 Dec 92	3 Jan 93
11.5	0.34	1.67	0.052	5	5	17	17 Dec 92	3 Jan 93
11.5	0.07	0.32	0.076	5	4	17	17 Dec 92	3 Jan 93
11.5	0.43	2.17	0.043	5	5	17	17 Dec 92	3 Jan 93