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PRIMARY RESEARCH PAPER

Mayfly production in a New Zealand glacial stream and the potential effect of climate change

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Abstract In contrast to the northern hemisphere where species of Chironomidae are usually the dominant benthic invertebrates in the coldest upper reaches of glacial streams, mayflies (*Deleatidium* spp.: Leptophlebiidae) predominate in equivalent conditions in New Zealand. We examined the life histories and annual production of *Deleatidium* spp. at two sites on the Matukituki River (South Island, New Zealand) and at three sites in its glacier-fed tributary, Rob Roy Stream. Mean annual water temperature at the five sites ranged from 2.1 to 7.0°C. Monthly sampling showed that mayfly populations were poorly synchronised at all sites but were probably univoltine. The large *Deleatidium cornutum* was the dominant mayfly species found at the upper sites (Sites 1 and 2) on Rob Roy Stream, whereas above the confluence with Matukituki River (Site 3) it co-existed with a complex of smaller species we refer to as *D.* "*angustum*". *Deleatidium* "*angustum*" also dominated at the Matukituki sites. *Deleatidium* production calculated for the five sites, assuming an 11-month nymphal life, ranged from 0.48 g dry weight/m^2/year (Site 1) to 3.07 g dry weight/m^2/year (Site 3). The values for *D. cornutum* at Sites 2 and 3 are high for a species of *Deleatidium* and reflect its large size. This species appears to be strongly adapted for growth at low temperatures. Climate change scenarios for New Zealand predict the gradual and ultimate loss of small South Island glaciers and a consequent warming of streams as runoff from rainfall and snow melt becomes more dominant in spring. As a result, suitable habitats will be lost for cold-water specialists such as *D. cornutum*, and they are likely to suffer reductions in their distributional range and local extinction. In contrast, species such as those in the *D.* "*angustum*" complex may extend their ranges into streams formerly dominated by glacial meltwater.

Keywords Ephemeroptera · *Deleatidium* · Secondary production · Global warming · Streams · New Zealand

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Introduction

Alpine streams provide physically harsh environments for aquatic invertebrates because of high shear stress, high sediment load and often unstable channels (McGregor et al., 1995). Their severe physical conditions are believed to limit the importance of biological interactions such as competition and predation in structuring benthic communities (Steffan, 1971; Brittain & Milner, 2001b), although interference competition among midge larvae was implicated by Flory & Milner (1999) as causing changes in the species composition of chironomids in a recently formed Alaskan glacial stream. Ward (1994) identified water temperature as the primary environmental variable influencing between stream ecological differences and longitudinal patterns of community structure in mountain streams and rivers. However, the hydrological regime and geomorphological processes such as channel migration and bed sediment movement are also important, especially downstream changes in physical habitat and disturbance (Milner & Petts, 1994).

Interest in glacial stream communities has increased in the last decade. A recent compilation of 18 papers (Brittain & Milner, 2001a) considers various aspects of invertebrate communities and their physico-chemical and hydrological relationships, and intensive ecological studies on the Tagliamento River, north–east Italy, are summarised by Ward & Uehlinger (2003). Most invertebrate studies in glacial streams have been undertaken in Europe and North America and show that where water temperature is typically <2°C in summer below the glacier terminus (the kryal zone), the fauna is typically limited to Chironomidae (Diamesinae and sometimes Orthocladiinae) (Stephan, 1971; Ward, 1994). However, Ward (1994) also noted that nymphal mayflies (*Iron montanus* Brodsky) and larval blephariceids (*Philorus nivia* Brodskij) were relatively abundant in glacier-fed headwaters of the Akbura River, central Asia (Kyrgystan), where water temperature was <1.5°C. Further downstream where the addition of groundwater results in an increase in flow and water temperature, faunal diversity typically increases and other insect groups such as Ephemeroptera (Baetidae, Heptageniidae) and Plecoptera (Chloroperlidae) are found (Milner & Petts, 1994). Temporal succession of macroinvertebrates in a stream newly formed by glacial recession in Alaska was found to be very similar to the longitudinal pattern described above and predictable at the generic or family level (Milner, 1997).

The South Island of New Zealand is a mountainous landmass with over 3,000 glaciers (Chinn, 2001). They range in area from about 1 to 10,000 ha, and those in the Southern Alps had a volume of 59.25 km^3 in 2001 (Chinn, 2004). Although these glaciers are the sources of numerous streams, most are difficult to reach and little ecological research has been carried out on them. Exceptions are longitudinal studies of the turbid Waiho and Fox Rivers that have their origins in the iconic Franz Josef and Fox glaciers near sea level on the western side of the Southern Alps (Milner et al., 2001; Taylor, 2001). In contrast with most glacial streams of the northern hemisphere, mayflies (Leptophlebiidae: *Deleatidium*) were found in the coldest water close to the glacier face along with Orthocladiinae and the endemic *Maoridiamesa* (Diamesinae). However, invertebrate densities in the turbid, flood-prone Waiho and Fox rivers were low (typically <500/m^2) (Milner et al., 2001).

Rob Roy Stream, the site of the present study, is fed by the small Rob Roy glacier (4.8 km^2) and supports a moderately rich invertebrate fauna dominated numerically by Ephemeroptera, Plecoptera and Chironomidae (Cadbury, 2007). Especially notable is the presence of *Deleatidium cornutum* Towns & Peters, which is the largest and most abundant benthic species throughout the stream. Our aim was to estimate production of *Deleatidium* in Rob Roy Stream and in the larger Matukituki River near its confluence with the Rob Roy. Production measurements integrate data on density, growth and survivorship and therefore are ideal indicators of population success (Benke, 1993; Oswood, 1997). We also consider our results in the context of projected climate change since the extinction of some endemic alpine invertebrates is predicted as glaciers recede and meltwater inputs to currently glacier-fed streams are reduced or lost (Brown et al., 2007).

Materials and Methods

Study area

Rob Roy Stream (44°26′ S, 168°43′ E) is a south-facing tributary of the Matukituki River in the southwest of the South Island, New Zealand (Fig. 1). Rob Roy Stream is within Mount Aspiring National

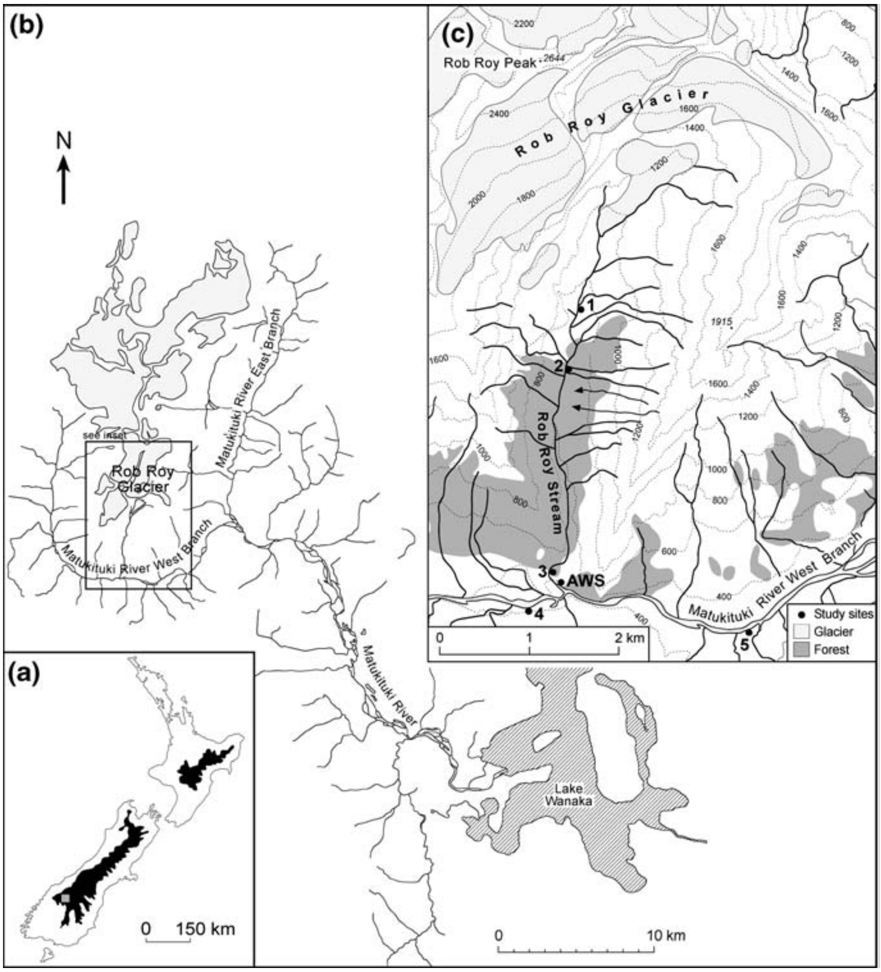

Fig. 1 Map of the study area in the South Island, New Zealand. (**a**) Location within New Zealand; (**b**) the Matukituki River system; (**c**) Sampling sites on Rob Roy Stream (1–3) and Matukituki River (4, 5). AWS = site of climate and discharge recording station

Park and is fed by the Rob Roy glacier at about 870 m a.s.l. and also by seasonal snow melt and runoff from rainfall that averages about 2,460 mm per year (Weingartner & Pearson, 2001). Meltwater contributed about 91% of baseflow discharge below the glacier face in spring and summer 2004–05 and about 85% at its mouth 4 km downstream (Cadbury, 2007). Discharge of the Rob Roy close to the mouth averages about 4 m^3/s (Cadbury et al., 2007). Geology of the Rob Roy catchment is predominantly schist and the principal vegetation is native beech forest (*Nothofagus* spp.), which extends up the valley to the treeline at about 800 m. At higher altitudes, plant cover is mainly tussock grass and subalpine scrub.

The floodplain of Rob Roy Stream is up to 20 m wide in its upper reaches and over 40 m wide at its confluence with the Matukituki River at 400 m a.s.l. The stream channel is 8–11 m wide and includes steep cascades, pools, riffle runs and a narrow gorge in its middle section. Substrata range from large boulders and bedrock to cobbles and coarse gravel. The source of the Matukituki is about 15 km northwest of the confluence with Rob Roy Stream (Fig. 1). It is fed by several glacial headwater streams as well as run-off from groundwater, snow melt and rainfall. Above and below the confluence, the Matukituki is a braided river 40–60 m wide that flows within a broad floodplain, although immediately below the entrance of the Rob Roy it narrows into a turbulent, single-thread river. Riparian vegetation in this section of the Matukituki includes beech forest and improved pasture grazed by cattle and sheep. The river channel is characterised by extensive runs and riffles except in the turbulent reach where large boulders predominate.

The *Deleatidium* species complex

Nymphs of the leptophlebiid mayfly *Deleatidium* are the most abundant benthic invertebrates in many stony New Zealand streams and rivers where they graze on epilithon and are a significant source of food for fish. Despite their ubiquity, individual species are difficult to distinguish, and many nymphs and winged stages cannot be identified with confidence either to species or from co-occurring species. However, the nymphs of *D. cornutum* (subgenus *Penniketellum*), the most abundant species in Rob Roy Stream (Cadbury, 2007), were easily distinguished by their uniformly black coloration, the dark pigmentation of all thoracic and abdominal ganglia and the large size they attain. Subimagoes (the only winged stage included in the original species description) were consistent with those described by Towns & Peters (1996), although they lacked the thoracic "horns" of the type specimens. However, these structures were not present on subimagoes from various sources examined by T. Hitchings (pers. comm.) and are not considered to be good taxonomic characters. *Deleatidium cornutum* seems to be confined to small, fast, alpine streams in South Canterbury, Central Otago and South Westland (South Island) (Towns & Peters, 1996; Hitchings, 2001). No previous studies have addressed aspects of its life history and ecology.

In contrast to *D. cornutum*, the common *Deleatidium* species present in the Matukituki River could not be identified with certainty. The most abundant species is referred to as *D.* "*angustum*" because its nymphs resemble those mentioned by Towns & Peters (1996) as occurring in the South Island and are possibly referable to the North Island species. Because of our inability to separate the nymphs of species in the Matukituki, they are considered together at the generic level.

Sampling sites

Sampling was carried out at five sites, three on the Rob Roy and two on the Matukituki, one above and one below the confluence. Site 1 was about 0.6 km from the face of Rob Roy glacier and was in the pro-glacial reach of the stream above the forest. The riparian zone was mainly bare rock and rubble with little vegetation. Site 2 was about 1 km further downstream within beech forest that bordered the stream on the true right bank; on the true left a narrow (~10 m wide) band of grass and scrub formed the riparian zone. Site 3 was at the mouth of the Rob Roy Stream where forest merged into grassland and the narrow glacial valley of the stream broadened. Sites 4 and 5 were on the Matukituki River 0.5 km above and 1 km below the confluence with Rob Roy Stream. Sampling was confined to major braids 20–30 cm deep, which were more stable and slow flowing at Site 5 (Cadbury, 2007). Both sites had broad floodplains, riparian zones with extensive gravel deposits and predominantly grassy vegetation along with beech forest on the true left of Site 5.

Water temperature was monitored continuously at all five sites from November 2004 to October 2005. Ranges of monthly mean temperatures were 1.2–3.7°C (Site 1), 1.9–4.1°C (Site 2), 2.3–5.8°C (Site 3), 4.4–9.9°C (Site 4) and 4.4–8.9°C (Site 5). Mean annual water temperatures at the five sites were 2.1, 2.7, 4.0, 7.0 and 6.7°C, respectively. Mean annual pH of stream water ranged from 7.5 to 7.7 at the 5 sites and conductivity was moderately low (60–85 μS_{25} cm^{-1}) (Cadbury, 2007; C. Ilg unpublished data).

Invertebrate sampling

Five benthic samples were taken with a Surber sampler (0.1 m^2, 250 µm mesh) from riffles at each site at approximately monthly intervals from September 2004 to October 2005, except at Site 1 where sampling began in November. Samples were preserved in the field in 70% alcohol. *Deleatidium* nymphs were sorted from other invertebrates in the laboratory and separated into two groups for analysis: (a) *D. cornutum* and (b) all other *Deleatidium* nymphs (referred to as *D.* "*angustum*").

Head capsule widths of all nymphs were measured across the eyes using an eyepiece micrometer at 10× magnification. Estimates of mayfly biomass were obtained from separate head capsule width: dry weight regressions for (a) *D. cornutum* and (b) other nymphs. The former were collected from Site 3 and the latter from Sites 3 and 5 and were preserved for less than a week in 4% formalin, which does not result in significant changes in dry weight (Leuven et al., 1985; authors' unpublished data). Nymphs in monthly collections could not be used because alcohol preservation resulted in loss of weight that continued over time. Mayfly production was calculated using the size frequency method (Benke, 1984) because specific nymphal cohorts could not be distinguished. Nymphs were assigned to 8 (*D. cornutum*) and 10 (*D.* "*angustum*") head width groups for analysis. Length of nymphal life was assumed to be 11 months (as in Huryn, 1996), so "cohort production" was multiplied by 12/11 to estimate annual production (Benke 1993). An example of the calculation procedure is given in Electronic supplementary material. Estimates of mean specific growth rates (instantaneous growth rates) of nymphs over the whole of nymphal life were calculated according to Benke (1993) where mean specific growth rate (%/day) = ln (final dry weight/initial dry weight)/365. Final dry weight was the average weight of measured final instar nymphs and initial weight was assumed to be 0.001 mg following Huryn (1996). To make comparisons with growth rates of *Deleatidium lillii*-group nymphs, ash-free dry weight was assumed to be 0.85% dry weight (Whiles & Wallace, 1995) and maximum nymphal biomass 3.5 mg (Huryn, 1996).

Results

Deleatidium cornutum

Deleatidium cornutum was the dominant *Deleatidium* species at Sites 1 and 2 where it had a mean annual density of 24.4/m^2 and 126.9/m^2, respectively. It was also abundant at Site 3 (88.3/m^2), but only occasional nymphs were found in the Matukituki River. Nymphal abundance peaked at the Rob Roy sites in late winter-early spring and mid-summer and was lowest in autumn (Fig. 2). Nymphs of all sizes were present in most months with the highest percentage of small individuals found in March, April and May. Although not easy to interpret, the head width data (Fig. 3) suggest there was probably a single annual generation in the Rob Roy with emergence starting in spring and continuing through summer. Nymphs with black wing pads that were about to emerge were not present in Surber samples, but subimagoes were found at all three Rob Roy sites. Their presence in the headwaters indicated that the life cycle could be completed even where mean water temperature was only 2.1°C.

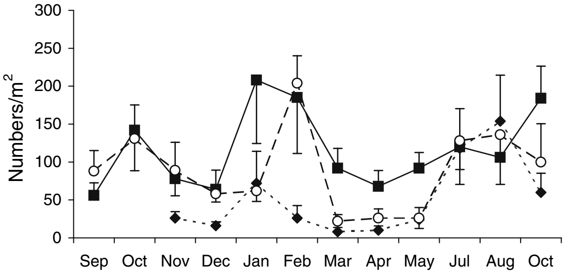

Fig. 2 Mean abundance of *D. cornutum* nymphs at Sites 1–3 on Rob Roy Stream, September 2004–October 2005. Site 1 (◆), Site 2 (■), Site 3 (○); error bars = 1SE

Deleatidium cornutum is the largest known species of *Deleatidium* and its final instar nymphs (2.3 mm head width) had an average dry weight (DW) of 9.77 mg. Mean annual biomass calculated for Site 1 was 98 mg DW/m^2, but it was almost four times greater at Sites 2 and 3 (392 and 377 mg DW/m^2,

Fig. 3 Monthly nymphal size distribution (head capsule width) of *D. cornutum* (upper; sites 1–3 combined) and *D.* "*angustum*" (lower; sites 3–5 combined), September 2004 to October 2005

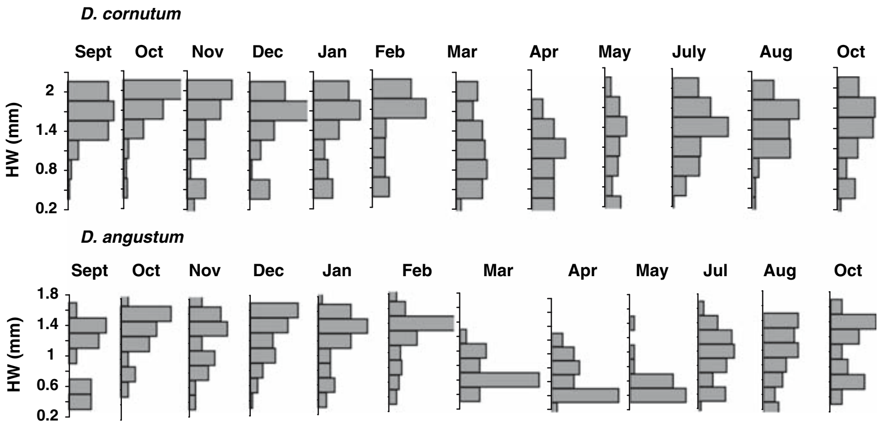

Table 1 Estimates of mean density, biomass (dry weight), production and the annual production: biomass ratio (P/B) for *D. cornutum* and *D.* “*angustum*” at Sites 1–3 on Rob Roy Stream and Sites 4 and 5 on Matukituki River

Site	Density (no/m^2)	Biomass (g/m^2)	Annual P (g/m^2)	P/B
D. cornutum				
S1	48	0.098	0.48	4.9
S2	127	0.392	2.02	5.1
S3	88	0.377	2.32	6.2
D. “*angustum*”				
S3	109	0.158	0.74	4.7
S4	259	0.191	0.90	4.7
S5	387	0.449	1.67	3.7
All *Deleatidium* spp.				
S3	197	0.535	3.07	5.8

Annual production estimates assume a larval life of 11 months

respectively). Estimates of annual production were highest at Site 3 (2.32 g DW/m^2) and lowest at Site 1 (0.48 g DW/m^2) (Table 1). Mean specific growth rate required to achieve full size by *D. cornutum* in 11 months was 2.8%/day.

Deleatidium “*angustum*” complex

Nymphs referred to as *D.* “*angustum*” were most abundant in the Matukituki River where mean annual densities were 259.3/m^2 and 387.1/m^2 at Sites 4 and 5, respectively. They were also common at Site 3 on Rob Roy Stream (101.3/m^2). Members of this species complex were absent from the two upper sites on Rob Roy Stream. Temporal patterns of abundance differed among sites (Fig. 4) and no consistent seasonal abundance patterns were apparent. Smaller nymphs predominated in most months (Fig. 3) and late-instar nymphs were most abundant in spring and summer.

The largest nymphs in the *D.* “*angustum*” complex attained a smaller size than *D. cornutum* (head width: 2.0–2.1 mm, average dry weight: 5.47 mg). Their mean annual biomass was greatest at Site 5 (449 mg DW/m^2) and lowest at Site 3 (158 mg DW/m^2) where nymphs co-occurred with *D. cornutum*. Estimates of annual production were also greatest at Site 5 (1.67 g/m^2) and lowest at Site 3 (0.74 g/m^2). Mean specific growth rate required to achieve full size by *D.* “*angustum*” in 11 months was 2.6%/day.

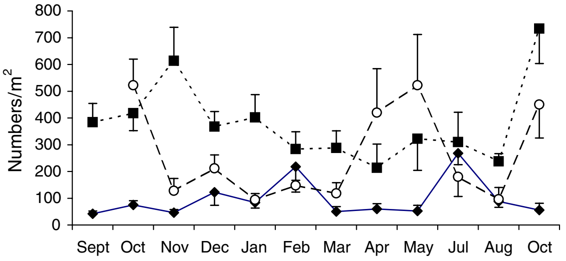

Fig. 4 Mean abundance of *D.* “*angustum*” nymphs at Sites 3–5 on Rob Roy Stream and Matukituki River, September 2004–October 2005. Site 3 (◆), Site 4 (○), Site 5 (■); error bars = 1SE

Overall, mean annual biomass and production of all *Deleatidium* species were greatest at Site 3 where 76% of production was attributable to *D. cornutum* (Table 1). The higher density, biomass and production of *D.* “*angustum*” at Site 5 than Site 4 on the Matukituki River probably reflect the greater physical stability of the river bed at Site 5, whereas the lower P/B ratio at Site 5 is brought about by the greater proportion of late-instar nymphs (head width: >1.8 mm) there (10.1% c.f. 5.8% at Site 4).

Discussion

Although annual production of stream macroinvertebrate communities can exceed 100 g DW/m^2, it was estimated to be less than 10 g DW/m^2/year in about half the studies (58 sites) reviewed by Benke (1993). Similarly, most published production estimates for grazer/scraper species are in the range 1–10 g DW/m^2/year ($n = 220$) and almost 90% had P/B ratios of 1–10. Some of the lowest estimates of community production are for cool-temperate and arctic streams and have been attributed to the constraints of low seasonal temperatures and nutrient or food limitation (Huryn & Wallace, 2000). Total invertebrate production was not calculated for Rob Roy Stream, but because *D. cornutum* is the largest and most abundant species present (Cadbury, 2007) it must account for a high proportion of it. Although the production estimates for *D. cornutum* suggest that total community production is low, they are surprisingly high for a single species at such low temperatures. Production estimates for populations of *Deleatidium* (species unidentified or questionable) have been made on at least 13 other New Zealand streams and rivers (Graesser, 1988; Collier et al., 2004) and range from 0.6 to 7.4 g DW/m^2/year. Our estimate for *D. cornutum* at Rob Roy Site 3 is exceeded by only four of these, and our estimate for all *Deleatidium* species combined at Site 3 is the fourth highest reported for the genus in New Zealand. All production estimates that exceed the highest values obtained in the present study were for populations in open pasture catchments with some probable nutrient enrichment and in all probability included several *Deleatidium* species.

The presence of a wide range of different sized nymphs in most months typifies many populations of *Deleatidium* in New Zealand but makes the interpretation of life cycles difficult. Towns (1983) concluded that stream-dwelling species in the north of the country had either univoltine or bivoltine life cycles, and slow-growing winter and fast-growing summer generations were inferred for some South Island stream populations studied by Winterbourn (1974), Scrimgeour (1991) and Huryn (1996). Our nymphal size distribution data for *D. cornutum* and more especially the *D.* "*angustum*" complex could be interpreted as encompassing a summer generation. However, the growth rates required to sustain a short summer generation would appear to be unrealistically fast at the low prevailing temperatures.

Humpesch (1979) found that water temperature was the main factor affecting the growth rates of three stream-dwelling species of *Baetis* (Ephemeroptera), with mean specific growth rates of *B. alpinus* Pictet, a species restricted to cold alpine streams, ranging from 0.82 to 2.97%/day over the temperature range 0.5–10.1°C. Huryn (1996) showed that temperature explained most of the variation in growth rate of *Deleatidium* nymphs belonging to the informal *lillii*-species group (similar to "*angustum*" in the Matukituki but smaller) in two South Island mountain streams with rates of <1%/day at 1–2°C, 2–5%/day at 6°C and 2–8%/day at 11°C obtained in 15–41 day trials in growth chambers held in two streams. Mean specific growth rates needed to attain full size by *D. cornutum* and *D.* "*angustum*" were slightly greater than the 2.5%/day for *D. lillii*-group larvae. The mean growth rate of *D. cornutum*, in particular, is impressive given that mean water temperature at the three Rob Roy study sites ranged from 2.1 to 4.0°C, and indicates it must be strongly adapted for growth at low temperature. Similarly, Brittain (1983) suggested that the mountain stonefly *Capnia atra* Morton had an inherent ability for growth at low temperature as indicated by a mean specific growth rate of 1.6%/day at 0.2–1.0°C, approximately twice that of three other co-occurring stonefly species.

Although determination of the trophic basis of production was not part of the present study, preliminary analyses of gut contents from nymphs at all sites indicated a predominance of diatoms and very little detritus of any kind (authors' unpublished data). Small species of *Achnanthidium*, *Encyonema* and *Diatoma* predominated in algal scrapings taken from the study sites (Cathy Kilroy, NIWA; pers. comm.) and chrysophytes were also common at Site 1 close to the glacier face. In addition to diatoms, the guts of many nymphs of *D. cornutum* contained large quantities of silt, which is presumably swept into the mouth by the broad maxillary brushes during grazing and may aid in the maceration of algal cells within the gut, thereby aiding digestion and assimilation of algal cell contents. Additionally, it is possible that bacteria adhering to silt particles could be an important component of the nymphal diet.

Implications for climate change

Speculation on the possible implications of projected climate change on the freshwater fauna of New Zealand has been minimal. Ryan & Ryan (2006) concluded that both higher temperatures and an increase in the predicted frequency of extreme climatic events have the capacity to change aquatic community structure as well as the geographical distribution, development and timing of life histories of individual species. Although direct links between alpine stream biota and meltwater inputs are poorly understood, reductions in the contribution of meltwater to streams are expected to have significant effects on stream communities. Brown et al. (2007) found that as the percentage of meltwater declined in streams of the French Pyrenees, water temperature, conductivity and pH all increased, while suspended sediment concentration decreased. Two common inhabitants of the glacial streams, the chironomid *Diamesa latitarsis* (Goetghebuer) and the trichopteran *Rhyacophila angelieri* Decamps, were no longer found where the meltwater contribution was less than 65% and could become at least locally extinct if glaciers continue to retreat (Brown et al., 2007).

Recent scenarios for climate change in New Zealand include average temperature increases of 1.5–2.0°C by the 2080s, higher rainfall in the west of the country, heavier and or more frequent extreme rainfall, a decrease in snow cover and a rise in the snowline and a continuing long-term reduction in ice volume and glacier length (Ministry for the Environment, 2007). Although regional climate projections are subject to considerable uncertainty (Wratt et al., 2007), the winter snowline in the general vicinity of Rob Roy Stream could rise 300–400 m and be accompanied by changes in riparian vegetation and greater runoff of winter rainfall. South Island glaciers can be expected to recede, as they have been for the last 100 years or so (Chinn, 2004) and eventually disappear. Consequences of such a scenario for glacier-fed streams such as the Rob Roy include more fluctuating discharge regimes and greater habitat instability. Less snow may also result in increased freeze-thaw cycles and also higher frequencies of floods (Sinclair, 2001). Water temperature is not likely to warm until glaciers have melted away (or nearly so), but if melting is accelerated, greater volumes of glacial sediments are likely to be released to the detriment of stream biota.

A climate warming scenario of this kind can be expected to have significant effects on members of the alpine stream fauna, especially cold stenothermal species such as *Deleatidium cornutum* that are restricted to very cold alpine streams (Füreder, 2007). With the complete loss of glacial meltwater, consequential reductions in flow (Melack et al., 1997) and an increase in water temperature, *D. cornutum* is likely to be lost from such streams, either because low temperature thresholds for growth and development of larvae and/or eggs are not met (Hauer et al., 1998), or because they may be less effective competitors at warmer temperatures. Furthermore, habitat loss may restrict winged adults from colonising streams other than their natal stream and lead to local extinction (Ryan & Ryan, 2006).

In contrast, an increase in stream water temperature could enable species such as members of the *Deleatidium* "*angustum*" complex to extend their distributions up formerly glacier-fed streams, although other factors may limit their ability to do so. For example, Oswood et al. (1992) noted that a less rigorous (warmer) thermal regime could result in the arrival of new predators, while the high gradient, larger substrata and flow conditions of streams like the Rob Roy differ markedly from those of the larger rivers downstream and may limit which species are capable of colonising, successfully.

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