Influence of environmental conditions on nymphal development and abundance of *Deleatidium fumosum* mayflies

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Abstract

We examined the effects of habitat type; (permanently flowing, forested stream sections versus intermittently flowing, stream sections flowing through scrubland) and the approach of winter on the abundance and nympahl development of the common leptophlebid mayfly *Deleatidium fumosum*. Life history traits of *D. fumosum* did not differ between stream habitat types, probably as a result of the close proximity of the habitats (forested sections were upstream of open sections). However, densities were two to four times lower in the warmer downstream intermittent sections, where there was a significant desiccation risk. Seasonal differences occurred in life history traits but not in abundance. Nymphs were significantly larger (up to 14%) in February than later in the growing season (April). These size differences were consistent across all instar categories and, combined with the apparent presence of two cohorts in February, indicate the probable presence of two generations; a fast growing summer one and a slower growing generation that over-wintered. This result was similar to that found for *Deleatidium fumosum,* in a North Island stream.

Keywords: mayfly - life history - time constraints - bivoltine.

Introduction

The physical environment of streams can be unpredictable and variable (Sheldon 1984), influencing the life histories of species that occur there (Robinson *et al.* 1992; Closs 1996; Williams 1996). Physical abiotic factors of many New Zealand streams, especially in the mountains, have been hypothesised as having more important roles in structuring aquatic communities than biotic conditions (Winterbourn 1997). The variability and unpredictability of environmental conditions may have resulted in the predominance of poorly synchronised life histories in New Zealand stream insects (Winterbourn *et al.* 1981; Scarsbrook 2000). Even relatively small changes in flow rate can affect life history traits and distribution of individuals of a single species (Collier 1994; Palmer 1995; Lake 2000).

Temperature and food availability can also influence the life history traits, for example, nymphal growth, adult size and fecundity of mayflies can be affected significantly by temperature (Sweeney 1984; Huryn 1996).

The mayfly genus *Deleatidium* (Leptophlebiidae) is ubiquitous in New Zealand and comprises a complex group of hard to distinguish species with asynchronous and overlapping life histories (Winterbourn 1978; Towns 1983). Despite the expectation that environmental conditions should strongly influence the life history of New Zealand stream insects there have been relatively few investigations of the details of their effects.

In this study we investigated how variations in abiotic factors associated with permanently flowing, forested compared to more open, intermittent stream sections (in scrubland) and the approach of winter influenced the abundances and life history traits of *Deleatidium fumosum* mayflies.

Materials and methods

Study Sites

Four streams close to the University of Canterbury's field station at Cass (43° 02'S, 171° 46'E), near Arthur's Pass, in the South Island, were chosen for study. They were Reservoir Bush Stream, Sugarloaf Stream and two streams that run through the forest patch of Middle Bush, differentiated in this study as Middle Bush Left and Middle Bush Right Streams. They are all first-order, fishless streams (McIntosh 2000) within the same subcatchment (Grasmere Stream) of the Waimakariri River and have similar climatic regimes. Within the Cass basin small fragments (3-4 ha; Rounick & Winterbourn 1982) of mountain beech (*Nothofagus solandri* var. *cliffortioides*) occur in gullies (Winterbourn & Davis 1976), whereas unforested areas are composed of tussock grassland and scrub, mainly matagouri (*Discaria toumatou)* and *Coprosma* species. All four study streams run through forest patches where flow is continuous year round, while the downstream, non-forested reaches often dry up (Molloy 1977; McLeod 1998).

Rainfall patterns are likely to affect the distance the streams flow before disappearing underground. Cass is located in a region where annual rainfall is high to the west and declines steeply in the east (Greenland 1977). Temporal variability in rainfall in the Waimakariri River catchment is high (Cowie *et al.* 1986) and records taken from 1917 to 1976 at the Cass field station show that rainfall varies considerably between years (Winterbourn & Davis 1976) with consequent variability in the extent of stream drying. Middle Bush Stream has been described as having a steep unstable streambed and unpredictable, sometimes torrential, flow (Winterbourn 1976; Ledger *et al.* 2002).

Sampling design

Physical stream characteristics were measured and invertebrates sampled at four sites in both the forested and lower non-forested (open) sections of each stream (i.e., 8 sites in 4 replicate streams, 32 sites in total). Benthic samples were taken between 23-24 February and between 3-4 April 2002 and the extent of stream drying was recorded approximately every three weeks from early February until the end of May.

Physical stream characteristics

To quantify differences in physical conditions between open and forested stream sections over time, stream discharge and spot measurements of water temperature and dissolved oxygen were made at all 32 sampling sites during February and April, whereas light levels and substrate size were measured once. Substrate composition was estimated by randomly selecting ten particles at each site and measuring their longest axis. This was converted to a substrate index comprising three size classes: cobble or larger (> 6.1 cm), coarse gravel (3.1 -6 cm) and fine gravel or smaller (<3 cm). Photosynthetically active radiation readings were recorded at each site, between 1100 and 1300 h on a clear and sunny day using a Licor LI250 meter. Readings were made close to the stream surface and in open areas near the stream to allow the proportion of ambient light reaching the streambed to be calculated.

Invertebrate sampling

Two Surber samples (0.023 m^2, 250 µm mesh) were collected from riffles at each site and preserved in ethanol in the field. A Malaise trap was placed in the open section of the right branch of Middle Bush Stream from 25 March to 5 May 2002 to catch emerging adults to aid identification of *Deleatidium* species. Adults and nymphs from open and forest sections of each stream were identified according to Towns & Peters (1996).

Deleatidium nymphs were sorted from samples in the laboratory and the presence of individuals with black wingpads (indicating imminent emergence to the adult) was recorded. Total body length (anterior end of head capsule to posterior end of the abdomen, excluding caudal filaments), headcapsule width and wingpad length were measured with a linear eyepiece micrometer at 20x magnification. Wingpad length was used to indicate development stage (Delucchi & Peckarsky 1989) and was measured from the anterior end of the mesonotum to the tip of the wingpad.

Statistical analysis

To evaluate differences in physical environmental factors between streams and between forested compared to scrub-covered stream sections, a multivariate comparison of the mean physical factors measured in these sections of the four streams, on both sampling dates, was conducted. Principal Component Analysis (PCA) (PCORD version 4.01) was performed on the normalised data using the correlation matrix to extract components that described the habitat in terms of a limited number of easily comparable independent variables.

The scores of the first three components, with eigenvalues greater than one, were then used as dependent variables in repeated measures ANOVAs to test for significant differences between sampling dates and sections within sampling dates. In interpreting the PCA, physical variables with an absolute loading >0.5 to a component were assumed to be important.

To test whether densities of *Deleatidium* varied between intermittently and permanently flowing stream sections, or between months, a repeated measures ANOVA was performed. Sizes of three instar categories (final instar, final -1, < final-1) were also tested with a repeated measures analysis. The size of black wingpad individuals, indicating imminent emergence, were tested between months. Generally, streams were used as replicates and average values were calculated for each stream section. However, few nymphs had black wingpads (BWPs), so individuals were used as replicates in this analysis. Residual plots were used to test for normality and variables were Log_e transformed where necessary to satisfy assumptions of normality and homoscedasity. All statistical tests, other than PCA, were performed in Systat version 10; statistical significance was judged at alpha = 0.05.

Results

Physical stream conditions

Current velocity was higher in the forested sections than the downstream open stream sections and did not change from February to April (Table 1). However, the permanently flowing forested stream sections were, on average, wider and shallower in April than in February (Table 1). Even though differences in physical conditions between open and forest stream sections were consistent across all four streams they were generally small compared to differences between months. For example, the mean temperature in open stream sections was only 0.8 °C warmer than in forest sections in April, and 1.3 °C warmer in February. However, mean stream temperatures were 4.1 °C and 6.6 °C warmer in February than in April for forest and open sites, respectively.

The first three components identified by PCA accounted for 86.8% of the total variation in physical variables measured. Scores for the first component identified by PCA differed significantly between permanently flowing, forested stream sections (forest) and scrub-covered, intermittently flowing stream sections (open); forest sections had higher scores for component I (Table 2; Figure 1). Environmental variables that were positively correlated with component I included stream discharge, current velocity, substrate size and dissolved oxygen concentration. Water temperature and stream depth were negatively correlated with component I. Thus, substrate was larger, temperature lower and dissolved oxygen levels were higher in the forest sections than the intermittently

Table 1. Mean (± SE) value for environmental variables measured at open and forested sites in four streams at Cass, during February and April 2002.

Variable	February		April	
	Open sites	Forest sites	Open sites	Forest sites
Temperature (°C)	10.7±0.4	9.4±0.2	6.6±0.4	5.8±0.5
Dissolved oxygen (mg l^{-1})	13.0±0.2	13.6±0.2	14.7±0.3	15.2±0.2
Current velocity (m s^{-1})	0.06±0.02	0.14±0.05	0.05±0.01	0.14±0.03
Discharge (cm^3 s^{-1})	0.20±0.01	0.41±0.01	0.12±0.04	0.40±0.08
Width (cm)	48±5	48±6	47±4	58±6
Depth (cm)	5.6±0.9	6.2±0.4	6.4±1.1	5.6±0.2
Substrate size (cm)	5.3±0.3	7.8±0.7		
Incident light at stream bed (%)	0.23±0.13	0.14±0.05		

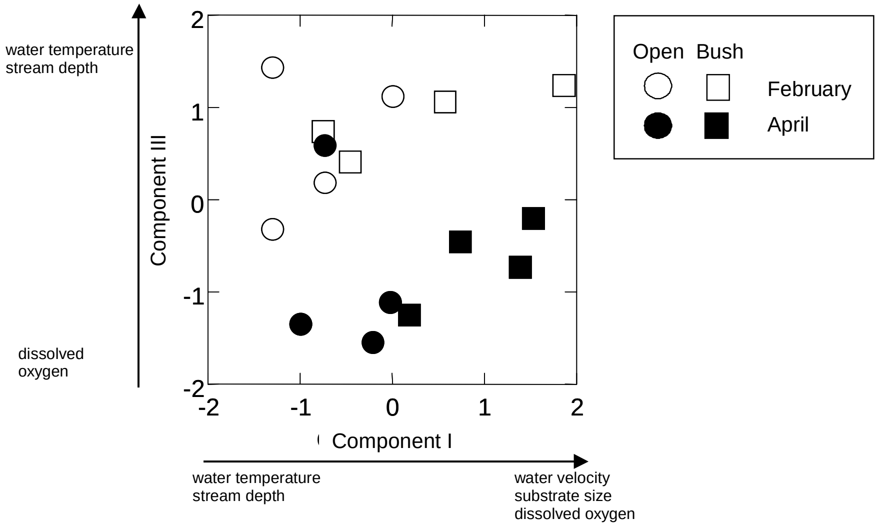

Figure 1. Principal Components Analysis of physical variables measured in open and forested sections of four streams at Cass on two sampling dates (February and April 2002). Physical variables shown on the axes were correlated with the respective component by absolute values of >0.5.

Table 2. Results of repeated measures ANOVA on factor scores of a) component I, b) component II, and c) component III identified by principal components analysis on physical stream characteristics. See Figure 1 for PCA details.

	Source of variation	df	MS	*F* ratio	*P* value
a) Component I					
Within subjects	Section	1	6.71	6.80	0.04
	Error	6	0.99		
Between subjects	Time	1	1.02	4.86	0.07
	Time x Section	1	0.10	0.46	0.52
	Error	6	0.21		
b) Component II					
Within subjects	Section	1	0.11	0.07	0.80
	Error	6	1.62		
Between subjects	Time	1	3.51	16.53	0.007
	Time x Section	1	0.38	1.80	0.23
	Error	6	0.21		
c) Component III					
Within subjects	Section	1	0.21	0.26	0.63
	Error	6	0.83		
Between subjects	Time	1	8.92	61.06	<0.001
	Time x Section	1	0.004	0.02	0.88
	Error	6	0.15		

flowing, scrub-covered stream sections (Table 1).

Factor scores of the second and third components identified by PCA differed significantly with respect to sampling date (Figure 1; Table 2). Temporal changes were most obvious for Component III, which was positively correlated with water temperature and negatively correlated with dissolved oxygen concentration (Figure 1).

Development of Deleatidium *nymphs*

Species identity

Nymphs in the forested and open sections of the four streams looked identical morphologically and were identified as *D. fumosum*. Adults and subimagos taken in the Malaise trap on Middle Bush Stream also belonged to this species. *D. fumosum* is very widely distributed and often the dominant *Deleatidium* species present in South Island streams (Hitchings 2001).

Abundance

Mean *Deleatidium* densities in open stream sections were 1055 m^2 and 1871 m^2 in February and in April, respectively. Densities in the forested sections were much higher, 4633 m^2 in February and 4676 m^2 in April. The difference in densities was significant between forested and open stream sections (ANOVA section effect: $F_{1,3} = 23.52$, $P = 0.02$) but not between months (ANOVA month effect: $F_{1,3} = 0.70$, $P = 0.46$; Table 3). All four streams had similar *Deleatidium* densities (ANOVA stream effect: $F_{3,3} = 3.375$, $P = 0.17$).

Cohorts

In February, size frequency histograms for nymphs in all four streams sampled in permanently flowing forest sections were bimodal, with a high frequency of small individuals (<4 mm body length) and a slightly lower peak in frequency of large (>5 mm) nymphs (Figures 2a, b, c and d). Few nymphs were of intermediate size. This pattern was consistent across all four streams and indicates there were two overlapping cohorts of nymphs in each stream. Few small mayflies were present in the downstream intermittently flowing, open sections where large nymphs were more common. In April, small *Deleatidium* nymphs (<4 mm body length) were most abundant in both open and forest sections and very few

Table 3. Results of repeated measures ANOVA on the density of *Deleatidium* nymphs in open and forested stream sections of four streams during February and April 2002.

Source of variation	df	MS	*F* ratio	*P* value
Between subjects				
Stream	3	1.03	3.38	0.17
Section	1	7.14	23.52	0.02
Error	3	0.30		
Within subjects				
Month	1	0.22	0.70	0.46
Month x Stream	3	0.80	2.50	0.24
Month x Section	1	0.34	1.06	0.38
Error	3	0.32		

nymphs > 4 mm body length were found at any site (Figure 2e). This indicates the probable presence of only one cohort in April and implies that the second cohort present in February had emerged as adults. Overall, the proportion of individuals with wingpads (> ~4 mm body length) decreased from 0.30 in February to 0.08 in April.

Instar categories

Instars can be very difficult to determine in mayfly species as they exhibit indeterminate growth and many techniques for defining mayfly instar categories can produce flawed results, especially those using size frequency data (Fink 1984). We distinguished three instar categories by plotting wingpad length against body length of nymphs (n = 1281; Figure 3). Individuals with wingpads formed two non-overlapping groups and were classified as the final two instar categories. The final instar category (F) had wingpads longer than 1.4 mm and the penultimate instar category (F-1) had wingpads 0.1 to 1.3 mm long and may have included individuals in more than one actual instar. Individuals with no wingpads were designated <F-1.

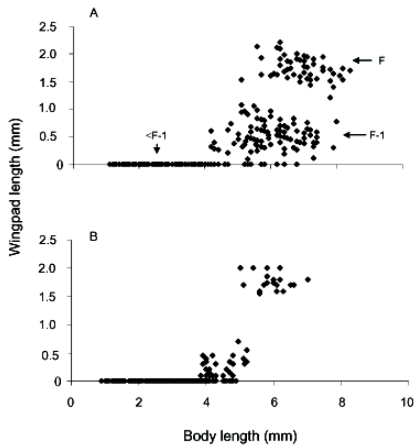

Figure 3. Wingpad length plotted against total body length for *Deleatidium* nymphs from four streams at Cass in a) February and b) April. F, F-1 and <F-1 labels indicate nymphs classified as final instar, penultimate instar group and younger nymphs, respectively.

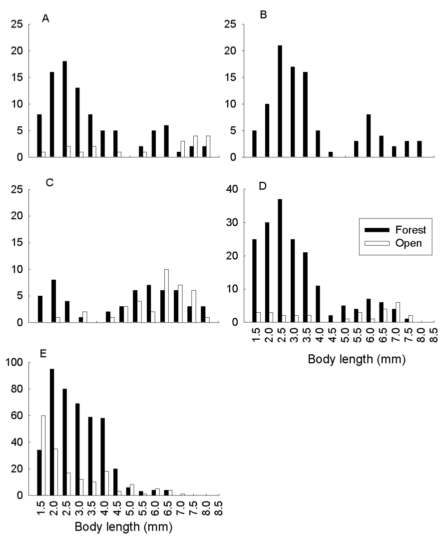

Figure 2. Body lengths of *Deleatidium* nymphs from four streams, a) Middle Bush Left, b) Reservoir Bush, c) Middle Bush Right, and d) Sugarloaf, at Cass during February (a, b, c, and d) and April (e) in forested and open stream sections. Reservoir Bush Stream flowed underground in the open sites during February. All four streams are combined for April (e).

No differences in body lengths of instar categories were found between the intermittently and permanently flowing stream sections (indicated by no section effects in the ANOVA; Table 4). However, the body lengths of instar categories did differ significantly between months (Table 4). Body lengths of nymphs in all three instar categories were significantly smaller (up to 2 mm) in April than in February (Figure 4) and the ANOVA indicated a significant instar by sampling month interaction (Table 4). Body lengths of

Table 4. Results of repeated measures ANOVA on body length of instar categories of *Deleatidium* nymphs in open and forested stream sections of four streams in February and April 2002.

Source of variation	df	MS	*F* ratio	*P* value
Between subjects				
Stream	3	0.69	1.14	0.39
Section	1	0.31	0.52	0.49
Instar	2	47.42	78.05	<0.001
Section x Instar	2	0.07	0.11	0.89
Error	9	0.61		
Within subjects				
Month	1	6.99	45.28	<0.001
Month x Stream	3	0.38	2.47	0.13
Month x Section	1	0.002	0.01	0.92
Month x Instar	2	1.22	7.92	0.01
Month x Section x Instar	2	0.16	1.04	0.39
Error	9	0.15		

black wingpad *Deleatidium* (all sites combined) varied significantly between months ($F_{1, 21}$ = 12.7, P = 0.002). These individuals close to emergence had body lengths nearly 1 mm shorter in April than in February (Figure 4).

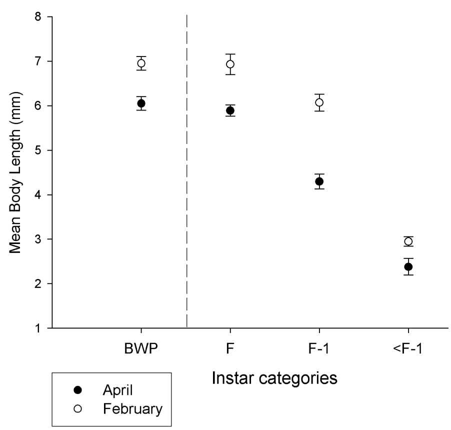

Figure 4. Mean (±1 SE) body length of *Deleatidium* nymphs within three instar categories on two sampling dates, February and April. Black wingpad (BWP) data points are also included in the final (F) instar category. F, F-1 and <F-1 means were calculated using streams as replicates, whereas BWP means were calculated using individuals as replicates (N = 14 and 11 for February and April, respectively).

Discussion

We found consistent differences in water temperature, water velocity and dissolved oxygen concentration between the two types of stream sections considered in our study. *Deleatidium* densities also varied consistently between the upstream, permanently flowing, forested sites and the downstream, intermittently flowing, scrubland sites. Densities were two to four times lower in the warmer downstream sites of all four streams where, during summer, the mayflies are exposed to the risk of desiccation. Increased levels of algal food resources in the forested sections are unlikely to explain this pattern. Winterbourn (1990) found higher levels of epilithic algae in the intermittent, open section of Middle Bush Stream compared to the upstream forested reach (mean algal chlorophyll *a* (and phaeophytin) 0.87 g cm^{-2} and 0.27 g cm^{-2}, respectively). Although there was a greater difference in abiotic factors between February and April, than occurred between the intermittent and permanently flowing sites, there was no seasonal effect on mayfly densities. In addition, as would be expected if individuals from the upstream sites were drifting down, there was no difference in life history traits of *Deleatidium* mayflies between section types.

Differences in temperature and dissolved oxygen concentration were larger between February and April than they were between the open and forest stream sections in either month. Instar category size differed between months with all three instar classes of *Deleatidium* being larger (up to 2 mm on average) in summer (February) than in autumn (April). In addition, individuals about to emerge were nearly 1 mm shorter in April. Fecundity is related to adult body size at emergence because adult mayflies do not feed (Peckarsky *et al.* 1993), so a 14 % decrease in body length is likely to affect female adult fecundity significantly. There is also some evidence that larger male mayfly body size is associated with increased mating success (Flecker *et al.* 1988; Harker 1992; but see Peckarsky *et al.* 2002). Thus, seasonal effects are likely to have affected the fecundity and probable reproductive success of individual *Deleatidium* in the streams studied at Cass.

The smaller body size of mayflies in April was found across all instar categories, even the smallest (<F-1). Thus, the difference seen was not caused solely by individuals close to emergence detecting unfavourable conditions, the approach of winter acting as time constraint on growth, and increasing development to emerge sooner at smaller body size. Furthermore, two overlapping cohorts were present in February, whereas by April only the smaller cohort was left. Together these differences imply the presence of a slow growing, over-wintering population hatching in late summer and emerging the following summer, and a fast growing summer generation that emerged at a smaller body size than the over-wintering generation.

In ectotherms, reduced growth rates at low temperatures often result in delayed maturity at a larger size (Atkinson 1994; Berrigan & Charnov 1994). Consistent with this pattern, *Deleatidium* hatching from eggs in summer may have remained in the stream over winter and emerged in early summer at a larger body size than summer-growing individuals. Because it is likely that a critical body size needs to be reached before emergence can occur (Forrest 1987) a limit is placed on which individuals can emerge before winter and which must remain in the stream. *Deleatidium* species generally have long emergence and oviposition periods resulting in individuals of many sizes being in a stream at any one time (Towns 1983). The occurrence of two generations in some *Deleatidium* species was also indicated by the life history studies of Towns (1983), Scrimgeour (1991) and Huryn (1996) in various parts of the country. Similarly, Winterbourn & Harding (1993) found that the stream-dwelling caddisfly *Aoteapsyche colonica* could have a fast-growing summer generation in addition to a longer winter generation in some Canterbury streams. Towns (1983) found that *Deleatidium* sp. C, later identified as *Deleatidium fumosum* (Towns & Peters 1996), had a life cycle in the Waitakere Ranges near Auckland that he interpreted as being basically bivoltine, with overlapping summer and winter generations. From the seasonal size distribution graph in Towns (1983) the winter generation of *D. fumosum* appear to mature at larger sizes than the summer generation, as was found in this study. Thus, the life history pattern of *D. fumosum* appears generally similar between a North Island catchment and the South Island one studied here.

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