

Density-dependent life history differences in a stream mayfly (*Deleatidium*) inhabiting permanent and intermittent stream reaches

C. T. ROBINSON

Department of Aquatic Ecology
Swiss Federal Institute of Aquatic Science and
Technology
8600 Dübendorf, Switzerland
email: robinson@eawag.ch

T. BUSER

Department of Environmental Sciences
ETH Zürich
8092 Zürich, Switzerland

Keywords Ephemeroptera; temporary; drift; alluvial river

INTRODUCTION

Temporary waters are a common feature of landscapes worldwide (Williams 1987). In running waters, temporary waters range from ephemeral streams that display a high degree of seasonal predictability to intermittent streams that can show highly unpredictable flows (Williams 1996). Falling water conditions in predictable temporary waters impose a time constraint on invertebrate and vertebrate development and life histories because of habitat loss (De Block & Stoks 2005). Most species inhabiting predictable temporary waters have evolved various life-history traits to meet the time constraint of falling water and thereby reduce mortality by desiccation. Falling water often acts as a seasonal cue, e.g., most predictable temporary systems fall dry in late summer/early autumn, for aquatic organisms to either complete development and leave the system (Delucchi & Peckarsky 1989; Donath & Robinson 2001) or enter into a stage of diapause to wait for resumption of flowing water (Williams 1996). For instance, many insects have drought resistant eggs that allow them to survive seasonal dry periods (Brock et al. 2003).

Falling water conditions in unpredictable aquatic environments often require organisms to develop a plastic life history response, e.g., increased development, to limit mortality from habitat drying and desiccation (Julianno & Stoffregen 1994; Johannsson et al. 2001; Shama & Robinson 2006). Stream insects can also display behavioural responses to falling water that may lessen mortality, such as moving into saturated hyporheic sediments or under rocks (Fowler 2002), drifting, or moving upstream (Delucchi 1989). However, behavioural displacement to alternative habitats is not a guarantee against mortality and may even increase rates of predation (Stanley et al. 1994; Shearer et al. 2003).

Abstract A life-history response by the mayfly *Deleatidium* (Ephemeroptera: Leptophlebiidae) from a permanent-flowing and an intermittent-flowing reach of the Selwyn River, New Zealand, to falling water conditions was examined using field populations and laboratory experiments in January 2006. Field populations had similar densities under flowing water conditions, but size distributions were skewed towards larger larvae in the intermittent reach relative to the permanent reach. Under field conditions of falling water at the intermittent reach, more larvae were caught in the drift during the day and more adults at dusk at the intermittent than at the permanent reach. A desiccation study in the laboratory showed that larvae survived up to 3 days under moist conditions, whereas larvae died within 3 h under dry conditions. Another laboratory experiment revealed that both populations increased emergence under falling water in the high density treatment but not in the ambient density treatment. We conclude that a density increase caused by falling water cues late instar larvae to hasten emergence, an adaptive trait that may reduce population mortality from stream drying.

In this study, we tested a life-history response, i.e., adult emergence, of a common stream mayfly to unpredictable falling water conditions in an intermittent alluvial river. *Deleatidium* is a common mayfly in streams and alluvial rivers in New Zealand (Scrimgeour 1991), often reaching high densities (c. 4000 ind/m², Scrimgeour 1991). It has a hemimetabolous life cycle and an asynchronous life history (Scrimgeour 1991; Huryn 1996); adults can be found throughout the year (Winterbourn & Gregson 1989). Larvae are herbivores, feeding on periphyton growing on rocks (Fowler 2004).

We hypothesised that the mayfly would show a plastic response, i.e., a change in a life-history parameter that increased survivorship, to falling water in its unpredictable environment. One example of this sort of response is a change in emergence behaviour, where individuals in intermittent reaches would emerge earlier than in permanent ones. We expected falling water conditions in the field to increase the density of the mayfly because of a reduction in surface water habitat (e.g., Larned et al. in press) and thereby cause a behavioural response that induces early emergence by late instar larvae. We tested our hypothesis using field observations and a laboratory experiment on two populations, one from a permanent-flowing reach and another from an intermittent-flowing reach in the river, during January 2006.

MATERIALS AND METHODS

Field measures

The Selwyn River (43°30'S, 172°59'E) is an alluvial river on the South Island of New Zealand. The upper reaches of the river are permanent, whereas the river often dries in its lower reaches as it flows through the central plains that are composed of glacio-fluvial gravels (Larned et al. in press). An area of transition, a perennial losing reach, exists along a 3-km section of the river where the channel responds rapidly to changes in flow, quickly drying or flooding in a matter of hours. This section, river km 7.4–10.4, has a rainfall dominated flow regime and loses surface water at a rate of 0.2 m³ s⁻¹ km⁻¹ (Larned et al. in press). We selected one site in this active downwelling zone where flow permanency averages c. 60% and another site c. 2 km upstream with permanent flow. Although annual temperature records were not available for the study sites, spot temperatures taken during the study showed sites had similar water temperatures, average c. 15 ± 4°C

during the study month (January 2006), when surface flow occurred.

We estimated mayfly densities at both sites using a Hess sampler (0.085 m², 250-µm mesh, $n = 4$) on 5 January 2006. Samples were preserved with 70% isopropyl-alcohol and taken to the laboratory for processing. In the laboratory, *Deleatidium* were handpicked from each sample, counted, and interocular widths measured (± 0.01 mm) with an ocular micrometer at 10× magnification. On the same day benthic samples were collected, we also collected 60 min drift samples (1-m long net, 14-cm diam. aperture, 250-µm mesh, $n = 4$) at both sites at dawn (c. 06:00), noon (c. 12:00), mid-afternoon (c. 15:00), and dusk (c. 19:00). Flow velocity through each net was measured using a Marsh-McBirney velocity meter (± 0.2 cm/s) and used to calculate the volume of water sampled by each net. The number of *Deleatidium* caught in each drift sample was counted and each mayfly recorded as larva or adult (subimago). We assessed differences in subimago *Deleatidium* numbers in the drift as an indicator of emergence in field populations.

Laboratory experiments

Larval mortality to stream drying was estimated using a desiccation experiment in a climate-controlled room maintained at 15°C. We collected 100+ late instar larvae from each site and returned them alive to the laboratory. Larvae were kept aerated in aquaria overnight and any dead larvae removed the following morning. Groups of 10 larvae from each site were each placed in 10 Petri dishes. Five Petri dishes were fitted with a single layer of dry paper towel; larvae were placed on the paper towel and then covered by another dry paper towel. The other five dishes were fitted with a layer of moist paper towel; larvae were placed on the moist towel and then covered with another layer of moist paper towel. Larvae were assessed for mortality by touching with forceps every 30 min until all larvae were dead. Larvae believed dead were placed in a flask with aerated water to assess death feigning. As larvae survived considerably longer in the moist treatment after the first 4 h, these dishes were examined every 4 h until all larvae had died.

A laboratory experiment was used to test the effects of mayfly density (natural and high) and water level (constant and falling water) on adult emergence of the two populations. The experiment used a replicated ($n = 10$ each) full factorial design (2 populations × 2 densities × 2 water treatments). Density at the permanent site, based on Hess samples

(above), was used for the natural density treatment with the high density treatment two-fold greater than the natural density. This treatment resulted in 10 larvae per aquarium (10 cm × 15 cm × 7 cm) in the natural density treatment (250 larvae/m²) and 20 larvae per aquarium in the high density treatment (500 larvae/m²). Last instar larvae collected the previous day (10 January 2006) from each population were used in the experiment. All collected larvae had visible black wing pads and were of similar size (length 6.81–7.28 mm).

Aquaria were maintained in a climate-controlled room at 15°C with a 12h:12h day:night light regime that reflected ambient field conditions. Water levels were maintained at 700 ml in the constant treatment with half of the water exchanged with new water every 2 days. In the falling water treatment, 150 ml of water (corresponding to c. 1.3 cm loss in water depth) was removed from each aquarium every 2 days. This falling water regime translated to an 86% reduction in water volume and a 44% reduction in usable surface area in each aquarium at the end of the experiment.

One small stone (5–7 cm wide) with periphyton was placed in each aquarium to supply food and habitat for larvae, and each aquarium was aerated. Stones collected from the same reach were used for the experiment and each had a thin visible layer of periphyton. A coarse mesh was fitted over each aquarium to collect adults (subimagos) as they emerged, and the experiment was terminated on day 11. Aquaria were assessed each day for dead larvae and emerged adults. Emerged adults were dried at 40°C and weighed to the nearest microgram. Dry mass was determined as previous studies have shown that insect larvae may trade size of emergence with early development (De Block & Stoks 2005). Sex was not determined.

Data analysis

Differences in benthic densities between the two sites were tested with a *t* test and differences in size distribution with a Kolmogorov-Smirnov test (Zar 1984). Differences in drift parameters between sites were tested using 2-way ANOVA (site and time of day) on log₁₀(x+1)-transformed data. Differences in survival time between sites and treatments in the desiccation experiment were tested using two-way ANOVA. Three-way ANOVA was used to test for differences in adult emergence (percentage emerged) and adult biomass between treatments in the aquaria experiment, followed by Tukey's test when differences were found. Data were

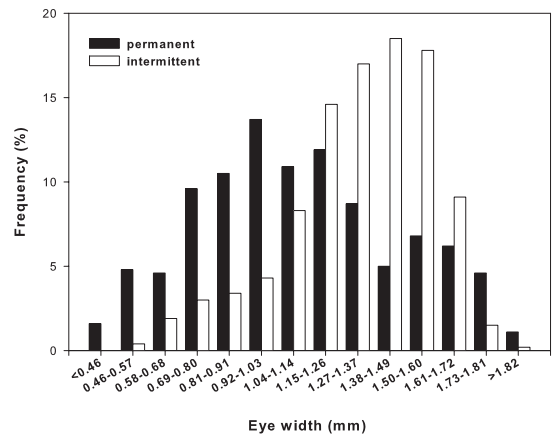


Fig. 1 Size frequency histogram of mayfly (*Deleatidium*) larvae collected from the permanent ($n = 438$) and intermittent ($n = 529$) study sites. Size was measured using the inter-ocular widths of head capsules.

transformed (arcsine square-root for percentage data and log₁₀(x+1) for biomass data) before analysis to meet ANOVA assumptions (Zar 1984).

RESULTS

Field populations

The density of *Deleatidium* was not significantly different at the two sites (*t* test, $P = 0.76$) and averaged 263 ind/m² (± 26 SD) at the permanent site and 261 ind/m² (± 84) at the intermittent site. The size distribution of larvae was strongly skewed towards larger individuals (inter-ocular widths of 1.15–1.72 mm) at the intermittent site and towards smaller individuals (inter-ocular widths 0.69–1.14 mm) at the permanent site (Fig. 1) (Kolmogorov-Smirnov test, $D = 0.093$ $P < 0.05$). A total of 46% of collected larvae were late instar nymphs at the intermittent site, whereas they represented only 20% of the collected nymphs at the permanent site.

Deleatidium larvae were collected in the drift throughout the day at the intermittent reach, whereas drift peaked at dusk at the permanent site and was absent during the day (Fig. 2). Adults were found in the drift at dusk at both sites, but represented 62% of the mayflies collected at the intermittent site and only 4% of the individuals collected at the permanent site. These adults may represent emerged subimagos or dead females that oviposited in upstream areas.

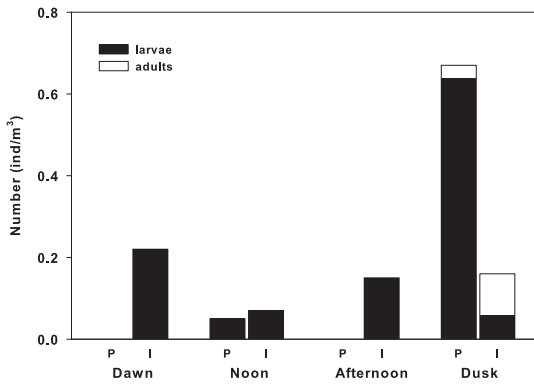


Fig. 2 Number (ind/m³) of mayfly (*Deleatidium*) larvae and adults collected in drift samples from the permanent and intermittent study sites at dawn, noon, afternoon, and dusk ($n = 4$ each).

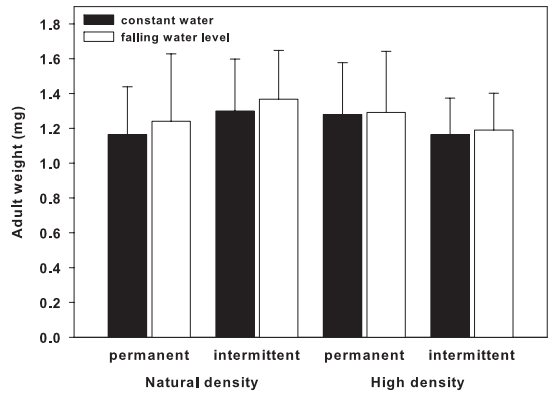


Fig. 4 Weight (dry mass) (mean + 1SD) of emerged adults from each treatment of the aquarium experiment.

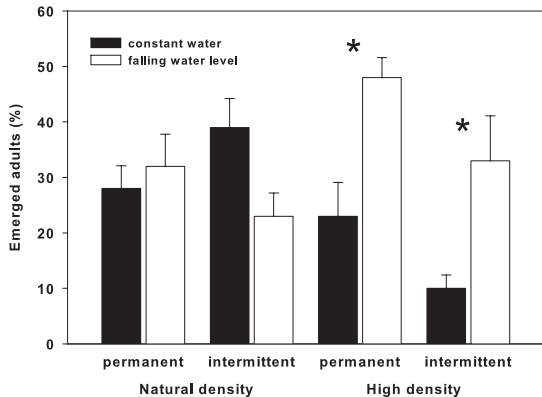


Fig. 3 Percentage emergence (mean + 1SE) of mayfly adults from the different treatments in the aquarium experiment ($n = 10$ each). Asterisks indicate significant differences between pairs (constant versus falling water level) in the high density treatment for both populations based on Tukey's test results ($P < 0.05$).

Laboratory experiments

The desiccation experiment showed that 50% of larvae from both populations died within 3 h in the dry paper towel treatment, whereas the same level of mortality was achieved after 30 h in the moist towel treatment ($F_3 = 4.82, P < 0.0001$). Eight percent of the mayflies lived up to 3 days in the moist towel treatment.

In the aquarium experiment, there was a significant density-dependent effect on mayfly emergence to falling water (Fig. 3) (water \times density: $F_6 = 14.87,$

$P < 0.0001$). The percentage emergence of adults was two-fold greater (permanent site) and three-fold greater (intermittent site) in the high density treatment under falling water (Tukey's test, $P < 0.05$). There was no significant increase in adult emergence to falling water for either population at natural density. In the intermittent site population at natural density, average percentage emergence was lower, although non-significantly so, by c. 15% in the falling water treatment than in constant water treatment (Tukey's test, $P > 0.05$). The average weight (mg dry mass) of emerged adults did not differ between sites and treatments (Fig. 4) (3-way ANOVA: $F_7 = 1.25, P = 0.297$). Average adult weights ranged from 1.16 to 1.37 mg, and varied on average c. 23% (CV) within each treatment. Larval mortality averaged about 20% for the experiment, and did not differ among treatments ($F_7 = 1.37, P = 0.513$).

DISCUSSION

Field data suggest that larger larvae accumulated in the intermittent reach, either from large larvae moving downstream in the drift or those that actively move upstream in response to falling water in downstream areas. Another explanation may be that life histories differed between the two sites, being faster in the intermittent site, in response to, for example, temperature differences or some other environmental factor (Huryn 1996). As *Deleatidium* nymphs cannot be identified to species and we had only subimagos for analysis, our results may be based on 1 or 2 species. However, the proximity

of the two study sites and life-history similarity of the two examined populations suggest that a single species was most likely used in the present study.

The lower density of early instar larvae in the intermittent reach further suggests that emerged adults fly upstream to oviposit. Upstream flight is a common characteristic of stream mayflies and other aquatic insects (Müller 1982; Monaghan et al. 2002). We noticed that larvae recolonise previously dry channels by migrating downstream as a periphyton layer develops on stones (C. T. Robinson & T. Buser pers. obs., see Fowler 2004).

An increase in night drift is a common characteristic of aquatic insects in streams with predatory fish (Elliot 1977), and has been observed for *Deleatidium* in New Zealand streams (Glova & Sagar 1989). What is important in this study is the active drift of mayflies during the day at the intermittent site when water levels were falling. Discharge in the river decreased by >50% during the day that drift was sampled at the intermittent site, whereas little change in discharge was observed at the permanent site (C. T. Robinson & T. Buser pers. obs.). The area of available habitat for larvae decreases as water levels fall, thereby increasing densities and potential encounters between larvae as larvae disperse to more favourable habitat. An increase in contact may cause larvae to drift, or the falling water conditions may act as a cue for larvae to leave the system (both behavioural responses). Fowler (2002) noted that *Deleatidium* larvae also use subsurface or hyporheic areas. Larvae were observed to actively swim towards the surface during the day in stream areas during falling water conditions (C. T. Robinson & T. Buser pers. obs.). The increase in drift also may increase mortality from predation by drift-feeding fish (Shearer et al. 2003).

When comparing the adult drift percentages with those of larger larvae at each of the sites, it is probable that adult emergence substantially increased at the intermittent site during this period of falling water relative to the permanent site. That is, more adult mayflies (subimagos and imagos) were found in the drift at the intermittent site than the permanent site relative to the number of large larvae present at the two sites. It is possible the adults collected in the drift were from ovipositing females that died and may not be related to increased emergence. Falling water has been found to be an important cue for amphibians to metamorphose earlier (Denver et al. 1998; Lane & Mahony 2002), and plasticity in life history responses to falling water have been documented for an alpine caddisfly (Shama & Robinson 2006).

De Block & Stoks (2005) found various responses by a damselfly that inhabits temporary ponds to falling water related to egg hatching date. Eclosion in aquatic insects is controlled by various hormones such as adult development hormones (Butler 1984), but presently no information exists on how an environmental cue such as falling water (or an associated factor) stimulates hormone release to hasten adult emergence in aquatic insects, especially in unpredictable waters in which the response is probably plastic. The drift results suggest that larval activity is enhanced under falling water conditions and this behaviour may be related to increased adult emergence.

In the field, live larvae were often found on the undersides of stones in the dry channel of the intermittent reach, and the undersides of these stones were moist, whereas larvae attached to undersides of stones that were dry in the same area were always dead. We observed larvae to crawl under stones in the field to escape falling water conditions. The undersides of these stones typically were moist and may allow larvae to survive periodic dry periods (C. T. Robinson & T. Buser pers. obs.). Larval mayflies have external gills that require a moist surface for effective diffusion of oxygen across gill membranes. The response to move to the undersides of stones once a channel dries out may be a bet-hedging strategy of larvae to stay alive until the next rain that resumes surface flow in channels. These rains can occur within days in the headwaters of coastal plain streams in New Zealand, providing surface-flowing water to intermittent channels of rivers (Larned et al. in press). Fowler (2002) noted that *Deleatidium* larvae can use subsurface sediments, perhaps in response to changes in flow conditions.

Some studies have found a trade-off between size and rate of development of insects (e.g., Johansson & Rowe 1999), whereas others have found contrasting patterns (Day & Rowe 2002). Because we selected similar-sized last instar larvae from both sites for the laboratory experiment, no treatment effect was expected or found for adult size. In this study, we were interested only in the response of last instar larvae to falling water, as would be expected in intermittent streams with unpredictable dry periods.

The aquarium experiment results suggest that the density increase associated with falling water conditions cues the mayfly to emerge, and that this response occurs under high density. For instance, increased emergence did not occur in the natural density falling water treatment, but only in the high density falling water treatment. Emergence

during the experiment may have reduced any density effect in the natural density falling water treatments below that found in the high density falling water treatments. In the field, larvae that fail to emerge may move under stones as the river dries, and if flowing water resumes within a few days these larvae may survive. The emergence response appears to be plastic as both populations responded in a similar way. Plasticity in emergence may be a common response by this stream mayfly, even for those in permanent channels, as channel turnover in braided rivers can be relatively high (Arscott et al. 2002; van der Nat et al. 2003).

Plastic responses are theoretically expected in unpredictable environments such as that at the intermittent site where drying and wetting occur frequently within an annual cycle (Loman & Claesson 2003; Frisch & Santer 2004). However, empirical data testing theoretical predictions for aquatic insects are few (see, e.g., Johansson et al. 2001; Shama & Robinson 2006). This is the first study, to our knowledge, that assessed life-history plasticity in stream mayflies. *Deleatidium* is a common mayfly of intermittent alluvial streams throughout New Zealand (Winterbourn & Gregson 1989), thus being able to emerge quickly under falling water conditions is an important life-history trait for population persistence. Although falling water is unpredictable in this intermittent river, a major increase in density with falling water may be a sufficiently strong signal to stimulate emergence. For example, no increase in emergence occurred in the natural-density falling-water treatment, even though density may have increased as the water level decreased. Alternatively, a density increase was offset in the natural-density falling-water treatments by adult emergence during the experiment. Additional research including physiological parameters would improve our understanding of how aquatic insects persist in unpredictable temporary water bodies, a common habitat type in many landscapes.

ACKNOWLEDGMENTS

The research was conducted at the National Institute of Water and Atmospheric Research (NIWA), Christchurch, New Zealand. The authors thank S. Larned and B. Biggs for logistic support during the study. We also thank two anonymous reviewers who made constructive comments that improved the manuscript.

REFERENCES

- Arscott DB, Tockner K, Ward JV 2002. Geomorphic dynamics along a braided-river corridor in the Alps (Fiume Tagliamento, NE Italy). *Ecosystems* 5: 802–814.
- Brock MA, Nielson DL, Shiel RJ, Green JD, Langley JD 2003. Drought and aquatic community resilience: the role of eggs and seeds in sediments of temporary wetlands. *Freshwater Biology* 48: 1207–1217.
- Butler MG 1984. Life histories of aquatic insects. In: Resh VH, Rosenberg DM ed. *The ecology of aquatic insects*. New York, Praeger Publishers. Pp. 24–55.
- Day T, Rowe L 2002. Development thresholds and the evolution of reaction norms for age and size at life-history transitions. *American Naturalist* 159: 338–350.
- De Block M, Stoks R 2005. Pond drying and hatching date shape the tradeoff between age and size at emergence in a damselfly. *Oikos* 108: 485–494.
- Delucchi CM 1989. Movement patterns of invertebrates in temporary and permanent streams. *Oecologia* 78: 199–207.
- Delucchi CM, Peckarsky BA 1989. Life history patterns of insects in an intermittent and a permanent stream. *Journal of the North American Benthological Society* 8: 308–321.
- Denver RJ, Mirhadi N, Phillips M 1998. Adaptive plasticity in amphibian metamorphosis: response of *Scaphiopus hammondi* tadpoles to habitat desiccation. *Ecology* 79: 1859–1872.
- Donath U, Robinson CT 2001. Ecological characteristics of lake outlets in alpine environments of the Swiss Alps. *Archiv für Hydrobiologie* 150: 207–225.
- Elliot JM 1977. Diel changes in invertebrate drift and the food of trout *Salmo trutta*. *Linnaean Journal of Fish Biology* 2: 161–165.
- Fowler RT 2002. Relative importance of surface and subsurface movement on benthic community recovery in the Makaretu River, North Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 36: 459–469.
- Fowler RT 2004. The recovery of benthic invertebrate communities following dewatering in two braided rivers. *Hydrobiologia* 523: 17–28.
- Frisch D, Santer B 2004. Temperature-induced responses of a permanent-pond and a temporary-pond cyclopoid copepod: a link to habitat predictability? *Evolutionary Ecology Research* 6: 541–553.
- Glova GJ, Sager PM 1989. Prey selection by *Galaxias vulgaris* in the Hawkins River, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 23: 153–161.

- Huryñ AD 1996. Temperature-dependent growth and life cycle of *Deleatidium* (Ephemeroptera: Leptophlebiidae) in two high-country streams in New Zealand. *Freshwater Biology* 36: 351–361.
- Johansson F, Rowe L 1999. Life history and behavioral responses to time constraints in a damselfly. *Ecology* 80: 1242–1252.
- Johansson F, Stoks R, Rowe L, De Block M 2001. Life history plasticity in a damselfly: effects of combined time and biotic constraints. *Ecology* 82: 1857–1869.
- Juliano SA, Stoffregen TL 1994. Effects of habitat drying on size at and time to metamorphosis in the tree hole mosquito *Aedes triseriatus*. *Oecologia* 97: 369–376.
- Lane SJ, Mahony MJ 2002. Larval anurans with synchronous and asynchronous development periods: contrasting responses to water reduction and predator presence. *Journal of Animal Ecology* 71: 780–792.
- Larned ST, Hicks DM, Schmidt J., Davey AJH, Dey K, Scarsbrook M, Arscott D, Woods RA in press. The Selwyn River of New Zealand: a benchmark system for alluvial river ecosystems. *River Research and Applications*.
- Loman J, Claesson D 2003. Plastic response to pond drying in tadpoles *Rana temporaria*: tests of cost models. *Evolutionary Ecology Research* 5: 179–194.
- Monaghan MT, Spaak P, Robinson CT, Ward JV 2002. Population genetic structure of 3 alpine stream insects: influences of gene flow, demographics, and habitat fragmentation. *Journal of the North American Benthological Society* 21: 114–131.
- Müller K 1982. The colonization cycle of freshwater insects. *Oecologia* 52: 202–207.
- Scrimgeour GJ 1991. Life-history and production of *Deleatidium* (Ephemeroptera, Leptophlebiidae) in an unstable New Zealand River. *New Zealand Journal of Marine and Freshwater Research* 25: 93–99.
- Shama LNS, Robinson CT 2006. Sex-specific life-history responses to seasonal time constraints in an alpine caddisfly. *Evolutionary Ecology Research* 8: 169–180.
- Shearer KA, Stark JD, Hayes JW, Young RG 2003. Relationships between drifting and benthic invertebrates in three New Zealand rivers: implications for drift-feeding fish. *New Zealand Journal of Marine and Freshwater Research* 37: 809–820.
- Stanley EH, Buschman DL, Boulton AJ, Grimm NB, Fisher SG 1994. Invertebrate resistance and resilience to intermittency in a desert stream. *American Midland Naturalist* 131: 288–300.
- Van der Nat D, Tockner K, Edwards PJ, Ward JV, Gurnell AM 2003. Habitat change in braided rivers (Tagliamento, NE-Italy). *Freshwater Biology* 48: 1799–1812.
- Williams DD 1987. *The ecology of temporary waters*. Portland, Oregon, Timber Press.
- Williams DD 1996. Environmental constraints in temporary fresh waters and their consequences for the insect fauna. *Journal of the North American Benthological Society* 15: 634–650.
- Winterbourn MJ, Gregson KLD 1989. *Guide to the aquatic insects of New Zealand*. Bulletin of the Entomological Society of New Zealand 9.
- Zar JH 1984. *Biostatistical analysis*. Englewood Cliffs, NJ, United States, Prentice-Hall, Inc.