*Hydrobiologia* **523:** 17–28, 2004.

# The recovery of benthic invertebrate communities following dewatering in two braided rivers

R.T. Fowler
*Institute of Natural Resources – Ecology, Massey University, Private Bag 11-222, Palmerston North, New Zealand*
*Present address: 65B Portal Street, Wanganui, New Zealand*
*E-mail:reecevegas@yahoo.co.nz*

Received 6 June 2002; in revised form 12 December 2003; accepted 4 February 2004

*Key words:* benthic communities, braided rivers, colonisation, dewatering, drift, drought, hyporheic zone, New Zealand, periphyton, recovery

## Abstract

The recovery of benthic invertebrates was investigated in the braided Tukituki and Waipawa Rivers (North Island, New Zealand) following extended channel dewatering of sites for 6, 10 or 14 weeks during summer 1997/1998. After rewatering, invertebrates rapidly colonised each denuded site and, although some invertebrates were numerically dominant at different times, $95^{+}$% of the taxa list were present after 7 days of rewatering. The number of individuals also increased over time, but significantly greater numbers were collected in reference sites and those dry for 6 weeks compared to sites dewatered for longer periods. Taxa such as *Tanytarsus* spp., *Maoridiamesa* spp. (Diptera: Chironomidae) and the riffle beetle Elmidae (Coleoptera) were abundant early, while *Deleatidium* spp. (Ephemeroptera: Leptophlebiidae) dominated communities later. The greater abundance of *Deleatidium* in sites dewatered for a short time may be because desiccation was less significant at determining taxa present at these sites, or that reference sites provided a closer source of colonists and periphyton propagules to allow a more rapid numerical recovery of this taxon. In contrast, Elmidae dominated communities at sites dewatered for longer periods because Elmidae may be more resilient to desiccation than *Deleatidium*. These data suggest that the duration of dewatering may regulate taxonomic composition in the short term by subjecting taxa to desiccation and/or food resource restrictions, but not in the long term because food resources recovered over time and sites with similar physicochemical conditions should have similar communities.

## Introduction

Colonisation of denuded habitats by benthic invertebrates has been an active area of stream ecology research over the last three decades (Williams, 1977; Sagar, 1983; Mackay, 1992; Williams & Smith, 1996). Experimental studies investigating colonisation dynamics in benthic communities have shown invertebrates are present immediately after disturbances such as floods and channel dewatering (Williams & Hynes, 1976; Sagar, 1983), although pre-existing community composition may not be achieved for months (Cairns et al., 1971). The ability of invertebrates to colonise benthic habitats is influenced by the type of disturbance (Lake & Barmuta, 1986; Resh et al., 1988), frequency of disturbance (Lake et al., 1989), and the number (Marchant et al., 1991) and type of taxa present pre-disturbance. Adaption of instream fauna to regular disturbance (e.g., floods and dewatering), along with the availability (Cairns et al., 1971) and proximity (Gore, 1982) to potential disturbance refugia will also play a role in the duration of community recovery following disturbance events.

Habitats including stream banks, log debris, the hyporheic zone and undisturbed side braids have been suggested as sources of colonists in river systems following disturbance (e.g., Cooling & Boulton, 1993; Lancaster & Hildrew, 1993). However, how rapidly benthic communities recover following channel rewatering has received little attention (Larimore et al., 1959; Sagar, 1983; Cowx et al., 1984; Doeg et al., 1989). Stream systems may rely on other sources of colonists such as downstream drift, aerial oviposition from flying adults (beetles, bugs etc.) and crawling to repopulate disturbed systems. Migration of benthic animals into the hyporheic zone may also play a major role in the survival of invertebrates during droughts (Williams, 1977). The benthos may migrate into wetted interstitial substrates that provide refugia while the surface channel is dry (Williams, 1977; Malicky, 1982; Boulton, 1989). The benthos may then be repopulated by immature stages moving from the hyporheos (Williams & Hynes, 1976, Cooling & Boulton, 1993), wetted reaches upstream, or emerging from perenating lifestages present in interstices once channel flow resumes (Abell, 1984). Benthic invertebrates present in the river bed may colonise the benthos post-disturbance as long as interstitial flow is maintained during and after the period of disturbance (see Godermakers & Pinkster, 1981; Boulton et al., 1992; Cooling & Boulton, 1993). Therefore, the significance of wetted upstream reaches and the vertical extent of interstitial dessication may be influenced by the longitudinal extent and duration of disturbance. Thus, the extent and duration of disturbance will determine the type of refugium that will provide suitable colonists for denuded stream systems, as interstitial flow can cease after extended dry periods, resulting in the dessication of refugia (Boulton & Stanley, 1995), and altered recovery patterns for stream systems.

Physical and physicochemical disturbance to the stream channel is considered a major structuring force in stream invertebrate communities (Power et al., 1988; Resh et al., 1988). However, despite the fact that New Zealand rivers have rapidly changing and unpredictable flow regimes (Winterbourn et al., 1981; Winterbourn, 1987), entire river channels do not annually dewater in New Zealand for extended periods of time. Rather, smaller river sections dewater after extended periods of low rainfall through the loss of surface waters to underlying aquifers. Thus, although many New Zealand studies have focused on the effects of high flow events on the stream fauna (e.g., Sagar, 1986; Scrimgeour et al., 1988; Quinn & Hickey, 1990), few studies have investigated the effects of channel dewatering on the benthic fauna, or how the community recovers following dewatering (refer Sagar, 1988). The objective of this study was to examine whether channel dewatering changed the rate of benthic community recovery and composition in two braided rivers. Increasing the duration of dewatering may increase the desiccation of potential colonisation sources (i.e., wetted upstream reaches and the hyporheic zone) and thus restrict community recovery for the denuded benthos.

## Study sites

The Tukituki and Waipawa Rivers (40 ° 00′ S, 176 ° 20′ E) originate in the Ruahine Ranges (North Island, New Zealand) from 1700 m a.s.l, have a greywacke fluvial geomorphology (Ruataniwha alluvium) and meander through predominantly agricultural land within fluvial deposits up to 150 m wide and 60 m deep (Hawkes Bay Regional Council, 1999). Overhead riparian cover at each sample site is minimal because the meandering braided channel often flows over exposed alluvial gravels up to 10 m from the riparian zone. Willow trees (*Salix* sp.) are common beside both rivers. Substrate composition is similar in both rivers, comprising 5% boulders (>26 cm), 30% large cobbles (13–26 cm), 30% small cobbles (6–12 cm), 30% gravels (0.2–6 cm) and 5% sand/silt (<0.2 cm). The Hawkes Bay Regional Council (local governing body) assessed substrate composition during 1997 and showed similar substrate composition to the current survey in the immediate vicinity of the study sites for both rivers.

Four Tukituki (NZMS 260 series; U22 027 351) and four Waipawa (NZMS 260 series; U22 064 444) riffle sites (each 10 m long ± 1 m) were located at 100 m intervals along a 340 m reach of river. Reference sites (i.e., sites that did not dewater) were located farthest upstream, followed by sites naturally dewatered for ‘6 weeks’, '10 weeks' and '14 weeks', respectively. The duration of dewatering was estimated from aerial photographs taken monthly by the Hawkes Bay Regional Council during the 1997/1998 summer, followed by on-site visual assessments of the dry streambed prior to rewatering. On-site visual assessment involved exposing the dry river gravels to a depth of 10 cm (greater depth at which Surber samples were collected) to show gravels were dry to at least 10 cm depth. The study sites selected had dewatered at similar rates between sites and rivers. Sites labelled 14 weeks went dry on 9 January 1998, with all other sites dewatering at 4 or 8 weeks thereafter. Sites were dewatered for 6, 10 and 14 weeks before flows resumed following rain on 3 April 1998. The dewatered conditions for the two rivers were the result of the lowest groundwater levels during 1997/1998 (reference BH 1376, site 894001) since 1992 (Hawkes Bay Regional Council, 1999). One section from each river that remained wetted throughout the summer period was considered a reference for those sites dewatered. The reference sites were not considered controls as flows were reduced in these riffle sites during the summer period.

## Methods

### *Sampling protocol*

On four sampling occasions at 7, 14, 28 and 42 days after flows resumed, three randomly placed 0.1 $m^2$ Surber samples (300 $\mu$m mesh) to a depth of approximately 7 cm were collected from the reference site and from each dewatered region (dry for 6, 10 and 14 weeks). Samples were stored in 70% ethanol for later sorting and identification using the keys of Winterbourn & Gregson (1989). Conductivity (standardised to 25 °C) and temperature were measured from the river channel using an Orion 122 portable conductivity meter. The water pH was analysed using an Orion 250A pH meter. Dissolved oxygen was measured in the river channel using a YSI 59 dissolved oxygen meter. River depth and velocity were assessed from four points randomly selected along each sampled riffle using a velocity head rod, while width was measured half way along each sampled riffle.

Algal biomass was assessed by extracting photosynthetic pigments (chlorophyll *a* and phaeophytin) with 90% acetone at 5 °C for 24 h from five randomly selected gravels (mean diameter = 5 cm). Gravels were collected at each site (reference, 6, 10 and 14 weeks) on each sampling occasion. Total pigment concentration was calculated using the formulae outlined in Moss (1967a, b) and corrected for stone surface area using the approach described by Graham et al. (1988).

### *Data analysis*

To assess whether sampling occasion, duration of dewatering and differences between rivers affected community characteristics, a univariate repeated measures analysis of variance (ANOVA) was performed using SYSTAT (SYSTAT, 1998). Tukeys HSD test was used *post-hoc* to assess differences between sampling occasion, dewatering and rivers. Individual counts, total pigment concentration, community composition data (for multivariate analyses) and abundance of the seven most common taxa were log transformed to improve normality and homogeneity of variances prior to analysis. Diversity was measured as species number, Simpson's index (Simpson, 1949) and Margalefs' index (Clifford & Stevenson, 1975).

Detrended correspondence analysis (DCA) and a multiresponse permutation procedure (MRPP) (using Sorensens distance measure) (Beals, 1984; McCune & Grace, 2002) were performed using the PCORD statistical package (McCune & Mefford, 1999) to assess the variation in community composition between dewatered treatments and each sampling occasion. The DCA uses abundance data for a sample to arrange communities within ordination space in relation to how similar they are in composition to each other. Thus, samples from communities that have more species in common are arranged more closely in ordination space. In contrast, MRPP is a non-parametric procedure for testing the hypothesis of no difference between two or more groups of entities using abundance data. The MRPP is similar to a multivariate analysis of variance without the requirement of multivariate normality and homogeneity of variance (Berry et al., 1983; Mielke, 1984).

## Results

### Periphyton biomass

Total pigment concentration (chlorophyll *a* and phaeophytin) increased through time in both rivers ($F_{3,9} = 19.01$; $p < 0.01$), but was significantly higher in the Tukituki River overall ($F_{1,3} = 0.41$; $p = 0.57$). Total pigment concentrations were highest in reference sites and lowest in all dewatered treatments ($F_{3,9} = 10.35$; $p < 0.01$) (Fig. 1). Total pigment concentrations in the reference sites were low at day 7, but increased over time, so that concentrations peaked by day 42 in reference sites. By comparison, periphyton in the dewatered treatments showed a slower recovery rate and concentrations did not peak until at or after 42 days. A significant interaction was observed between sampling occasion and dewatered treatment ($F_{3,9} = 2.44$; $p < 0.01$). Environmental characteristics for the Tukituki and Waipawa Rivers are presented in Table 1.

### Diversity patterns

The number of taxa present in both rivers (Fig. 2a and b) increased rapidly within the first 7 days of rewatering and did not change over the 42 day sampling period overall ($F_{3,9} = 0.31$; $p = 0.82$). Number of taxa did not change between dewa-

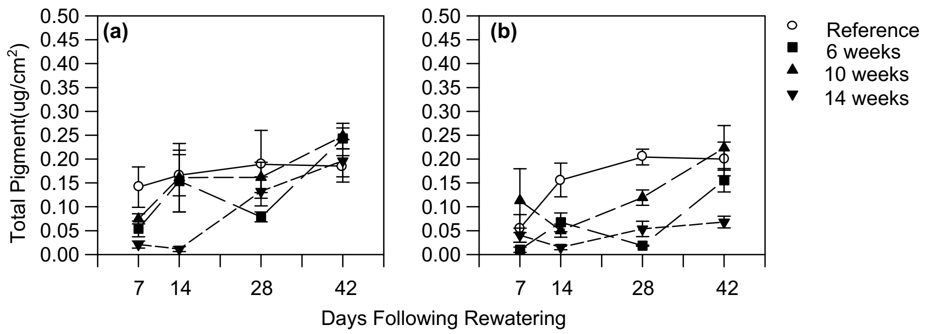

*Figure 1.* Mean total pigment concentration (±1 SE) for samples collected at four sites within the Tukituki (a) and Waipawa (b) Rivers (North Island, New Zealand) after flow resumed on 3 April 1998.

*Table 1.* Mean (with range in parentheses) environmental variables measured on four occasions between 10 April and 15 May 1998 in the Tukituki and Waipawa Rivers (North Island, New Zealand)

| Sampling occasion | Tukituki | | | | Waipawa | | | |
|---|---|---|---|---|---|---|---|---|
| | 7 | 14 | 28 | 42 | 7 | 14 | 28 | 42 |
| Conductivity ($\mu$S/cm) | 107.6 | 108.9 | 100.9 | 101.4 | 123.9 | 125.7 | 121.2 | 122.0 |
| | (100–109) | (100–109) | (100–101) | (–) | (123–124) | (125–126) | (121–122) | (–) |
| Depth (cm) | 16 | 14 | 15 | 18 | 20 | 12 | 18 | 20 |
| | (13–19) | (11–17) | (12–20) | (13–21) | (15–26) | (7–15) | (15–18) | (16–29) |
| Oxygen (mg/l) | 9.0 | 8.9 | 10.2 | 12.5 | 9.0 | 9.6 | 10.5 | 11.5 |
| | (8.8–9.1) | (8.8–9.1) | (10.1–10.3) | (11–15.5) | (8.7–9.3) | (9.4–10) | (10.4–10.6) | (11.3–11.8) |
| pH (no range) | 6.8 | 7.1 | 7.6 | 7.9 | 6.8 | 7.3 | 7.4 | 7.4 |
| Temperature (°C) | 19 | 19 | 16 | 11 | 19 | 19 | 20 | 12 |
| | (18.7–19) | (18.7–19.3) | (15.8–16.3) | (10.8–11) | (19–19.1) | (16.4–17.4) | (15.6–16.4) | (11.1–12) |
| Width (m) | 6.9 | 7.0 | 7.8 | 9.1 | 7.4 | 7.5 | 9.1 | 9.4 |
| | (5–9.6) | (5.1–9.7) | (5.1–12.2) | (5.2–12.3) | (4.5–11.2) | (4.8–11.3) | (6.1–13.1) | (6.1–13.2) |
| Velocity (m/s) | 0.99 | 0.94 | 0.94 | 0.92 | 0.97 | 0.70 | 0.87 | 1.01 |
| | (0.8–1.1) | (0.7–1.1) | (0.8–1.1) | (0.8–1.1) | (0.8–1) | (0.7–0.9) | (0.6–1) | (0.7–1.1) |

Values are represented as means (with range in parentheses) from the four sites on each sampling occasion.

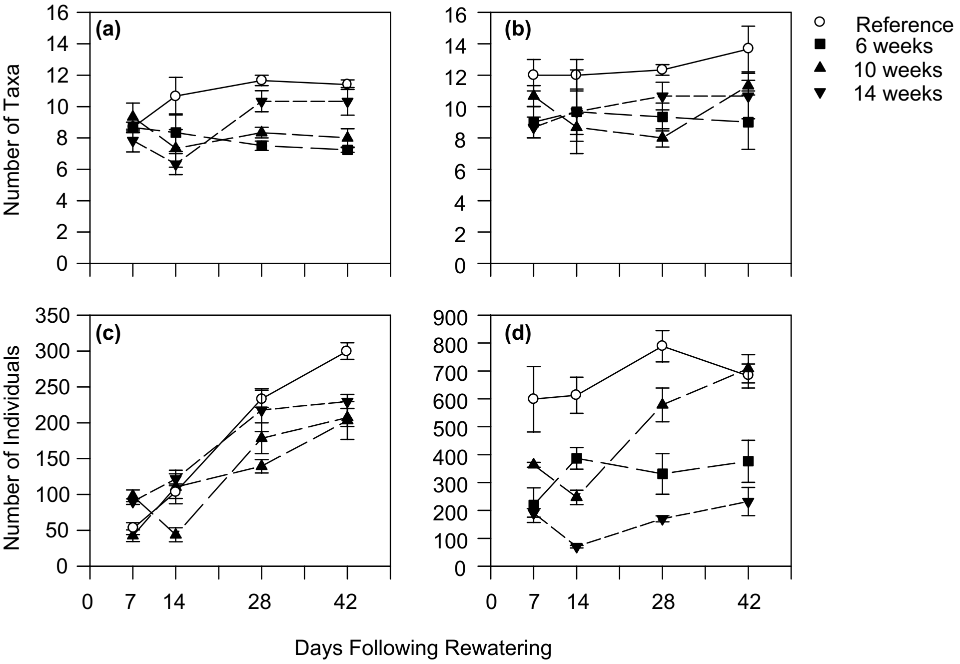

*Figure* 2. Mean ( ± 1 SE) number of taxa (a and b) and individuals (c and d) collected in three 0.1 m$^2$ Surber samples at four sites within the Tukituki (a and c) and Waipawa Rivers (b and d) (North Island, New Zealand) after flow resumed on 3 April 1998.

tering treatments within each river ($F_{3,3} = 1.32$; $p = 0.41$). Overall, similar numbers of taxa were identified in both the Tukituki and Waipawa Rivers ($F_{3,9} = 3.23$; $p = 0.17$). A total of 26 taxa were collected from the Tukituki River. The leptophlebiid mayfly larvae *Deleatidium* spp. (Ephemeroptera) comprised the greatest total abundance of the fauna (Fig. 3a–d). The larvae of the riffle beetle Elmidae (Coleoptera), the Chironomidae *Tanytarsus* sp. and *Maoridiamesa* sp. (Diptera), and the caddisflies *Aoteapsyche* spp., *Oxyethira albiceps* and *Pycnocentrodes* spp. (Trichoptera) were collected in moderate numbers from all Tukituki sites.

Twenty-six taxa were collected from the Waipawa River and, although *Deleatidium* was numerically most abundant, Elmidae, *Pycnocentrodes*, *Tanytarsus* and *Maoridiamesa* were also collected during the course of the study (Fig. 4a–d). Species eveness (i.e., Simpson's scores) was low throughout the sampling period ($F_{3,3} = 3.48$; $p = 0.07$) (Table 2), but significant interactions were identified between sampling occasion and river ($F_{3,9} = 1.17$; $p = 0.03$), suggesting that species eveness changed differently between rivers. By comparison, species richness (Margalefs' index scores) was similar between sampling occasion ($F_{3,9} = 0.96$; $p = 0.49$) and between treatments ($F_{3,9} = 1.89$; $p = 0.11$) (Table 2). A significant interaction for species richness was observed between sampling occasion and dewatered treatment ($F_{3,9} = 4.16$; $p = 0.02$).

### *Invertebrate abundance*

The total number of individuals (Fig. 2c and d) was significantly higher in the Waipawa River than the Tukituki River ($F_{1,3} = 369.4$, $p < 0.01$). The lowest mean number of individuals was present on day 14 for treatments dewatered for 6 and 10 weeks in the Tukituki, and treatments dewatered for 10 and 14 weeks in the Waipawa ($F_{3,9} = 54.01$, $p < 0.01$). Invertebrate abundance was significantly highest in the reference sites and lowest in treatments dry for 14 weeks in both rivers overall ($F_{3,9} = 21.36$; $p < 0.01$). However, an interaction was observed between the time of sampling and river sampled ($F_{3,9} = 22.72$; $p < 0.01$), and dewatered treatment and river sampled ($F_{3,9} = 63.15$; $p < 0.01$). The interactions indi-

*Table 2.* Mean species richness (Margalef's index) and species eveness (Simpsons index) for the Tukituki and Waipawa Rivers between dewatered treatments and sampling occasions calculated from the benthic invertebrate taxa (North Island, New Zealand)

| | Tukituki | | | | Waipawa | | | |
|---|---|---|---|---|---|---|---|---|
| | 7 days | 14 days | 28 days | 42 days | 7 days | 14 days | 28 days | 42 days |
| *Richness* | | | | | | | | |
| 0 (reference) | 2.07 | 1.97 | 1.29 | 1.06 | 1.74 | 1.72 | 1.7 | 1.94 |
| 6 weeks | 1.95 | 1.71 | 2.08 | 1.45 | 1.50 | 1.45 | 1.45 | 1.35 |
| 10 weeks | 1.82 | 1.68 | 1.42 | 1.31 | 1.46 | 1.24 | 1.08 | 1.58 |
| 14 weeks | 1.48 | 1.11 | 1.74 | 1.72 | 1.46 | 2.05 | 1.88 | 1.81 |
| *Evenness* | | | | | | | | |
| 0 (reference) | 0.29 | 0.35 | 0.64 | 0.60 | 0.43 | 0.44 | 0.41 | 0.40 |
| 6 weeks | 0.24 | 0.26 | 0.36 | 0.56 | 0.65 | 0.78 | 0.77 | 0.82 |
| 10 weeks | 0.35 | 0.26 | 0.60 | 0.75 | 0.59 | 0.59 | 0.58 | 0.64 |
| 14 weeks | 0.21 | 0.65 | 0.45 | 0.47 | 0.35 | 0.22 | 0.53 | 0.61 |

cated the timing of highest abundance varied between rivers depending on dewatering duration. The interactions indicated that abundance in the Tukituki was lowest on day 14 in sites dewatered for 6 and 10 weeks, while lowest in the Waipawa on day 14 for sites dry for 10 and 14 weeks.

### *Community composition*

With the exception of *Eriopterini* sp. (Diptera) and *Aoteapsyche* between rivers, and sampling occasions, numerical abundance of the most common taxa were significantly different between time, dewatering treatment and river (Table 3). The greatest number of *Deleatidium* were collected on day 42 and the lowest on day 7, whereas Diptera and Elmidae were evenly abundant throughout the experiment. Absolute abundance of higher-order benthic invertebrate groups in the Tukituki (Fig. 3a–d) and Waipawa (Fig. 4a–d) were similar over time between references (Fig. 3a) and sites dry for 6 weeks (Fig. 3b) in the Tukituki; and for references (Fig. 4a) and sites dry for 6 (Fig. 4b) and 10 (Fig. 4c) weeks in the Waipawa. By comparison, Ephemeroptera abundance (i.e., *Deleatidium*) increased more slowly in sites dry for longer periods (i.e., dry for 10 and 14 weeks in the Tukituki and 14 weeks in the Waipawa), with an initial reduction in abundance at day 14. By comparison, Chironomidae (i.e., *Tanytarsus* and *Maoridiamesa*) comprised greater abundance early in sites with longer dewatering duration.

*Table 3.* *F* values testing the hypothesis that the abundance of individual taxa are significantly different between rivers, treatments and sampling occasions for the seven most common taxa collected in the Tukituki and Waipawa Rivers (North Island, New Zealand).

| | River df = 1, 3 | | Dewatered treatment df = 3, 3 | | Sampling occasion df = 3, 9 | |
|---|---|---|---|---|---|---|
| | *F* value | *p* | *F* value | *p* | *F* value | *p* |
| *Deleatidium* spp. | 81.08 | <0.01 | 11.07 | <0.01 | 17.60 | <0.01 |
| Elmidae | 38.36 | <0.01 | 10.74 | <0.01 | 10.16 | <0.01 |
| *Aoteapsyche* spp. | 26.94 | <0.01 | 1.69 | 0.18 | 2.64 | 0.06 |
| *Pycnocentrodes* sp. | 2.83 | 0.10 | 6.79 | <0.01 | 8.48 | <0.01 |
| *Eriopterini* sp. | 1.44 | 0.23 | 12.10 | <0.01 | 2.37 | 0.08 |
| *Tanytarsus* sp. | 214.10 | <0.01 | 5.24 | <0.01 | 18.8 | <0.01 |
| *Maoridiamesa* sp. | 12.72 | <0.01 | 3.32 | 0.02 | 39.10 | <0.01 |

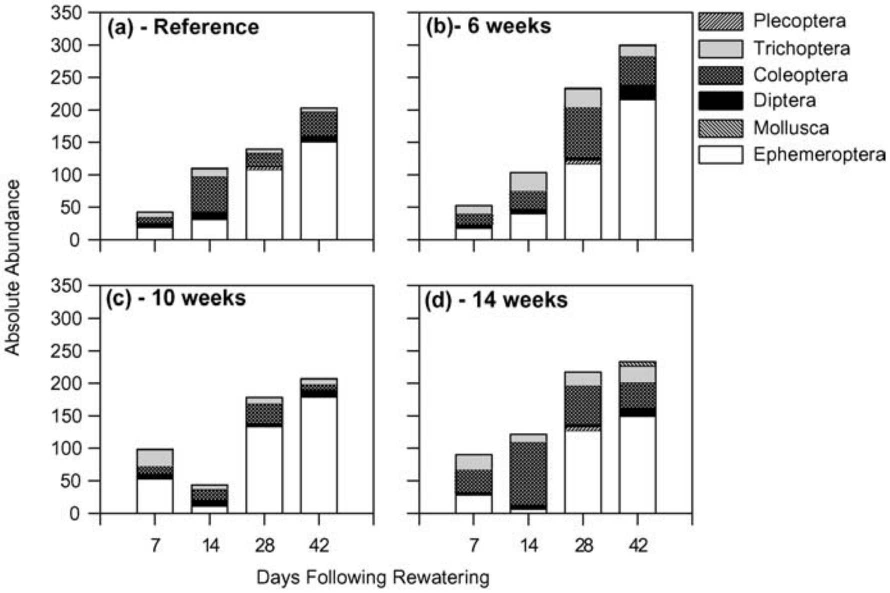

*Figure* 3. Absolute abundance of benthic invertebrates in the Tukituki River (North Island, New Zealand) at a reference site (a) and sites dewatered for 6 (b), 10 (c) and 14 weeks (d) during summer 1997/1998.

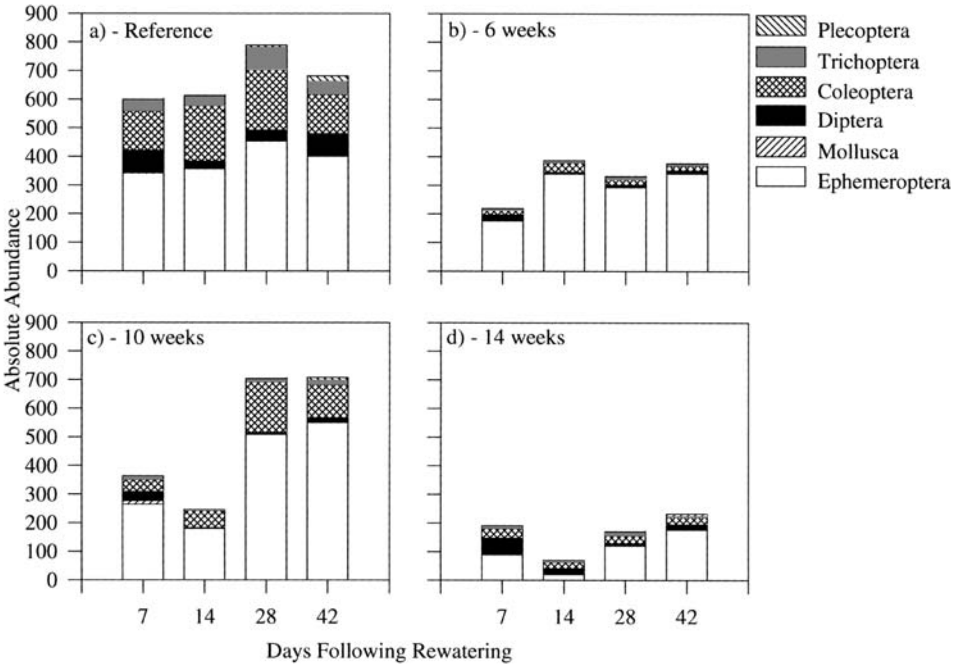

*Figure* 4. Absolute abundance of benthic invertebrates in the Waipawa River (North Island, New Zealand) at a reference site (a) and sites dewatered for 6 (b), 10 (c) and 14 weeks (d) after flow resumed on 3 April 1998.

Sites were grouped during DCA ordination of assemblage structure in the Tukituki (Fig. 5a) and Waipawa (Fig. 5b). Rivers according to the time after rewatering. This pattern was generally

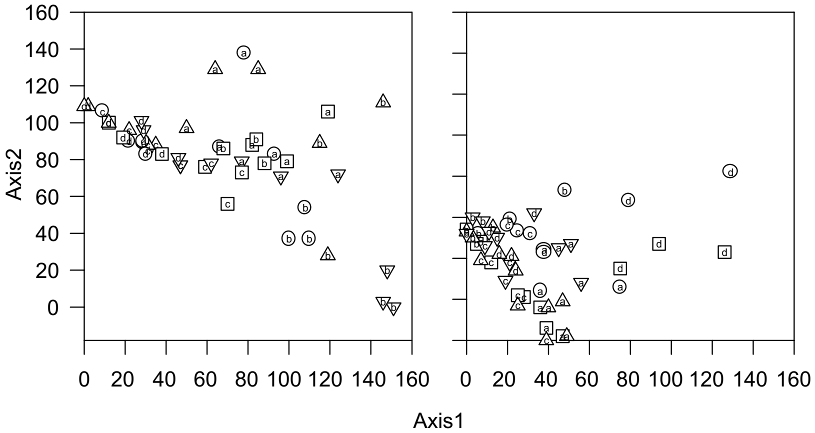

*Figure* 5. DCA of benthic community structure between sites in the Tukituki (a) and Waipawa (b) Rivers (North Island, New Zealand). Shapes represent the duration each site remaining dry, so that circle = reference, square = 6 weeks, triangle = 10 weeks and inverted triangle = 14 weeks.

consistent between the references and dewatered treatments for both rivers. Overall, samples collected 7 and 14 days after rewatering showed a greater spread along Axis 1 (to the right), while sites collected 28 and 42 days after rewatering had low scores on Axis 1. Samples in the Tukituki with high scores on Axis 1 were associated with greater number of *Aoteapsyche*, *Tanytarsus*, Elmidae and Eriopterini. In contrast, *Maoridiamesa* sp., *Deleatidium* and *Psilochorema* sp. (Trichoptera) were more abundant to the left of Axis 1. Elmidae was also positively correlated with Axis 2. Samples with high scores on Axis 1 in the Waipawa River were associated with greater number of *Tanytarsus, Maoridiamesa* and *O. albiceps*, while *Deleatidium* and *Psilochorema* were more abundant to the left of Axis 1. Elmidae and Eriopterini were more abundant to the bottom (positively correlated) of Axis 2. Conductivity (Tukituki $r = 0.82$; Waipawa $r = 0.46$) and water temperature (Tukituki $r = 0.79$; Waipawa $r = 0.47$) were positively correlated with Axis 1 in both rivers, while dissolved oxygen (Tukituki $r = -0.56$; Waipawa $r = -0.48$) was negatively correlated with Axis 1 in both rivers. Axis 1 accounted for 48.4% (Tukituki) and 32.6% (Waipawa) of the variance in the data, while Axis 2 accounted for 1.7% (Tukituki) and 4.9% (Waipawa) of the variance in the data for the DCA.

Community composition from the Tukituki (MRPP, $r = 0.04$, $p = 0.04$) and the Waipawa (MRPP, $r = 0.35$, $p = 0.01$) were significantly different between dewatering treatments. Community composition was also different between each sampling occasion in the Tukituki (MRPP, $r = 0.36$, $p < 0.02$), but similar in the Waipawa with time (MRPP, $r = 0.03$, $p = 0.11$).

## Discussion

This study investigated the colonisation patterns of the benthos following rewatering in two braided rivers where flows ceased in the river channel for between 6 and 14 weeks. Benthic recovery was predicted to differ between sites with different dewatering duration. This prediction was based on the premise that colonisation and refuge potential of wetted upstream reaches and the hyporheic zone would decline with distance downstream and increasing periods of dewatering (Cooling & Boulton, 1993). The significance of wetted upstream regions as a source of colonists was expected to decline with increasing distance downstream (Gore, 1982) and with increasing duration of channel dewatering. In the present study, length of dewatering did not significantly alter the recovery of taxa numbers in the dewatered sites overall as all taxa were present within 7 days after the return of the surface water, nor was abundance different from the references after 28 days of colonisation. Doeg et al. (1989), investigating substrate disturbance, also found that intensity of disturbance did not affect the rate of overall benthic recovery as much as disturbance duration. However, recovery of individual taxa did change with dewatering duration, with longer dewatered periods favouring different types of colonising taxa in the short term.

Periodic drought conditions may be an important factor affecting diversity patterns in stream systems (Everard, 1996), and the few studies investigating invertebrate recolonisation following dewatering in New Zealand show communities recover rapidly (e.g., Sagar, 1983). The lack of groundwater discharge in the sites surveyed (Hawkes Bay Regional Council, 1999) compared to those in some other systems (e.g., Wood & Petts, 1999; Wright & Symes, 1999) may increase the importance of upstream sources of colonists and the direct disturbance of dewatering on habitat and food resources. The alteration in useable habitat (Jowett & Richardson, 1990) driven by the change in flow volume and the braided channel morphology may have been a significant determinant of benthic community composition at these braided river sites.

The invertebrate composition in braided rivers throughout New Zealand is often dominated by taxa resilient to physical disturbance (e.g., *Dealatidium*), or taxa that are suggested to colonise disturbed sites early (e.g., riffle beetles, Chironomidae) (Sagar, 1986; Quinn & Hickey, 1990; Fowler & Death, 2000). However, the duration of time required for species diversity and abundance to recover following disturbance was similar temporally compared to a system where dewatering occurred for approximately 4 months (refer Extence, 1981; Wright & Symes, 1999). A notable difference between the New Zealand rivers studied and the English chalk streams studied by Wright & Symes (1999) was that the dewatered sites in New Zealand recovered dramatically over a short period. The differing responses of the benthic fauna in different river systems suggest invertebrate recovery may be influenced by the presence of colonists in some sites (Sedell et al., 1990), the environmental conditions present within each river system and the longitudinal extent of dewatering.

Benthic invertebrates rapidly colonised each dry site and the reference sites of the Tukituki and Waipawa, with diversity in the dewatered treatments resembling those in the references within 7 days of rewatering in both braided rivers. However, density was only comparable to the references after 28 days of rewatering. Recovery patterns suggest animals such as Diptera (*Tanytarsus*) and Coleoptera (Elmidae) larvae were initially the most abundant benthic colonists before declining in abundance after 14 days. In contrast, Ephemeroptera (*Deleatidium*) became numerically dominant towards the end of the study, but were less common earlier in the study. Ephemeroptera were consistently most abundant in the reference sites and those dry for 6 weeks, but the proportion of Ephemeroptera was lower in the first 14 days after rewatering in sites that were dry for 10 and 14 weeks in the Tukituki and 14 weeks in the Waipawa. This was in contrast to findings of Sagar (1983), where *Deleatidium* rapidly colonised the denuded benthos in a South Island (New Zealand) river. However, in the alluvial gravels of the southern Hawkes Bay (North Island, New Zealand), longer dewatering periods and lowering of the water table may have influenced some sources of potential benthic colonists, especially for *Deleatidium*, which may commonly colonise from the hyporheic zone (Fowler, 2002). Alternatively, fewer *Deleatidium* may have colonised the sites dewatered for longer because of the lower algal standing crop compared to reference sites and those dewatered for a short period.

The increase in abundance of *Deleatidium* with time was consistent in both rivers and for a nearby braided river (approximately 8 km south west of the Waipawa and Tukituki Rivers). Fowler (2002) used artificial substrates in the Makaretu River to assess the influence of different sources of colonists on benthic community recovery, showing that riffle beetle larvae (i.e., Elmidae) appeared rapidly in the artificial baskets in the Makaretu. The early abundance of Elmidae suggested this taxon may colonise primarily by drift and crawling, or that riffle beetles are more resistant to desiccation than mayflies (i.e., *Deleatidium*) (refer to Fowler, 2002 for explanation of methods). In contrast, the lower proportion of mayflies in sites dry for 10 and 14 weeks during the first 14 days after rewatering in the current study river may be due to lower resilience to desiccation, and/or the inadequate food resources (e.g., algal propagules) for such taxa.

Previous authors have also noted that mayflies (i.e., *Baetis* spp.) and certain other invertebrates may seek refuge (i.e., from discharge increase) within bed substrates (Lehmkuhl & Andersen, 1972; Goedermakers & Pinkster, 1981). This may explain why many invertebrates can rapidly recolonise the benthos after disturbances such as floods in some systems (e.g. Williams & Hynes, 1976; Sagar, 1986; Scrimgeour et al., 1988). Benthic animals may also colonise from eggs left in dewatered substrates as long as these do not become desiccated in the dry riverbed, or are adapted to drying. However, the current study suggests that recovery could be slower in sites dewatered for longer periods because dewatering may have removed the hyporheic zone as a colonisation source. If this is the case then invertebrate recovery would be heavily reliant on wetted upstream regions (i.e., drift), aerial oviposition or crawling. Benthic recovery was rapid in all sites in the Waipawa and Tukituki, but sites dry for 10 and 14 weeks showed different recovery patterns for individual taxa compared to reference sites or those dewatered for short periods. Thus, the rapid benthic community recovery was probably the result of drifting invertebrates (Williams & Hynes, 1976; Brittain & Eikeland, 1988), and the hyporheic zone. Whereas the recovery of sites dewatered for longer may have relied more heavily on upstream sources and were more restricted by available food resources compared to reference sites and those dewatered for short periods.

The algal standing crop was measured following variable periods of dewatering of the streambed within the two sampled rivers. Mosisch (2001) found that desiccation is a significant factor controlling periphyton communities in stream systems, with periphyton recovery not expected for periods over 30 days in some rivers. After rewatering, the photosynthetic pigments indicated algal biomass was low early in all Tukituki and Waipawa sites, including the reference sites, but was consistently higher in the reference sites over the period of recovery because low flows and warm temperatures allowed a visibly abundant periphyton community to persist. Overall, algal biomass increased steadily over time in both rivers, but increased in biomass more readily in the reference sites due to the persistence of a low periphyton standing crop. In contrast, algal biomass recovered more slowly where no standing crop was present because algae must first reach the denuded sites from upstream. This study also suggests that the algal communities had not recovered from the dewatering disturbance after 42 days of recovery in the dewatered sites surveyed, but algal recovery was considered complete in the reference sites. The variable time taken for algal recovery may have important implications for invertebrate/algal interactions and the ability of some taxa to persist within a sampled site through resource (i.e., food and habitat) availability. For example, Chironomidae larvae are generally more abundant where algal biomass is high because these taxa are more capable of utilising the larger algal standing crop as a food and habitat resource. By comparison, mayflies are more common with low algal standing crops (e.g., Winterbourn, 1990; Botts, 1993; Quinn et al., 1997).

Overall, invertebrates rapidly colonised each denuded site after rewatering, and although some invertebrates were numerically dominant at different times, 95% of the taxa list were present after 7 days of rewatering. Absolute animal abundance also rapidly increased over time, but significantly greater numbers were collected in the reference sites and sites dry for 6 weeks compared to sites previously dry for longer periods. The pattern of invertebrate community recovery indicated that sites dewatered for short periods (and references) probably relied on a combination of wetted upstream reaches and the hyporheic zone for sources of colonists. Whereas sites dewatered for longer periods were more heavily reliant on wetted upstream sources of invertebrate colonists for recovery, thereby altering the type of taxa present in these sites in the short term (i.e., < 28 days). The greater abundance of *Deleatidium* in sites dewatered for a short time may be because desiccation was less significant at determining taxa present at these sites, or that reference sites provided a closer source of colonists and periphyton propagules to allow a more rapid recovery of this taxon. In contrast, Elmidae dominated communities at sites dewatered for longer because Elmidae may be more resilient to desiccation than *Deleatidium*. These data suggest that the duration of dewatering may regulate taxonomic composition in the short term by subjecting taxa to desiccation and/or food resource restrictions, but not in the long term because food resources recovered over time and sites with similar physicochemical conditions should have similar communities.

## Acknowledgements

I would like to thank Mike Scarsbrook and Russell Death for manuscript review, along with Gil Coombe and Melanie Norgate for assistance in the field. Comments from Mike Winterbourn, Andrew Boulton and Alastair Robertson also greatly improved an earlier draft of this manuscript. The paper has also benefited greatly from reviews by H. J. Dumont and an annonymous referee for which I am grateful. A grant from the Hawkes Bay Regional Council (New Zealand) and postgraduate funding from the Institute of Natural Resources – Ecology, Massey University, Palmerston North (New Zealand) supported this research.

## References

Abell, D. L., 1984. Benthic Invertebrates of Some California Intermittent Streams. Davis Institute of Ecology, CA.

Beals, E. W., 1984. Bray–Curtis ordination: an effective strategy for analysis of multivariate ecological data. Advances in Ecological Research 14: 1–55.

Berry, K. J., K. L. Kvamme & P. W. Mielke Jr., 1983. Improvements in the permutation test for spatial analysis of distribution of artifacts into classes. American Antiquity 48: 547–553.

Botts, P. S., 1993. The impact of small chironomid grazers on epiphytic algal abundance and dispersion. Freshwater Biology 30: 25–33.

Boulton, A. J., 1989. Over-summering refuges of aquatic macroinvertebrates in two intermittent streams in central Victoria. Transactions of the Royal Society of South Australia 113: 23–34.

Boulton, A. J., H. M. Valett & S. G. Fisher, 1992. Spatial distribution and taxonomic composition of the hyporheos of several Sonoran Desert streams. Archiv für Hydrobiologie 125: 37–61.

Boulton, A. J. & E. H. Stanley, 1995: Hyporheic processes during flooding and drying in a Sonoran Desert stream. Archiv für Hydrobiologie 134: 27–52.

Brittain, J. E. & T. J. Eikeland, 1988. Invertebrate drift – a review. Hydrobiologia 166: 77–93.

Cairns, J., J. S. Crossman, J. L. Dickson & E. E. Herricks, 1971. The recovery of damaged streams. Association of the Southeastern Biological Bulletin 18: 79–106.

Clifford, H. T. & W. Stevenson, 1975. An Introduction to Numerical Classification. Academic Press, London, England.

Cooling, M. P. & A. J. Boulton, 1993. Aspects of the hyporheic zone below the terminus of a South Australian arid-zone stream. Australian Journal of Marine and Freshwater Research 44: 411–426.

Cowx, I. G., W. O. Young & J. M. Hellawell, 1984. The influence of drought on the fish and invertebrate populations of an upland stream in Wales. Freshwater Biology 14: 165–177.

Doeg, T. J., P. S. Lake & R. Marchant, 1989. Colonisation of experimentally disturbed patches by stream macroinvertebrates in the Acheron River, Victoria. Australian Journal of Marine and Freshwater Research 14: 207–220.

Everard, M., 1996. The benefits of drought on the aquatic environment. Freshwater Forum 7: 33–50.

Extence, C. A., 1981. The effect of drought on benthic invertebrate communities in a lowland river. Hydrobiologia 83: 217–224.

Fowler, R. T., 2002. The 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(3).

Fowler, R. T. & R. G. Death, 2000. The effects of channel morphology on temporal variation in invertebrate community structure in two North Island, New Zealand Rivers. New Zealand Journal of Marine and Freshwater Research 34: 231–240.

Godermakers, A. & S. Pinkster, 1981. Population dynamics of three gammarid species (Crustacea: Amphipoda) in a French chalk stream. Migration. Bijdr. Dierk. 51: 145–180.

Gore, J. A., 1982. Benthic invertebrate recolonisation: source distance effects on community composition. Hydrobiologia 94: 183–194.

Graham, A. A., D. J. McCaughan & F. S. McKee, 1988. Measurement of stone surface area of stones. Hydrobiologia 157: 85–87.

Hawkes Bay Regional Council, 1999. Ruataniwha Plains Conceptual Hydrological Model. Pattle Delamore, Technical Report, No. ISSN 1174-3077.

Jowett, I. G. & J. Richardson, 1990. Microhabitat preferences of benthic invertebrates in a New Zealand river and the development of instream flow-habitat models for *Deleatidium* spp. New Zealand Journal of Marine and Freshwater Research 24: 19–30.

Lake, P. S. & L. A. Barmuta, 1986. Stream Benthic Communities: Persistent Presumptions and Current Speculations. Dr W. Junk Publishers, Melbourne, Australia.

Lake, P. S., T. J. Doeg & R. Marchant, 1989. Effects of multiple disturbance on macro-invertebrate communities in the Acheron River, Victoria. Australian Journal of Ecology 14: 507–514.

Lancaster, J. & A. G. Hildrew, 1993. Flow refugia and microdistribution of lotic macroinvertebrates. Journal of the North American Benthological Society 12: 385–393.

Larimore, R. W., W. F. Childers & C. Hechrote, 1959. Destruction and re-establishment of stream fishes and invertebrates affected by drought. Transactions of the American Fisheries Society 88: 262–285.

Lehmkuhl, D. M. & N. H. Andersen, 1972. Microdistribution and density as factors affecting the downstream drift of mayflies. Ecology 53: 661–667.

Mackay, R. J., 1992. Colonisation of lotic macro-invertebrates: a review of processes and patterns. Canadian Journal of Fisheries and Aquatic Sciences 49: 617–628.

Malicky, H., 1982. Adaptations of two stonefly species to intermittent streams in Crete. Ann. Mus. Goulandris 5: 179–182.

Marchant, R., P. S. Lake & T. J. Doeg, 1991. Longitudinal variation in recolonisation rates of macro-invertebrates along an upland river in southeastern Australia. Freshwater Biology 25: 349–356.

McCune, B. & J. B. Grace, 2002. Analysis of Ecological Communities. MjM Software Design, Gleneden Beach, Oregon.

McCune, B. & M. J. Mefford, 1999. PC-ORD 4.0. Multivariate Analysis of Ecological Data. MjM Software Design, Gleneden Beach, Oregon, USA.

Mielke, P. W. Jr., 1984. Meteorological applications of permutation techniques based of distance functions. In Krishnaiah, P. R. & P. K. Sen (eds), Handbook of Statistics, Vol. 4. Elsevier Scientific Publishers, 813–830.

Mosisch, T. D., 2001. Effects of desiccation on stream epilitihic algae. New Zealand Journal of Marine and Freshwater Research 35: 173–180.

Moss, B., 1967a. A spectrophotometric method for the estimation of percentage degradation of chlorophylls to phaeo-pigments in extracts of algae. Limnology and Oceanography 12: 335–340.

Moss, B., 1967b. A note on the estimation of chlorophyll *a* in freshwater algal communities. Limnology and Oceanography 12: 340–342.

Power, M. E., R. J. Stout, C. E. Cushing, P. P. Harper, F. R. Hauer, W. J. Matthews, P. B. Moyle, B. Statzner, I. R. Badgen & Wais de Bagden, 1988. Biotic and abiotic controls in river and stream communities. Journal of the North American Benthological Society 7: 456–479.

Quinn, J. M. & C. W. Hickey, 1990. Magnitude effects of substrate particle size, recent flooding, and catchment development on benthic invertebrates in 88 New Zealand rivers. New Zealand Journal of Marine and Freshwater Research 24: 411–427.

Quinn, J. M., A. B. Cooper, R. J. Davies-Colley, J. C. Rutherford & R. B. Williamson, 1997. Land use effects on habitat, water quality, periphyton and benthic invertebrates in Waikato, New Zealand, hill-country stream. New Zealand Journal of Marine and Freshwater Research 31: 579–597.

Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace & R. Wissmar, 1988. The role of disturbance in stream ecology. Journal of the North American Benthological Society 7: 433–455.

Sagar, P. M., 1983. Invertebrate recolonisation of previously dry channels in the Rakaia River. New Zealand Journal of Marine and Freshwater Research 17: 377–386.

Sagar, P. M., 1986. The effect of floods on the invertebrate fauna of a large, unstable braided river. New Zealand Journal of Marine and Freshwater Research 20: 37–46.

Scrimgeour, G. J., R. J. Davidson & J. M. Davidson, 1988. Recovery of benthic macro-invertebrate and epilithic communities following a large flood, in an unstable, braided, New Zealand river. New Zealand Journal of Marine and Freshwater Research 22: 337-344.

Sedell, J. R., G. H. Reeves, F. R. Hauer, J. A. Stanford & C. P. Hawkins, 1990, Role of refugia in recovery from disturbances: modern fragmented and disconnected river systems. Environmental Management 14: 711–724.

Simpson, E. H., 1949. Measurement of diversity. Nature 163: 688.

SYSTAT, 1998. SYSTAT. Evanston IL, USA, SYSTAT Inc. 1800 Sherman Ave.

Williams, D. D., 1977. Movements of benthos during the recolonisation of temporary streams. Oikos 29: 306–312.

Williams, D. D. & H. B. N. Hynes, 1976. The recolonisation mechanisms of the stream benthos. Oikos 27: 265–272.

Williams, D. D. & M. R. Smith, 1996. Colonisation dynamics of river benthos in response to local changes in bed characteristics. Freshwater Biology 36: 237–248.

Winterbourn, M. J., 1987. Chapter 6. Wellington, New Zealand, DSIR Scientific Information Publication Centre.

Winterbourn, M. J., 1990. Interactions amount nutrients, algae and invertebrates in a New Zealand mountain stream. Freshwater Biology 23: 463–474.

Winterbourn, M. J. & K. D. L. Gregson, 1989. Guide to the aquatic insects of New Zealand. Bulletin of the Entomological Society of New Zealand 9. 94.

Winterbourn, M. J., J. S. Rounick & B. Cowie, 1981. Are New Zealand streams really different? New Zealand Journal of Marine and Freshwater Research 15: 321–328.

Wood, P. J. & G. E. Petts, 1999. The influence of drought on chalk stream macroinvertebrates. Hydrological Processes 13: 387–399.

Wright, J. F. & K. L. Symes, 1999. A nine-year study of the macroinvertebrate fauna of a chalk stream. Hydrological Processes 13: 371–385.