The impacts of reduced flow on instream habitat condition and macroinvertebrate behaviour

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Alexander Bryan Wilfried James
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Abstract

The allocation of water and setting of minimum flows is a contentious issue. Despite this, there is little research into the impacts of reduced stream flows on instream habitat and biota. Previous studies tend to concentrate on fish or macroinvertebrate community structure with few studies investigating the behavioural responses of macroinvertebrates to flow reduction. Therefore the aim of my thesis was to assess the impact of severe flow reduction on habitat condition and macroinvertebrate behaviour (drift and refugia use) using before-after, control-impact (BACI) experimental manipulations in natural (Wairarapa, New Zealand) and artificial stream channels (Canterbury, New Zealand). Instream channels were also used to assess the impact of flow reduction duration and magnitude on macroinvertebrate community structure and vertical distribution in the substrate. Reduced flow tended to decrease depth, velocity, and wetted width and increase fine sediment deposition. However, the common assertion that it would lead to increased temperatures and lowered dissolved oxygen levels was not supported by my results, although this may occur in some streams. I found that severely reduced flow in small streams had minimal effect on water temperature, although it can depress nighttime dissolved oxygen minima. Flow reduction markedly increased the drift propensity of some taxa immediately following flow reduction, before it fell back to near background levels for the rest of the reduced flow period. This increased drift occurred as animals redistributed themselves to more suitable microhabitats within the stream. Additionally, flow reduction reduced the drift distance of animals making it unlikely that drifting would be a viable way of escaping low flow conditions. Flow reduction had no impact on the densities or vertical distribution of animals within the substrate, however, most species were present at all depths sampled in the hyporheic zone, providing a source of colonists should some event (flood or drying) denude the benthos of animals. An instream channel experiment showed that apart from changes to the relative abundances of a few common taxa, flow reduction magnitude (up to 98% reduction) had little impact on the macroinvertebrates of a lowland river. Overall, my results suggested that severe flow reduction stresses a number of taxa, causing them to drift as they redistribute themselves within the stream. I found no evidence that animals actively seek refuge in the hyporheic zone, and in a lowland river, the magnitude and duration of flow reduction had minimal effect on the macroinvertebrate community.

Acknowledgements

I express my appreciation to my main supervisor Russell Death who has provided guidance and encouragement as well as occasional discouragement. I particularly liked Russell's hands-off approach that allowed me to develop my own ideas and organise my own business. I thank Ian Henderson, Mike Joy and the various students who have gone through the 'Stream Team' over the last few years for their advice and critical comment. I also appreciated the help of Massey University Ecology staff, especially Erica Dahya who helped organise various things and Barbara Just who helped me purchase all the equipment I required and was great at organising funding to attend numerous conferences. I am grateful for the Massey University Doctoral Scholarship that supported me for three years although it is a shame these scholarships do not go for four years which is a more realistic timeframe to produce a quality Ph.D. thesis.

I would not have been able to produce this work without the logistical and emotional support of Zoë Dewson who for the last 9 ½ years has shared all aspects of my life including this project. Stanley (English Cocker Spaniel) and Archer (Schnauzer) have provided much amusement and a welcome distraction. They ensure I get up early and many ideas have come to me whilst walking them. My parents, Hertha and Bryan James have provided endless encouragement, financial and logistical support. Zoë's parents have always been encouraging and I thank them for letting me have their daughter.

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I thank John Richardson and Carin Bondar at the University of British Columbia for logistical support and access to the streamside channels in the Malcolm Knapp Research Forest where I conducted the short-term experiment included in Chapter 3. I thank Alastair Suren of the National Institute of Water and Atmosphere who allowed me to collaborate on the experiment that has formed Chapter 5.

Lastly I thank the numerous anonymous reviewers from journals I have submitted manuscripts to for their comments and suggestions.

Thesis structure and authorship note

This thesis consists of a series of manuscripts each produced for publication in relevant journals. Thus, there is a certain amount of repetition especially in the methods sections. The numbering of figures, tables and photographic plates restarts at the beginning of each chapter. Manuscripts are co-authored to acknowledge the input of others as appropriate. My main thesis supervisor, Russell Death was instrumental in the design and funding of the New Zealand flow reduction experiment and the idea of the Canadian streamside channel experiment originated with him. Russell edited manuscripts and provided guidance on all aspects of my work. Zoë Dewson completed her Ph.D. thesis alongside mine using the same experimental setup (natural channel severe flow reduction) thus she helped with all the fieldwork. She also processed the benthic invertebrate samples while I processed all drift, hyporheic and pool samples. The literature review that forms chapter 1 originated from Russell's idea to combine two separate reviews on macroinvertebrate community (ZD) and individual (AJ) responses to flow reduction into one complete review for publication. Zoë and I had the greatest and equal input into this review. I was responsible for all aspects (design, fieldwork, sample processing, and analysis) of Chapters 2, 3 and 4. Chapter 5 was the result of a collaborative experiment with Alastair Suren of NIWA. Alastair designed and installed the experiment whilst I assisted in the sampling, processed all the samples, conducted all the analyses of biotic data and wrote the manuscript. Alastair did much of the abiotic analysis, wrote some parts of the methods (abiotic measurements), and had editorial input.

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PDF file of published paper derived from Chapter 1

PDF file of published paper derived from Chapter 3A

PDF file of published paper derived from Chapter 4

General Introduction

Humans have been always been preoccupied with water. Initially, a reliable source of water could only be ensured by dwelling near a river, stream or lake. With the advent of agriculture and permanent settlements, rainfall alone often could not provide enough water for crops and sustenance. Thus began the human appropriation of the world's freshwater resources that continues today. Early efforts involved simple techniques such as hand watering which evolved into the use of canals and ditches to divert water to where it was required. With the industrial revolution and rapid increase in population seen in the last few centuries, the appropriation of water has grown exponentially so that humans now take more than half of all accessible runoff (Postel *et al.*, 1997). In the past, little thought was given to the effects of damming and diverting flow on river ecosystems. Some of the world's larger rivers (e.g. Nile, Ganges, Yellow) no longer flow to the sea for part of the year because so much water is diverted (Postel *et al.*, 1997). In order to sustain large human populations in arid regions, water may be diverted for hundreds of kilometres. For example, water from the Colorado basin provides municipal supply for the desert city of Las Vegas (Plate 1) and some of Los Angeles.

In recent decades water managers have shown a growing acceptance that rivers are legitimate 'users' of water. There is also increased public demand for the preservation of the aesthetic, recreational and cultural features of waterways (Baron *et al.*, 2002; Richter *et al.*, 2003). Through environmental flow assessment, water managers attempt to balance the needs of river ecosystems with the needs of those who wish to take water. Whatever approach is adopted in setting flows for a particular river, be it simple hydrological, hydraulic habitat or ecosystem encompassing 'holistic' methods (e.g. Poff *et al.*, 1997; Arthington *et al.*, 2003), some knowledge of biotic and abiotic responses to flow alteration is required if biologically relevant flows are to be set. Often environmental flow assessment revolves around the setting of minimum flow levels at which water abstraction must cease or reduce. Despite this being a contentious, often controversial issue, there is little research into the impacts of reduced stream flows on river habitat and biota, with the exception of economically important fish species and larger damming projects. Bunn & Arthington (2002) state, "Currently, evidence about how rivers function in relation to flow regime and the flows that aquatic organisms need exists largely as a series of untested hypotheses".

Plate 1. The irrigation of an amenity garden (and pavement) on 'The Strip' in Las Vegas (11/6/06). Prudent use of water appropriated from the Colorado River basin?

While the development of large irrigation and hydroelectric schemes gets public scrutiny and media coverage, innumerable smaller water takes and diversions for municipal supply and small-scale irrigation tend to go unnoticed and unstudied. In New Zealand, most effort has gone into modelling and researching appropriate flows in large rivers (e.g. Jowett *et al*., 1991). Such models and findings may not apply in smaller streams and currently there are no simple methods for setting flows in small streams even though the ecological value of small streams can be high (Ministry for the Environment, 1998). In New Zealand, the demand for water from small streams usually peaks during summer when streams are naturally running low and particularly vulnerable to increased water temperature and algal proliferation. If we wish to protect smaller waterways from over extraction by allocating sensible volumes of water then more research is essential.

The removal of water can alter various aspects of the instream environment, including water velocity, depth and wetted width (e.g. Gore, 1977; Cowx, 1984; Kinzie *et al*., 2006), rates of sedimentation (Wood & Petts, 1999) and water temperature (Rader & Belish, 1999). Such physicochemical variables can be important in structuring macroinvertebrate communities. For example, in New Zealand, stoneflies tend to be absent from streams that attain temperatures greater than 19ºC (Quinn & Hickey, 1990). Thus flow reduction, through changes to habitat, will affect macroinvertebrates at the individual and community level. In response to flow reduction, some invertebrates may enter the water column and drift downstream (e.g. Minshall & Winger, 1968). It has also been hypothesised that some animals may move into the hyporheic zone (wetted interstitial zone below and alongside rivers) to avoid harsh surface conditions (Brunke & Gonser, 1997; Boulton *et al*., 1998). Additionally, the duration and magnitude of a reduced flow period is important in determining its impact. Intuitively, the longer and more severe a flow reduction, the greater effect it will have on stream biota.

Previous studies of flow reduction impacts in smaller streams are generally either observational assessments of the effects of drought (e.g. Caruso, 2002; Dahm *et al*., 2003) or surveys involving sampling upstream and downstream of some pre-existing structure that removes water (e.g. McIntosh *et al*., 2002; Dewson *et al*., 2003). Few experimental studies that allow before and after reduction sampling in non-reduced (control) and reduced (impact) reaches (BACI design, see Downes *et al*., 2002) have been conducted. Additionally, previous work tends to be poor at measuring the impacts of flow reduction on instream habitat condition, especially important variables such as temperature and dissolved oxygen concentration. While most previous studies investigate changes to macroinvertebrate abundance and community composition, few contemplate the impacts of flow reduction on invertebrate behaviour.

To address the lack of knowledge on the impacts of reduced flow on small stream habitat and macroinvertebrate behaviour, the goal of this thesis was to investigate the impact of severe flow reduction (but not complete drying) on habitat condition and the drift behaviour and hyporheic zone usage of benthic macroinvertebrates. I hypothesised that flow reduction would decrease the preferred habitat of some taxa leading to increased drift and that some taxa would move deeper in the substrate in an attempt to escape unfavourable surface conditions and avoid potential drying of the surface. I also expected that the greater the magnitude of flow reduction, the greater the impact on macroinvertebrate community composition and structure.

The objectives of this study were to:

1. Review the literature about the consequences of reduced flow on instream habitat condition and aquatic macroinvertebrates (Chapter 1).

2. Investigate the impact of severe flow reduction in natural streams by creating diversions and collecting before-after, control-impact information to:
    - Assess the impact of severe reduced flow on instream habitat condition especially temperature and dissolved oxygen (Chapter 2).
    - Test a computer program (Water Allocation Impact On River Attributes – WAIORA) that predicts flow related changes to hydraulic habitat, temperature, dissolved oxygen levels and the abundance of certain taxa (Chapter 2).
    - Assess the influence of flow reduction on macroinvertebrate drift propensity and distance (Chapter 3).
    - Examine how flow reduction influences macroinvertebrate usage of the hyporheic zone and pools (Chapter 4).
3. Use instream channels to investigate the impact of magnitude and duration of flow reduction on:
    - Benthic macroinvertebrate abundance and use of the hyporheic zone (Chapter 5).

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Chapter 1

A review of the consequences of decreased flow for instream habitat and macroinvertebrates

This chapter has been published in the Journal of the North American Benthological Society as:

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Abstract

The effects of drought on stream invertebrates have been reviewed, but the effects of artificially reduced flows have not. We addressed this knowledge gap by reviewing the literature on the effects of natural low flows and artificially reduced flows (without complete cessation of flow). We considered the effects of low water volume on habitat conditions and on invertebrate community structure, behaviour, and biotic interactions. Decreases in discharge usually cause decreased water velocity, water depth, and wetted channel width, increased sedimentation, and changes in thermal regime and water chemistry. Invertebrate abundance increases or decreases in response to decreased flow, whereas invertebrate richness commonly decreases because habitat diversity decreases. Invertebrate species differ in their environmental tolerances and requirements, and any loss of habitat area or alteration of food resources from decreased flow can influence organism behaviour and biotic interactions. Invertebrate drift often increases immediately after flow reduction, although some taxa are more responsive to changes in flow than others. Natural low flows and artificially reduced flow have similar effects on invertebrates, but the severity (duration and magnitude) of the flow decrease can influence invertebrate responses. Certain invertebrate taxa are especially sensitive to flow decreases and might be useful indicators for reduced flows or flow restoration. The effect of low flow on streams is an important issue, but few empirical studies of the impacts of decreased flow on stream ecosystems have been done, and more manipulative experiments are needed in order to understand the ecological consequences of decreased flow.

Introduction

Management of rivers and streams to maintain biological integrity in the face of increasing water extraction is becoming ever more difficult (Baron *et al.*, 2002; Poff *et al.*, 2003a; Richter *et al.*, 2003). Major human uses of water include irrigated agriculture, industry, and household water supply. Humans already use over half of accessible runoff (Postel *et al.*, 1996). The global distribution of water does not coincide with the global distribution of humans. In many countries, available water is insufficient to sustain the population (Postel, 1997). Even greater challenges for water resource management will occur in the future as the global distribution of freshwater resources is altered by climate change (Jackson *et al.*, 2001).

Natural flows span a wide range, including periods of low flow resulting from precipitation deficits. Low flows are often seasonal and occur at a similar time each year (Smakhtin, 2001), but human activities can artificially create or extend low flows that deviate from the natural flow regime. Artificial flow reductions are those created by human activities, such as groundwater extraction, water diversion, or dam closure (e.g. Bickerton *et al.*, 1993; McIntosh *et al.*, 2002). The demand for water often peaks during dry periods of the year when stream flows are naturally low, with the consequence that natural low flows are exacerbated by water extraction (Gasith & Resh, 1999; Suren *et al.*, 2003a, b).

Flowing water is the defining characteristic of streams (Allan, 1995) and clearly has an important influence on aquatic biota (Allan, 1995; Hart & Finelli, 1999). Flow exerts a direct physical force on stream organisms, and affects them indirectly by influencing substrate composition, water chemistry, the delivery rate of nutrients and organic particles (Statzner *et al.*, 1988; Allan, 1995; Hart & Finelli, 1999; Crowder & Diplas, 2000), and habitat availability and suitability (Statzner & Higler, 1986; Hart & Finelli, 1999). Assessing how much water a river needs to prevent adverse effects on the environment while still allowing water abstraction is a task many water resource managers face. However, predicting how the biota will respond to altered flow regimes is difficult (Bunn & Arthington, 2002). Instream flow incremental methodology (IFIM) has been used successfully for salmonids, but its application for invertebrates and other fishes is limited because of difficulties associated with the collection of large numbers of samples, taxonomic identification, and the application of habitat suitability curves to benthic macroinvertebrates (Gore *et al.*, 1998, 2001).

Boulton (2003) and Lake (2003) highlighted the paucity of information available on the effects of drought on stream invertebrates and fish. Seasonal low flows, water extraction, and dams on both large and small regulated rivers have been investigated, but these findings have yet to be synthesised. As a first step in developing strategies for managing water allocation issues, we reviewed published information on the effects of naturally low and artificially reduced flows on instream habitat and invertebrates. My goals were to determine whether consistent abiotic or biotic changes result from natural low flows and artificial flow reductions (Table 1) and to identify variables that have received little attention in studies of decreased flow. First, we considered the effects of decreased water volume on habitat conditions such as water velocity, depth, water temperature, sedimentation, and algae. Then we examined how changes in habitat conditions manifest themselves in patterns of benthic community structure, invertebrate behaviour, and biotic interactions.

Our review includes published literature on natural low flows (droughts, seasonal low flows) and artificially reduced flows (damming, diversion, water abstraction) in permanent streams. Studies in which the stream channel dried completely or the stream was naturally intermittent were excluded because these types of situations would have different consequences for invertebrates (i.e. no surface habitat remaining) than low flow. We did not exclude large rivers and large dams from our review, but the review is biased toward smaller streams because we included only those studies in which the effects of reduced discharge, rather than other aspects of the altered flow regime, were the focus.

Table 1. Summary of the magnitudes and durations of natural and artificial low flows. Where available, stream location, description, and size are included for each stream and a range of sizes is given where more than one stream was studied. Table continued on following page.

Type of low-flow event	Location	Description	Stream size or order	Size of discharge reduction	Duration of flow reduction	Source
Natural	Otago, New Zealand	Various	12 streams with mean annual low flow: 0.2–5.5 m^3/s	Various	4–6 month drought	Caruso, 2002
	Central Wales	Upland stream	Width: 8 m	60% reduction	3 month drought	Cowx *et al.*, 1984
	New Mexico, USA	Spring-fed mountain stream	1st order; <0.001 m^3/s during drought	Various	Analysis of drought from long-term flow records	Dahm *et al.*, 2003
	New York, USA		Permanent stream summer discharge: 0.004–0.081 m^3/s	Up to 94% reduction	Summer flow recession	Delucchi, 1989
	Southeast UK	Lowland stream	Not stated	Not stated	3 month drought	Extence, 1981
	Canterbury, New Zealand	Lowland plains streams	2 streams with median discharge: 3.1–4.6 m^3/s	83–89% reduction	6 week summer flow recession	Suren *et al.*, 2003a, b
	Southeast UK	Chalk stream	Mean discharge: 0.73 m^3/s width: 1.5–8 m	Various	Long-term studies of drought in a chalk stream	Wood & Petts, 1994, 1999 Wood *et al.*, 2000 Wood & Armitage, 2004
	Southeast UK	Chalk stream	Discharge: 0.5–3.6 m^3/s width: 7–10 m	Various	9 year study including a minor and major drought	Ham *et al.*, 1981 Wright & Berrie, 1987 Wright & Symes, 1999

Table 1 (continued). Summary of the magnitudes and durations of natural and artificial low flows. Where available, stream location, description, and size are included for each stream, and a range of sizes is given where more than one stream was studied. Table continued on following page.

Type of low-flow event	Location	Description	Stream size or order	Size of discharge reduction	Duration of flow reduction	Source
Artificial	UK	Various	22 streams with discharge: 0.13–15 m^3/s width: 1–40 m	Various	Many years, ongoing	Armitage & Petts, 1992 Castella *et al.*, 1995
	Southeast UK	Chalk stream	3 streams with discharge: 0.01–0.39 m^3/s width: 7–10 m	55–100% reduction	Many years, ongoing	Bickerton *et al.*, 1993
	Southeast France	Regulated Mediterranean river	Mean discharge: 80–190 m^3/s width: 33 m	~60% reduction	Many years, ongoing	Cazaubon & Giudicelli, 1999
	Northwest Portugal	Regulated mountain river	Width: 6–33 m	Various	Many years, ongoing	Cortes *et al.*, 2002
	North Island, New Zealand	Lowland streams	4 streams with mean annual low flow: 0.06–0.24 m^3/s	22–81% reduction	Many years, ongoing	Dewson *et al.*, 2003
	Montana, USA	Prairie river	Mean discharge: 12.7 m^3/s width: 30 m	60–87% reduction	6 weeks of reduced flow	Gore, 1977
	Kaua'i, Hawaii, USA	Mountain stream	2^{nd}–3^{rd} order	Average 83% reduction, but up to 100%	Many years, ongoing	Kinzie *et al.*, 2006

Table 1 (continued). Summary of the magnitudes and durations of natural and artificial low flows. Where available, stream location, description, and size are included for each stream, and a range of sizes is given where more than one stream was studied.

Type of low-flow event	Location	Description	Stream size or order	Size of discharge reduction	Duration of flow reduction	Source
Artificial continued....	Sweden	Central and northern mountain streams	52 streams with discharge: 0.5–258 m^3/s	92–99.5% reduction	Many years, ongoing	Malmqvist & Englund,1996 Englund & Malmqvist, 1996
	Maui, Hawaii, USA	Mountain stream	2nd order	92–97% reduction	Many years, ongoing	McIntosh *et al.*, 2002
	Switzerland	European Alps stream	Width: 1–7 m	100% of glacial melt water	Dam completed in 1961	Petts & Bickerton, 1994
	Colorado, USA	Rocky Mountains headwater streams	3 streams: 2nd–3rd order	Mild: ~25% reduction; severe: nearly 100% reduction	Dammed and diverted since 1957	Rader & Belish, 1999
Experimental	Oregon, USA		Artificial channel width: 6 m	50–95% reduction	4 week	Corrarino & Brusven, 1983
	California, USA		Base flow: 0.23–0.5 m^3/s; width: 2.0–3.4 m	30–80% reduction	Weirs and diversions manipulated flow over 1 week	Hinckley & Kennedy, 1972 Hooper & Ottey, 1988
	Montana, USA		Summer discharge: ~1 m^3/s	Up to 90% reduction	3 month	Kraft, 1972
	Idaho, USA		1st order; width: 0.5 m	63–100% reduction	4 day	Minshall & Winger, 1968
	Colorado, USA		Autumn discharge: 0.51–0.62 m^3/s	Not stated	2 day	Poff & Ward, 1991 Poff *et al.*, 1991
	Oregon, USA		Artificial channel width: 6 m	50–95% reduction	1–2 week	Ruediger, 1980
	Canterbury, New Zealand		Artificial channel width: 3 m	To base flow of 0.11 m^3/s	5 month	Rutledge *et al.*, 1992

Decreased Stream Flow and Habitat Conditions

Velocity, depth, and wetted width

Decreased discharge causes decreases in water velocity and depth (Table 2). Wetted width typically decreases with discharge, but differences in channel morphology cause considerable variation among and within streams (Larimore *et al.*, 1959; Stanley *et al.*, 1997; Gippel & Stewardson, 1998; Jowett, 1998). For example, a decrease in discharge causes wetted width to decrease in streams with high width-to-depth ratios but causes depth to decrease in streams with lower width-to-depth ratios (Gordon *et al.*, 2004). Occasionally, wetted width does not change in response to decreased flow, and the absence of change is noted particularly because of the important relationship between wetted width and habitat size. For example, wetted width was unchanged below diversions in headwater streams in the central Rocky Mountains, USA (Rader & Belish, 1999) and in an English chalk stream during a major drought (Wright & Symes, 1999) even though discharge decreased substantially. These results suggested that water depth, rather than width, responded to decreases in flow.

Decreases in velocity, depth, and wetted width tend to develop gradually with the onset of natural low flows. However, changes can be sudden when damming or water diversions artificially reduce flow. For example, a 32% reduction in discharge caused average stream width to decrease from 30 m to 7 m downstream from the Tongue River Reservoir Dam in Montana, USA (Gore, 1977). Loss of wetted width decreases available habitat (Cowx *et al.*, 1984; Stanley *et al.*, 1997; Brasher, 2003), reduces habitat diversity (Cazaubon & Giudicelli, 1999), alters habitat suitability (Cowx *et al.*, 1984), and causes the stream ecosystem to contract (Stanley *et al.*, 1997).

Temperature

Solar radiation, wind, and groundwater usually have a greater influence on surface water temperatures at low than at high discharge. Several researchers have suggested that low flows cause water temperatures to increase (Riggs, 1980; Everard, 1996). A model by Meier *et al.*, (2003) predicted a temperature increase downstream of a diversion in a small stream in the Swiss Alps, but empirical evidence to support this assertion is scarce. Water temperature usually increases as discharge decreases during natural droughts (e.g. Cowx *et al.*, 1984). However, increases in air temperatures often co-occur with drought, and the effects of low discharge and high air temperature can be confounded as causes of increases in water temperature during drought. When reductions in flow are artificial, temperatures can be measured simultaneously in reaches with reduced and unreduced flow. Temperatures were higher in reaches with reduced flow than in reaches with unreduced flow in large rivers (Cazaubon & Giudicelli, 1999) and in small streams (Petts & Bickerton, 1994; Rader & Belish, 1999). On the other hand, substantial groundwater inputs can cause streams to become cooler during low or reduced flows when surface runoff is reduced (Grant, 1977; Mosley, 1983; Kinzie *et al.*, 2006). This effect can be particularly strong in small streams where groundwater contributes a high proportion of total discharge (Grant, 1977; Mosley, 1983).

Chemical characteristics

Dissolved oxygen concentrations increase in streams during daylight because of photosynthesis and decrease at night because of respiration. We found no evidence that low or reduced flows affect dissolved oxygen concentrations (Cazaubon & Giudicelli, 1999; Rader & Belish, 1999; Caruso, 2002; Table 2). However, most measurements of dissolved oxygen are made during the day; therefore, the minimum O_2 levels that might stress stream biota are rarely recorded.

Natural low flows are caused by periods of low precipitation in rain-fed streams. In an acidic UK stream, reduced runoff from the surrounding acidic landscape during a period of little rain was implicated as a cause of a rise in the pH in the stream (Woodward *et al.*, 2002). Lower nutrient levels in New Zealand streams were explained by the absence of storms and runoff during a low-flow period (Caruso, 2002). The influence of groundwater on surface-water chemistry can increase when discharge is low and might explain some of the variation found between streams. Decreased stream water nutrient levels were attributed to the relatively greater contribution of low-nutrient groundwater to surface flow during periods of lower discharge (Dahm *et al.*, 2003). In contrast, relatively greater inputs of solute-rich groundwater to surface water during periods of lower discharge can lead to increased electrical conductivity (Rader & Belish, 1999; Caruso, 2002).

Sedimentation

Increased sedimentation is often a consequence of low or reduced flow (Table 2) because lower velocities allow more sediment to settle out of suspension (Wright & Berrie, 1987; Wood & Petts, 1994; Castella *et al.*, 1995; Wood & Armitage, 1999).

Within the confines of catchment geology, substrate size generally increases with water velocity (Jowett, 1992). However, fine sediment deposition occurs on stream margins, the streambed, and within interstitial spaces as flow decreases with the onset of drought (Wood & Petts, 1999). These accumulated fine sediments can remain in the stream if high or flushing flows do not occur (Bickerton *et al.*, 1993; Wood & Petts, 1999). Ham *et al.* (1981) found that sediment that accumulated within *Ranunculus* beds during low flows remained in place when the macrophyte beds receded. In contrast, low flow can decrease sedimentation because suspended sediment levels in the water decrease (Wright & Symes, 1999; Caruso, 2002; Bond, 2004). Turbidity and sediment supply in southern New Zealand streams were lower during periods of low flow when storms that induce runoff and erosion were absent (Caruso, 2002).

Algae and macrophytes

Flow regime is an important determinant of periphyton development in gravel-bed rivers (Biggs & Close, 1989). Water velocity can affect colonisation, production, and loss of periphyton (Biggs & Close, 1989; Jowett & Biggs, 1997), and investigators have found both positive and negative relationships between velocity and periphyton (McIntire, 1966; Poff *et al.*, 1990; Biggs & Hickey, 1994; Jowett & Biggs, 1997). These contrasting results are probably caused by differences in periphyton growth forms among rivers. For instance, dense, prostrate periphyton can increase with velocity because it benefits from increased nutrient delivery rates at higher velocities, whereas filamentous algae decrease as scouring of filaments increases with water velocity (Biggs *et al.*, 1998).

Periphyton typically changes from a low-biomass diatom assemblage to a high-biomass filamentous green algal mat during low or reduced flows. This change occurs in response to increased temperatures, higher nutrient concentrations, and reduced current velocity (McIntire, 1966; Poff *et al.*, 1990; Suren *et al.*, 2003b; Table 2). High flows generally scour periphyton, whereas periphyton can proliferate under low-flow conditions (Biggs, 1985; Biggs *et al.*, 2005). Responses of periphyton to low flow can differ among rivers with different levels of nutrient enrichment. Suren *et al.* (2003b) measured substantial increases in filamentous algae during low flow in a nutrient-enriched river, whereas low-biomass diatoms remained dominant during low flow in an unenriched river. Benthic algal biomass can decrease because of insufficient water when flow reduction is especially severe (Kinzie *et al.*, 2006). Accumulation of epiphytic algae on macrophytes was responsible for retarding macrophyte growth during low discharge in an English chalk stream (Ham *et al.*, 1981).

Table 2. Summary of effects reported in the literature for decreased stream flow on habitat conditions. Table continued on following page.

Variable	Increase	No change	Decrease
Velocity			Minshall & Winger, 1968 Kraft, 1972 Ham *et al.*, 1981 Wright & Berrie, 1987 Bickerton *et al.*, 1993 Malmqvist & Englund, 1996 McIntosh *et al.*, 2002 Brasher, 2003
Depth			Minshall & Winger, 1968 Kraft, 1972 Gore, 1977 Extence, 1981 Cowx *et al.*, 1984 Bickerton *et al.*, 1993 McIntosh *et al.*, 2002 Brasher, 2003 Kinzie *et al.*, 2006
Wetted width		Wright & Symes, 1999 Rader & Belish, 1999 Dewson *et al.*, 2003	Kraft, 1972 Gore, 1977 Cowx *et al.*, 1984 Wright & Berrie, 1987 Stanley *et al.*, 1997 Gippel & Stewardson, 1998 Cazaubon & Giudicelli, 1999 McIntosh *et al.*, 2002 Brasher, 2003 Kinzie *et al.*, 2006
Temperature	Cowx *et al.*, 1984 Petts & Bickerton, 1994 Cazaubon & Giudicelli, 1999 Rader & Belish, 1999 Meier *et al.*, 2003	Kraft, 1972 McIntosh *et al.*, 2002	Grant, 1977 Mosley, 1983 Kinzie *et al.*, 2006

Table 2 continued. Summary of effects reported in the literature for decreased stream flow on habitat conditions.

Variable	Increase	No change	Decrease
Dissolved oxygen		Rader & Belish, 1999 Cazaubon & Giudicelli, 1999 Caruso, 2002	
pH	Close & Davies-Colley, 1990 Woodward *et al.*, 2002	Rader & Belish, 1999	McIntosh *et al.*, 2002
Nutrient concentration			Caruso, 2002 Dahm *et al.*, 2003
Electrical conductivity	Rader & Belish, 1999 Caruso, 2002 Dewson *et al.*, 2003 Kinzie *et al.*, 2006		
Sedimentation	Kraft, 1972 Ham *et al.*, 1981 Wright & Berrie, 1987 Bickerton *et al.*, 1993 Wood & Petts 1994 Castella *et al.*, 1995 Malmqvist & Englund, 1996 Wood & Petts, 1999 Wood & Armitage, 1999	Wright & Symes, 1999	
Suspended sediment			Caruso, 2002 Bond, 2004
Algae	McIntire, 1966 Ham *et al.*, 1981 Biggs, 1985 Poff *et al.*, 1990 Suren *et al.*, 2003b Biggs *et al.*, 2005	Suren *et al.*, 2003b	Kinzie *et al.*, 2006

Decreased Flows and Macroinvertebrates

Invertebrate density

Invertebrate densities change in response to flow. In some cases, natural low flows and artificially reduced flows cause decreases in invertebrate densities (Table 3). For example, reduced-flow sites on large regulated rivers had lower invertebrate densities than sites on unregulated rivers (Englund & Malmqvist, 1996; Malmqvist & Englund, 1996; Cazaubon & Giudicelli, 1999). Invertebrate densities also decreased downstream of diversions in two Hawaiian streams (McIntosh *et al*., 2002; Kinzie *et al*., 2006). McIntosh *et al*. (2002) suggested that density decreased in response to changes in competition and predation because habitat area decreased and food quality and quantity were altered by flow reduction. The same argument could be used to explain decreased invertebrate densities during natural low flows in other small streams (Cowx *et al*., 1984; Wood *et al*., 2000).

In other situations, density of benthic invertebrates increases when flows decrease (Table 3). Reduced wetted area can sometimes explain these increases because individuals are concentrated into a smaller area (Gore, 1977; Wright & Berrie, 1987). However, changes in habitat suitability or food resources can cause invertebrate densities to increase, even when wetted area remains constant (Wright & Symes, 1999; Dewson *et al*., 2003).

Table 3. Summary of effects reported for decreased stream flow on invertebrate communities. Table continued on following page.

Variable	Increase	No change	Decrease
Density	Gore, 1977	Cortes *et al*., 2002	Cowx *et al*., 1984
	Extence, 1981	Suren *et al*., 2003a	Hooper & Ottey, 1988
	Wright & Berrie, 1987		Wood & Petts, 1994
	Rader & Belish, 1999		Englund & Malmqvist, 1996
	Wright & Symes, 1999		Malmqvist & Englund, 1996
	Dewson *et al*., 2003		Cazaubon & Giudicelli ,1999
	Suren *et al*., 2003a		Rader & Belish, 1999
			Wood & Petts, 1999
			Wood *et al*., 2000
			McIntosh *et al*., 2002
			Wood & Armitage, 2004
			Kinzie *et al*., 2006

Table 3 continued. Summary of effects reported for decreased stream flow on invertebrate communities.

Variable	Increase	No change	Decrease
Taxonomic richness		Armitage & Petts, 1992 Cortes *et al.*, 2002 Dewson *et al.*, 2003	Englund & Malmqvist, 1996 Rader & Belish, 1999 Wright & Symes, 1999 Cazaubon & Giudicelli, 1999 Wood & Armitage, 1999 Wood *et al.*, 2000 McIntosh *et al.*, 2002 Wood & Armitage, 2004 Kinzie *et al.*, 2006

Studies that report variable density responses provide some insight into the factors that might influence invertebrate responses to changes in flow (e.g. Armitage & Petts, 1992; Rader & Belish, 1999; Suren *et al.*, 2003a). For example, invertebrate densities and algal resources were compared between two New Zealand rivers with different levels of nutrient enrichment during low flow (Suren *et al.*, 2003b). In the river with high nutrient concentrations, filamentous green algae and invertebrate density increased significantly during summer low flows. In the river with low nutrient concentrations, the diatom-dominated periphyton assemblage supported a stable invertebrate community (Suren *et al.*, 2003b). Thus, responses of food resources, such as algae and organic matter, to low flow can strongly influence invertebrate density responses (Hart & Finelli, 1999; Smakhtin, 2001).

Changes in habitat suitability affect each taxon differently. Thus, the taxonomic composition of the invertebrate community can cause variable density responses to flow reduction. For example, when fine sediments accumulated in a small English chalk stream during a drought, density of *Sialis lutaria* (alder fly larvae) increased and density of *Gammarus pulex* (amphipod) decreased (Wood & Petts, 1994). The severity of flow reduction also can influence the direction of density responses. Rader & Belish (1999) observed that mean invertebrate densities increased 57% downstream of mild diversions, whereas invertebrate densities decreased 50% downstream of severe diversions. The direction of the density responses probably differed because the magnitude of change to habitat suitability varied with the severity of flow reduction.

Invertebrate richness

Low or reduced flows in permanent streams often cause decreases in taxonomic richness (Table 3). Loss of richness can be attributed to loss of habitat types (e.g. fast flows, rapids) during reduced flows (Cazaubon & Giudicelli, 1999; McIntosh *et al.*, 2002). The reduction in richness can be modest if habitat diversity is maintained under extreme low-flow conditions (Wood & Petts, 1999). McIntosh *et al.*, (2002) compared macroinvertebrate communities above and below a diversion in a Hawaiian stream. Taxa preferring fast-flowing cascade habitats were lost downstream of the diversion because their habitats were lost when flow downstream of the diversion was reduced by 92 to 97% during summer (McIntosh *et al.*, 2002). The number of taxa in benthic invertebrate communities in a large river with greatly reduced residual flow was lower than in similar unregulated rivers because braided channel habitats were lost in the regulated river (Cazaubon & Giudicelli, 1999).

The importance of habitat diversity is reinforced by studies comparing multiple streams. For example, water abstraction generally had less effect on the fauna of upland streams than on the fauna of small lowland streams in the UK (Armitage & Petts, 1992). Habitat diversity and connectivity decreased in the lowland streams, whereas a diverse range of suitable microhabitats remained available in the upland streams following water abstraction, and the presence of numerous tributaries facilitated recolonisation in the upland streams.

The effects of low or reduced flow on richness also can vary among habitats within streams. In a perennial section of a UK chalk stream, Wright & Symes (1999) observed that some biotopes (*Berula*, *Ranunculus*, and silt) supported fewer invertebrate taxa than normal during a major drought, whereas taxonomic richness was unchanged in other biotopes (*Callitriche* and gravel).

Changes to instream environments, such as increased water temperature, increased sedimentation, and altered periphyton assemblages might cause changes in taxonomic richness as flow decreases. Cazaubon & Giudicelli (1999) suggested that higher than normal summer water temperatures and larger than usual annual temperature ranges at reduced flow sites contributed to lower invertebrate richness. Wood & Armitage (1999) suggested that richness in a small gravel-bed stream was lower than in other English lowland streams because sediments gradually covered gravel surfaces as flow declined. Species richness in the same gravel-bed stream generally increased with increased flow over a 6-year period (Wood *et al.*, 2000). Taxa with preferences for low water velocities and fine sediments characterised sites during drought years, and taxa with preferences for high velocities and gravel substrate characterised sites during non-drought years (Wood *et al.*, 2000). Englund & Malmqvist (1996) concluded that species richness was lower in sites with reduced flow than in sites with normal flow because food supply for grazing invertebrates was lower at the sites with reduced flow.

Responses of taxonomic richness to low or reduced flow often can be explained by changes to habitat diversity or instream conditions. Channel morphology can strongly influence invertebrate community responses to decreases in flow. A homogeneous section of stream probably maintains its range of habitats during extreme decreases in flow, whereas sections that are more heterogeneous are likely to lose a large proportion of the habitat types that are available during high flows (Wood & Petts, 1994). The severity of the flow reduction will influence invertebrate responses because it affects the amount of habitat lost and the magnitude of change in instream conditions. Rader & Belish (1999) reported strongly reduced richness in severely diverted (almost 100% of flow diverted for 10–11 months) headwater streams of the central Rocky Mountains, USA, but weakly reduced richness in similar streams that were only mildly diverted (25% of flow diverted for 5 months). Castella *et al.* (1995) found that minor abstractions generally had less effect on biota than major abstractions.

Invertebrate community composition

Invertebrate community composition often changes in response to low or reduced flow (Table 4). These changes probably are a result of increased habitat suitability for some species and decreased suitability for others (Gore *et al.*, 2001). Low flows should favour taxa that prefer slower water velocities (Jowett, 1997). For instance, invertebrate assemblages at regulated sites were generally more tolerant of stresses such as oxygen depletion, preferred slower flowing water, and had shorter life cycles than assemblages at unregulated sites (Cortes *et al.*, 2002). In a Hawaiian stream, taxa preferring fast-flowing cascade habitats were lost downstream of a diversion, but the relative abundances of other taxa were unchanged because all dominant taxa decreased in density (McIntosh *et al.*, 2002). Sediment accumulation also influences habitat suitability. Increased sedimentation and a loss of macrophytes were responsible for changes in macroinvertebrate community composition during drought in an English chalk stream (Wright & Berrie, 1987), and increased sedimentation and reduced macrophyte cover were important factors contributing to invertebrate community changes with water abstraction in 22 UK streams (Castella *et al.*, 1995).

Table 4. Summary of studies that have reported changes to invertebrate community species composition in response to decreased stream flow.

Changes in species composition reported	
Gore, 1977	Rader & Belish, 1999
Extence, 1981	Wood & Petts, 1999
Cowx *et al.*, 1984	Wright & Symes, 1999
Wright & Berrie, 1987	Wood *et al.*, 2000
Hooper & Ottey, 1988	Cortes *et al.*, 2002
Bickerton *et al.*, 1993	McIntosh *et al.*, 2002
Wood & Petts, 1994	Dewson *et al.*, 2003
Petts & Bickerton, 1994	Suren *et al.*, 2003a
Castella *et al.*, 1995	Wood & Armitage, 2004
Englund & Malmqvist, 1996	Kinzie *et al.*, 2006

Drift behaviour

If low flow creates unsuitable conditions for invertebrates, individuals might seek refuge or leave the stream reach. Drift enables organisms to escape unfavourable conditions and can occur actively or passively (Brittain & Eikeland, 1988). Passive drift decreases in response to low water velocities during periods of low flow, but many studies have shown that active drift increases during periods of low flow (Table 5). Invertebrates might drift actively at low water velocities because flow is insufficient to meet their nutritional, physiological (Walton, 1980a; Vinikour, 1981; Kohler, 1985), or preferred habitat requirements (Leudtke & Brusven, 1976; Dudgeon, 1983; Brittain & Eikeland, 1988). Active drift can also be caused by predator avoidance behaviour, which can increase at low flows if predator density increases (Peckarsky, 1980; Walton 1980b; Malmqvist & Sjostrom, 1987; Kratz, 1996).

Drift responses to reduced flows differ among taxa. For example, reduced flow increased active drift by some taxa (*Baetis* spp., *Epeorus longimanus*, Simuliidae, *Brachycentrus americanus*) and decreased active drift by other taxa (*Paraleptophlebia heteronea*, *Ephemerella infrequens*, *Triznaka signata*, *Lepidostoma ormea*) (Poff & Ward, 1991). Moreover, some taxa drifted passively because drift density was positively related to flow (Poff & Ward, 1991). Hooper & Ottey (1988) found that the drift rates of many taxa (*Simulium* sp. in particular) increased when discharge was experimentally decreased at night. A sudden reduction in discharge following the closure of the Tongue River Dam was associated with a ten-fold increase in invertebrate drift (Gore, 1977).

Refugia

The hyporheic zone can be a refuge for benthic fauna when surface conditions become unfavourable (e.g. Williams & Hynes, 1974; Boulton *et al.*, 1998). Hyporheic water can provide a thermal refuge for invertebrates because it is often cooler than surface water, a consequence of its high groundwater content and the insulating properties of the substrate (Evans & Petts, 1997). However, Gilpin & Brusven (1976) found no difference between sections of a stream with normal or reduced flow in the abundance of invertebrates colonising hyporheic chambers. Moreover, the vertical distribution of benthic invertebrates within experimental channels was unaffected by surface flow reductions (Ruediger, 1980), and little vertical movement of invertebrates in the substrate of a permanent stream was observed as flow decreased (Delucchi, 1989). These studies suggest that the hyporheic zone is not used as a refuge in permanent streams (Table 5).

Predation and competition

Low or reduced flow can alter the direction and strength of predator–prey and competitive interactions by decreasing water velocity and habitat size (wetted area). Contraction of wetted width as flow decreases can cause invertebrate densities to increase and can lead to increases in predation and competition (Table 5). Extence (1981) attributed increased predator numbers following a severe drought to increased prey density in a lowland English stream. In contrast, prey densities decreased when the hydraulic regime was favourable to the predator within enclosures in a German stream (Peckarsky *et al.*, 1990). Reduced velocities also could remove velocity-mediated predation refugia when predators and prey normally have different velocity preferences. For instance, in laboratory chambers, most encounters between predatory flatworms (*Dugesia dorotocephala*) and their larval black fly (*Simulium vittatum*) prey occurred in slower regions where predation efficiency was greatest (Hansen *et al.*, 1991). The black fly (*Simulium ornatum*) appears to select microhabitats with high current velocities despite a reduction in feeding efficiency because stonefly predation on black flies is eased in high-current microhabitats (Malmqvist & Sackmann, 1996). Zhang *et al.* (1998) found that species richness and abundance of simuliid larvae was greater than predicted at low-flow sites and attributed this result to lower densities of predators and less competition at low-flow sites than at high-flow sites.

Water velocity controls the rate of food delivery for filter feeders (Nowell & Jumars, 1984). For instance, hydropsychid caddisfly larvae tend to aggregate in high-velocity water where feeding rates are higher than in low-velocity water (Georgian & Thorp, 1992). Larvae might react to flow reduction by moving to zones of more rapid flow (Edington, 1965), thereby increasing competition for space and food. Individuals of *Hydropsyche morosa* are less tolerant of conspecifics at low velocities than at high velocities, possibly because of reduced food delivery rates at low velocities (Matczak & Mackay, 1990).

Grazer–periphyton interactions

Water velocity can influence the foraging efficiency of grazers and alter their role in structuring algal assemblages. The velocity differences associated with decreased discharge can influence grazer–periphyton interactions. *Cladophora* (macroalgae) was present in a Michigan stream only when water velocity was greater than 50 cm/s because high velocity impaired the foraging of the crayfish *Orconectes propinquus* (a major herbivore) (Hart, 1992). At low velocities, the grazing caddisfly *Agapetus boulderensis* reduces periphyton biomass and alters the structure of the algal assemblage, but at high velocities, they decrease only biomass (Poff & Ward, 1995). The effect of water velocity on grazing efficiency is species specific. Poff *et al.* (2003b) showed that a caddisfly (*Glossosoma verdona*) was a more effective grazer at higher velocity, whereas the grazing efficiency of two mayflies (*Baetis bicaudatus* and *Drunella grandis*) did not change significantly with velocity. Water velocity also influences the behavioural responses of invertebrates to algal resources. At low velocities, drift of *Helicopsyche borealis* is greater when periphyton levels are low, whereas at high velocities, passive drift is the predominant source of drift and no relationship exists between drift and periphyton levels (Vaughn, 1986).

Table 5. Summary of effects reported for decreased stream flow on invertebrate individuals and populations.

Variable	Increase	No change	Decrease
Drift	Minshall & Winger, 1968 Pearson & Franklin, 1968 Radford & Hartland-Rowe, 1971 Gore, 1977 Ruediger, 1980 Corrarino & Brusven, 1983 Hooper & Ottey, 1988 Poff & Ward, 1991 Poff *et al.*, 1991 Rutledge *et al.*, 1992		Poff & Ward, 1991 Poff *et al.*, 1991 Kinzie *et al.*, 2006
Hyporheic use		Gilpin & Brusven, 1976 Ruediger, 1980 Delucchi, 1989	
Predation	Extence, 1981 Malmqvist & Sackmann, 1996		Zhang *et al.*, 1998
Competition	Matczak & Mackay, 1990		Zhang *et al.*, 1998

Summary

Periods of low flow are an integral part of the natural flow regime (Humphries & Baldwin, 2003) and can be important for maintaining freshwater ecosystem diversity (Wood *et al.*, 2000; Humphries & Baldwin, 2003). However, human activities can artificially create or extend low flows because the demand for water often peaks during dry periods of the year when stream flows are naturally low. The body of literature on the definition of and potential problems associated with low flows is large, but relatively few empirical studies have been done to investigate the influence of reduced flows on the abiotic and biotic properties of permanent streams. Basic measurements of the physical habitat such as velocity, depth, wetted width, water temperature, and sedimentation generally are well documented in the literature on the effects of decreased flow, and most of these variables show fairly consistent responses (Fig. 1). In contrast, important chemical measurements such as dissolved oxygen, pH, and nutrient levels are reported infrequently in the literature. Measurements of invertebrate density, richness, and community composition are reported frequently in the literature, but behavioural responses (except drift) and biotic interactions are rarely considered, even though they may provide valuable information on the potential mechanisms underlying patterns of community-level responses to low flow.

The responses of certain invertebrate taxa to flow reduction suggest that invertebrates might be useful indicators in assessments of reduced-flow impacts or in measurements of the success of flow restoration. It should be possible to identify taxa that are sensitive to flow reduction, such as those that drift when flows change, are affected by sedimentation, or have specific velocity requirements. For example, Gore (1977) recommended using a mayfly as an indicator of adequate stream flow conditions because of its strong drift response to flow reduction. Natural low flows and artificial flow reductions appear to have similar effects on invertebrates. However, the severity of the flow decrease has an important influence on invertebrate responses because it determines the magnitudes of changes in the environment, including changes in habitat diversity, sedimentation, and periphyton availability as a food resource. The impact of low flow is greatest where habitat diversity is lost and habitat conditions change the most.

Our review of the published literature highlights several areas where more research is needed, including: 1) What are the effects of the duration and timing of flow reductions? For example, do long periods of flow reduction have more impact on invertebrates than short periods of flow reductions? 2) What are the influences of water quality, land use, and stream type on invertebrate responses to flow reduction? Comparative studies are required to address this issue and should include detailed measurements of habitat characteristics such as dissolved oxygen and the periphyton community. 3) What are the effects of stream size and morphology on responses to flow reduction? For example, does taking 80% of discharge from a river with discharge of 1 m^3/s differ from taking 80% from a river with a discharge of 100 m^3/s? 4) Does decreased flow change oviposition behaviour because of reduced water depth? For example, recent studies show that many stream invertebrates preferentially lay their eggs on the undersides of large rocks protruding above the water surface (Peckarsky *et al*., 2000; Reich, 2004). We suggest that experimental manipulations of flow, or studies comparing different flow-reduction regimes are needed to address these knowledge gaps.

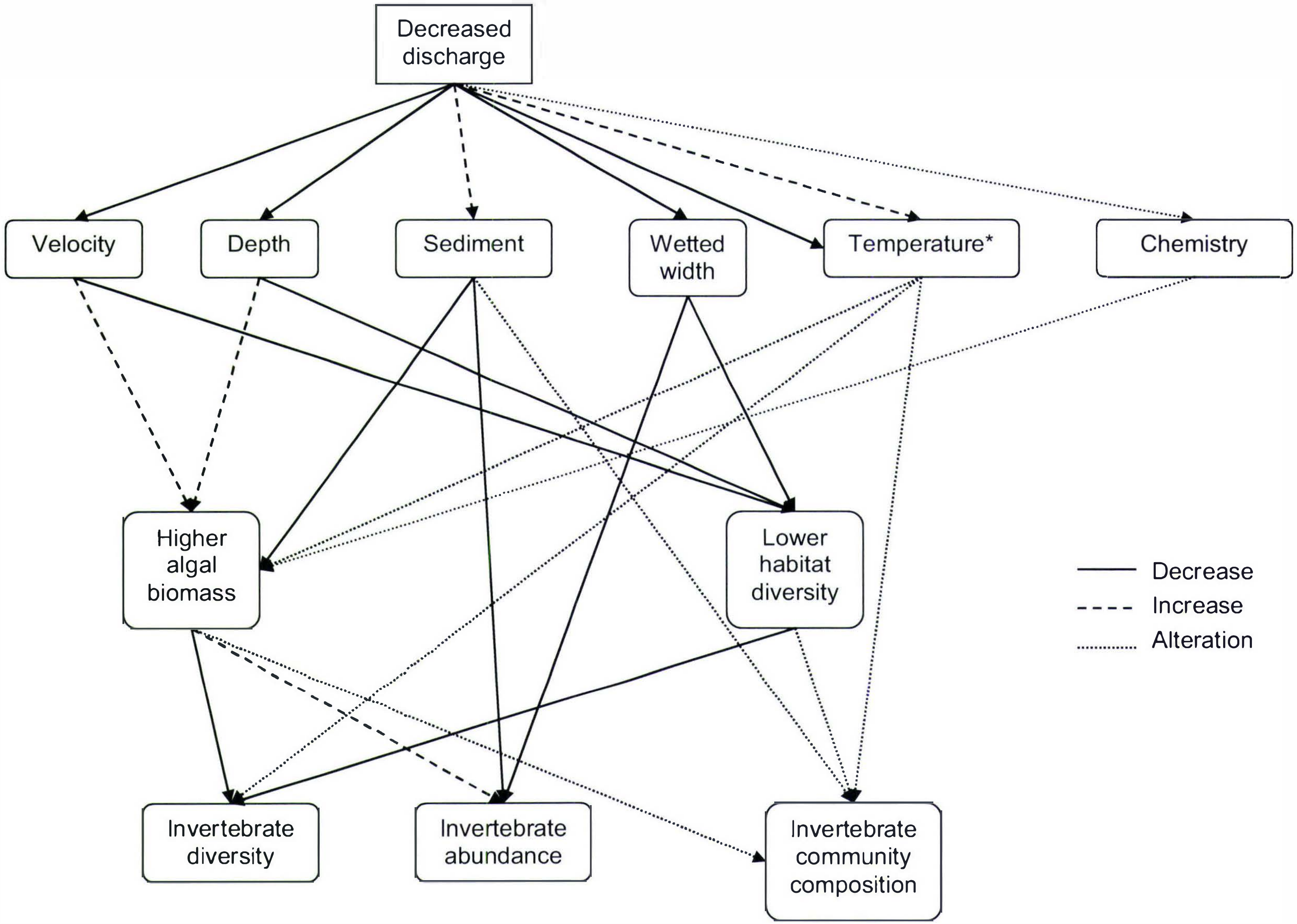

Figure 1. Summary of the effects of decreased stream flow on habitat conditions and invertebrate community abundance, diversity, and composition.
* Response for temperature varies among studies.

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Chapter 2

What happens to small stream habitat condition when flow is reduced? Observations from experimental flow reductions and a test of a predictive computer program

Abstract

In many parts of the world, increasing human population and the intensification of agriculture is increasing the demand for freshwater. There is also an increasing acceptance of streams as legitimate users of water and many resource managers now strive to balance stream ecosystem requirements with out-of-stream needs for water. To assist in achieving this balance, managers need to know what habitat characteristics of streams are impacted by reduced flows.

We reduced flows by over 85% for approximately 100-m reaches, in three, small New Zealand streams to assess impacts on habitat condition. We found water depth, velocity, wetted width and dissolved oxygen levels decreased, fine sediment cover increased and chlorophyll-*a*, pH and temperature were unchanged by flow reduction, although there was considerable variability among the three streams. Additionally, we tested the depth, velocity and wetted width predictions of the computer program Water Allocation Impacts on River Attributes (WAIORA) as well as the weighted usable area - abundance relationship for two macroinvertebrate taxa (*Deleatidium* sp. and *Aoteapsyche* sp.).

WAIORA accurately predicted velocity and wetted width changes as a result of flow reduction, but overestimated temperature and underestimated dissolved oxygen minima. Generalised habitat curves for two taxa correctly predicted a decline in abundance with severe flow reduction from a single mid-summer sampling. In a control reach (no experimental flow reduction) over a range of flows, predicted weighted usable area for those taxa was not related to observed abundance.

Our findings are consistent with some of the commonly measured effects of flow reduction (e.g. decreased depth and velocity). However, the impact of flow reduction on other variables has seldom been measured adequately and there is little empirical evidence to support the generally held ideas of increased temperatures and decreased dissolved oxygen levels. In the rush to report biotic changes, many studies poorly describe the abiotic impacts of flow reduction and we suggest workers studying reduced flows should make a greater effort to measure the effects on habitat condition.

Introduction

Ever-escalating demand for water is a significant challenge in the sustainable management of rivers and streams to maintain biological integrity (Baron *et al.*, 2002; Poff *et al.*, 2003; Richter *et al.*, 2003). In order to balance the needs of humanity with those of aquatic ecosystems, water managers need to know how much water can be removed before there are significant detrimental effects on aquatic biota. To determine sensible levels of water removal that retain ecological integrity, one must first consider which habitat variables are the most important in maintaining community structure. These variables must then be kept within their natural ranges of variability if we want to maintain the survival potential of existing native species (Resh *et al.*, 1988).

Variables related to the flow of water perhaps have the greatest influence on benthic organisms (Hart & Finelli, 1999). Recently, the maintenance of natural flow regimes, especially downstream of large dams, has been advocated as a way of mitigating the effects of reduced flows (Poff *et al.*, 1997; Richter *et al.*, 1997). This usually involves the alteration of dam operations to recreate pre-dam flow variability, for example, the periodic release of stored water to emulate spates. Small streams may be subject to many discrete water abstractions along their length and usually lack large storage structures. Thus, the ability to augment flows via the periodic release of water to emulate floods is not possible. In such streams, management often revolves around minimum flow levels as managers can have some influence over these.

Often, demand for water is greatest at times when streams are naturally running low and thus, there is large potential for conflict between water users and those wanting to maintain some level of minimum flow. One of the most sophisticated and commonly used methods of determining minimum flow levels is the Instream Flow Incremental Methodology (IFIM) (Bovee, 1982), which usually includes some form of physical habitat simulation (e.g. Physical HABitat SIMulation System – PHABSIM) (Milhous *et al.*, 1981). These techniques are expensive and most often applied to salmonid populations in large rivers. There is little information on simple methods for setting flows in small streams (Ministry for the Environment, 1998) and it would be useful if key habitat variables that preserve biotic diversity in these small streams could be identified and maintained.

In New Zealand, IFIM uses a PHABSIM derivative, River Hydraulics and HABitat SIMulation (RHYHABSIM) to quantify the response of instream habitat to changes in flow (Jowett, 1996). Additionally, a simplified computer package, Water

Allocations Impacts On River Attributes (WAIORA), has been developed and described as "a decision support system designed to provide guidance on whether a flow change could have adverse impacts on the following environmental parameters: dissolved oxygen, total ammonia, water temperature and habitat for aquatic life" (NIWA, 2004). Habitat data (discharge, width, depth) are collected at two levels of discharge and a variety of temperature and dissolved oxygen parameters (e.g. mean and maximum daily air temperature, humidity, elevation, dissolved oxygen range and daily mean) are entered by the user. An amount of abstraction (or addition) of water is entered and numerical models estimate changes to the previously mentioned environmental parameters. WAIORA also contains generalised habitat suitability curves for several fish and invertebrate species. Such curves are generated from detailed measurements of depth, velocity and substrate preferences of taxa and converted to weighted usable area (WUA) (see Jowett *et al.*, 1991). WUA can be plotted against discharge, giving an indication of how much optimal habitat is lost or gained as discharge changes. The relationship between changes in WUA and the abundance of any particular taxon is crucial to whether this approach is useful in determining the impacts of flow reduction (or addition). Some have questioned the existence of a relationship between WUA and abundance (e.g. Mathur *et al.*, 1985; Wills *et al.*, 2006), however, other workers have demonstrated such relationships in rivers where habitat suitability curves have been calculated (e.g. Morin *et al.*, 1986; Jowett & Richardson, 1990).

Such modelling approaches rely on the assumption that the included habitat variables determine the distribution and abundance of biota. Taxa have differing preferences for depth and velocity (Jowett *et al.*, 1991; Collier *et al.*, 1995), thus, flow reductions can increase or decrease the habitat depending on the species' individual requirements (Ministry for the Environment, 1998). The wetted width of a stream dictates the area of available habitat, while its temperature regime influences ecosystem structure and function and can act as a habitat limiter (Quinn *et al.*, 1994; Allan, 1995). Dissolved oxygen levels are crucial to many aquatic invertebrates and overall stream health (Alabaster & Lloyd, 1980) whilst pH affects the toxicity of ammonia (Ministry of the Environment, 1998). Other variables, not included in most habitat modelling techniques such as siltation (see Wood & Armitage, 1997) and algal biomass (e.g. Suren *et al.*, 2003) have been shown to influence invertebrate community structure, and should be considered in flow reduction studies.

Previous studies into the effects of reduced flow often measure basic habitat variables (e.g. depth, width, velocity) but few include important variables such as temperature, dissolved oxygen and algae (see Chapter 1 and Dewson *et al.*, 2007 for full review). Additionally, previous studies are usually surveys sampling upstream and downstream of some existing diversion/abstraction structure (e.g. Castella *et al.*, 1995; McIntosh *et al.*, 2002). Such studies do not allow pre-reduction sampling of the downstream impact reach and can thus never completely eliminate the potential confounding influence of other upstream – downstream changes (e.g. land use).

Experimental flow reductions in natural channels are rare in the published literature, making it difficult to establish if there are consistent impacts from flow reduction. We have manipulated the flows of three small (< 200 L/s base flow) streams to investigate the impacts of flow reduction on habitat condition and stream invertebrates. Our study seeks to emulate flow reductions that occur commonly in New Zealand for irrigation of pasture. We predicted decreases in depth, velocity, wetted width, dissolved oxygen and increases in temperature, conductivity, algal biomass and sediment cover. We also tested the depth, velocity, width, temperature and dissolved oxygen predictions of the WAIORA computer package (NIWA, 2004), and examined the validity of using invertebrate habitat curves as predictors of abundance in response to reduced flows.

Methods

Study sites

The three study sites were small (< 200 L/s base flow) stony-bottomed streams in the southern North Island, New Zealand. Table 1 summarises stream characteristics. Booths Creek (Plate 1) is situated on the Wairarapa Plains approximately 5 km south of Carterton (41°04′S 175°31′E) after the stream has passed through 10 km of predominantly dairy farmland. The other two sites are approximately 20 km north of Masterton. They are unnamed and will be referred to by the name of the stream they feed. Kiriwhakapapa Stream is located on private land having passed for 2 km through low intensity sheep and beef farmland (40°49′S 175°34′E). Reef Creek (Plate 2) is in the Tararua Forest Park (40°48′S 175°32′E) and surrounded by predominantly second growth indigenous forest.

Plate 1. The construction of the diversion channel at Booths Creek. The natural channel is visible at mid-right.

Plate 2. The diversion pipes and weir under construction at Reef Creek prior to flow reduction.

Table 1. Physicochemical attributes of the study streams. Substrate expressed as % boulder (>256 mm): large cobble (128-256 mm): small cobble (64-128 mm): gravel (2-64 mm): sand/silt (<2 mm). Ranges are given in brackets where means are presented.

	Booths Creek	Kiriwhakapapa Stream	Reef Creek
Coordinates	41°04′S 175°31′E	40°49′S 175°34′E	40°48′S 175°32′E
Landuse	Dairy farming	Sheep and beef farming	Native forest
Altitude (m)	50	280	350
Slope	0.4:100	1:100	12:100
Mean discharge (L/s)	275 (40-4527)	96 (17-7720)	56 (2-5000)
Mean wetted width (m)	3.58 (2.40-7.80)	2.24 (0.75-5.50)	2.16 (0.65-4.10)
Mean depth (m)	0.16 (0.09-0.28)	0.12 (0.06-0.21)	0.09 (0.04-0.17)
Mean velocity (m/s)	0.55 (0.20-1.01)	0.62 (0.22-1.15)	0.31 (0.04-0.71)
Substrate size	0:13:51:27:9	0:6:21:58:15	19:31:20:28:2
Mean specific conductivity (µS/cm)	163 (143-179)	72 (66-83)	54 (46-60)
Mean pH	7.8 (7.3-8.4)	7.5 (7.0-8.6)	7.0 (6.5-7.9)
Mean dissolved oxygen (mg/L)	9.7 (6.3-11.6)	9.4 (8.7-10.9)	10.0 (8.9-11.3)
Mean annual temperature (°C)	13.9 (5.4-26.8)	13.0 (3.7-28.2)	9.7 (4.8-15.9)

Flow reduction

The creation of flow reductions involved the digging of diversion channels in two streams (Booths Creek and Kiriwhakapapa Stream (Plate 3 and 4)) and installation of pipes at Reef Creek. We constructed pole and board weirs to form header pools for the diversion channels/pipes, to reduce flow by over 80% for approximately 100 m in each stream. This created reduced flow (impact) reaches, which could be compared to unreduced (control) reaches upstream. The diversions operated for one month in the summer of 2003 - 2004 and have operated continuously since the summer of 2004 - 2005.

Invertebrate sampling

Five replicate Surber samples (0.1 m^2, 250µm mesh) of benthic invertebrates were collected three times before (between November 2004 and January 2005) and five times after (after 1 week, 1 month, 2 months 9 months and 1 year) the flow reductions were imposed in January 2005. All samples were preserved in 10% formalin for later sorting and enumeration. For large samples, a sample splitter was employed to divide the sample into four parts. Sequential subsamples were sorted until at least 200 individuals were removed. The entirety of each subsample was processed. Vinson & Hawkins (1996) found a rapid increase in the number of taxa as the number of individuals examined increased up to 200 individuals after which the rate of increase slowed considerably. To avoid missing rare taxa, we scanned the remainder of the sample for taxa not present in the subsample. Invertebrates were identified to the lowest possible taxonomic level using the keys of Winterbourn (1973), Chapman & Lewis (1976), Towns & Peters (1996), Winterbourn *et al*., (2000) and Smith (2003). Chironomids were identified to sub-family level and Oligochaeta to class.

Plate 3. The diversion pipe and iron pole supports for weir prior to flow reduction at Kiriwhakapapa Stream.

Plate 4. An overview of Kiriwhakapapa Stream. The diversion weir is circled at mid-left with diversion channel flowing left to right across centre of photo. The reduced flow reach (impact) meanders across bottom of photo.

Physicochemical measurement

Temperature. Water temperature was logged in both control and impact reaches at 30-minute intervals using Onset temperature loggers (Onset Computer Corporation, Bourne, MA, USA.) from November 2004 until August 2006.

Discharge. Discharge was estimated at a fixed transect on each sampling occasion with a minimum of 12 depth and velocity measures per transect recorded with a Marsh-McBirney Model 2000 Flowmate (Marsh-McBirney Inc., Fredrick, MD, USA.) to an accuracy of 0.01 m/s. TruTrack Ltd. WT-HR water level dataloggers (TruTrack Ltd., Christchurch, New Zealand) (Plate 5) recorded stage height to an accuracy of 1 mm every 20 minutes in control and impact sections from January 2005 – August 2006. We calculated stage-discharge rating curves following Gordon *et al.* (2004) for each section, giving discharge records for the duration of the water level datalogger deployment. In Booths Creek, a high flow event damaged a water height recorder resulting in only a two-month discharge record for this site.

Plate 5. The exhilarating process of offloading water level data from a TruTrack WT-HR water height datalogger to a Palm m505 PDA at Booths Creek.

Sediment. The coverage of fine sediment (silt material deposited on top of stony substrate) on the substrate was visually estimated at 15 randomly selected transects at each study site on three occasions while diversions were operating. At each transect, the same person on each occasion, estimated the percentage of substrate covered by fine sediment within a 300 mm wide strip across the width of the stream. Sediment traps similar to those described by Bond (2002) were also installed in control and impact sections. Traps consisted of small plastic buckets (depth = 200 mm, radius = 82.5 mm), providing a settlement area of 0.02 m^2. Once installed, traps were flush with the streambed and covered with a layer of coarse substrate, supported by wire mesh over the trap to minimize the alteration of hydraulic conditions (Bond, 2002). Sediment was trapped for 24 hours at control and impact sites on four occasions during discharge reduction. On each occasion, we also collected 500 mL water samples at midstream to measure suspended sediments. We analysed ash-free dry mass (AFDM) of suspended and trapped sediment samples by vacuum filtration, using pre-weighed Whatman glass fibre filters (GF/C) (Whatman International Ltd., Brentford, England). Filtration was followed by drying at 50°C for 24 hours. Filters were then weighed, ashed for four hours at 450°C and reweighed.

Periphyton. Adjacent to each invertebrate sample, a stone (< 60 mm, a-axis) was selected for chlorophyll-*a* analysis. Stones were transported on ice in the dark and stored at -20°C. Photosynthetic pigments were extracted from stones by submergence in 90% acetone for 24 hours at 5°C. Absorbency was read at 750, 665 and 664 nm on a Varian Cary 50 Conc. UV-Visible spectrophotometer (Varian Australia Pty Ltd., Mulgrave, Australia) before and after 0.1M HCl was added. We calculated the amount of chlorophyll-*a* ($\mu g/cm^2$) on each cobble as described by Steinman & Lamberti (1996), and corrected for stone surface area calculated using length, width and depth of each cobble following Graham *et al.* (1988).

In February 2006, periphyton scrapings were taken from Kiriwhakapapa Stream and Reef Creek to assess algal community composition. We used a scalpel to remove algae from a 2-cm^2 area on each of 10 cobbles from randomly selected riffles in each reach. Samples were stored on ice and frozen as soon as possible. Samples were processed by the National Institute of Water and Atmosphere (NIWA) where relative abundances were assessed with a point scoring methodology ranging from 8 ("Dominant") to 1 ("Rare") as described by Biggs & Kilroy (2000).

Physicochemical. Depth and velocity were measured at five points where invertebrate benthic samples were collected. We measured wetted width every 5 m over 65 m in each stream section. Specific conductivity, pH and dissolved oxygen were logged at one-minute intervals for approximately an hour with a YSI 556 Multiprobe System (Yellow Springs Instruments Inc., Yellow Springs, OH, USA.) on each sampling occasion. Logged data were averaged to obtain a single value. Dissolved oxygen was also logged simultaneously for 24 hour periods in riffles at control and impact sections with the YSI probes.

Analysis

A two-way analysis of variance (ANOVA) was used to examine, Season (winter, spring, summer, autumn) and Treatment (control, impact) effects on water temperature. Both were treated as fixed factors. We also calculated the percentage of time mean daily temperature exceeded 19°C in control and impact reaches, since this temperature is hypothesised to inhibit stonefly distribution (Quinn & Hickey, 1990).

One-way ANOVA was used for discharge data, 24 hour logged dissolved oxygen data and the three sediment measures, as only control-impact comparisons were made during the flow reduction.

All other variables were analysed in a before-after-control-impact paired in time (BACIP) format (Downes *et al.*, 2002). This design focuses on any changes at the impact location relative to the control, by comparing the difference between control and impact values within each period. One-way ANOVA tested for differences between before and after treatments.

All analyses were conducted using Statistix 8.1 (Analytical Software, Tallahassee, FL, USA.). The *post hoc* Tukey multiple comparisons test evaluated significant differences when found and data were $\log_{10}$ transformed where necessary to improve normality and ensure homogeneity of variances.

WAIORA: a test of predictions

Kiriwhakapapa Stream was chosen as a case study site to test WAIORA predictions. WAIORA Version 2.0 and manual are available online at http://www.niwascience.co.nz/ncwr/tools/waiora/. We measured depth, width, velocity, temperature and dissolved oxygen parameters between December 2005 and March 2006 during summer low flows. Data collected in the control reach was used to make predictions of changes to depth, wetted width, velocity, temperature mean and maxima and dissolved oxygen (DO) minima for a fixed level of abstraction. Predicted values were then compared with actual measurements in the impact reach. An index flow (flow to which changes in habitat, DO and temperature are compared) was determined from flow gauging and water height records and the length of the reduced flow reach was 100 metres.

Habitat data. Survey data were collected at two flow levels. We measured depth at 10 cm increments along each of nine transects encompassing pool, run and riffle habitats. The stage change between the two surveys was calculated as the mean change in depth at each 10 cm increment. Width was determined as the mean of the nine transects. Predicted depth, velocity and width were compared to those measured in the impact reach in December 2005.

Temperature. All temperature parameters were measured on site except bed conductivity, bed thickness and bed temperature which were estimated as described in the WAIORA manual (NIWA, 2004). Predicted mean daily and maximum daily temperatures were compared with those logged at 20-minute intervals between December 10, 2005 and February 2, 2006.

Dissolved oxygen. Dissolved oxygen parameters were acquired from the smoothest 24-hour curve from a three-day continuous log at ten-minute intervals. A value of 2 for Q_{10} (ratio of respiration 10°C apart) was selected following Phinney & McIntire (1965) (R. Young, Cawthron Institute, pers. com.). The predicted dissolved oxygen minima was compared to that measured in the impact reach during the same 24 hour period.

Invertebrate generalised habitat curves. WAIORA includes generalised habitat curves for *Deleatidium* sp. and *Aoteapsyche* sp. and predicts the proportion of suitable habitat (Weighted Usable Area (WUA)) that is present at the index flow and the amount this decreases as a result of flow reduction. We compared this predicted decrease in theoretical habitat with actual change in abundances collected in mid-January, 2006. To show whether the volume of theoretical optimum habitat was related to invertebrate abundance over a longer period, WUA was also regressed against the abundances of *Deleatidium* sp. and *Aoteapsyche* sp. in the control reach, sampled in the summers of 2004 - 2005 and 2005 - 2006.

Results

Physicochemical and periphyton

Discharge. Discharge was significantly lower in the impact reaches of each stream (Table 2). Discharge was reduced by around 95% at Booths Creek, 88% at Kiriwhakapapa Stream and 96% at Reef Creek.

Temperature. For all streams, daily mean, range and maximum temperatures were greater in summer and spring than in autumn and winter (Figure 1, Table 3). Flow treatment had no effect on temperature at Reef Creek. Flow reduction increased mean daily temperature at Kiriwhakapapa Stream, but decreased daily range and maximum temperatures. Daily maximum temperatures also decreased at Booths Creek. Flow reduction increased the time mean daily temperature was greater than 19°C by only a few percent, except in Reef Creek where temperatures never reached 19°C (Figure 2).

Sediment. Fine sediment cover increased as a result of flow reduction in Booths Creek and Kiriwhakapapa Stream, but not at the forested Reef Creek site (Figure 2a, Table 2). More sediment was collected in the sediment traps in the control reach of Kiriwhakapapa Stream, but suspended sediment was unaffected by flow reduction in any stream (Table 2).

Periphyton. Chlorophyll-*a* was unchanged by flow reduction in any stream (Table 2). The algal community of Reef Creek was dominated by *Batrachospermum* sp. (Rhodophyta) in both the control and impact reaches during flow reduction (Table 4). The diatom *Navicula radiosa*, was more abundant in the impact reach. At Kiriwhakapapa Stream, the diatom *Synedra ulna* dominated the control reach whilst the filamentous alga, *Spirogyra* sp. (Chlorophyta) dominated in the impact reach. Flow reduction did not influence the number of algal taxa present (Table 4).

Physicochemical. Depth only decreased with flow reduction at Booths Creek (Figure 2b, Table 2). In all streams, velocity was lower in the impact reach (Figure 2c, Table 2) whilst wetted width was only significantly smaller in Kiriwhakapapa Stream but showed a decreasing trend with flow reduction in the other two streams (Figure 2d, Table 2). Spot measures of dissolved oxygen (DO) decreased at impact sites following flow reduction in Booths Creek and Reef Creek (Table 2). Dissolved oxygen logging showed levels were lower in impact reaches of Kiriwhakapapa Stream (Figure 3) and Reef Creek (Table 2), especially at night. Specific conductivity increased with flow reduction in Kiriwhakapapa Stream and Reef Creek (Figure 2e, Table 2) whilst pH remains unchanged in all streams (Figure 2f, Table 2).

Table 2. ANOVA *F*-values of differences in physicochemical variables in each stream: A. measured summer 2003 - 2004 and summer 2004 - 2005 and B. measured summer (sediment variables) and during year 2005 (discharge, dissolved oxygen). df = degrees of freedom, nd = no data, **Bold** = significant at 5% level. *Post hoc* Tukey multiple comparison test results shown where significant. ↑ = increase in impact reach following flow reduction, ↓ = decrease in impact reach following flow reduction. C = control reach, I = impact reach.

Parameter	**Hypothesis**	**Booths Creek**		**Kiriwhakapapa Stream**		**Reef Creek**	
A. BACI differences		df	*F* – value	df	*F* – value	df	*F* – value
Depth	H_o: difference between control and impact *before* reduction = difference between control and impact *after* reduction	1, 9	**6.37** ↓	1, 11	0.12	1, 11	0.05
Velocity		1, 9	**10.53** ↓	1, 11	**20.80** ↓	1, 11	**8.88** ↓
Wetted width		1, 8	1.83	1, 11	**85.69** ↓	1, 11	1.38
Dissolved oxygen – spot measures		1, 9	**10.98** ↓	1, 11	1.16	1, 11	**14.2** ↓
pH		1, 9	0.01	1, 11	1.82	1, 11	0.55
Specific conductivity		1, 9	0.38	1, 11	**6.87** ↑	1, 11	**15.98** ↑
Chlorophyll-*a*		1, 8	0.03	1, 10	2.76	1, 10	1.71
B. Control – impact only							
Discharge	H_o: control = impact	1, 9022	**23472.8** C>I	1, 47460	**1335.17** C>I	1, 43246	**1626.15** C>I
Dissolved oxygen – logged data		nd	nd	1, 862	**188.09** C>I	1, 288	**2395.66** C>I
Visual sediment cover		1, 4	**28.59** I>C	1, 4	**29.76** I>C	1, 4	0.08
Sediment traps		1, 6	4.14	1, 6	**7.77** C>I	1, 6	1.48
Suspended sediment		1, 6	0.21	1, 6	0.00	1, 6	0.34

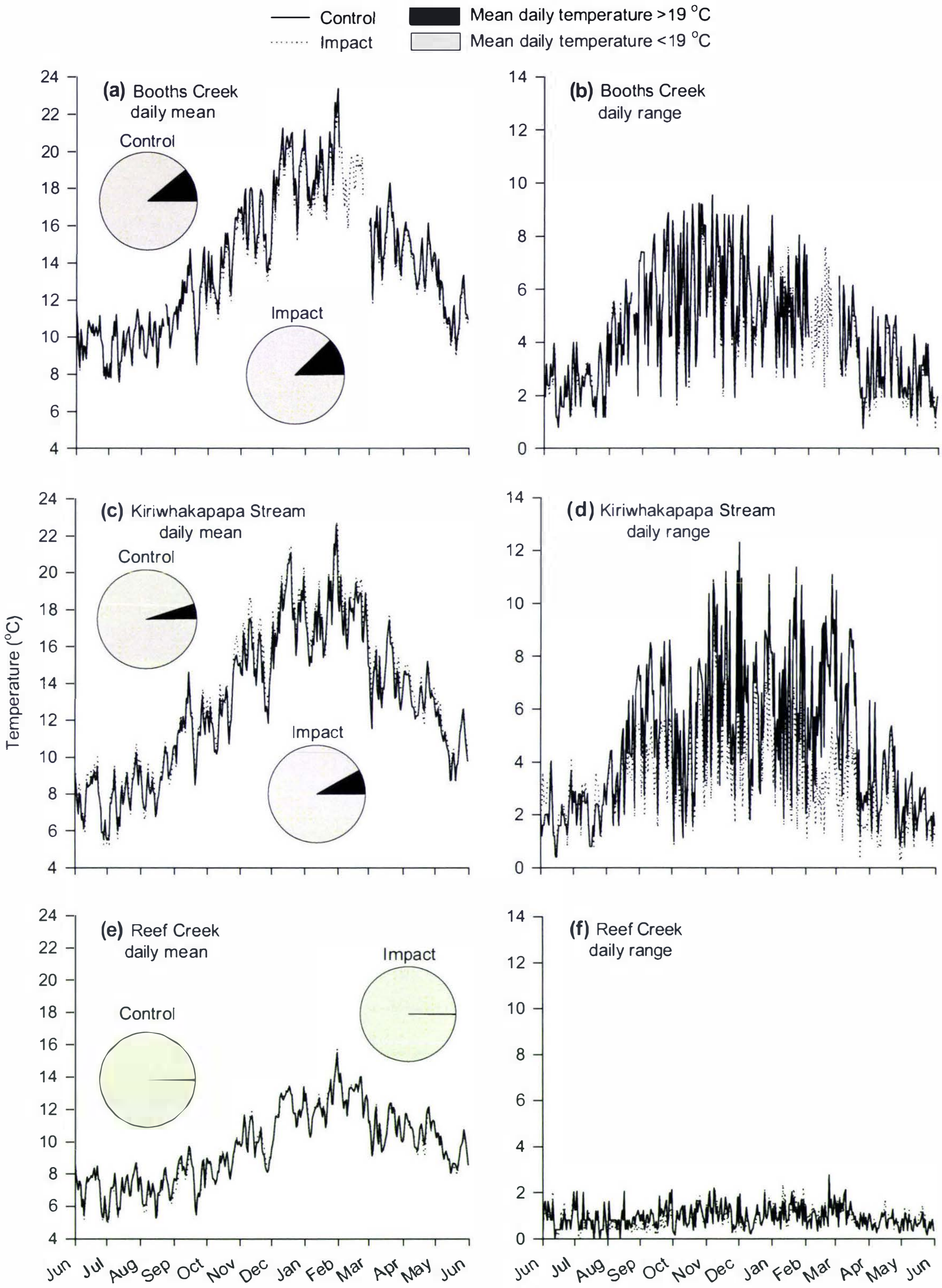

Figure 1. Mean daily temperature and range (line graphs) at control and impact sites and the percentage of the year that temperatures were above or below 19°C (pie charts) using data collected between June 2005 and May 2006 in Booths Creek, Kiriwhakapapa Stream and Reef Creek.

Table 3. ANOVA *F*-values of seasonal (spring, summer, autumn, winter) and treatment (control and impact) differences in temperature measured between June 2005 and May 2006 in three Wairarapa streams. *Post hoc* Tukey means test results are given where significant. **Bold** = significant at 5% level, df = degrees of freedom, Sm = summer, Sp = spring, A = autumn, W = winter, C = control, I = impact.

Temperature parameter	**Factor**	**Booths Creek**		**Kiriwhakapapa Stream**		**Reef Creek**	
2-Way ANOVA		df	*F* – value	df	*F* – value	df	*F* – value
Daily mean	Season	3, 670	**770.70** Sm>Sp=A>W	3, 716	**957.30** Sm>Sp=A>W	3, 716	**812.82** Sm>A>Sp>W
	Treatment	1, 670	3.64	1, 716	**9.09** I>C	1, 716	0.05
	Season × Treatment	3, 670	0.50	3, 716	0.42	3, 716	0.29
Daily range	Season	3, 670	**155.22** Sp>Sm>W=A	3, 716	**97.77** Sm=Sp>A=W	3, 716	**15.14** Sm=Sp>A=W
	Treatment	1, 670	3.58	1, 716	**71.52** C>I	1, 716	0.69
	Season × Treatment	3, 670	0.03	3, 716	**11.02** CSm=CSp>Isp=Ism≥ CA≥IW=CW≥IA	3, 716	2.18
Daily maximum	Season	3, 670	**731.65** Sm>Sp>A>W	3, 716	**714.80** Sm>Sp>A>W	3, 716	**820.07** Sm>A>Sp>W
	Treatment	1, 670	**6.22** C>I	1, 716	**7.77** C>I	1, 716	0.05
	Season × Treatment	3, 670	0.36	3, 716	1.57	3, 716	0.43

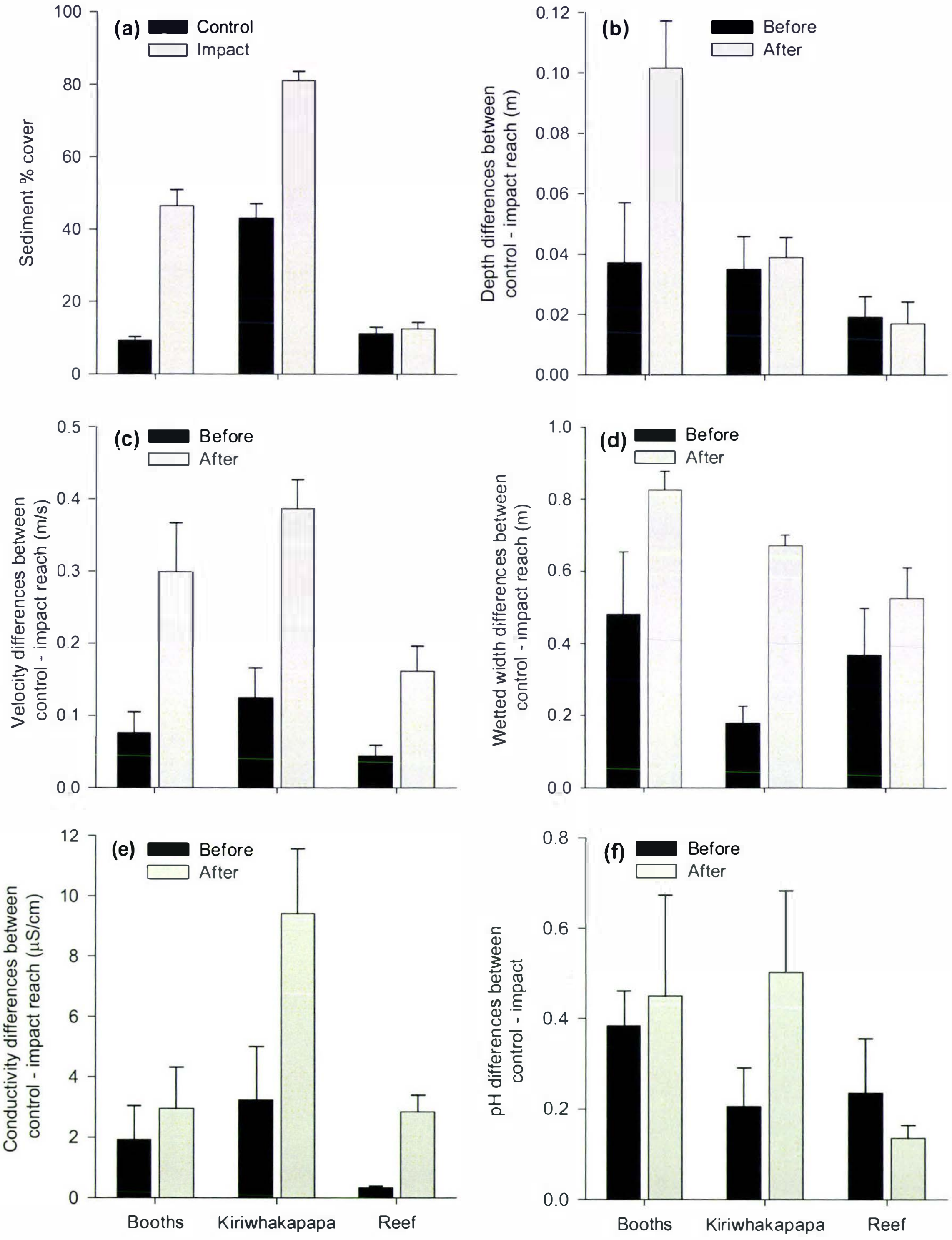

Figure 2. (a) Mean (+ 1 SE) sediment cover at control and impact sites (n = 3); and differences between control and impact reaches (+ 1 SE) before and after initiation of flow reduction for (b) depth, (c) velocity, (d) wetted width, (e) conductivity and (f) pH (n = 13).

Table 4. Relative abundances of algal taxa in the control and impact reaches of Kiriwhakapapa Stream and Reef Creek collected during February 2006. Taxa are ranked, relative to the dominant taxon, according to their contribution to the biovolume of the sample using the methods of Biggs & Kilroy (2000). 8 = dominant, 7 = abundant, 6 = common to abundant, 5 = common, 4 = occasional to common, 3 = occasional, 2 = rare to occasional, 1 = rare.

Major algal group	Taxa	Kiriwhakapapa Stream control	Kiriwhakapapa Stream impact	Reef Creek control	Reef Creek impact
Chlorophyta	*Spirogyra* sp.	6	8		
Chlorophyta	*Oedogonium* sp.	4	4		
Cyanobacteria	*Oscillatoria* sp.		1		
Rhodophyta	*Batrachospermum* sp.			8	8
Diatom	*Cocconeis placentula*	4		1	
Diatom	*Cymbella aspera*	1			
Diatom	*Cymbella kappii*	4	2		
Diatom	*Cymbella tumida*	5	7		
Diatom	*Encyonema minutum*	3			
Diatom	*Epithemia* cf. *adnata*		1		
Diatom	*Eunotia* sp. (cf. *rhomboidea*)		1		
Diatom	*Fragilaria vaucheriae*	2			
Diatom	*Gomphoneis minuta* var. *cassieae*	1			
Diatom	*Gomphonema parvulum*	3	3		
Diatom	*Gomphonema truncatum*	1	3		
Diatom	*Melosira varians*	3			
Diatom	*Navicula cryptocephala*	1			
Diatom	*Navicula radiosa*		1	1	5
Diatom	*Navicula rhynchocephala*	1			
Diatom	*Navicula* sp. (small species)	2	4		
Diatom	*Nitzschia* sp. (cf. *intermedia*)		2		
Diatom	*Reimeria sinuata*	1			
Diatom	*Rhoicosphenia abbreviata*		1	1	1
Diatom	*Synedra acus*		3		
Diatom	*Synedra ulna*	8	5		

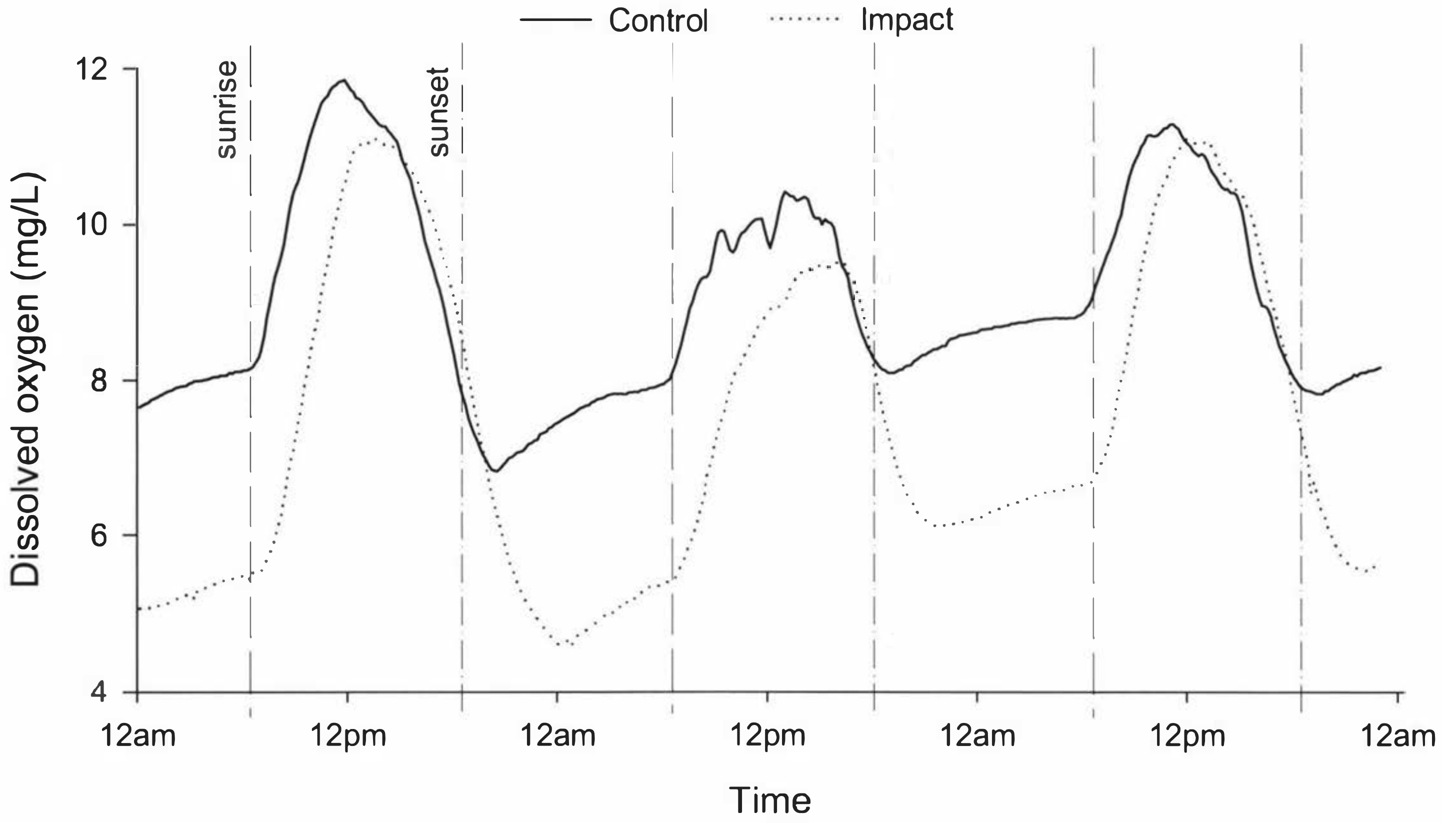

Figure 3. Dissolved oxygen at Kiriwhakapapa Stream in control and impact reaches logged continuously between 20 May and 22 May 2006.

WAIORA: a test of predictions in Kiriwhakapapa Stream

WAIORA underestimated depth by 5 cm but not velocity or wetted width (Figure 4). Mean daily temperature was overestimated by 2-3°C in both the control and impact reaches (Figure 5a). WAIORA underestimated the increase in mean daily temperature because of flow reduction, but only by 0.5°C (Figure 5b). The maximum water temperature was also overestimated by a few degrees (Figure 5c) but WAIORA failed to estimate the direction of the flow reduction impact. It estimated maximum water temperature would increase by over 1°C, but maximum temperature was actually nearly 1°C lower in the impact reach (Figure 5d). WAIORA predicted lower dissolved oxygen minima than were observed in both control and impact reaches (Figure 5e), however, the amount this was depressed by flow reduction was similar (Figure 5f).

Deleatidium sp. were found in lower densities in the impact reach (Figure 6a) than the control reach in mid January, 2006, after one year of continuous reduced flow. This decrease was similar in magnitude to the decrease in habitat predicted by WAIORA (Figure 6b). *Aoteapsyche* sp. densities displayed a similar trend (Figure 6c) and again the decrease was similar to the predicted decrease in habitat (Figure 6d). In the absence of experimental flow reduction (control reach) over a number of sampling occasions there was a poor relationship between WUA and the densities of *Deleatidium* sp. (Figure 7a) and *Aoteapsyche* sp. (Figure 7b).

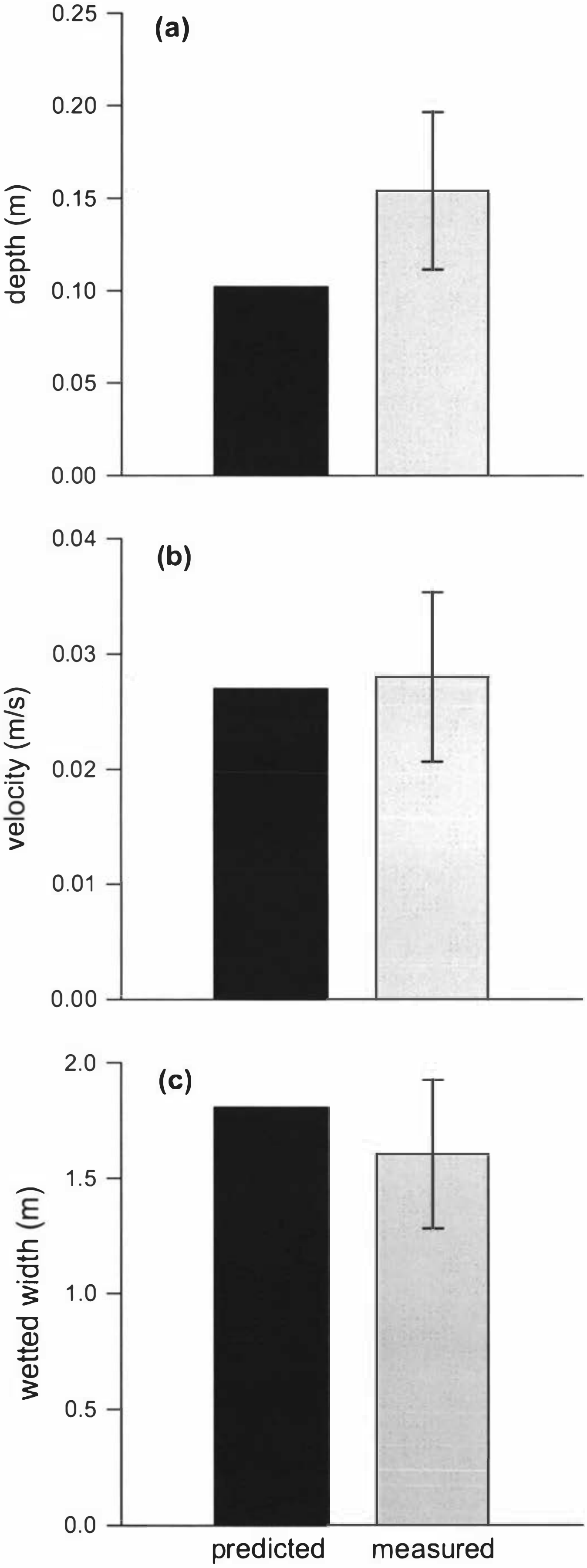

Figure 4. WAIORA predictions for changes to (a) depth, (b) velocity, and (c) wetted width resulting from flow reduction compared to measured mean (± 1 SE) values at the impact site on Kiriwhakapapa Stream during summer, 2005 - 2006. Black bars = predicted and grey bars = measured values.

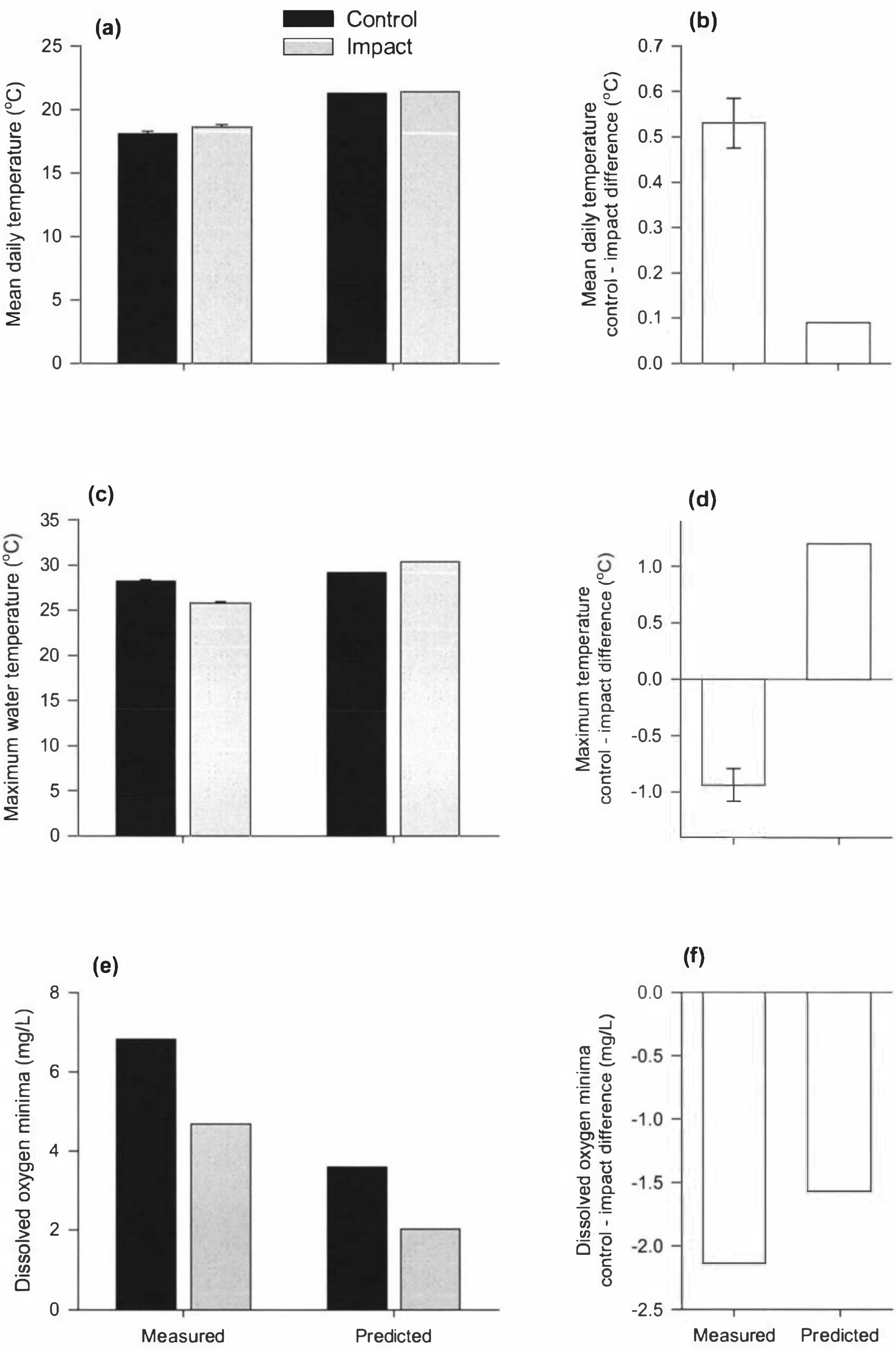

Figure 5. (a) Mean daily temperature, (c) maximum water temperature and (e) dissolved oxygen minima measured (± 1 SE) at Kiriwhakapapa Stream, summer 2005 - 2006, and corresponding values predicted by WAIORA. (b), (d), and (f) give the size of predicted and measured differences in these parameters between control and impact reaches.

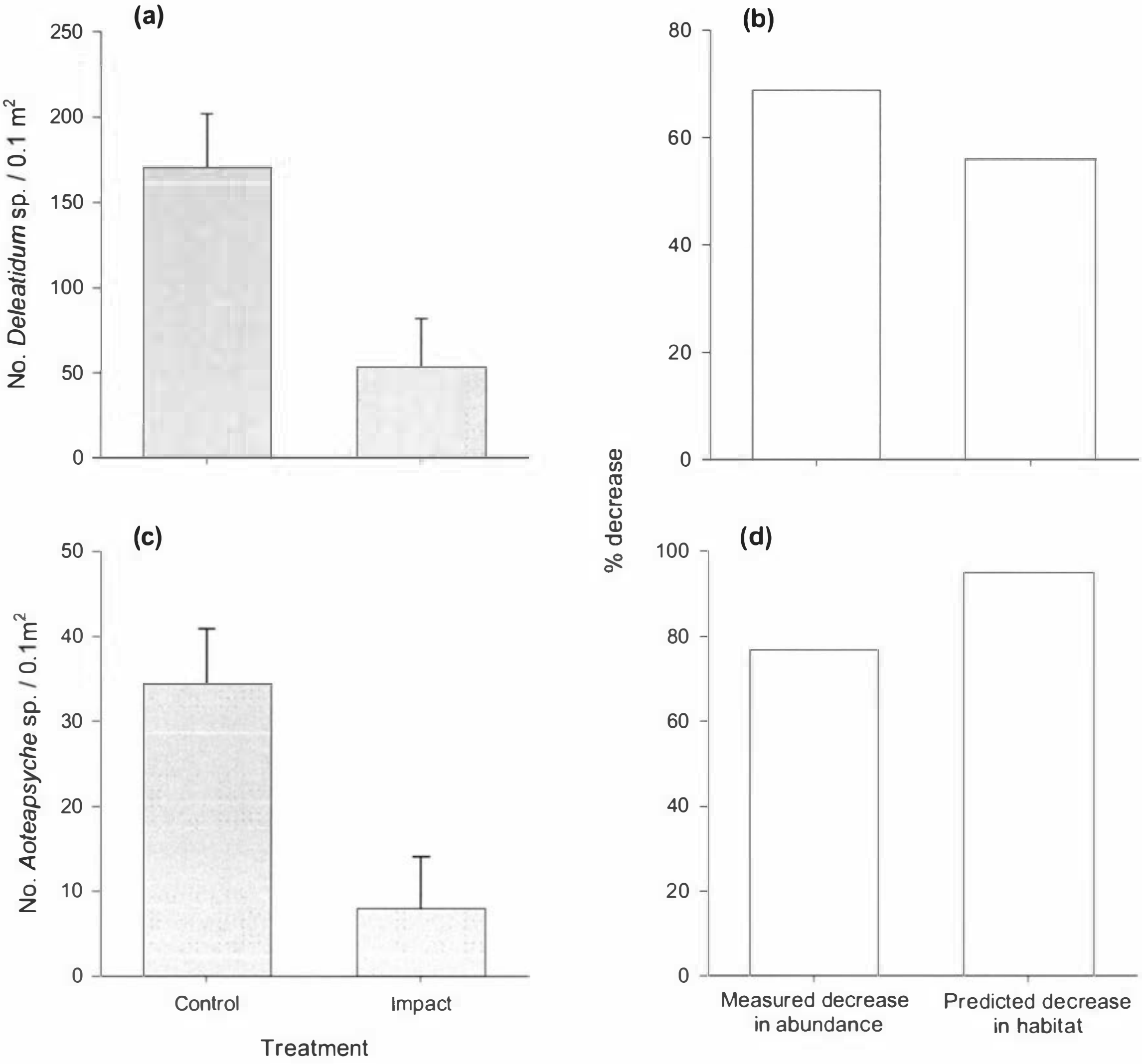

Figure 6. (a) *Deleatidium* sp. density (+ 1 SE) in control and impact reaches of Kiriwhakapapa Stream in mid-January 2006, (b) the observed percent decrease in *Deleatidium* sp. abundance and predicted decrease in habitat as a result of flow reduction, (c) the density of *Aoteapsyche* sp. (+ 1 SE) in control and impact reaches of Kiriwhakapapa Stream in mid-January 2006, and (d) the observed percent decrease in *Aoteapsyche* sp. abundance and predicted decrease in habitat as a result of flow reduction.

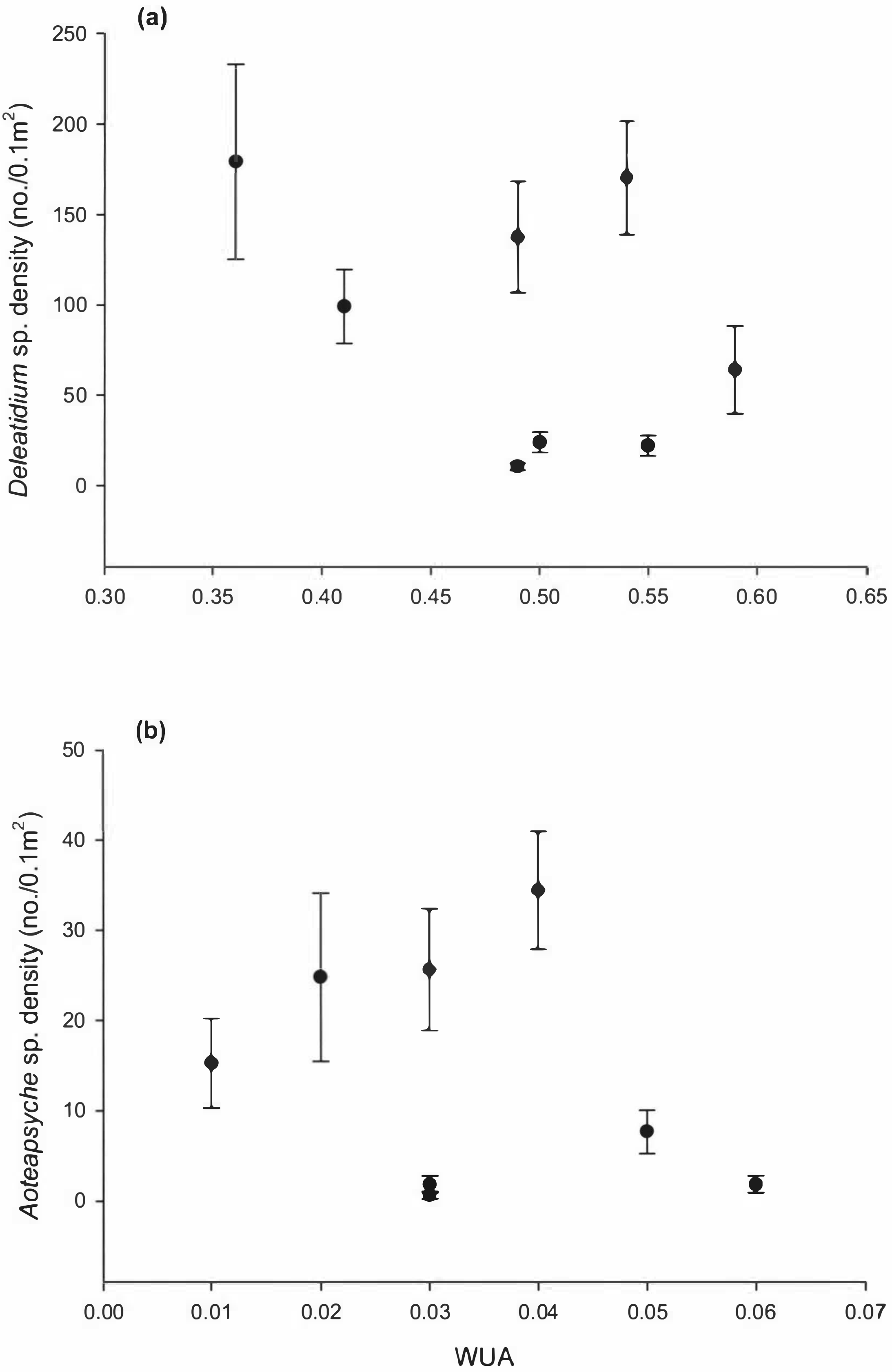

Figure 7. The relationship between weighted usable area (WUA) and (a) *Deleatidium* sp. abundance and, (b) *Aoteapsyche* sp. abundance in the control reach of Kiriwhakapapa Stream, sampled in the summers of 2004 - 2005 and 2005 - 2006. Each point represents a sampling date (average of five samples).

Discussion

Field measurements

Small changes to temperature in these streams are unlikely to be biologically significant. Flow reduction increased daily mean temperatures by 0.39ºC in Kiriwhakapapa Stream, whilst flow reduction depressed the daily maximum temperature in Booths Creek and had no impact on temperatures in the forested Reef Creek. Our finding may result from an increased influence of cooler groundwater on surface water temperatures (Grant, 1977; Mosley, 1983). Similar effects on temperature have been observed in at least one other flow reduction study (Kinzie *et al.*, 2006). In contrast to expected increases in temperature with reduced flow, our severe flow reductions had minimal influence on water temperature compared to the influence of season, meteorological variability and riparian vegetation. All taxa have a preferred temperature range and water temperature is an important determinant of the distribution of many aquatic species (Allan, 1995). It has been observed that in New Zealand, stoneflies are absent from rivers where summer temperatures are greater than 19ºC (Quinn & Hickey, 1990). Such temperatures were exceeded in the two open canopy streams, where stoneflies were absent (authors, pers. obs), but the proportion of the time that stream temperatures were greater than 19ºC was barely altered by our severe flow reductions.

Flow reduction decreased water velocity in all the study streams as has been found in previous work (see Chapter 1 and Dewson *et al.*, 2007). Depth only decreased in the larger Booths Creek. Flow reduction had little impact on water depth in Kiriwhakapapa Stream and Reef Creek. At base flow these streams were relatively shallow even in the absence of flow reduction. Previous studies have found depth to decrease with flow reduction (e.g. Bickerton *et al.*, 1993; McIntosh *et al.*, 2002), although this is not always the case with water abstractions, especially where relatively small proportions of the flow are removed (Dewson *et al.*, 2003).Wetted width tended to decrease in all streams with flow reduction but was only statistically significant in Kiriwhakapapa Stream. Previous studies have also shown wetted width to either decrease (Cowx *et al.*, 1984) or remain unchanged (Rader & Belish, 1999) with decreased flow.

Dissolved oxygen (DO) levels decreased in response to flow reduction. Logging the full diurnal cycle in Kiriwhakapapa Stream and Reef Creek showed that DO levels were similar at control and impact sites during daylight but fell to lower minima at impact sites overnight. It appears that rates of respiration/photosynthesis per unit volume of stream water are increased by flow reduction and the increase in re-aeration (from increased surface/volume ratio) is not great enough to overcome this (Ministry for the Environment, 1998). Impact sites had DO minima of around 5 mg/L and 9.5 mg/L at Kiriwhakapapa Stream and Reef Creek, respectively. The minimum at Reef Creek will have no impact on existing taxa and even the lower levels at Kiriwhakapapa Stream are unlikely to have a great impact on taxa. Alabaster & Lloyd (1980) and Dean & Richardson (1999) found a minimum level of 5 mg/L would be satisfactory for many European and New Zealand fish, respectively. Little is known about the oxygen requirements of New Zealand macroinvertebrates but elsewhere, taxon specific low DO tolerances (Kolar & Rahel, 1993) and behavioural responses (Wiley & Kohler, 1980) have been demonstrated.

Reduced flows tend to cause more sediment to settle out of suspension, covering underlying larger substrates (e.g. Wright & Berrie, 1987; Castella *et al.*, 1995) and potentially changing the quality and availability of food and habitat for macroinvertebrates. Whilst suspended sediment remained unchanged by flow reduction in all streams, sediment cover increased in both of the open canopy, farmland streams. The lack of an increase at the forested Reef Creek site was most likely a result of the lower background sediment levels in this stream. Clearly, larger scale variables such as land use influence the impacts of reduced flow. In the study streams, settled sediment was mobilised by high flow events that breached the weirs (authors, pers. obs.), however, such suspended sediment may negatively impact stream habitat in drought situations or where instream structures effectively prevent downstream flushing flows.

The algal community of the forested Reef Creek site was unchanged by flow reduction, whilst there was an increase in the dominance of the filamentous *Spirogyra* sp. in Kiriwhakapapa Stream. This result mirrors the findings of Suren *et al.* (2003) who observed that low flow led to a shift from diatoms to filamentous algae in an enriched river while diatom dominated communities persisted in a nearby similar sized un-enriched river.

Existing literature

A comparison of our findings to those of other studies was difficult due to the limited number of similar studies in the literature. Many previous studies fail to clearly describe the changes to habitat condition that result from decreased flows, especially in smaller streams. We suspect there is a large amount of unpublished information on reduced flows that has been compiled by various management authorities and consultancies, but these results are not readily accessible. Studies of naturally induced flow reduction (i.e. drought) are particularly poor at describing changes to key habitat variables such as velocity, wetted width and temperature (e.g. Wood & Petts, 1994; Wood & Armitage, 2004). This probably results from a lack of pre-drought information or alternately, the authors thought the impacts to such variables were so obvious that they did not present or measure them. Studies of human induced flow reductions tend to have more information on changes to habitat condition, but conclusions about important characteristics that have significant temporal variability such as temperature and dissolved oxygen are commonly made from spot measures only (e.g. McIntosh *et al.*, 2002).

Despite the apparent lack of empirical information, numerous generalisations about some habitat variables are made in the literature (e.g. Riggs, 1980; Jowett, 1997). Many of these are somewhat predictable, such as decreases in depth, velocity and wetted area, and increases in sediment cover. These are generally supported by empirical studies, although local stream geomorphology can influence flow reduction impacts. Other changes, such as increases in temperature and algae, and decreases in dissolved oxygen levels lack such support. Apart from the present study, we are unaware of any studies that have simultaneously logged temperature in reduced and non-reduced flow reaches over a full year, or simultaneously logged dissolved oxygen over full 24 hour periods. Without these measurements it is impossible to tease apart and contrast the relative size of the effects of reduced flow and seasonal and meteorological variability. Our results suggest that reduced flow will not necessarily increase temperature in small streams, probably because of cooler subsurface water contributing a greater proportion of surface flow in many instances. Dissolved oxygen levels, specifically minimum levels will probably be reduced by flow reduction, but further study is needed.

A test of WAIORA

The WAIORA computer package was successful at estimating the effect of flow reduction on velocity and wetted width at Kiriwhakapapa Stream. Depth did not decline as much as predicted, possibly because measurements included a large deep pool in the impact reach and the stream channel was fairly incised. Mean daily temperature was overestimated by around 3°C in both control and impact reaches. The difference between control and impact reaches was underestimated by approximately 0.4°C but the direction of change (temperature increase in impact reach) was correct. Maximum temperature was overestimated by a few degrees in each reach. WAIORA correctly predicted the size of the control – impact difference in maximum temperature (approximately 1°C), but indicated that flow reduction would increase the maximum temperature when in reality it decreased. The overestimation of both mean daily and maximum temperatures by WAIORA probably results from the influence of cooler subsurface water. The temperature modelling facility of WAIORA is able to include a correction for tributary inflow, but groundwater input is more difficult to account for and quantify. Dissolved oxygen minima predicted by WAIORA were lower than those measured in both the control and impact reaches by 2.5 – 3 mg/L. The predicted and measured effects of flow reduction on DO minima were similar, with decreases of 1.57 and 2.14 mg/L respectively. Thus, the DO model predicted the magnitude of the flow reduction impact adequately, although not the actual values.

WAIORA predicted some parameters more effectively than others. Models that attempt to predict physicochemical responses to physical changes invariably include a number of assumptions. If breached, these assumptions will affect the accuracy of predictions. Additionally, the quality of the information fed to the model will affect the quality of the predictions. We believe that key assumptions of the DO and temperature models, including that the characteristics of the selected reach or site would represent the characteristics of a longer reach or site further downstream, and that daily water temperature variability is small (<5°C) are met in this stream. Factors that may have affected the accuracy of the models include the relative short length (approximately 100 m) of the reach tested, however, the effects of a severe flow reduction in a small stream will be most obvious in the reach directly after the point of reduction, before flow is augmented by tributaries, seeps and groundwater. That the natural flow in this stream is truncated by a weir structure is something the models may not cope with, however, such structures are often required in small streams to form header ponds for water abstraction. The main source of error in the models is likely to be that they are designed and developed in larger streams and rivers. For example, groundwater input will have a greater influence during reduced flow periods and re-aeration may be high at reduced flows because of the relatively shallow nature of smaller streams.

For a single mid summer sampling occasion testing the impact of a severe flow reduction, the predicted decrease in habitat (WUA) was mirrored by observed decreases in densities of the mayfly, *Deleatidium* sp. and caddisfly, *Aoteapsyche* sp. in Kiriwhakapapa Stream. However, over a number of sampling occasions, in the absence of experimental flow reduction there was no relationship between WUA and the abundance of these two taxa in the control reach. The habitat curves included in the WAIORA program for these taxa were derived from four relatively large New Zealand rivers (>10 cumecs mean flow) (see Jowett *et al.*, 1991). Such curves are not transferable to small streams, where maximum water depths and velocities are likely to be less than preferred depths and velocities in larger rivers (Jowett, 2000). Our findings show that these curves appear to correctly predict the decrease in abundance of these taxa in response to a severe flow reduction. Perhaps, where the change in hydraulic habitat is drastic, curves derived in larger rivers may be adequate, but where changes are lesser, other factors such as life cycle, food supply and flood disturbance may be more important in determining invertebrate abundance than simple hydraulic habitat. In light of this, WAIORA may lack the precision to adequately predict the outcome of smaller volumes of abstraction from smaller streams. In any case, WAIORA is described as a “decision support system” (NIWA, 2004) and users should not base their recommendations solely on the output of such programs.

Conclusion

Good environmental decision-making relies on the support of quality empirical data. With water allocation and the setting of minimum flow levels increasingly becoming a catalyst for conflict, basic data on how reduced flows actually impact stream habitat is vital. Unfortunately, most reduced flow studies (drought and human induced) are not that helpful when it comes to actually formulating policy and regulations. Rules of thumb need to be developed, as more complex flow assessments are never going to be financially viable in smaller streams. The trick is making such simplified rules biologically relevant. Programs such as WAIORA have a place, but the applicability of the underlying models for smaller streams needs to be addressed. Little is known about which habitat variables are the most important in maintaining the native biota of streams. Unfortunately, in their rush to describe reduced flow impacts on fish and/or macroinvertebrates, few workers adequately describe what happens to such habitat variables. We make a plea to workers doing such studies, to measure habitat variables and publish their findings.

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Chapter 3

Macroinvertebrate drift in response to reduced flows

This chapter consists of two stand-alone papers:

A. "The effect of experimental flow reductions on macroinvertebrate drift in natural and streamside channels" has been published as:
James A.B.W., Dewson Z.D. & Death R.G. (2008). The effect of experimental flow reductions on macroinvertebrate drift in natural and streamside channels. *River Research and Applications*, **24**, 22-35.

B. "The influence of flow reduction on macroinvertebrate drift propensity and distance in three New Zealand streams".

The effect of experimental flow reductions on macroinvertebrate drift in natural and streamside channels

Abstract

Understanding how much water must remain in a stream to maintain a healthy functioning ecosystem has become an important focus in stream ecology research. The drift of stream invertebrates is important as a mechanism of dispersal, recolonisation and as a food source for fish in flowing water. Drift behaviour of stream invertebrates in response to flow reduction was examined in natural (New Zealand) and streamside (Canada) channels. We hypothesised that the drift of some taxa would increase following flow reduction as they attempted to avoid unfavourable conditions. Taxa such as *Baetis* sp. (Ephemeroptera) in Canadian streamside channels and *Coloburiscus humeralis* (Ephemeroptera) and *Austrosimulium* sp. (Simuliidae) in streams in New Zealand exhibited a short-term increase in drift following flow reduction. This appears to be in response to decreased velocities and available habitat in flow reduced areas. The majority of taxa displaying this response in New Zealand were filter feeders, suggesting a decline in food delivery with reduced flow contributed to increased drift. Some taxa (e.g. the amphipod *Paracalliope fluviatilis*) had a sustained increase in drift throughout the reduced flow period, probably because a preference for reduced flows increased their abundance or levels of activity. Water allocation decisions should consider potential impacts on the drift behaviour of the more commonly drifting taxa in a stream.

Introduction

The sustainable management of rivers and streams to maintain biological integrity in the face of ever escalating demands for water extraction is becoming an increasingly difficult task (Baron *et al*., 2002; Poff *et al*., 2003; Richter *et al*., 2003). Maintenance of natural flow regimes is often touted as a mechanism for the sustainable management of river ecosystems (Poff *et al*., 1997). Natural flow regimes encompass a range of flow conditions from high to low flows (McMahon & Finlayson, 2003) and most unregulated streams are subject to natural periods of low flow as a result of seasonal rainfall deficits. Demand for water often coincides with periods of naturally low flow, thereby potentially increasing both the severity and duration of low flows. Low flow periods may result in an increase in taxa that are suited to low velocity, high periphyton biomass conditions (e.g. worms, snails, chironomid midges) to the detriment of mayflies and caddisflies (Jowett & Duncan, 1990). Where the duration, severity and frequency of low flow periods is extended beyond that which occurs naturally there is the potential for taxa that prefer higher flow conditions to be greatly impacted. Instream structures for storage and/or diversion of water may create almost permanent low flow conditions, which can have catastrophic impacts on some taxa. For example, McIntosh *et al.* (2002a) found a number of native aquatic invertebrate taxa to be absent or in reduced densities downstream of a water diversion in a Hawaiian stream.

Increasingly, water resource managers need to know how much water can be removed from a river before there are significant detrimental effects on biological integrity. Although there have been some studies on the effects of reduced flows on invertebrates (e.g. Petts & Bickerton, 1994; Rader & Belish, 1999; Wood & Petts, 1999; Dewson *et al*., 2003) there are no generally applicable techniques that can be used to predict how low the flow can become without a stream community becoming temporarily or permanently impaired. While the instream flow incremental methodology (IFIM) has been used successfully for salmonids, its application for invertebrates and other fish remains limited, because of perceived difficulties in the collection of large sample sizes, taxonomic identification, and the generation of habitat suitability curves for benthic macroinvertebrates (Gore *et al*., 1998, 2001). There is a paucity of information on the way flow reductions influence non-salmonid components of stream ecosystems.

Invertebrate drift is the entrainment and transport of individuals in the water column. It is an important mechanism in the dispersal of invertebrates, recolonisation of denuded areas and feeding ecology of many fish (Merritt & Cummins, 1996). Brittain & Eikeland (1988) outline several types of drift (e.g. catastrophic, behavioural, distributional) and note that the uncritical usage of such categories has led to much confusion. For our purposes, we will divide drift into two categories, passive drift (where animals enter the water column unintentionally) and active drift (where animals intentionally enter the water column). It is well established that increases in water velocity accompanying flood events elevate levels of passive drift (e.g. McLay, 1968; Pearson & Franklin, 1968; Bogatov, 1978). Passive drift also results from animals losing hold of the substrate whilst foraging during lower flow conditions. Reasons for active drift include predator avoidance (e.g. Peckarsky, 1980) and competition (e.g. Hildrew & Townsend, 1980). Increased drift results from food shortage for some taxa (e.g. Hildebrand, 1974). However, it is not always clear whether animals actively enter the water column in search of food, or are simply more vigorously foraging on the substrate surface and thus more prone to passive drift entry.

Low flow caused by drought or water regulation has been implicated in increasing drift (Minshall & Winger, 1968; Gore, 1977; Corrarino & Brusven, 1983; Poff & Ward, 1991). At low current velocities, drift may enable invertebrates to avoid unfavourable habitats such as pools (Luedtke & Brusven, 1976; Dudgeon, 1983) and certain invertebrates may attempt to stay in the drift when flow conditions are insufficient to meet their nutritional or physiological needs (Walton, 1980a; Vinikour, 1981). Few studies have continually sampled drift before and after reducing flows in natural streams, or examined which associated changes in the physicochemical environment initiate these increases. Our aim in this study was to investigate the drift responses of invertebrate communities to experimentally reduced flows to determine what physicochemical changes resulting from flow reduction are responsible for any drift response. To do this we have used experimental flow reductions in natural and streamside channels in New Zealand and Canada.

Methods

Experiment 1 – Streamside channel experiment, Canada

Study site location and channel design

The streamside channels (Plate 1) used for this experiment were located in the University of British Columbia's Malcolm Knapp Research Forest (49°16′N 122°34′W) about 60 km east of Vancouver, near Maple Ridge, British Columbia, Canada. The channels were adjacent to Mayfly Creek, a 3 metre wide, second order oligotrophic stream draining a coastal western hemlock forest catchment. Average annual pH of the stream is 6.8 and electrical conductivity, 20 µS/cm. Mayfly Creek is generally shaded with water temperature ranging no more than 3°C daily and rarely getting above 17.5°C (Richardson, 1991). Water from Mayfly Creek was gravity fed into twelve PVC lined channels (15 m × 0.35 m). Each channel had valves to control inflow. Channels were colonised naturally by macroinvertebrates for two weeks prior to the experiment. Channel substrate consisted of rounded gravel (3-4 cm, a-axis) to a depth of 0.2 m. See Richardson (1991) and Rowe & Richardson (2001) for further details of channels.

Plate 1. The streamside channels in the Malcolm Knapp Research Forest, British Columbia, Canada.

Experimental design

Three levels of flow were randomly allocated to each of four replicate channels. These comprised a control flow based on the flow the channels had been receiving prior to the experiment (i.e. 100% flow) and flow reductions of approximately 50% and 75% (mean discharges, 1.16 L/s, 0.50 L/s and 0.20 L/s, respectively). Channel discharge was measured by timing the collection of a known volume of water from each channel in a graduated bucket. Because of the rectangular cross-section of these channels, flow reduction did not decrease wetted width. Depth in the 75% reduction channels was less than 3 cm and some of the substrate was exposed. Depths in the other treatments were between 4 – 6 cm. Velocity was less than 0.05 m/s in the 75% reduction and between 0.1 – 0.2 m/s in the other treatments. Temperature, pH and conductivity were not measured, but given the channels were only 15 metres long, these parameters were not expected to change with flow reduction. Invertebrate drift was sampled for a 24-hour period prior to flow reduction, then after one day and three days of flow reduction (June 15 – 19, 2004). All animals drifting were captured in drift nets at the end of each channel (mouth size: 0.35 m × 0.35 m, mesh size: 250 μm). Samples were preserved in 10% formalin for later sorting and enumeration. Invertebrate samples were rinsed through a 500 μm Endecott sieve and identified to the lowest possible taxonomic level using Merritt & Cummins (1996). Chironomidae were identified to sub-family level and Oligochaeta to class.

Data analysis

Drift densities were corrected for discharge and expressed as the number of animals per m^3. We did not calculate drift propensity (drift density/benthic density) as there was no reason to assume benthic densities differed among channels over the short period of the experiment. The drift density of replicate channels was measured three times, so we used a repeated measures analysis of variance (ANOVA) to assess any differences in the five most abundant taxa, total individuals and total number of taxa under the three levels of flow reduction (Statistix 8, Analytical Software, Tallahassee, FL, USA). The Tukey multiple comparison test was used to evaluate significant differences that were identified in the ANOVA. The Shapiro-Wilk test was used to test whether data were normally distributed and if not, data were $\log_{10}$ transformed to improve normality.

Experiment 2 –Whole stream flow manipulation, New Zealand

Study sites

The three selected study streams were small (< 200 L/s base flow, 2 – 3 m wide, less than 17 cm mean depth), stony bottomed streams in the southern North Island, New Zealand with contrasting land use (see Chapter 2, Table 1 for summary of stream attributes). The Booths Creek study site is situated on the Wairarapa Plains approximately 5 km south of Carterton (41°04′S 175°31′E) after the stream has passed through 10 km of predominantly dairy farmland. The other two sites are approximately 20 km north of Masterton. They are unnamed and will be referred to by the name of the streams they feed. The Kiriwhakapapa Stream site is located on private land, having passed for 2 km through low intensity sheep and beef farmland (40°49′S 175°34′E). The Reef Creek site is in the Tararua Forest Park (40°48′S 175°32′E) and surrounded by predominantly second growth indigenous forest.

Flow reduction

The creation of flow reductions involved the digging of diversion channels in two streams (Booths Creek and Kiriwhakapapa Stream) and installation of pipes at Reef Creek. We constructed pole and board weirs to form header pools for the diversion channels/pipes, to reduce flow by over 85% for approximately 100 m in each stream. The Kiriwhakapapa Stream and Reef Creek diversions operated in the Austral summer-autumn between March and April 2004. Persistent high flows in Booths Creek following an unusual mid-February storm meant that the diversion was not operating properly until late April 2004.

Experimental design

We sampled reaches upstream (control) and downstream (impact) of the diversion weir, two times before (2.5 and 1 month prior) and four times after (3, 10, 17 and 31 days) the flow reduction began. The delayed start in Booths Creek only allowed two samplings following the reduction in late April and early May 2004.

Physicochemical measurements

On each sampling occasion in each reach, water temperature, conductivity, pH and dissolved oxygen were logged for around an hour within a few hours of midday with a YSI 556 Multiprobe System (Yellow Springs Instruments Inc., Yellow Springs, OH, USA). Logged values were averaged. We also logged temperature at 30-minute intervals for the duration of the study using Onset H8 Hobo temperature loggers (Onset Computer Corporation, Bourne, MA, USA.) housed in waterproof cases. Discharge was estimated with the velocity-area method (Gordon *et al*., 2004) at the same point on each sampling occasion with a minimum of 12 depth and velocity measures per transect recorded with a Marsh-McBirney Model 2000 Flowmate (Marsh-McBirney Inc., Fredrick, MD, USA) to an accuracy of 0.01 m/s. Wetted width was measured every 5 m over 65 m in each stream section. Depth and velocity were measured at five points where invertebrate benthic samples were collected.

Invertebrate sampling

On each sampling occasion, benthic invertebrates were collected in five Surber (0.1 m^2) samples taken from riffles. The day prior to each sampling occasion two drift nets (10.5 cm × 5.5 cm mouth × 80 cm long, 250 μm mesh) were installed side by side at the same fixed points every sampling occasion. These were left overnight for a period of 18-20 hrs. All samples were preserved in 10% formalin for later sorting and enumeration. Invertebrate samples were rinsed through a 500 μm Endecott sieve and subsampled. We used a sample splitter to divide the sample into four parts and sorted sequential subsamples until at least 200 individuals were removed. The entirety of each subsample was processed. Vinson & Hawkins (1996) found a rapid increase in the number of taxa as the number of individuals examined increased up to 200 individuals after which the rate of increase slowed considerably. To avoid missing rare taxa, we scanned the remainder of the sample for taxa not present in the subsample. Invertebrates were identified to the lowest possible taxonomic level using the keys of Winterbourn (1973), Chapman & Lewis (1976), Towns & Peters (1996), Winterbourn *et al.* (2000) and Smith (2003). Chironomidae were identified to sub-family level and Oligochaeta to class.

Plate 2. The collection of macroinvertebrate drift samples at Reef Creek. One net is still installed in the stream whilst the other is being washed into a collection bag.

Data analysis

The average of the two drift nets at each site and time were used for all analyses. To compare the differences between the benthic community and the composition of the drift, the relative abundances of seven taxa groupings were calculated for before-after, control-impact treatments. Data were fourth root transformed to down-weight the influence of abundant taxa (Clarke & Warwick, 2001) and analysis of similarities (ANOSIM) used to determine any differences in invertebrate communities among streams and between drift and benthic samples (PRIMER 6, PRIMER-E Ltd., Plymouth, UK).

To determine the influence of flow reduction on drift behaviour, drift densities of individual taxa were corrected for discharge (using the average riffle depth and velocity) and expressed as the number of animals per m^3. Drift propensity (drift density/benthic density) was used for subsequent analysis to eliminate the possibility that patterns observed were merely reflections of variations in benthic density (McIntosh *et al*., 2002b). Since drift was measured simultaneously in impact and control reaches on a number of occasions before and after flow reduction, we used a before-after, control-impact paired (BACIP) analysis (Downes *et al*., 2002). This approach focuses on any changes at the impact location, relative to the control. The variable analysed is the difference between control and impact values (H_0: control-impact reach difference before = control-impact reach difference after). We hypothesised that drift may increase directly after flow reduction before decreasing to background levels. Thus, our BACIP analysis had three treatments (before reduction, within the 1st week of reduction, and the rest of reduction period) and one-way analysis of variance (ANOVA) was used to test for differences between these (Statistix 8, Analytical Software, Tallahassee, FL, USA). The Tukey multiple comparison test was used to evaluate significant differences when identified in the ANOVA. The Shapiro-Wilk test was used to test whether data were normally distributed and if not, data were $\log_{10}$ transformed to improve normality. As different taxa were dominant in each stream, we analysed streams separately. The five most abundant taxa and total number of individuals were examined for treatment differences. Feeding guilds were assigned to each taxon with the aid of Winterbourn (2000). Physicochemical measures were analysed in a similar manner except that only two treatments (before and after flow reduction) were used as the impact of flow reduction on these parameters is not often subtle (e.g. obvious decreases in velocity and wetted width) and were thought likely to persist through the reduced flow period, unlike the drift propensity of some taxa.

Results

Experiment 1 – Streamside channel experiment, Canada

The greatest densities of invertebrates drifted in the lowest flow (75% reduction) channels over the first day of reduction (Fig 1a, Table 1). *Baetis* sp. (Ephemeroptera: Baetidae) (Fig. 1b) responded most dramatically, but similar patterns were observed for Tanypodinae (Diptera: Chironomidae) (Fig. 1c) and *Ecclisomyia* sp. (Trichoptera: Limnephilidae) (Fig. 1d). The total number of taxa drifting, Orthocladiinae (Diptera: Chironomidae) and Oligochaeta showed no drift response to flow reduction (Table 1).

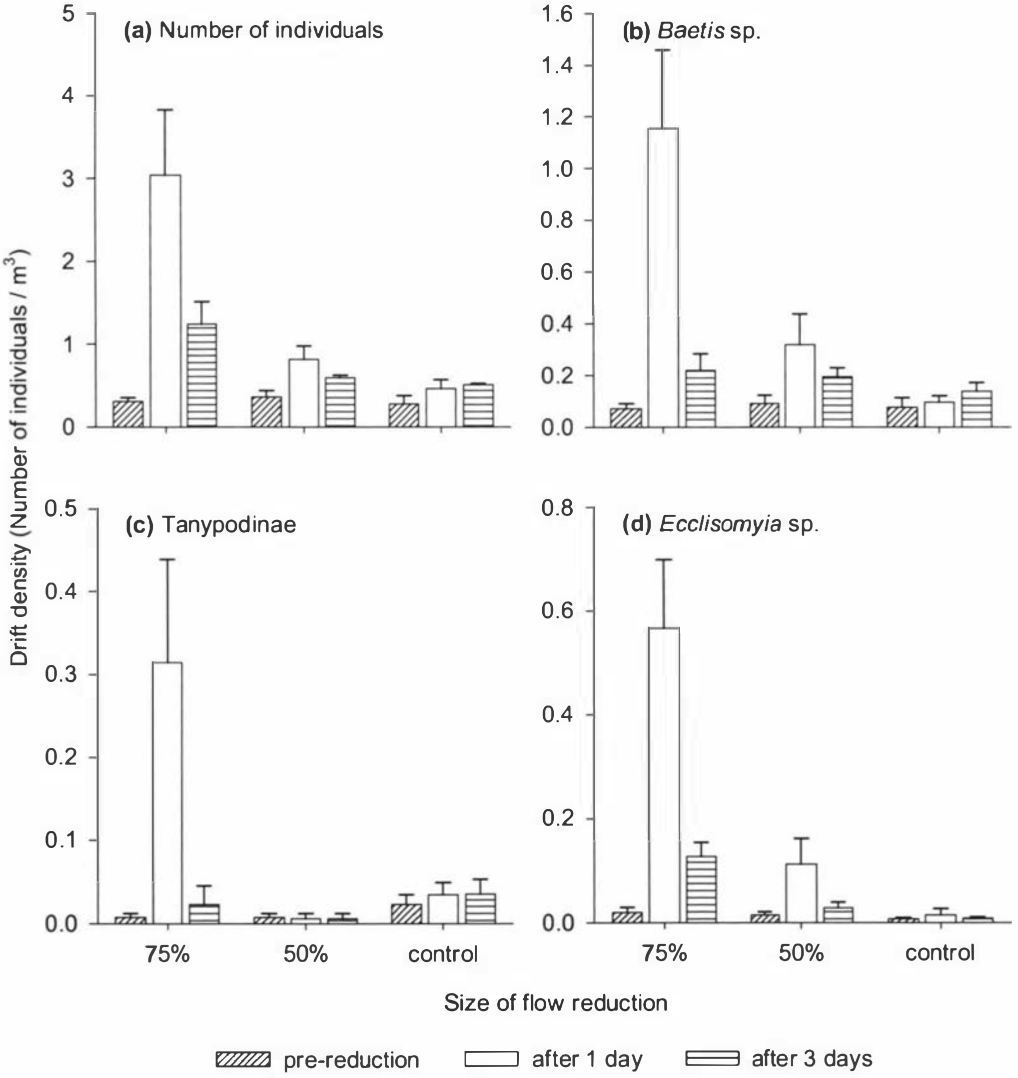

Figure 1. Mean drift densities (+1 SE) of (a) total individuals and selected taxa ((b) *Baetis* sp.; (c) Tanypodinae Chironomidae; (d) *Ecclisomyia* sp.) collected in Canadian streamside channels, 15-19 June, 2004, under three levels of flow reduction.

Table 1. Repeated measures ANOVA *F*-values for Canadian streamside channel experiment testing for differences in the number of individuals, number of taxa and drift densities of the 5 most abundant taxa among treatment (3 levels: control, 50% and 75% reduction) and time (3 levels: before, 1 day after, 3 days after). Results significant at 5% level in **bold**. The results of *post hoc* Tukey multiple comparisons are given in brackets where significant. C = control, 50 and 75 = respective reduction percentages and -1, +1 and +3 = days ± flow reduction. df = degrees of freedom. Taxa are listed in order of decreasing abundance in the drift.

Factor	df	Number of individuals	Number of taxa	*Baetis* sp.	Orthocladiinae	Oligochaeta	*Ecclisomyia* sp.	Tanypodinae
Treatment	2, 35	**10.77** (75)(50 C)	0.26	**20.13** (75)(50 C)	2.27	1.09	**23.03** (75)(50 C)	4.04
Time	2, 35	**16.06** (+1)(+3 -1)	0.52	**8.99** (+1(+3) -1)	**5.75** (+3(+1)-1)	2.56	**13.12** (+1)(+3 -1)	**6.60** (+1)(+3) -1)
Treatment × Time	4, 35	**7.47**	4.09	**7.89**	0.67	1.64	**14.79**	**6.42**

Experiment 2 – Whole stream flow manipulation, New Zealand

Physicochemical parameters

Discharge was reduced by greater than 90% in all three streams (Fig. 2a, Table 2). Riffle velocities were reduced to below 0.3 m/s and depth to below 10 cm in all streams. Flow reduction resulted in an approximate loss of 30% of wetted area in all streams (Fig. 2b, Table 2). Conductivity increased by approximately 10 μS/cm after flow reduction in Kiriwhakapapa Stream but remained unchanged in the others (Fig. 2c, Table 2), while pH remained circumneutral in all streams. There was a tendency for decreased dissolved oxygen concentrations at the start of the reduced flow period in Booths Creek and Reef Creek (Fig. 2d, Table 2), but levels remained relatively high (> 8.5 mg/L). Flow reduction had little impact on water temperature except at Kiriwhakapapa Stream where the main change was an increased temperature range in the impact reach (Table 2).

Drift composition

The benthic communities differed among the three streams (ANOSIM Global $R = 0.91$, $P < 0.01$). Booths Creek was dominated by Crustacea (Fig. 3a), Reef Creek by Ephemeroptera, Plecoptera, Trichoptera (EPT) taxa (Fig. 3e) and Kiriwhakapapa Stream by a combination of Mollusca, Chironomidae, Oligochaeta and EPT (Fig. 3c). The composition of the drift generally followed these patterns, but the drift assemblage did differ to that of the benthos (Booths Creek: Global $R = 0.71$, $P < 0.01$; Kiriwhakapapa Stream: Global $R = 0.85$, $P < 0.01$; Reef Creek: Global $R = 0.44$, $P < 0.01$). At Booths Creek, *Paracalliope fluviatilis* (Crustacea: Amphipoda), was more dominant in the drift than the benthos (Fig. 3a and b). At Kiriwhakapapa Stream, the Chironomidae and 'other' category contributed a much greater proportion to the drift than to the benthos. This was largely a result of high numbers of *Austrosimulium* sp. (Diptera: Simuliidae) in the drift. Also in this stream, *Potamopyrgus antipodarum* (Mollusca: Gastropoda) was common in the benthos but not the drift (Fig. 3c and d). Apart from the EPT group comprising a greater proportion of the drift in the after-impact treatment at Reef Creek (Fig. 3e and f), flow reduction did not have any impact on the taxonomic composition of the drift (Booths Creek: Global $R = -0.1$, $P = 0.68$; Kiriwhakapapa Stream: Global $R = 0.29$, $P = 0.03$; Reef Creek: Global $R = 0.21$, $P = 0.06$).

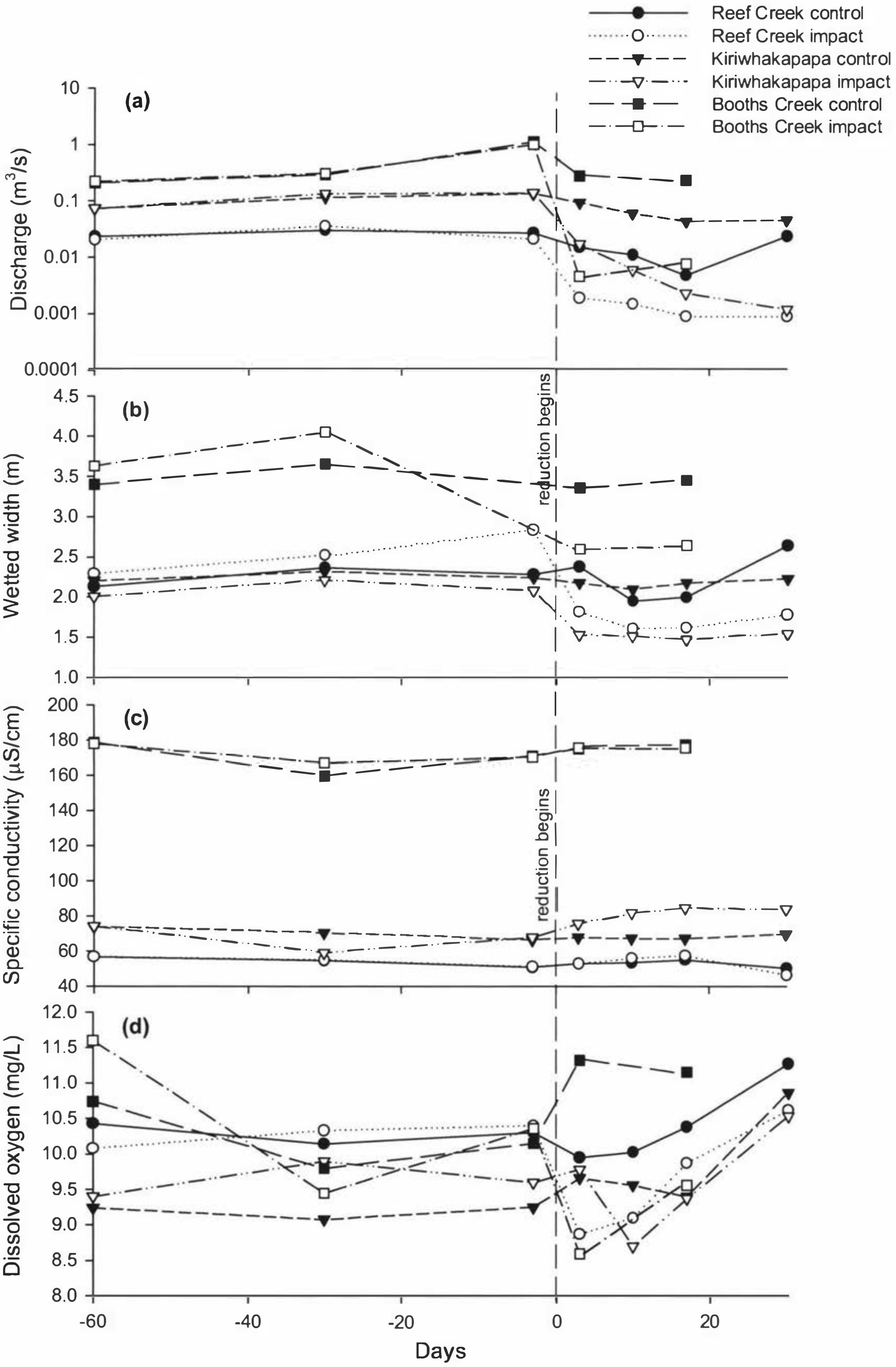

Figure 2. (a) Discharge, (b) wetted width, (c) specific conductivity and (d) dissolved oxygen measured in three Wairarapa, New Zealand streams before and during experimental flow reduction, December 2003 – May 2004.

Table 2. ANOVA BACIP *F*-values for the New Zealand stream experiment evaluating the effect of flow reduction on physicochemical measures at each of the three streams. Results significant at 5% level in **bold**. The results of *post hoc* Tukey multiple comparison tests given in brackets where significant (1= control-impact reach difference before flow reduction, 2 = control-impact reach difference after flow reduction). *missing before-upstream temperature logger at Reef Creek means BACIP procedure could not be used. One-way ANOVA instead compares after period control-impact reach means only.

	Booths Creek (BC)		Kiriwhakapapa Stream (KS)		Reef Creek (RC)		
	d. f.	*F*-value	d. f.	*F*-value	d. f.	*F*-value	Trend
Discharge	1, 3	**17.09** (2>1)	1, 5	**18.53** (2>1)	1, 5	2.55	Decrease in response to flow reduction
Velocity	1, 3	5.30	1, 5	**6.55**	1, 5	**9.18** (2>1)	Decrease in response to flow reduction
Depth	1, 3	0.90	1, 5	1.16	1, 5	0.54	Decrease in response to flow reduction
Wetted width	1, 3	**15.23** (2>1)	1, 5	**178.40** (2>1)	1, 5	1.97	Decrease in response to flow reduction
Dissolved oxygen	1, 3	**11.54** (2>1)	1, 5	0.16	1, 5	**12.58** (2>1)	Decrease in response to flow reduction but always greater than 8.5 mg/L
pH	1, 3	3.95	1, 5	0.19	1, 5	0.56	No change
Specific conductivity	1, 3	0.44	1, 5	5.49	1, 5	4.30	No change
Daily mean temperature	1, 46	0.99	1, 58	**29.73** (2>1)	1, 88	0.02*	At KS, impact reach up to 0.5°C cooler than control during reduction
Daily temperature range	1, 46	1.28	1, 58	**78.61** (2>1)	1, 88	0.11*	At KS, impact reach up to 2°C greater than control during reduction
Daily maximum temperature	1, 46	1.23	1, 58	**25.91** (2>1)	1, 88	0.00*	At KS, impact reach maximum temperature up to 1°C greater than control.

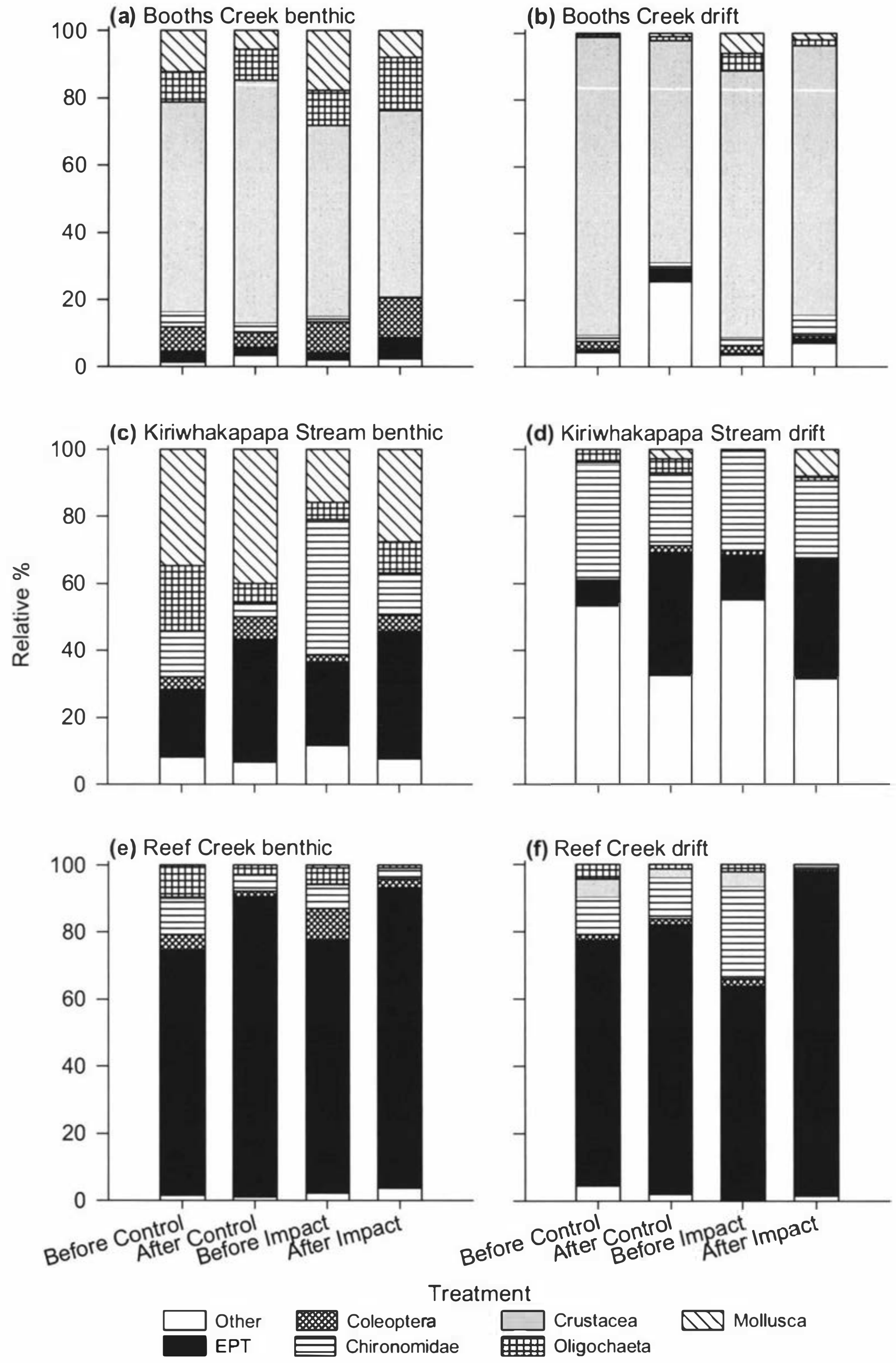

Figure 3. The relative abundance of higher order taxonomic groups collected from the benthos ((a) Booths Creek; (c) Kiriwhakapapa Stream; (e) Reef Creek) and drift ((b) Booths Creek; (d) Kiriwhakapapa Stream; (f) Reef Creek) in three Wairarapa, New Zealand streams, before and during experimental flow reduction, December 2003 – May 2004.

Drift propensity

We identified three types of drift response (Table 3). These were a sustained increase in drift throughout the reduction period, short-term drift increase only within the first week of flow reduction, and no or inconsistent drift response to flow reduction. Sustained increases in drift propensity at Booths Creek (Fig. 4a), and short-term increases in Kiriwhakapapa Stream and Reef Creek (Fig. 4b-c) were observed for total individuals. *Austrosimulium* sp. (Fig. 4e) and *Coloburiscus humeralis* (Ephemeroptera: Coloburiscidae) (Fig. 4f) showed a short-term response to flow reduction (Table 3). Taxa displaying a sustained increase in drift throughout the flow reduction period included *P. fluviatilis*, Orthocladiinae, and *P. antipodarum* in Booths Creek (Table 3). Some taxa differed in their responses between streams with Orthocladiinae having a sustained increase in drift at Booths Creek but no response at Kiriwhakapapa Stream (Fig. 4d, Table 3). Other taxa to exhibit no or variable responses to flow reduction include *Deleatidium* sp. (Ephemeroptera: Leptophlebiidae), *Oxyethira albiceps* (Trichoptera: Hydroptilidae), *Hydrobiosella* sp. (Trichoptera: Philopotamidae) and *Zelandoperla* sp. (Plecoptera: Gripopterygidae) (Table 3). Drift densities showed the same general pattern as drift propensity (Fig. 4).

Many taxa that exhibited short-term drift responses are filter feeders (e.g. *Austrosimulium* sp., *C. humeralis*), whilst those with sustained drift are mostly grazers and deposit feeders (e.g. *P. fluviatilis, P. antipodarum*, Orthocladiinae). However, other members of these guilds show no or inconsistent drift responses to flow reduction (Table 3).

Table 3. ANOVA *F*-values for BACIP differences in drift propensity resulting from flow reduction in the New Zealand experiment. The five most abundant drifting taxa listed in decreasing order of abundance. Results significant at 5% level in **bold**. Results of *post hoc* Tukey multiple comparison given in brackets where significant (1= control-impact reach difference before, 2 = difference >1 week after, 3 = difference <1 week after flow reduction). Drift trend: Short = Short term (< 1 week) drift increase following reduction, Sustained = elevated drift throughout reduction period, None = no or inconsistent drift response to flow reduction.

Stream	Taxa	*F*-value	Drift trend	Feeding method
Booths Creek (d. f. 2, 1)	*Paracalliope fluviatilis*	**839.86** (2>3=1)	Sustained	Browser
	Austrosimulium sp.	**464.04** (3≥2≥1)	Short	Filterer
	Orthocladiinae	**641.00** (2>3>1)	Sustained	Grazer
	Oligochaeta	**4779.87** (3>2>1)	Short	Deposit feeder
	Potamopyrgus antipodarum	**6155.12** (2>3>1)	Sustained	Grazer, scaper, deposit feeder
	Number of individuals	**785.98** (2>3=1)	Sustained	
Kiriwhakapapa Stream (d. f. 2, 3)	*Austrosimulium* sp.	**9.21** (3≥2≥1)	Short	Filterer
	Orthocladiinae	1.85	None	Grazer
	Oxyethira albiceps	0.35	None	Algal piercer
	Deleatidium sp.	0.37	None	Grazer, browser
	Hydrobiosis spp.	0.55	None	Predator
	Number of individuals	7.53	None	
Reef Creek (d. f. 2, 3)	*Coloburiscus humeralis*	**26.45** (3>2=1)	Short	Filterer
	Deleatidium sp.	5.54	None	Grazer, browser
	Orthocladiinae	0.39	None	Grazer
	Hydrobiosella sp.	2.14	None	Filterer
	Zelandoperla sp.	2.76	None	Filterer
	Number of individuals	**48.58** (3>2=1)	Short	

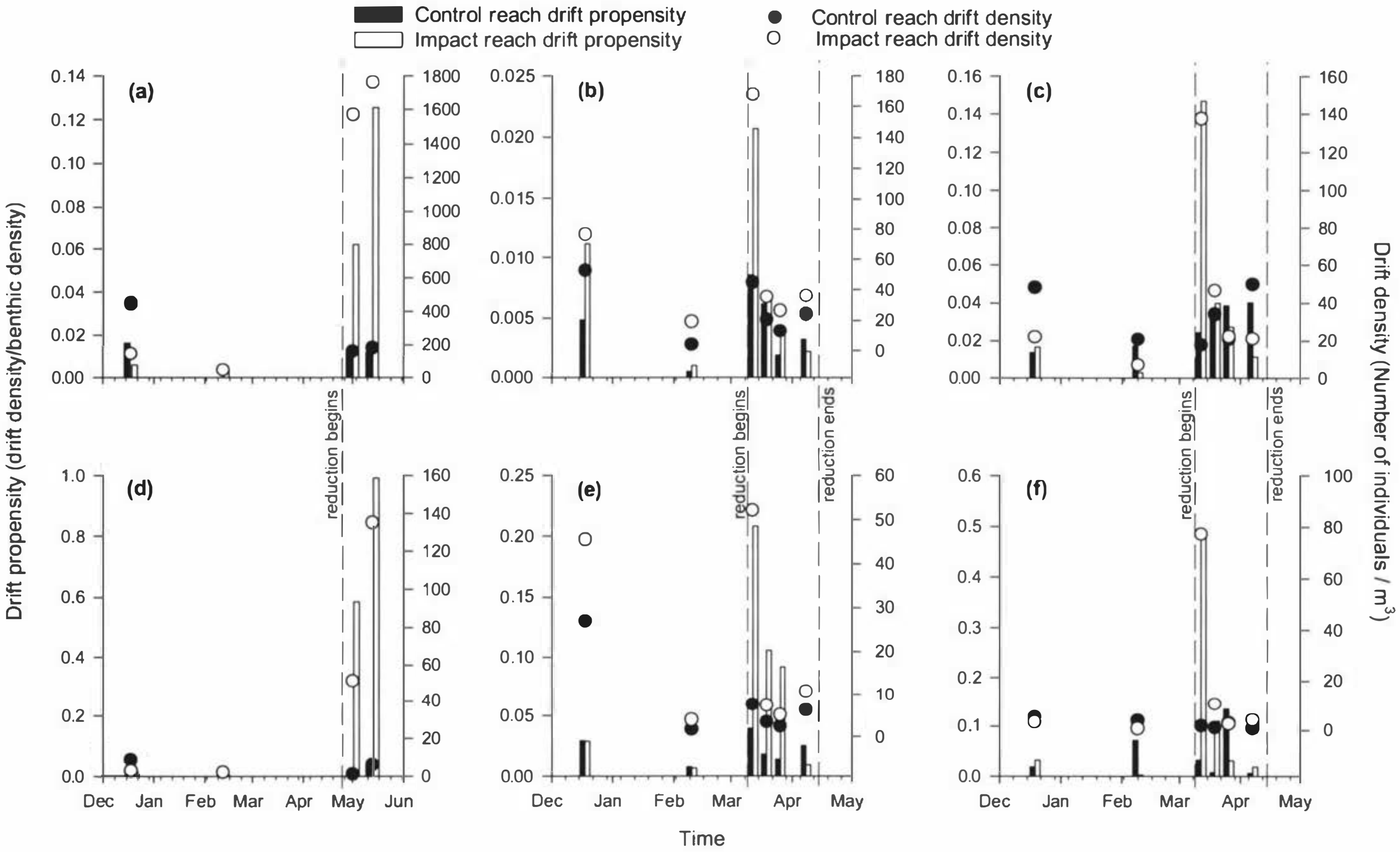

Figure 4. The drift propensity (bars, left y-axis scale) and density (circles, right y-axis scale) for the total number of individuals captured in the drift of (a) Booths Creek*, (b) Kiriwhakapapa Stream and (c) Reef Creek. The same is also shown for (d) Orthocladiinae in Booths Creek, (e) *Austrosimulium* sp. in Kiriwhakapapa Stream and (f) *Coloburiscus humeralis* in Reef Creek. Sampling occurred before and during experimental flow reduction, December 2003 – May 2004. *Note that in Booths Creek, the amphipod, *Paracalliope fluviatilis* accounts for 80% of the total individuals captured.

Discussion

The drift of invertebrates is a ubiquitous and important function of stream ecosystems. As a behaviour, it acts to redistribute and disperse animals and as a resource, it provides food for many fish and other invertebrate species. Drift can be initiated by numerous abiotic and biotic factors including changes to water velocity (e.g. Gore, 1977), resource scarcity (Hildebrand, 1974), predation (Peckarsky, 1980) and competition (Hildrew & Townsend, 1980). Drift may be 'passive' where an individual unintentionally enters the water column (e.g. loses hold of the substrate whilst foraging) or 'active', where the individual intentionally releases the substrate (e.g. to escape a predator). Many taxa are found in the drift and typically, the dominant groups of the benthos dominate the drift (Brittain & Eikeland 1988). However, taxa do differ in their drift propensity. We found the composition of the drift to be broadly similar to that of the benthos. However, some taxa contributed a greater (e.g. *Austrosimulium* sp., Chironomidae) or lesser (e.g. *P. antipodarum*) proportion to the drift than they did to the benthos, probably reflecting the microhabitat conditions they prefer (i.e. *P. antipodarum* lower velocity, *Austrosimulium* sp. higher velocity) and their ability to remain in contact with the substrate.

Reduced flow alters the instream environment by decreasing flow velocity (e.g. Kraft, 1972; Bickerton *et al*., 1993), depth, (e.g. Gore, 1977), wetted width (e.g. Cowx *et al*., 1984) and taxonomic richness (McIntosh *et al*., 2002a), increasing sedimentation (e.g. Wood & Petts, 1999) and altering invertebrate densities and community composition (e.g. Rader & Belish, 1999; Dewson *et al*., 2003). Such changes can directly or indirectly influence the drift behaviour of benthic invertebrates. We observed short-term increases in the drift of some benthic taxa following flow reduction in natural streams and streamside channels. This involved increased drift in the days following flow reduction before levels returned to pre-reduction levels. Other workers have reported similar responses to flow reduction (Minshall & Winger, 1968; Radford & Hartland-Rowe, 1971; Gore, 1977; Ruediger, 1980). Whilst there is compelling evidence that flow reduction leads to increased invertebrate drift in some taxa, it is more difficult to identify the underlying causal factors.

Dissolved oxygen, pH, conductivity and temperature did not differ between control and impact reaches or if they did, differences were too small to be biologically relevant. The most obvious and consistent changes (although not always statistically significant) in response to flow reduction were decreases in velocity, depth and wetted width. Since taxa have flow (i.e. depth, velocity) preferences (e.g. Jowett *et al*., 1991;

Collier *et al.*, 1995), the reaction of invertebrates to the sudden change in these parameters is likely to explain much of the observed short-term increase in drift. Poff & Ward (1991) also attributed an increase in drift after flow manipulations to changes in depth and velocity, since other variables such as dissolved oxygen and seston were unaffected. Taxa may be actively entering the drift in an attempt to escape unfavourable microhabitat conditions or may simply be entering the drift passively as more individuals move about on the substrate surface in search of optimal spots for foraging.

Some of the more common taxa to respond strongly to flow reduction by drifting included the filter feeding *Austrosimulium* sp. and *C. humeralis* (as well as the less common hydropsychid trichopterans *Aoteapsyche* sp. and *Orthopsyche* sp.). Other workers have also noted filter feeders to be common in the drift following flow reduction (e.g. Ruediger, 1980; Corrarino & Brusven, 1983). Filter feeders often prefer areas of higher velocity (e.g. Georgian & Thorp, 1992) where filtering rates are greater. The reduction in flow volume and velocity means less water passing through their filtering mechanisms and thus less food. The filter-feeding taxa show a short-term drift response as individuals relocate themselves because of a combination of reduced wetted habitat area and lower flow velocities leading to a reduction in entrainment of food particles and/or desirable filtering sites.

Increased drift could also result from elevated levels of biotic interaction. A concurrent study of benthic invertebrate responses to reduced flow found invertebrate densities increased in the month following flow reduction as a result of invertebrates crowding into the reduced wetted area (Dewson *et al.*, 2007). Increased benthic densities in these streams increase the likelihood of contact between animals. Some taxa respond to competitive interactions (e.g. Hildrew & Townsend, 1980) and predatory encounters (e.g. Peckarsky, 1980; Walton, 1980b) by drifting, however such a mechanism is unlikely to account for short-term increases in drift.

At Booths Creek, flow reduction led to a sustained increase in drift through the low flow period in some taxa. This response to flow reduction has not been reported elsewhere and was strongest in *P. fluviatilis*. It is possible that flow reduction increases the proportion of habitat available for this taxa, thus it is active over a wider area and a greater number of individuals are exposed to the current and passively enter the drift. Similarly, Hughes (1970) observed that in flow chambers the amphipod *Gammarus pulex* was more active, fed more on stone surfaces and drifted more in slower velocities

(0.09 m/s compared to 0.23 m/s). Sustained increased invertebrate drift could potentially lead to greater food availability for drift feeding fish during reduced flow conditions.

It was interesting that increased drift densities in our streamside channels only occurred where discharge was reduced by 75%, but not 50%, indicating that taxa are responding to some threshold of flow and not just change in flow per se. The identification of such thresholds in common taxa could enable drift to be used as an indicator of too little flow. The sudden increase of *Rhithrogena hageni* (Ephemeroptera: Heptageniidae) in the drift following the reduction of discharge in the Tongue River to below 3.68 m^3/s led Gore (1977) to recommend it as an indicator of adequate flow conditions. The mayfly *Austroclima sepia* (Ephemeroptera: Leptophlebiidae) drifted in relatively low numbers in all three New Zealand streams but did display a consistent short-term peak in drift following flow reduction. More detailed work would be required to ascertain if any drift initiation flow thresholds exist for this or any other taxa. If such thresholds were found, the drift of such taxa could be included in establishing limits to water removal before invertebrates are stressed enough to drift in significant numbers.

The increase in drift observed in the New Zealand study did not lead to reduced benthic densities (see Dewson *et al.*, 2007). This is because the proportion of invertebrates drifting relative to those present in the benthos is very small. Additionally the small size of the study streams meant drift distances were likely to be small and most drifting invertebrates remained in the reach. Flow reduction initiates drift through altering the nature and location of microhabitats within the channel. Animals, especially filter feeders, enter the drift either actively or passively as they attempt to redistribute themselves to areas of their preferred microhabitat. The sustained drift of some taxa is a novel finding and suggests that for some taxa there is an increase in usable habitat resulting from flow reduction. Most studies, including this one, show that some taxa respond to relatively sudden and severe flow reductions (i.e. a pulse disturbance) by drifting, but few studies have measured drift regularly through a period where flow is naturally decreasing more slowly (e.g. drought, a press disturbance). More work is required to tell whether elevated levels of drift result purely from a rapid change in discharge or if there is a discharge threshold, below which the drift propensity of some taxa increases. If there were such a threshold, we would expect to see elevated drift at some point during the decreasing limb of the hydrograph as a stream descended into low or drought flows.

Since drift is a major means of redistribution and dispersal of stream invertebrates (Minshall & Petersen, 1985) and a food resource for many ecologically and economically important fish species, we believe the drift behaviour of at least the more abundant taxa in a given stream deserves consideration when making water allocation decisions. Holistic environmental flow methodologies (Arthington *et al*., 1992; Tharme, 2003) that aim to maintain flow regimes that support a range of biotic, abiotic and functional elements could include an invertebrate drift component.

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The influence of flow reduction on macroinvertebrate drift propensity and distance in three New Zealand streams

Abstract

In many parts of the world, the demand for water is increasing. The removal of water from streams has the potential to affect aquatic biota. The protection of the ecological value of streams is of increasing interest to water managers and the public. However, there is a dearth of experimental studies about the impacts of flow reduction on stream habitat condition and biota.

To quantify the effects of flow reduction on habitat condition and macroinvertebrates, we reduced discharge (approximately 90%) in three small, stony bottomed streams (<4 m width) in the southern North Island, New Zealand, using weirs and diversion channels/pipes. We sampled benthic and drifting macroinvertebrates before and during a two-month period of continuous reduced flow. We also measured invertebrate drift distance in control and impact reaches to determine the impact of flow reduction on drift distance. We measured the head capsule width of common drifting taxa to determine if larval size interacted with discharge to influence drift distance.

The drift propensity of several taxa increased dramatically in the days following flow reduction and then drift dropped back to pre-reduction levels for the remainder of the period. Some taxa displayed increased drift propensity through the reduced flow period. Under reduced flow conditions, few individuals drifted more than 1 or 2 metres. The mayfly *Coloburiscus humeralis* was the only taxon where larval size influenced drift distance.

We concluded that some taxa respond to the stress of reduced flow by drifting. It is unclear whether animals are actively entering the drift or if increased drift propensity results from increased benthic activity that in turn initiates increased passive drift entry. Reduced discharge limits the distance an individual may travel in the water column. In small, shallow streams, it is unlikely that drifting would be a viable strategy for escaping unfavourable conditions.

Introduction

Over the last century, water usage has risen exponentially along with the human population (Postel, 1997; Jackson *et al*., 2001). The appropriation of ground or surface water for human use potentially has impacts on aquatic biota. Although the ecological impacts of removing water from aquatic environments are of increasing interest to water management authorities and the public, there are few experimental studies on the impacts of flow reduction on stream ecosystems (see Chapter 1 and Dewson *et al*., 2007). To date, the majority of studies have been observational surveys that either examine the impacts of drought (e.g. Cowx *et al*., 1984; Caruso, 2002) or look above and below some point where water is being removed from a stream (e.g. McIntosh *et al*., 2002a; Dewson *et al*., 2003). Drought studies provide some information about reduced flow impacts but since they can be extreme, gradual, often-regional scale disturbance events, ecosystem responses may differ from those of more discrete flow reductions resulting from water abstraction. Additionally, drought is generally outside the influence of even the most omnipotent water managers, whereas they can exact some control on how much water must remain downstream of water takes. Although above/below surveys are the best way to examine the effects of existing water abstractions, they are limited in that pre-abstraction variability between upstream and downstream sites is usually unknown. To enable the use of the more robust before-after, control-impact (BACI) experimental design (Downes *et al*., 2002) more experimental flow manipulation studies are required to provide reliable information on the effects of human-induced flow reduction on aquatic ecosystems.

Most studies of flow reduction impacts on macroinvertebrates tend to concentrate on community level variables (e.g. density, taxonomic richness) and community composition with little consideration of the individual and taxon specific behavioural responses that may be responsible for community level changes (e.g. Rader & Belish, 1999; Wood *et al*., 2000; McIntosh *et al*., 2002a). To understand why reduced flows alter community composition we must first consider its effects on physicochemical parameters and then on the behaviour and survivability of individuals and specific taxa. A number of studies have documented at least the most obvious and easily measured changes to physicochemical variables in response to flow reduction (see Dewson *et al*., 2007). The only macroinvertebrate behavioural response that has received much attention in relation to reduced flow is drift (e.g. Minshall & Winger, 1968; Gore, 1977; Poff & Ward, 1991; Kinzie *et al*., 2006).

Drift is "the downstream transport of aquatic organisms in the current" (Brittain & Eikeland, 1988) and may be 'active' where entry results from an individual choosing to release hold of the substrate or it can be 'passive' where an individual loses hold of the substrate accidentally (e.g. washed off by high shear stress). Invertebrates may drift for a number of reasons including increases in water velocity during floods (e.g. McLay, 1968; Bogatov, 1978), predator avoidance (e.g. Peckarsky, 1980) and competition (e.g. Hildrew & Townsend, 1980). Food shortage has led to increased drift in some taxa (e.g. Hildebrand, 1974). Previous information on drift responses to reduced flow is derived from studies that have either looked at short-term responses (e.g. Minshall & Winger, 1968 only sampled for 15-30 minutes directly following flow diversion), concentrated on flow regulation and fluctuation rather than reduced flow, specifically (e.g. Hooper & Ottey, 1988) or been artificial channel experiments (e.g. Corrarino & Brusven, 1983). Additionally, most previous studies look at drift density rather than drift propensity (drift density/benthic density), where observed changes over time may simply reflect changes in benthic density (e.g. Pearson & Franklin, 1968). As drift is an important process relating to the distribution of invertebrates and feeding ecology of many fish, we believe an examination of drift propensity in actual streams over a period of continuous reduced flow is warranted.

The aims of this study were to determine how flow reduction affects the drift propensity and drift distance of benthic macroinvertebrates. We reduced the flow of three small, New Zealand streams and sampled benthic and drifting macroinvertebrates before and after flow reduction. We created artificial disturbances of the substrate to determine the impact of discharge on drift distance. Additionally, for some common taxa we investigated whether larval size had any impact on drift distance. We hypothesised that for some taxa, natural drift propensity would increase and disturbance induced drift distance would decrease with flow reduction and that at lower discharges, larger individuals may not travel as far as smaller ones.

Methods

Study sites and flow reduction

The three study streams were small, stony bottom streams in the southern North Island, New Zealand. Booths Creek is the only named stream, thus the others are referred to by the name of the stream they feed. Stream attributes are summarised in Chapter 2, Table 1. The creation of flow reductions involved the digging of diversion channels in two streams (Booths Creek and Kiriwhakapapa Stream) and installation of pipes at Reef Creek. We constructed pole and board weirs to form header pools for the diversion channels or pipes, to reduce flow by over 80% for approximately 100 metres in each stream. This created an impact (reduced flow) reach and a control (unreduced flow) reach upstream. The diversions operated from late January to March 2005.

Experiment 1 – Flow reduction effects on macroinvertebrate drift propensity

Invertebrate sampling

In each reach, benthic invertebrates were collected via five Surber (0.1 m^2, 250 μm mesh) samples in riffles, three times before (11 weeks, 6 weeks, 1 week) and three times after (1 week, 4 weeks, 8 weeks) flow reduction. The day prior to each sampling occasion two drift nets (10.5 cm × 5.5 cm mouth × 80 cm long, 250 μm mesh) were installed side by side at the same fixed points on each sampling occasion. In addition, drift was assessed 1 day, 2 days and 3 days after flow was reduced in late January 2005. Drift nets were left overnight for 24 hours. All samples were preserved in 10% formalin. In the laboratory, invertebrate samples were filtered through a 500 μm Endecott sieve and one quarter of the sample sorted. A further quarter was sorted until at least 200 individuals were counted (each successive quarter was counted in entirety). The remainder of each sample was scanned for taxa not present in the subsample. Invertebrates were identified to the lowest possible taxonomic level using the keys of Winterbourn (1973), Chapman & Lewis (1976), Towns & Peters (1996), Winterbourn *et al.* (2000) and Smith (2003). Chironomidae were identified to sub-family level and Oligochaeta to class.

Physicochemical measurement

Spot surface water measures of conductivity, pH and dissolved oxygen were taken on three occasions before flow reduction (11 weeks, 6 weeks, 1 week) and three times after (1 week, 4 weeks, 8 weeks). On each occasion, parameters were logged for around an hour within a few hours of midday with a YSI 556 multi-probe system (Yellow Springs Instruments Inc., Yellow Springs, OH, USA.). Logged values were averaged. Dissolved oxygen was logged simultaneously in reduced and unreduced reaches over two to three day periods in Kiriwhakapapa Stream and Reef Creek using two YSI 556 multi-probes. Surface water temperature was logged at 30-minute intervals throughout the period of the experiment using Onset Hobo H8 (housed in waterproof cases) and Water Temp Pro temperature loggers (Onset Computer Corporation, Bourne, MA, USA.).

Discharge was estimated at a fixed transect on each occasion with a minimum of 12 depth and velocity measures per transect recorded with a Marsh-McBirney Model 2000 Flowmate (Marsh-McBirney Inc., Fredrick, MD, USA.) to an accuracy of 0.01 m/s. TruTrack WT-HR water level dataloggers (TruTrack Ltd., Christchurch, New Zealand) recorded stage height to an accuracy of 1 mm every 20 minutes in control and impact reaches from January 2005 until the end of the experiment. We calculated stage-discharge rating curves following Gordon *et al.* (2004) for each reach giving continuous discharge records from January 2005 onwards. Wetted width was measured every 5 m over 65 m in each stream reach. We measured depth and velocity at five points in riffles on each sampling occasion.

Adjacent to where depth and velocity were measured, a stone (< 60 mm, A axis) was selected for chlorophyll-*a* analysis. Stones were transported on ice in the dark and stored at -20°C. Photosynthetic pigments were extracted from stones by submergence in 90% acetone for 24 hours at 5°C. Absorbency was read at 750, 665 and 664 nm on a Varian Cary 50 Conc. UV-Visible spectrophotometer (Varian Australia Pty Ltd., Mulgrave, Australia) before and after 0.1M HCl was added. We calculated the amount of chlorophyll-*a* ($\mu g/cm^2$) on each cobble as described by Steinman & Lamberti (1996), and corrected for stone surface area calculated using length, width and depth of each cobble following Graham *et al.* (1988).

The coverage of fine sediment on the substrate was visually estimated at 15 randomly selected transects at each study site on three occasions while diversions were operating. At each transect, the same person on each occasion, estimated the percentage of substrate covered by fine sediment within a 300 mm wide strip across the width of the stream. From these measurements, an average percentage cover was calculated for each site and time. Water samples were collected midstream to measure suspended sediment. We analysed ash-free dry mass (AFDM) of suspended sediment samples by vacuum filtration, using pre-weighed Whatman (Whatman plc, Brentford, UK) glass fibre filters (GF/C). Filtration was followed by drying at 50°C for 24 hours. Filters were then weighed, ashed for 4 hours at 450°C and reweighed.

Data analysis

The average of the two drift nets at each site and time were used for all analyses. To determine the influence of flow reduction on drift behaviour, drift densities of individual taxa were corrected for discharge (using velocities measured at net mouths) and expressed as the number of animals per m^3. Drift propensity (drift density/benthic density) was used for subsequent analysis to eliminate the possibility that patterns observed were merely reflections of variations in benthic density (McIntosh *et al.*, 2002b). Since drift was measured simultaneously in impact and control reaches on a number of occasions before and after flow reduction, we used a before-after, control-impact paired (BACIP) analysis (Downes *et al.*, 2002). This approach focuses on any changes at the impact location, relative to the control. The variable analysed is the difference between control and impact values (H_0: control-impact reach difference before = control-impact reach difference after). Based on previous work (James *et al.*, 2007), we hypothesised that drift may increase immediately after flow reduction, before decreasing to background levels. Thus our BACIP analysis had three treatments (before reduction, the first three days, and the remaining reduction period) with sampling occasions as replicates within each treatment. One-way analysis of variance (ANOVA) was used to test for differences between these treatments using Statistix 8 (Analytical Software, Tallahassee, FL, USA). The Tukey *post hoc* multiple comparison test was used to evaluate significant differences identified in the ANOVA. The Shapiro-Wilk test was used to test for normality and plots of residuals versus fitted values tested for equality of variance. Where necessary, data were $\log_{10}$ or square root transformed to improve normality and equality of variances. As different taxa were dominant in each stream, we analysed streams separately. The five most abundant taxa and total number of individuals and taxa were examined for treatment differences.

Physicochemical measures were analysed in a similar BACIP design with only two treatments (control – impact differences *before* and *after* flow reduction) since these were not measured intensively in the first three days of flow reduction. Sediment cover, discharge (continuous record starting January 2005), and dissolved oxygen (24 hour logged) were not measured prior to flow reduction so the BACIP technique could not be employed. Instead, one-way ANOVA compared the control and impact reaches during the after period.

Experiment 2 – Flow reduction effects on macroinvertebrate drift distance

Measuring drift distance

In Kiriwhakapapa Stream and Reef Creek, the macroinvertebrate drift distance was measured in riffles on ten occasions using a disturbance – distance technique (e.g. McLay, 1970; Lancaster *et al*., 1996). In Booths Creek, macrophytes and edge vegetation covered most of the streambed at the time of experimentation making it impossible to measure drift distance. A Surber sampler acted as a drift net and a disturbance equivalent to taking a benthic Surber sample was created over a 0.1 m^2 area and drifting invertebrates were collected for five minutes. On each occasion, a disturbance was created at 0.5, 1.5, 2.5 and 5 m upstream of the net. It was not possible to examine distances greater than 5 m as riffles in the streams were always relatively short. On each occasion, three background drift samples were taken by collecting macroinvertebrate drift for 5 minutes in the absence of any disturbance. This procedure was performed five times in each control and impact reach in daylight hours. Invertebrates were preserved and processed as for Experiment 1, except samples were not subsampled. Prior to analysis, the mean background drift from each trial was subtracted from the experimental drift data.

Larval size

To assess the relationship between drift distance, discharge and larval size we measured the head capsule widths of *Deleatidium* sp., *Coloburiscus humeralis* and *Zelandobius* sp. from the Reef Creek drift distance experiment using an ocular micrometer. For samples containing fewer than 30 individuals, all animals were measured. For larger samples, a random subsample of 30 individuals was measured.

Data analysis

To assess the settlement rate and mean travel distance of invertebrates, we used the exponential model proposed by McLay (1970) and used by several others since (e.g. Death, 1988; Ledger *et al*., 2002). The change in numbers of drifting animals with distance (x) is given by: $N_x = N_0e^{-rx}$ or as a straight line: $\ln N_x = \ln N_0 - rx$, where N_x is the number of animals in the drift at distance (x) downstream of the point of entry, N_0 is the initial number in the drift and r is the instantaneous rate of settling from the drift. The mean distance travelled can then be derived from 1/r. Linear regressions were fitted and goodness of fit statistics calculated using SigmaPlot 2001 (SPSS Inc., Chicago, IL, USA).

Where the regression model fitted the natural logs of the drift distance data, analysis of covariance (ANCOVA) was used to test the effect of treatment (main effect) and distance (covariate) on the natural log numbers of animals in the drift.

ANCOVA was also used to test whether the size of larvae reaching the drift net was affected by flow reduction treatment (main effect) and distance from the experimental disturbance (covariate). Statistix 8 (Analytical Software, Tallahassee, FL, USA) was used for both the drift distance and larval size analyses. The Tukey multiple comparison test evaluated significant treatment differences while the covariate (distance) coefficients indicated the direction of the covariate relationship (e.g. a negative coefficient indicated that the numbers of drifting invertebrates decreased with distance from disturbance).

Results

Experiment 1 – Flow reduction effects on macroinvertebrate drift propensity

Macroinvertebrate drift propensity

There was an obvious increase in the propensity to drift for total individuals in the days following flow reduction (Fig. 1a-c, Table 1). At Booths Creek this tended to increase over the first three days (Fig. 1a), whilst at Reef Creek it declined after the first day (Fig. 1c). The greatest increase in drift propensity occurred on the first day of flow reduction at Kiriwhakapapa Stream (Fig. 1b), whilst levels remained higher than normal in Booths Creek and Reef Creek over the three days following flow reduction (Fig. 1a, c). Drift propensity tended to be greater in the impact reach than the control for all three streams over the entire flow reduction period. Several taxa exhibited increased drift propensity because of flow reduction (Fig. 1d-i, Table 1). Some taxa, such as *Paracalliope fluviatilis* at Booths Creek (Fig. 1d) and *Deleatidium* sp. at Reef Creek (Fig. 1f) showed an obvious increase in drift in the three days following flow reduction with variable but increased drift over the entire post reduction period. Orthocladiinae at Kiriwhakapapa Stream (Fig. 1h) showed a distinct peak in drift only on the day following the reduction of flow whilst *Austroclima sepia* (mayfly) at Booths Creek (Fig. 1g) and *C. humeralis* at Reef Creek (Fig. 1i) showed increased drift propensity over the three day period immediately after flow reduction before levels dropped off. The drift propensity of *Potamopyrgus antipodarum* at Kiriwhakapapa Stream tended to increase over the period of flow reduction (Fig. 1e).

Physicochemical

Flow reduction resulted in decreases to wetted width, depth and velocity, although these were not always statistically significant (Fig. 2, Table 2). Specific conductivity, pH and chlorophyll-*a* were generally unaffected by flow reduction with changes to conductivity in Reef Creek and pH in Booths Creek being small (Table 2). Water temperature was altered the most in the non-shaded Booths Creek and Kiriwhakapapa Stream, however observed differences were small. Mean temperature decreased in Booths Creek (by 0.3°C) and increased in Kiriwhakapapa Stream (by 0.3°C) whilst temperature range was decreased by flow reduction in both these streams (on average by 3.5°C and 0.9°C respectively). The daily maximum temperature was depressed in all three streams by flow reduction (on average by 3.3°C in Booths Creek, 0.6°C in Kiriwhakapapa Stream and 0.3°C in Reef Creek) (Table 2). Dissolved oxygen levels tended to be depressed by flow reduction with the main control-impact difference during the night in Kiriwhakapapa Stream and Reef Creek (Table 2). Coverage of the substrate by fine sediment increased after flow reduction only in the non-forested Booths Creek (from 9 to 46%) and Kiriwhakapapa Stream (from 43 to 83%) whilst suspended sediment was unchanged by flow reduction in any stream (Table 3).

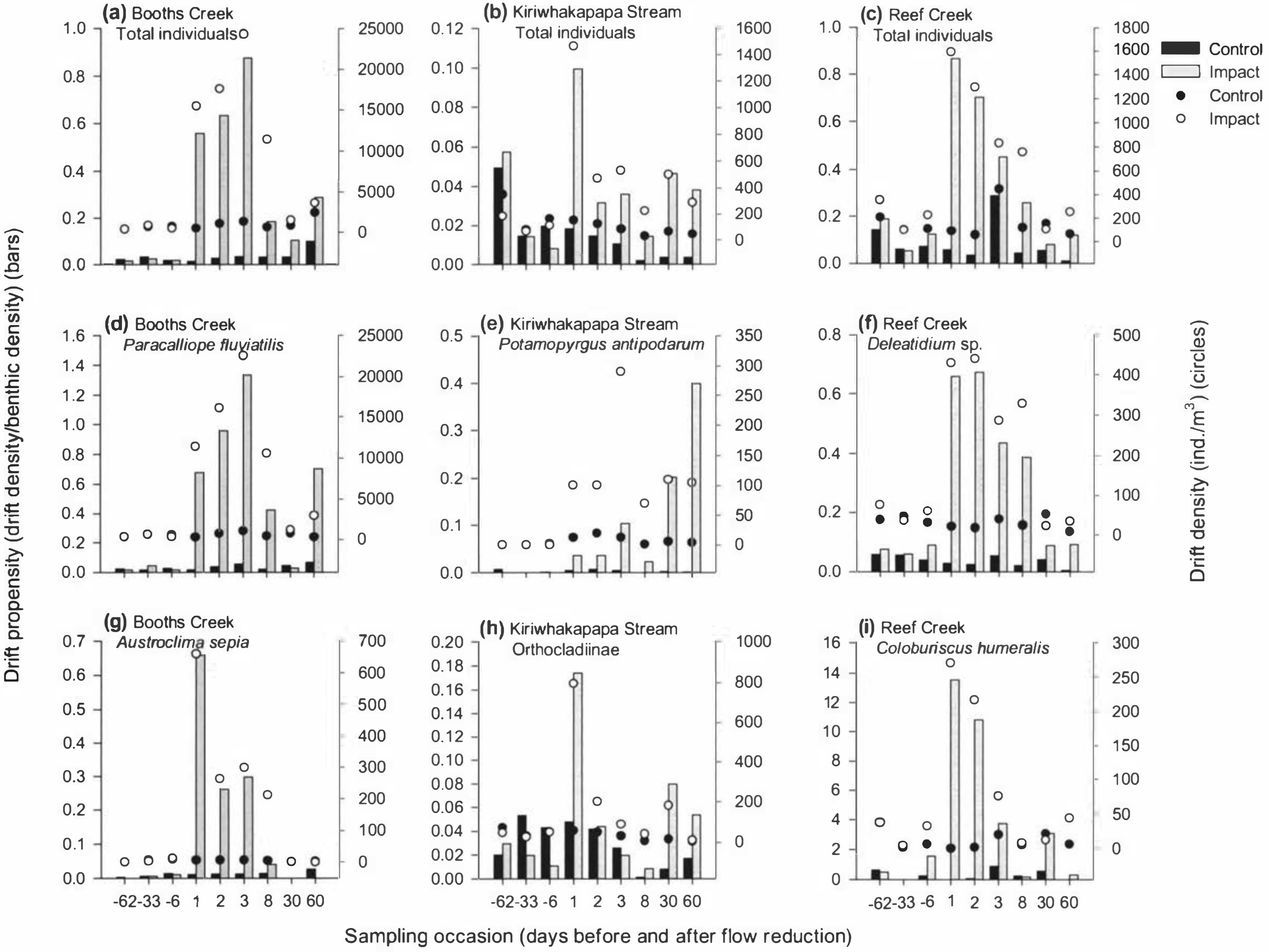

Figure. 1 The drift propensity (bars) and density (circles) of total individuals and selected common taxa in control and impact reaches of Booths Creek, Kiriwhakapapa Stream and Reef Creek before and after flow reduction.

Table 1. Drift propensity ANOVA *F*-values testing for control – impact reach differences before and after flow reduction. The five most common drifting taxa are shown in order of decreasing abundance. Results significant at the 5% level are in **bold**. Results of *post hoc* Tukey multiple comparison test given in brackets where significant (control-impact reach differences, 1 = before flow reduction, 2 = 1st three days of reduction, 3 = rest of flow reduction). df = degrees of freedom. ↑ = flow reduction increases drift, ↓ = flow reduction decreases drift.

Stream	Taxa	*F*- value
Booths Creek (df 2, 6)	*Paracalliope fluviatilis*	**10.45** (2≥3≥1) ↑
	Austrosimulium sp.	4.44
	Oxyethira albiceps	**175.64** (2>1=3) ↑
	Austroclima sepia	**23.80** (2>3=1) ↑
	Orthocladiinae	3.05
	Total individuals	**38.04** (2>3=1) ↑
	Total taxa	0.60
Kiriwhakapapa Stream (df 2, 6)	Orthocladiinae	0.15
	Potamopyrgus antipodarum	2.75
	Chironominae	0.43
	Oligochaeta	1.74
	Austrosimulium sp.	3.18
	Total individuals	2.97
	Total taxa	0.57
Reef Creek (df 2, 6)	*Deleatidium* sp.	**12.78** (2>3=1) ↑
	Zephlebia dentata	**69.74** (2>1=3) ↑
	Coloburiscus humeralis	**6.27** (2≥3≥1) ↑
	Orthocladiinae	0.83
	Orthopsyche sp.	**33.34** (2>1=3) ↑
	Total individuals	5.11
	Total taxa	1.99

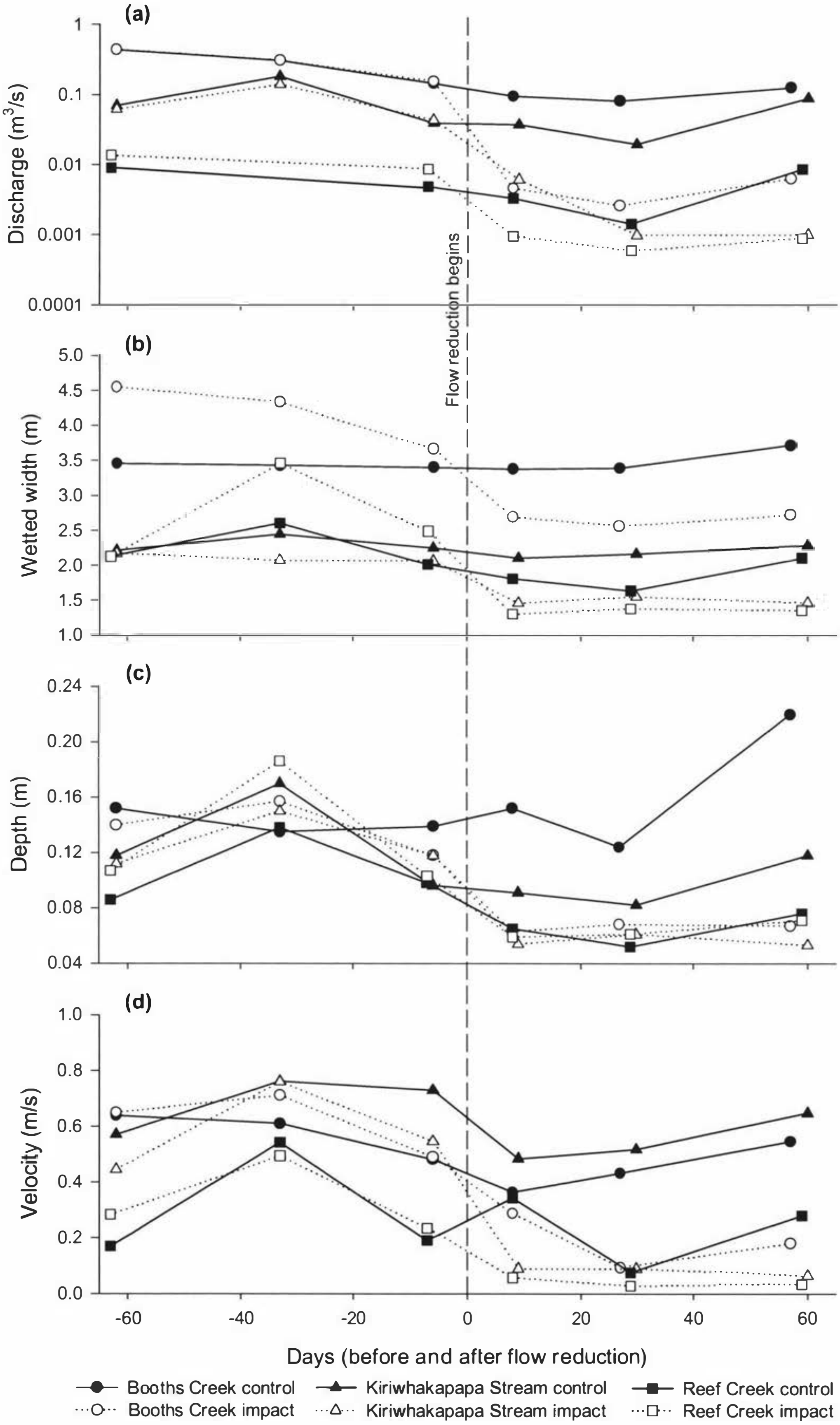

Figure. 2 Flow related measures recorded between November 2004 and March 2005 in control and impact reaches of Booths Creek, Kiriwhakapapa Stream and Reef Creek.

Table 2. ANOVA *F*- values testing for the impact of flow reduction on physicochemical measures recorded between November 2004 and March 2005 in three small New Zealand streams. Results significant at the 5% level are in **bold**. Results of *post hoc* Tukey multiple comparison test given in brackets where significant (1= control-impact reach difference before flow reduction, 2 = control-impact reach difference after flow reduction). ↓ = parameter decreases and ↑ = parameter increases with flow reduction. C = control and I = impact. df = degrees of freedom.

	Booths Creek		**Kiriwhakapapa Stream**		**Reef Creek**	
	df	*F*	df	*F*	df	*F*
Discharge	1, 9022	**23472.80** (C>I)	1, 8694	**11196.60** (C>I)	1, 8538	**384.64** (C>I)
Depth	1, 4	**7.99** (2>1) ↓	1, 4	3.28	1, 4	2.04
Velocity	1, 4	5.10	1, 4	**21.22** (2>1) ↓	1, 4	2.62
Wetted area	1, 4	0.11	1, 4	**17.50** (2>1) ↓	1, 4	0.04
Specific conductivity (spot)	1, 4	2.28	1, 4	1.26	1, 4	**51.33** (2>1) ↑
pH (spot)	1, 4	**13.96** (1>2) ↓	1, 4	12.80	1, 4	1.45
Dissolved oxygen (spot)	1, 4	**12.21** (2>1) ↓	1, 4	2.85	1, 4	2.33
Dissolved oxygen (logged)	No data	No data	1, 862	**188.09** (C>I)	1, 288	**2395.66** (C>I)
Sediment cover	1, 4	**28.59** (I>C)	1, 4	**29.76** (I>C)	1, 4	0.08
Suspended sediment	1, 6	0.21	1, 6	0.00	1, 6	0.34
Chlorophyll-*a*	1, 4	1.11	1, 4	0.67	1, 4	1.79
Daily mean temperature	1, 128	**100.71** (2>1) ↓	1, 130	**91.51** (2>1) ↑	1, 131	3.22
Daily temperature range	1, 128	**152.38** (2>1) ↓	1, 130	**39.58** (2>1) ↓	1, 131	0.25
Daily maximum temperature	1, 128	**145.43** (2>1) ↓	1, 130	**54.19** (2>1) ↓	1, 131	**16.63** (2>1) ↓

Experiment 2 – Flow reduction effects on macroinvertebrate drift distance and larval size

Macroinvertebrate drift distance

The number of animals in the water column decreased with distance from the experimental disturbance (Fig. 3, Table 3). Where the exponential model fitted or nearly fitted the observed pattern of drift distance, the mean travel distances were greater in the control than in the impact reaches (Table 3). More animals entered the drift as a result of experimental disturbance in the control reaches (Fig. 3, Table 3). Few *Deleatidium* sp. at Reef Creek remained in the drift in either the control or impact reach after an experimental disturbance at 5 metres (Fig. 3b). In contrast, around half of Orthocladiinae Chironomidae remained in the drift after 5 metres in Kiriwhakapapa Stream (Fig. 3d).

Larval size and drift distance

The size of *Deleatidium* sp. and *Zelandobius* sp. larvae had little effect on the distance drifted following experimental disturbance (Fig. 4a-b, Table 4). *Deleatidium* sp. larvae entrained in the drift were larger in the control compared to the impact reach (Table 4). Similarly, *C. humeralis* larvae in the drift were larger in the control reach (Table 4). Additionally, in the control reach, the size of *C. humeralis* remaining in the drift decreased with increasing distance from the experimental disturbance (Fig. 4c, Table 4).

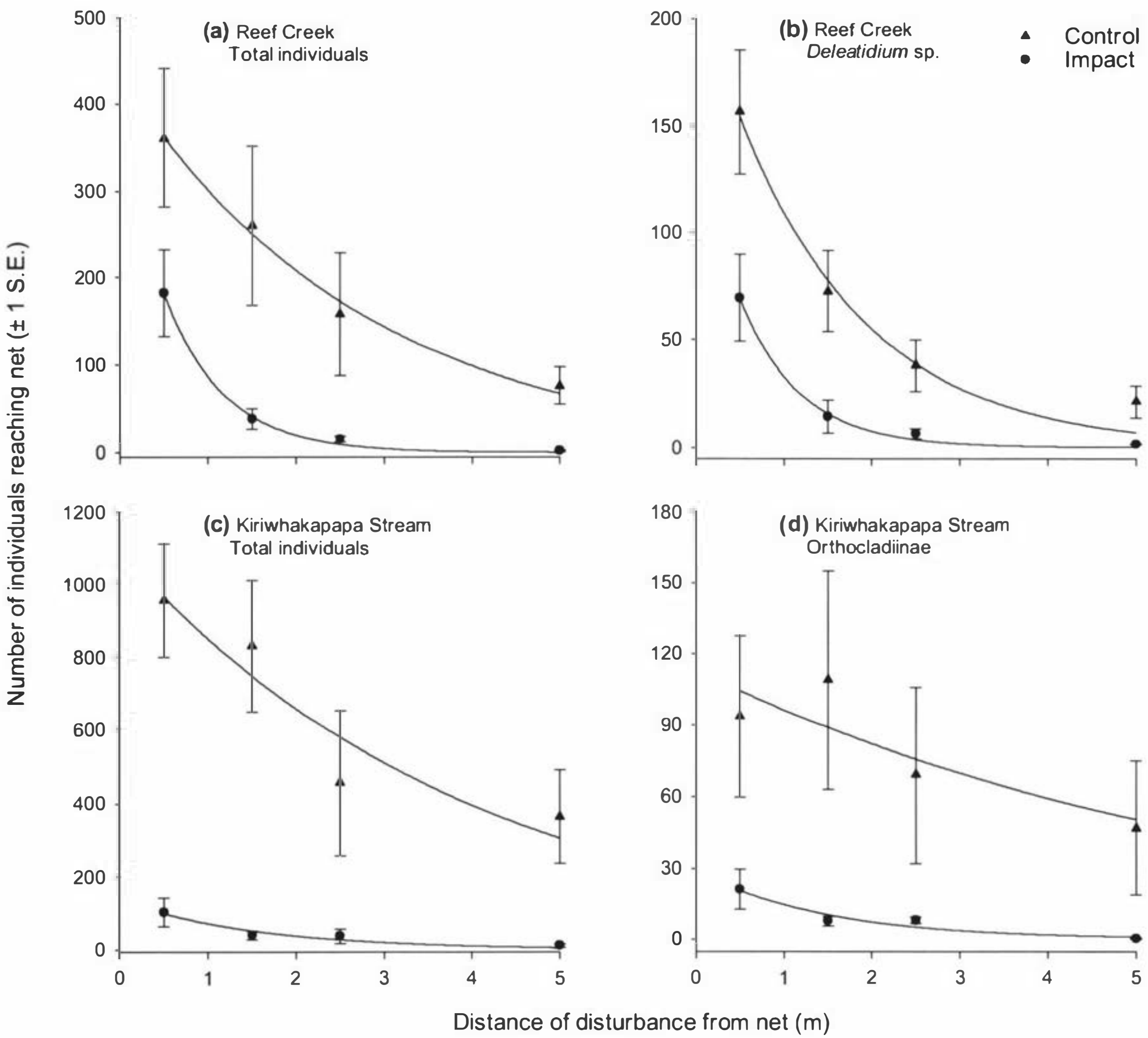

Figure. 3 The distance drifted in control and impact reaches of Reef Creek ((a) total individuals and (b) *Deleatidium* sp.) and Kiriwhakapapa Stream ((c) total individuals and (d) Orthocladiinae).

Table 3. Regression, goodness of fit and ANCOVA results describing the effect of flow reduction treatment and distance from experimental disturbance (n = 5 in each reach) on the number of animals in the drift. Only total individuals and those of the five most abundant taxa where the regressions were significant in at least one treatment are shown. 1/r is the mean drift distance in metres. The ANCOVA is one-way with treatment the main effect and distance the covariate. C = control, I = impact.

Stream	Taxon	Reach	y intercept	Slope±SE	R^2	*F*	*P*	1/r	ANCOVA results (all degrees of freedom: 1,7)	Tukey multiple comparisons and covariate coefficients
Reef Creek	Total individuals	Control	6.04	-0.35±0.03	0.99	180.34	**<0.01**	2.86	Treatment: *F* = 19.26, *P* < 0.01	C > I
		Impact	5.36	-0.96±0.01	0.98	87.42	**0.01**	1.04	Distance: *F* = 20.32, *P* < 0.01	-0.66
	Deleatidium sp.	Control	5.01	-0.42±0.09	0.91	19.88	**0.04**	2.38	Treatment: *F* = 20.03, *P* < 0.01	C > I
		Impact	4.20	-0.80±0.14	0.94	31.24	**0.03**	1.25	Distance: *F* = 28.51, *P* < 0.01	-0.61
	Coloburiscus humeralis	Control	3.85	-0.50±0.10	0.93	23.87	**0.04**	2.00	Treatment: *F* = 15.22, *P* = 0.01	C > I
		Impact	3.14	-1.01±0.18	0.94	30.18	**0.03**	0.99	Distance: *F* = 25.96, *P* < 0.01	-0.75
	Orthocladiinae	Control	3.21	-0.20±0.11	0.63	3.40	0.21	5	Treatment: *F* = 12.11, *P* = 0.02	C > I
		Impact	2.83	-0.65±0.13	0.93	26.48	**0.04**	1.54	Distance: *F* = 11.36, *P* = 0.02	-0.42
	Zephlebia sp.	Control	3.35	-0.51±0.04	0.99	164.99	**<0.01**	1.96	Treatment: *F* = 4.95, *P* = 0.08	C = I
		Impact	2.07	-0.56±0.42	0.47	1.77	0.31	1.78	Distance: *F* = 6.36, *P*= 0.04	-0.53
Kiriwhakapapa Stream	Total individuals	Control	6.93	-0.22±0.06	0.87	12.91	0.07	4.55	Treatment: *F* = 144.19, *P* < 0.01	C > I
		Impact	4.67	-0.46±0.08	0.94	32.86	**0.03**	2.17	Distance: *F* = 23.78, *P* < 0.01	-0.34
	Orthocladiinae	Control	4.75	-0.17±0.05	0.85	11.16	0.08	5.88	Treatment: *F* = 19.14, P < 0.01	C > I
		Impact	3.75	-0.97±0.19	0.93	27.36	**0.03**	1.10	Distance: *F* = 8.48, *P* = 0.03	-0.57
	Pycnocentrodes sp.	Control	6.04	-0.95±0.11	0.98	78.99	**0.01**	1.05	Treatment: *F* = 21.43, *P* < 0.01	C > I
		Impact	-1.35	0.28±0.18	0.54	2.34	0.27	3.57	Distance: *F* = 1.34, *P* = 0.30	

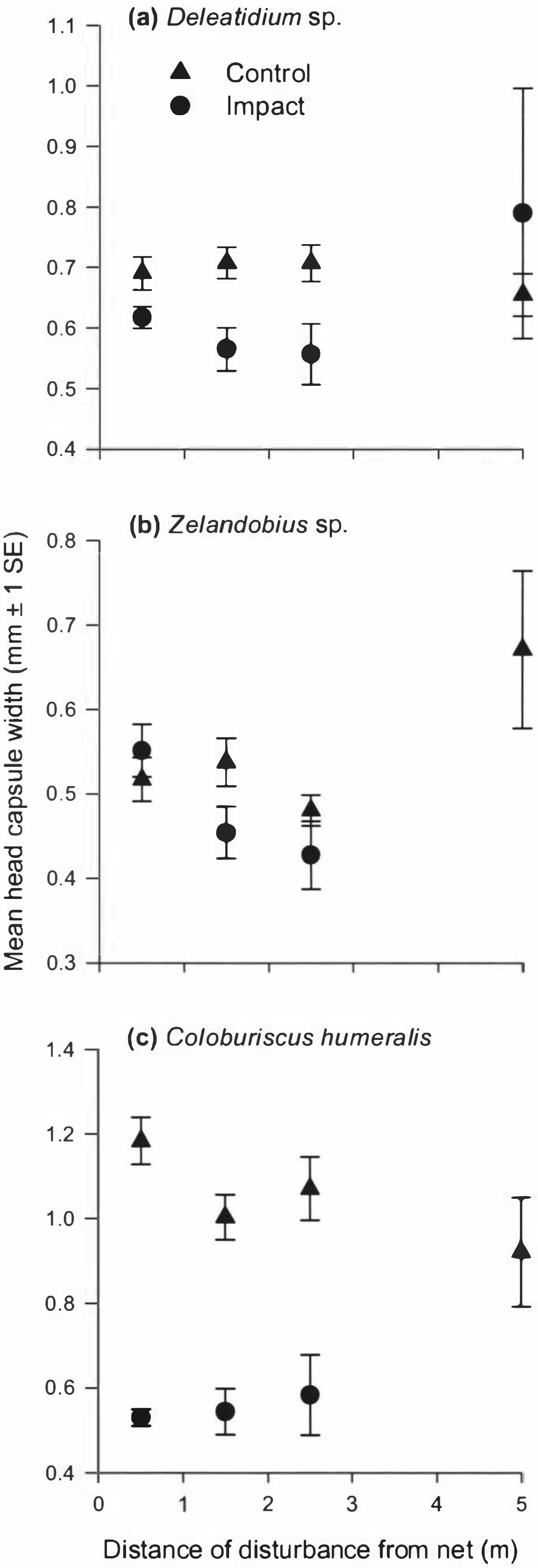

Figure. 4 The effect of larval size on the distance travelled following experimental disturbance in control and impact reaches for three Reef Creek taxa.

Table 4. ANCOVA results testing the relationship between treatment (main effect) and distance from experimental disturbance (covariate) on larval size for three common taxa in Reef Creek. Results significant at the 5% level are in **bold**. C = control, I = impact.

Taxon	Factor	Degrees of freedom	F- value	Tukey multiple comparisons and covariate coefficients
Deleatidium sp.	Treatment	1, 829	**16.72**	C > I
	Distance	1, 829	1.06	
Zelandobius sp.	Treatment	1, 281	0.04	
	Distance	1, 281	0.00	
Coloburiscus humeralis	Treatment	1, 409	**123.98**	C > I
	Distance	1, 409	**4.57**	-0.05

Discussion

Flow reduction increased the drift propensity of several taxa in our study streams. Several other authors have found drift density to increase with reduced flow in natural (e.g. Minshall & Winger, 1968; Pearson & Franklin, 1968) and artificial channels (e.g. Ruediger, 1980; Corrarino & Brusven, 1983). We would intuitively expect increased drift with increases in flow because animals can be 'washed' off the substrate and entrained in the water column by increased water velocity. The driver behind increased drift with decreased flow (and velocity) is less obvious. If drift was initiated by changes in thermal regime, dissolved oxygen levels or pH, then one might expect increased drift to be sustained throughout the period of reduced flow. However, for most taxa the response was short term, with increased drift over the first three days of flow reduction before levels returned to near pre-reduction levels. This suggests that these taxa are responding to the physical habitat changes caused by flow reduction as opposed to chemical factors. Additionally, flow reduction impacts on variables such as pH, dissolved oxygen and temperature were either small or absent in this study. Other changes, such as an increase in fine sediment cover take time to accumulate and will not occur immediately following flow reduction. A reduction in flow does however have an immediate impact on water depth, wetted width and velocity. Consequently, the location and size of microhabitats within the streambed will change. For example, high velocity areas may be lost while slow velocity areas and pools may increase.

Minshall & Winger (1968) attributed increased drift after flow reduction to decreases in depth and velocity, as wetted width did not change in their setup. Similarly, Poff & Ward (1991) ascribed an increase in drift after flow manipulations to changes in depth and velocity, as other variables (e.g. dissolved oxygen) were unaffected. Corrarino and Brusven (1983) attributed the increase in drift of the filter-feeding *Simulium* sp. following sudden flow reduction to its specific velocity requirements. The closely related *Austrosimulium* sp. in two of our study streams displayed no strong response to flow reduction. However, in an earlier study in the same streams, this taxon showed a strong increase in drift following flow reduction (see previous part of this chapter and James *et al*., 2007). A filter-feeding mayfly, *Coloburiscus humeralis*, common in the forested Reef Creek, increased greatly in the drift in the two days following flow reduction. Other workers (e.g. Ruediger, 1980; Hooper & Ottey, 1988) have also observed increased drift in filter feeding taxa after flow reduction, indicating that taxa that require the steady flow of water through their filtering mechanisms to obtain adequate nutrition may be more responsive to changes in velocity. Once these taxa have moved to an adequate microhabitat they will probably stay there as long as their nutritional requirements are met, hence the short-term drift response they display.

The distance travelled in the drift by an individual is related to a number of factors including species, life cycle stage, stream size, depth and the presence of pools (Brittain & Eikeland, 1988). Water velocity and discharge will play a significant role in determining the distance an individual will travel as it does with inanimate objects such as leaves and twigs (James & Henderson, 2005). Reduced discharge often results in lowered velocities (Chapter 1 and Dewson *et al*., 2007), thus one would expect drift distances to be decreased by flow reduction. Under low current velocity conditions (0 – 0.25 m/s), Townsend & Hildrew (1976) found 85% of invertebrates originated less than 2 metres upstream. Studies in smaller streams (i.e. < 4 m wide) have reported a range of mean drift distances (from below 2 m to greater than 70 m) depending on the species, but most report distances less than 10 m (e.g. McLay, 1970; Elliott, 1971; Death, 1988).

Flow reduction decreased mean travel distance by at least half for total individuals and most of the taxa that fitted the exponential decay model. Even in the control reaches it was evident that animals in the drift generally travelled no more than a few metres under summer base flow conditions. It has been proposed that drift may enable some benthic invertebrates to avoid unfavourable habitats (Luedtke & Brusven, 1976; Dudgeon, 1983) and that certain taxa may attempt to stay in the drift when flow conditions do not meet their nutritional or physiological requirements (Walton, 1980; Vinikour, 1981). Given that the drift distance experiments were performed in the higher velocity parts of the streams (i.e. riffles) and animals still only travelled relatively small distances, it is unlikely many invertebrates could actually use drift as a means of transport to escape reduced flow conditions in our small study streams. It is conceivable that animals could move downstream via a series of 'hops', but the prevalence of pools and fish would make such an exercise energy intensive and risky. The mayfly, *Deleatidium* sp. appeared to settle out of the water column rapidly as few individuals remained in the drift after an experimental disturbance five metres away. Ledger *et al.* (2002) also found that *Deleatidium* sp., especially early instar larvae, have high settlement rates. They attributed this rapid return to the streambed along with this taxon's low propensity to drift to be related to its broad diet, since it would be likely to find food resources wherever it settled.

Intuitively one would expect larger individuals to be both heavier and have a greater swimming ability (in those taxa that actively swim) and thus have greater control over drift entry and exit. Poff *et al.* (1991) found *Baetis* spp. to show size dependent responses to flow alteration with small individuals' drift rates increasing immediately following daytime flow alteration and larger individuals delaying drift until night. Thus for some taxa, size may affect drift behaviour. Since we induced invertebrates to drift via artificial disturbance we can only comment on size-related drift distance, not propensity to drift. We found little evidence of larval size-related differences in drift distance in control and impact reaches in Reef Creek for *Deleatidium* sp. or *Zelandobius* sp. and in the impact reach for *C. humeralis*. However, in the control reach of Reef Creek the mean size of *C. humeralis* remaining in the drift declined with increasing distance from the experimental disturbance. It appears larger individuals of this big-bodied, non-streamlined mayfly, because of their greater mass or swimming ability, settled out of the water column soon after being entrained. Thus, larval size may interact with discharge to influence the drift distance of some taxa, while for others size is of little consequence. Additionally, *Deleatidium* sp. and *C. humeralis* larvae reaching the catch net were smaller in the impact reach relative to the control. Perhaps larvae of these taxa were generally smaller in the impact reach. However, from the processing of benthic samples, there were no obvious size differences in these taxa between control and impact reaches. Therefore, it would appear that in impact reaches larger larvae settled out before reaching the catch net and were not captured.

We have shown that for many taxa flow reduction is a stressful event that results in increased drift. It is unclear whether flow reduction caused animals to actively enter the drift, whether the resulting changes to microhabitat structure increased benthic activity and more individuals passively entered the drift or if it was some combination of the two. Whatever the mode of drift entry, it is clear that under reduced flow conditions, individuals are unlikely to be transported more than a few metres even in riffles. Given the riffle – pool sequences common in these small streams, drift entry under low flow conditions is unlikely to be a useful option for individuals seeking more appropriate flow environments. This may be why larger individuals of the filter-feeding mayfly, *C. humeralis* settle out quickly following entrainment under low discharge conditions.

To further elucidate whether macroinvertebrate drift is a relevant phenomenon for consideration when making water allocation decisions, more work is required to ascertain the functional relevance of macroinvertebrate drift for the invertebrates themselves and organisms such as trout that feed on them. Specifically, studies are needed to investigate if invertebrate survival is altered by changes in drift dynamics and if the nutritional quality of drifting invertebrates (i.e. larval size, type of species) for drift feeding fish is altered by flow reduction.

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Chapter 4

Do stream macroinvertebrates use instream refugia in response to severe short-term flow reduction in three New Zealand streams?

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Abstract

Demand for water is increasing and water managers need to know how much they can remove from a stream before there are significant detrimental effects on its biological integrity. Flow reduction alters a number of habitat variables known to be important to aquatic invertebrates such as depth, velocity, temperature and fine sediment accumulation. Some taxa may attempt to use instream refugia to mitigate the effects of flow reduction.

We experimentally manipulated flows by constructing weirs and diversions in three small New Zealand streams. Discharge was reduced by 88-96%. We tested the hypothesis that macroinvertebrates would use pools and the hyporheic zone as refugia during short-term (1-month) periods of reduced flow. We sampled hyporheic invertebrates with colonisation chambers and pool invertebrates with kick nets within a before-after, control-impact (BACI) experimental design. A suite of physicochemical parameters was measured concurrently including surface and hyporheic temperatures.

Flow reduction significantly decreased velocity (60-69%) in all streams. Depth (18-61%) and wetted width (24-31%) tended to decrease but these changes were not always significant. Sediment cover increased the most in farmland streams (10-80%). Apart from decreasing temperature range (18-26%), flow reduction had little impact on the surface water temperatures. Flow reduction had no impact on the abundance of common pool macroinvertebrates or on the abundance, vertical distribution or community composition of hyporheic macroinvertebrates.

Our results suggest, in conjunction with those of Dewson *et al.* (2007) that aquatic macroinvertebrates are resistant to short-term, severe flow reduction as long as some water remains.

Introduction

The sustainable management of rivers and streams to maintain biological integrity in the face of escalating demands for water extraction is becoming more difficult (Baron *et al.*, 2002; Poff *et al.*, 2003; Richter *et al.*, 2003). Water managers need to know how much water can be removed from a river before there are significant detrimental effects on its biological integrity. Most empirical studies investigating the effects of flow reduction on benthic macroinvertebrates are surveys, often sampling upstream and downstream of some diversion/abstraction structure (e.g. Castella *et al.*, 1995; McIntosh *et al.*, 2002; Dewson *et al.*, 2003). Such studies usually do not allow sampling of the downstream impact reach prior to flow reduction and can thus never completely eliminate the potential confounding influence of other upstream – downstream changes such as land use.

Experimental manipulations that allow the application of more robust before-after, control-impact (BACI) analysis design (see Downes *et al.*, 2002) are required to establish if there are consistent impacts from flow reduction or if there are key habitat and/or biotic variables that might indicate too little flow. We manipulated the flows in three small (< 200 L/s base flow) streams in New Zealand to investigate the impacts of flow reduction on habitat condition and benthic, drifting and hyporheic invertebrates. Our study seeks to emulate a short-term flow reduction similar to those that occur commonly in New Zealand as a result of pasture irrigation. Such reductions may occur suddenly and during the warmest part of the year when demand for irrigation is greatest. Most previous flow reduction studies investigate changes to benthic macroinvertebrate abundance and community composition but few look at where animals move within the stream channel and substrate in response to flow reduction. If a normally perennial stream were to cease surface flow then pools and the hyporheic zone may be the only remaining wetted areas. This study seeks to determine whether pools and the hyporheic zone are refugia from severe flow reductions in perennial streams when some flow remains.

The hyporheic zone, defined by White (1993) "as the saturated interstitial areas beneath the stream bed and into the stream banks that contain some proportion of channel water or that have been altered by channel water infiltration" has received less attention from biologists than the stream benthos. Hyporheic fauna, known as the 'hyporheos' (Williams & Hynes, 1974), includes crustaceans, worms, mites and aquatic insect larvae (Boulton *et al.*, 1998). In New Zealand, fauna commonly collected from the hyporheic zone includes occasional hyporheic zone dwellers such as *Olinga feredayi* (Trichoptera: Conoesucidae), *Acanthophlebia cruentata* (Ephemeroptera: Leptophlebiidae), Elmidae (Coleoptera) and Chironomidae, and permanent resident taxa such as Acari, Copepoda, Ostracoda and Oligochaeta (Burrell & Scarsbrook, 2004).

The hyporheic zone is not often subject to stressors such as high water velocity and extreme temperature fluctuations, which can occur in surface waters. Additionally, if the surface channel dries out as happens in intermittent streams, water often remains in the hyporheic zone. Therefore, it is reasonable to propose that benthic invertebrates may use the hyporheic zone as a refuge from unfavourable surface conditions (Brunke & Gonser, 1997; Boulton *et al*., 1998). Some benthic invertebrates have been found to migrate into the substrate during high flow events to escape being scoured from the streambed and may then act as a source of post-flood colonists (e.g. Dole-Olivier & Marmonier, 1992). Several studies in intermittent streams have found this can occur in response to drying (e.g. Clifford, 1966; Cooling & Boulton, 1993) but not always (e.g. Boulton, 1989; Del Rosario & Resh, 2000). In perennial streams, Gilpin & Brusven (1976) and Ruediger (1980) found the use of the hyporheic zone by benthic invertebrates was unaffected by flow reduction. However, the former study had limited replication (6 chambers) whilst the latter only sampled to a depth of 17.5 cm and was not performed in natural channels.

Therefore, it remains unclear whether benthic invertebrates enter the hyporheic zone in perennial streams in response to flow reduction. We documented the community composition and vertical distribution of the hyporheos to determine if it and the abundance of pool macroinvertebrates were influenced by severe flow reduction. We predicted an increase in invertebrate abundance in these habitats and that surface taxa will move deeper into the hyporheic zone. At the scale of the stream, community composition of the hyporheos is probably related to factors such as land use, however within streams it may be altered because of decreased surface-hyporheic connectivity and/or increased sedimentation in flow reduced reaches.

Methods

Study sites and flow reduction design

The three study streams were small (2-4 m wide, 10-20 cm deep), cobble bottomed streams in the southern North Island, New Zealand. Booths Creek is the only named stream but the others are referred to by the name of the stream they feed. Mean discharge varied from 56-275 L/s and slope (estimated from topographic maps) differed

30-fold among the streams (for summary of stream characteristics see Chapter 2, Table 1).

The creation of flow reductions involved the digging of diversion channels in two streams (Booths Creek and Kiriwhakapapa Stream) and installing of pipes at Reef Creek. We constructed pole and board weirs to form header pools for the diversion channels or pipes to reduce flow by at least 80% for approximately 100 metres in each stream. This created an impact (reduced flow) reach and a control (unreduced) reach upstream. The diversions operated March to April 2004 and from late January to March 2005.

Physicochemical measurement

Surface water measures of conductivity, pH and dissolved oxygen were taken three times before (monthly) and four times after (3, 10, 17 and 31 days) the flow reductions were imposed in 2004 and three occasions before (monthly) and three times after (1 week, 1 month, 2 months) flow reduction in 2005. Parameters were logged for around an hour within 3 hours of midday with a YSI 556 multi-probe system (Yellow Springs Instruments Inc., Yellow Springs, OH, USA.), and averaged. Dissolved oxygen was logged simultaneously in reduced and unreduced reaches over two to three day periods in Kiriwhakapapa Stream and Reef Creek in summer 2005 using two YSI 556 multi-probe systems.

Discharge was estimated at a fixed transect on each occasion with a minimum of 12 depth and velocity measures per transect recorded with a Marsh-McBirney Model 2000 Flowmate (Marsh-McBirney Inc., Fredrick, MD, USA.) to an accuracy of 0.01 m/s. TruTrack WT-HR water level dataloggers (TruTrack Ltd., Christchurch, New Zealand) recorded stage height to an accuracy of 1 mm every 20 minutes in control and impact reaches from January 2005. We calculated stage-discharge rating curves following Gordon *et al.* (2004) for each reach giving continuous discharge records from January 2005 onwards. In both years wetted width was measured every 5 m over 65 m in each stream reach and depth and velocity measured at five points in riffles on each sampling occasion. On one occasion before reduction we assessed the percentage cover of each substrate size category (boulder, large and small cobble, gravel and sand/silt) by measuring 100 rocks, selected using the Wolman walk method (Wolman, 1954). This was not repeated as reduced flow is unlikely to mobilise the substrate.

Adjacent to where depth and velocity were measured, a stone (< 60 mm, A axis) was selected for chlorophyll-*a* analysis. Stones were transported on ice in the dark and stored at -20°C. Photosynthetic pigments were extracted from stones by immersion in 90% acetone for 24 hours at 5°C. Absorbency was read at 750, 665 and 664 nm on a Varian Cary 50 Conc. UV-Visible spectrophotometer (Varian Australia Pty Ltd., Mulgrave, Australia) before and after 0.1M HCl was added. We calculated the amount of chlorophyll-*a* ($\mu g/cm^2$) on each cobble as described by Steinman & Lamberti (1996), and corrected for stone surface area calculated using length, width and depth of each cobble following Graham *et al*. (1988).

The coverage of fine sediment on the substrate was visually estimated at 15 randomly selected transects at each study site on three occasions in summer 2005 while diversions were operating. At each transect, the same person on each occasion estimated the percentage of substrate covered by fine sediment within a 300 mm wide strip across the width of the stream. From these measurements, an average percentage cover was calculated for each site and time. We collected 500-mL water samples at midstream to measure suspended sediment in the water column. We analysed ash-free dry mass (AFDM) of suspended sediment samples by vacuum filtration, using pre-weighed Whatman glass fibre filters (GF/C) (Whatman International Ltd., Brentford, England). Filters were dried at 90°C for 24 hours, weighed, ashed for 4 hours at 450°C and reweighed.

Hyporheic water was collected via hand pump from depths of 15 cm, 25 cm and 35 cm through 10-mm diameter PVC pipes driven into the substrate and left in situ for the duration of the summer 2005 experiment. A YSI 556 multi-probe system instrument measured spot temperature, pH, conductivity and dissolved oxygen in the water samples. Samples were taken twice before (December 2004 and January 2005) and three times after (1 week, 1 month and 2 months) flow reduction in Kiriwhakapapa Stream and Reef Creek and once before (January 2005) and twice after (1 week, 1 month) at Booths Creek. Hyporheic fine sediment at 20 cm depth was estimated by hand pumping 1-L water samples from 10-mm diameter PVC pipes once while the diversions were operating. AFDM was analysed in the same manner as described for suspended sediment above. Prior to sediment pumping the same pipes were used as mini-piezometers (Lee & Cherry, 1978) to estimate the direction and magnitude of the vertical hydraulic gradient (VHG) in order to determine if downwelling or upwelling was occurring in the area where chambers had been buried. A hollow plastic tube was lowered into the pipe, blown into, with resultant bubbles indicating the waters meniscus. From this distance, the VHG was expressed relative to water depth (e.g. positive value indicative of upwelling and negative value indicative of downwelling).

Surface and hyporheic water temperature were logged at 30 minute intervals throughout the period of the experiment using Onset Hobo H8 (housed in waterproof cases) and Water Temp Pro temperature loggers (Onset Computer Corporation, Bourne, MA, USA.). Hyporheic temperature loggers were placed at the bottom of one colonisation chamber (~35 cm depth) upon burial in each reach.

Experimental design and invertebrate sampling

Colonisation chambers were constructed from 10-cm diameter PVC pipe following Scarsbrook (1995). They were 40 cm long with an outer PVC sleeve that was hammered down to seal the chambers prior to removal (Plate 1). Drilled along the sides were 11 rows of 1 cm diameter holes to allow horizontal movement of water and animals. Prior to burial, the chambers were filled with clean hyporheic substrate from the stream (a-axis 50 mm ± 0.7 mm). This size substrate was used as it was readily available at each of the three streams and it was important for comparability that the same size substrate was used at each site. Collection involved the slow uplift of chambers to minimise animals being moved or lost. The contents were carefully emptied into a half-circular tray and quickly divided evenly into four equal sized samples each representing a 10 cm vertical section to further prevent movement of animals.

The summer 2004 experiment involved the burial of six hyporheic colonisation chambers (Plates 2 & 3) in upstream (control) and downstream (impact) reaches in each stream. Two chambers were removed from each reach just prior to flow reduction, two more after one week of reduction and another two after one month of reduction. The data from these post-reduction chambers were pooled due to the loss of three chambers. Ideally, all chambers would have been buried for 4 weeks, but this was impossible due to uncontrollable circumstances including a major flood event and the time it took to get permission and then construct the diversions. For the summer 2005 experiment, two hyporheic colonisation chambers were buried in December 2004 and removed 4 weeks later in January 2005 before flow was reduced. Two more chambers were installed in each reach in February 2005 after flow reduction and again removed 4 weeks later. Chambers were installed in riffles, where they would remain wetted, even after flow reduction. Ideally, we would have installed a greater number of replicates, but this was impossible because the small size of the study streams meant there was not a lot of riffle habitat area, especially in the reduced flow reaches. In addition, we wanted to minimise the disturbance that chamber installation caused to the stream immediately around the chamber. This study occurred concurrently with an intensive benthic invertebrate sampling program and we needed to preserve suitable Surber sampling locations (see Dewson *et al.*, 2007).

Linear regression (SigmaPlot 2001, SPSS Inc., Chicago, IL, USA) showed that there was no relationship between time buried and the number of animals found in a chamber (control reach chambers: $R^2 = 0.08$, ANOVA $F = 2.33$, $P = 0.14$; impact reach chambers: $R^2 = 0.01$, ANOVA $F = 0.26$, $P = 0.61$), so we pooled all chambers into one data set. Analysis of similarities (ANOSIM, PRIMER-E Ltd., Plymouth, UK.) showed that there were no faunal differences between the two times the experiment was performed (Global $R = 0.04$, $P = 0.09$) so we have also combined the two years of data.

Pools were sampled before flow reduction in November 2004 and again after flow reduction in February 2005 with a 500-µm mesh kicknet (0.045 m^2 mouth). On each occasion within each reach, 15-second kick samples from an approximately 0.1 m^2 area were taken in three pools. Pool and hyporheic samples were preserved in 10% formalin for later processing.

Pool and hyporheic invertebrate samples were rinsed through a 500-µm Endecott sieve (Endecotts Ltd, London, UK.) prior to sorting as we were only interested in macroinvertebrates. Invertebrates were identified to the lowest possible taxonomic level using the keys of Winterbourn (1973), Chapman & Lewis (1976), Towns & Peters (1996), Winterbourn *et al.* (2000) and Smith (2003). Chironomids were identified to sub-family level and Oligochaeta to class.

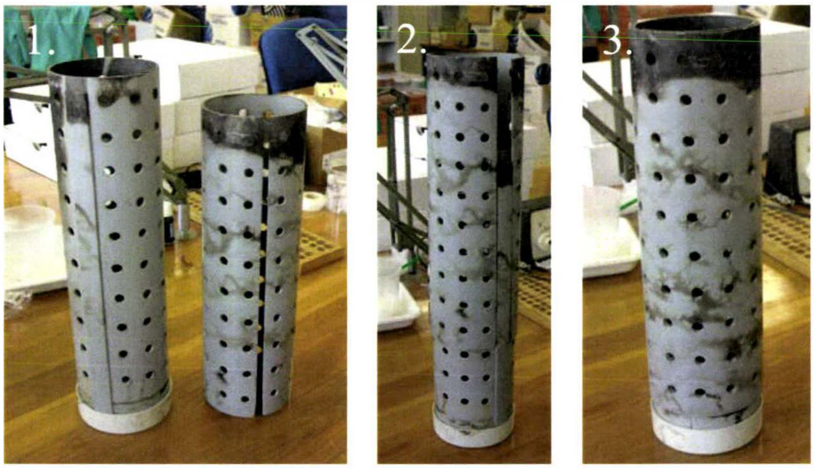

Plate 1. The design of the hyporheic colonisation chambers. 1. shows the inner and outer components side by side, 2. shows the outer fitting over the inner, and 3. shows the complete colonisation chamber.

Plate 2. Installation of hyporheic colonisation chambers at Booths Creek.

Plate 3. A freshly installed hyporheic colonisation chamber.

Analysis - surface physicochemical

Variables measured during flow reduction only (i.e. discharge, 24 hour logged dissolved oxygen and the three sediment measures), were analysed with one-way ANOVA to evaluate the effect of the two treatments (control and impact) using Statistix 8.1 (Analytical Software, Tallahassee, FL, USA.). Mean concentrations of fine sediment were compared among streams using a one-way ANOVA.

All other surface water physicochemical variables (depth, velocity, wetted width, spot dissolved oxygen, pH, conductivity, chlorophyll-*a*, daily temperature mean, maximum and range) were analysed in a before-after-control-impact paired in time (BACIP) format (Downes *et al.*, 2002). This design focuses on any changes at the impact location relative to the control by comparing the difference between control and impact values within each period. One-way ANOVA tested for differences between before and after treatments. The *post hoc* Tukey multiple comparisons test evaluated significant differences when found. Data were $\log_{10}$ transformed where necessary to improve normality and ensure homogeneity of variances.

Analysis – hyporheic physicochemical

Three-way ANOVA was used to assess the impact of flow reduction on hyporheic physicochemical parameters with the factors, time (before and after), treatment (control and impact) and depth all fixed. For physicochemical parameters, the depth factor consisted of three levels (surface, 15 cm and 25 cm) except for logged temperature data which had two levels (surface and 35 cm). The tests of interest from the three-way ANOVA were the time × treatment interaction which potentially shows a flow reduction effect irrespective of depth and the time × treatment × depth interaction which indicates whether flow reduction led to any changes in a parameter with depth.

Analysis – hyporheic macroinvertebrates

Within each stream, we analysed for hyporheic macroinvertebrates, the abundance of the five most common invertebrate taxa, total number of individuals, rarefied number of taxa, Margalef's Index and Simpson's Index. Samples were rarefied to correct for the fact that some chambers contained more individuals and thus potentially more taxa than samples comprising fewer individuals. Values for *N* were selected that were low enough to include the number of individuals found in most samples (e.g. *N*=100 for Booths Creek and Kiriwhakapapa Stream and *N*=30 for Reef Creek). Margalef's Index is a species richness measure which incorporates the total number of individuals. Simpson's Index is a measure of species evenness (Simpson, 1949). Data were $\log_{10}$ transformed where necessary to achieve normality and homogeneity of variances. The *post hoc* Tukey multiple comparisons test evaluated significant differences when found. Because each level in a hyporheic chamber is not independent from that above and below it, split-plot ANOVA was used in a similar fashion to Olsen & Townsend (2003). This design has two whole-plot effects (Time, Treatment) and Depth as a sub-plot effect with all factors fixed. Time was tested against the Chamber(Time) mean square, Treatment against Chamber(Treatment) and Time × Treatment against Chamber(Time × Treatment). Depth and all terms including Depth were tested against residual mean square using SAS 8.02 (SAS Institute Incoporated, Cary, NC, USA.).

Non-metric multidimensional scaling (NMDS) ordination and analysis of similarities (ANOSIM) using PRIMER 6 (PRIMER-E Ltd., Plymouth, UK.) compared the macroinvertebrate communities colonising hyporheic chambers among streams and treatments. Data were fourth root transformed to down-weight the influence of abundant taxa (Clarke & Warwick, 2001) and the Bray-Curtis distance measure was used. The similarity percentages (SIMPER) routine of PRIMER 6 was used to indicate which taxa were responsible for discriminating among groups of similar samples revealed by ordination.

Analysis – pool macroinvertebrates

The same dependent variables, data transformation and multiple comparison procedure as listed above for hyporheic invertebrates were used to assess the effects of flow reduction on pool macroinvertebrates. We used two-way ANOVA with the factors time (before and after) and treatment (control and impact) being fixed and the time × treatment interaction indicating any potential flow reduction effect using Statistix 8.1 (Analytical Software, Tallahassee, FL, USA.).

Results

Surface physicochemical characteristics

While there was an obvious trend towards decreased depth, velocity and wetted width with flow reduction, only velocity decreased significantly in all streams and also showed the greatest proportionate decrease (Fig. 1a, Table 1). Kiriwhakapapa Stream and Reef Creek showed small increases in conductivity with flow reduction (Table 1).

There was no statistically significant change to periphyton biomass in any stream. However, in Booths Creek a proportionately large decrease was observed (Table 1). Daily mean temperature declined by less than 1°C (Fig. 2a-c, Table 1). Similarly, daily maximum temperature was reduced a small amount by flow reduction in all streams (Table 1). Daily temperature range decreased in Booths Creek and Kiriwhakapapa Stream by around 2°C while temperature in Reef Creek never ranged more than 2°C in a 24 hour period (Fig. 2d-f, Table 1). Dissolved oxygen levels as indicated by spot measures show a small decrease in response to flow reduction with this significant in Booths Creek and Reef Creek only (Table 1). Logged data, especially in Kiriwhakapapa Stream showed a marked decline in DO minima overnight with reduced flow (Table 1). Fine sediment cover increased with flow reduction, being significant in Booths Creek and Kiriwhakapapa Stream (Fig. 1b, Table 1). Suspended sediment did not change with flow reduction (Table 1).

Hyporheic physicochemical characteristics

Apart from pH being higher in the surface water than the hyporheic water in Kiriwhakapapa Stream, there were no differences in pH, specific conductivity, dissolved oxygen, spot temperature or daily mean temperature with depth and flow reduction had no effect on these variables (Table 2). At Booths Creek, daily temperature range was greater at the surface than at 35 cm depth and least during the after-impact period, whilst at Kiriwhakapapa Stream temperature range was unchanged with depth but was again less during the after-impact period (Table 2). Daily maximum temperature was greater at the surface than at 35 cm in Booths Creek while the maximum did not differ with depth at Kiriwhakapapa Stream but was least during the after-impact period (Table 2). There were no differences in temperature with depth or flow reduction at Reef Creek.

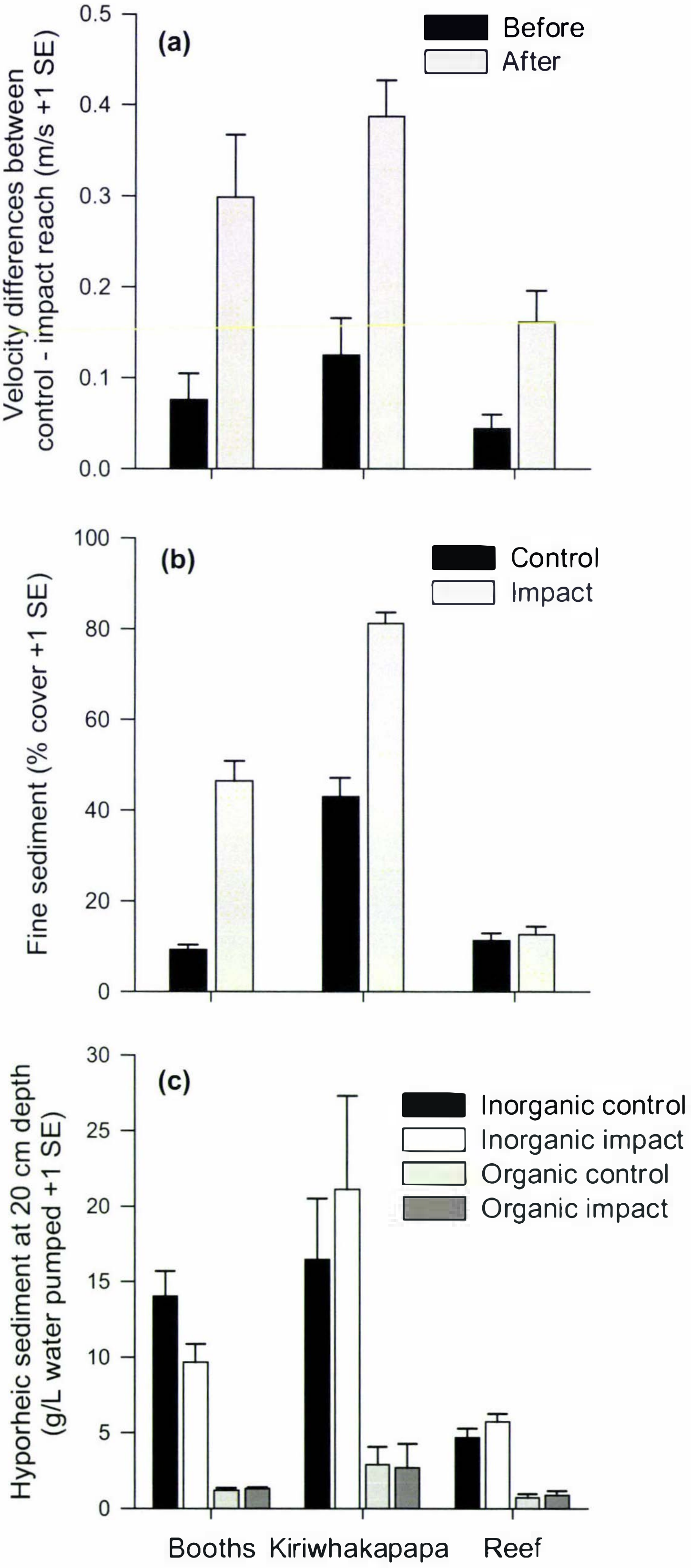

Figure 1. The effect of flow reduction on (a) velocity, (b) fine sediment cover and (c) hyporheic fine sediment in Booths Creek, Kiriwhakapapa Stream and Reef Creek

Table 1. ANOVA *F*-values of differences in physicochemical variables in each stream before and after flow reduction: A. measurements made in summer 2004 and summer 2005, B. measured in summer 2005 only (sediment variables) and during year 2005 (discharge, dissolved oxygen). df = degrees of freedom, nd = no data, **Bold** = significant at 5% level. Percent changes (in brackets) are from control to impact reaches during flow reduction, e.g. (-61%) shows a 61% decrease in the impact reach relative to the control.

Parameter	Hypothesis	Booths Creek		Kiriwhakapapa Stream		Reef Creek	
A. BACI differences		df	*F* – value	df	*F* – value	df	*F* – value
Depth	H_o: difference between control and impact *before* reduction = difference between control and impact *after* reduction	1, 9	**6.37** (-61%)	1, 11	0.12 (-36%	1, 11	0.05 (-18%)
Velocity		1, 9	**10.53** (-60%)	1, 11	**20.80** (-69%)	1, 11	**8.88** (-62%)
Wetted width		1, 8	1.83 (-24%)	1, 11	**85.69** (-31%)	1, 11	1.38 (-25%)
Dissolved oxygen – spot measures		1, 9	**10.98** (-8%)	1, 11	1.16 (-5%)	1, 11	**14.2** (-8%)
pH		1, 9	0.01 (-7%)	1, 11	1.82 (-6%)	1, 11	0.55 (+1%)
Specific conductivity		1, 9	0.38 (-2%)	1, 11	**6.87** (+12%)	1, 11	**15.98** (+3%)
Chlorophyll-*a*		1, 8	0.03 (-67%)	1, 10	2.76 (+9%)	1, 10	1.71 (-8%)
Daily mean temperature		1, 128	**100.71** (-1%)	1, 130	**91.51** (+0.1%)	1, 131	3.22 (-2%)
Daily maximum temperature		1, 128	**145.43** (-5%)	1, 130	**54.19** (-4%)	1, 131	**16.63** (-3%)
Daily temperature range		1, 128	**152.38** (-26%)	1, 130	**39.28** (-20%)	1, 131	0.25 (-18%)
B. Control – impact only							
Discharge	H_o: control = impact	1, 9022	**23472.8** (-95%)	1, 47460	**1335.17** (-88%)	1, 43246	**1626.15** (-96%)
Dissolved oxygen – logged data		nd	nd	1, 862	**188.09** (-18%)	1, 288	**2395.66** (-4%)
Visual sediment cover		1, 4	**28.59** (+80%)	1, 4	**29.76** (+47%)	1, 4	0.08 (+10%)
Suspended sediment		1, 6	0.21 (+12%)	1, 6	0.00 (-2%)	1, 6	0.34 (-26%)
Hyporheic sediment AFDM		1, 16	**4.53** (-31%)	1, 7	0.42	1, 16	1.85
Hyporheic sediment organic		1, 16	0.28	1, 7	0.02	1, 16	1.46

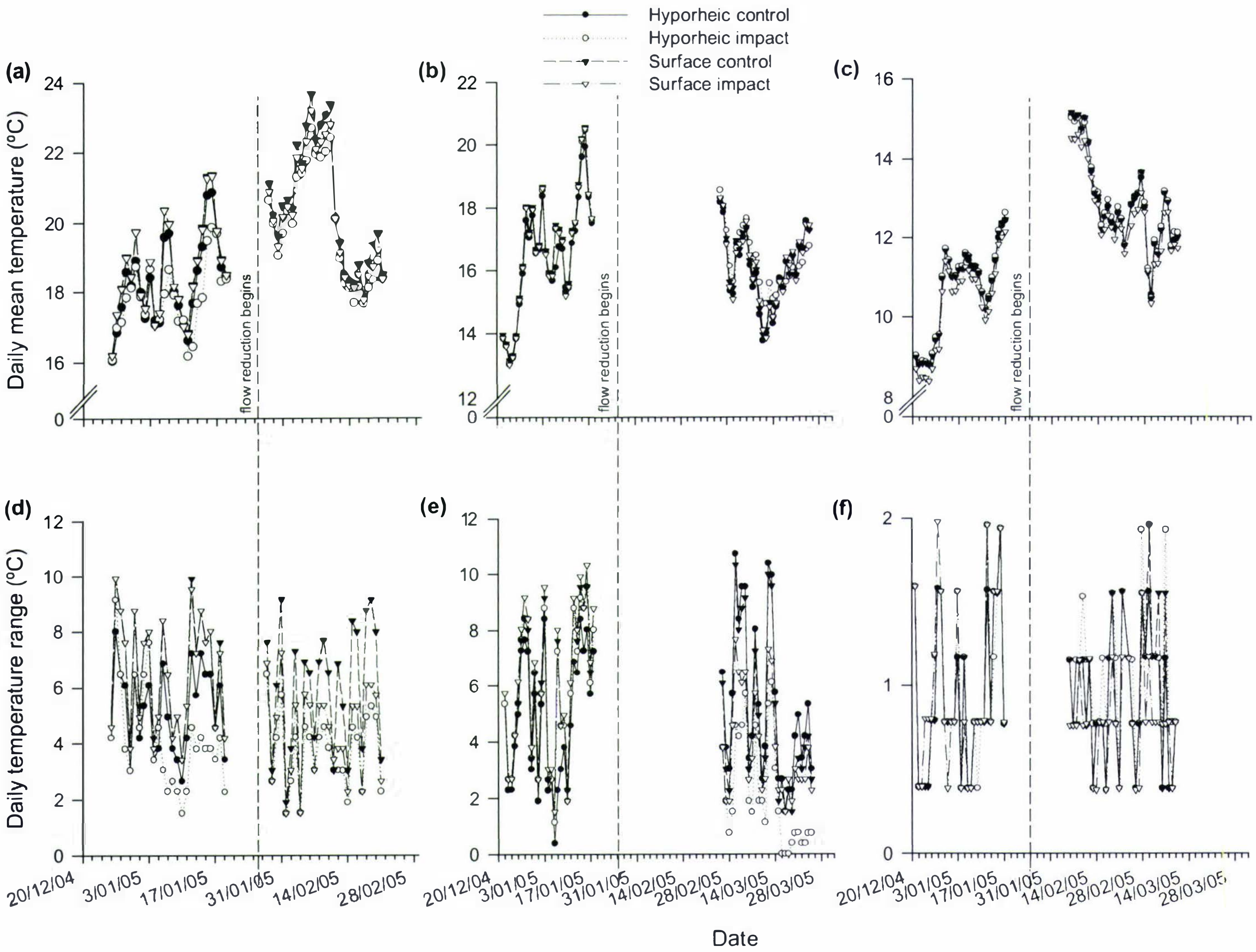

Figure 2. Hyporheic and surface daily mean temperature in the control and impact reaches of (a) Booths Creek, (b) Kiriwhakapapa Stream and (c) Reef Creek, and hyporheic and surface daily temperature ranges in (d) Booths Creek, (e) Kiriwhakapapa Stream and (f) Reef Creek. The breaks in the data indicate the separation between the before and after flow reduction periods.

Table 2. *F*-test results for three factor ANOVAs of the impact of flow reduction on hyporheic physicochemical characteristics. ANOVAs include the factors time (before and after), treatment (control and impact) and depth (either surface, 15 cm and 25 cm for pH, conductivity, dissolved oxygen and spot temperature or surface and 35 cm for other temperature parameters derived from logged data), measured between November 2004 and March 2005 in Booths Creek, Kiriwhakapapa Stream and Reef Creek. Insufficient before data and a damaged temperature logger in Booths Creek prevented all tests at this site. Only interactions of interest are shown. Results significant at the 5% level are in **bold.** *Post hoc* Tukey test results are given where significant. B = before, A = after, C = control, I = impact, S = surface, and 15, 25 and 35 = respective depth in cm below surface of substrate. Factor groups within brackets are equal, > denotes direction of difference between groups.

Booths Creek	pH	Specific conductivity	Dissolved oxygen	Spot temperature	Daily mean temperature	Daily temperature range	Daily maximum temperature
Depth	$F_{2,10} = 0.18$	$F_{2,10} = 2.18$	$F_{2,10} = 3.28$	$F_{2,10} = 0.22$	$F_{1,202} = 0.67$	**$F_{1,202} = 6.90$** (S) > (35)	**$F_{1,202} = 5.33$** (S) > (35)
Time × Treatment	No test	No test	No test	No test	$F_{1,202} = 0.15$	**$F_{1,202} = 4.17$** (AC, BC, BI) > (AI)	$F_{1,202} = 2.01$
Kiriwhakapapa Stream							
Depth	**$F_{2,15} = 5.48$** (S, 15) > (25)	$F_{2,15} = 1.86$	$F_{2,15} = 2.97$	$F_{2,15} = 0.87$	$F_{1,228} = 0.10$	$F_{1,228} = 2.56$	$F_{1,228} = 1.12$
Time × Treatment	$F_{1,15} = 3.63$	$F_{1,15} = 0.01$	$F_{1,15} = 0.01$	$F_{1,15} = 0.01$	$F_{1,228} = 0.09$	**$F_{1,228} = 17.99$** (BI, BC, AC) > (AI)	**$F_{1,228} = 5.28$** (BI, BC, AC) > (AC, AI)
Time × Depth × Treatment	$F_{2,15} = 0.65$	$F_{2,15} = 3.01$	$F_{2,15} = 0.38$	$F_{2,15} = 0.12$	$F_{1,228} = 0.01$	**$F_{1,228} = 5.86$** (BI35, BIS, BCS, AC35, BC35, ACS) > (AIS, AI35)	$F_{1,228} = 1.26$
Reef Creek							
Depth	$F_{2,18} = 3.24$	$F_{2,17} = 0.50$	$F_{2,18} = 1.57$	$F_{2,18} = 0.12$	$F_{1,232} = 1.42$	$F_{1,232} = 1.04$	$F_{1,232} = 1.74$
Time × Treatment	$F_{1,18} = 0.09$	$F_{1,17} = 0.12$	$F_{1,18} = 0.14$	$F_{1,18} = 0.26$	$F_{1,232} = 0.00$	$F_{1,232} = 0.07$	$F_{1,232} = 0.01$
Time × Depth × Treatment	$F_{2,18} = 0.13$	$F_{2,17} = 0.98$	$F_{2,18} = 1.03$	$F_{2,18} = 0.07$	$F_{1,232} = 0.00$	$F_{1,232} = 2.68$	$F_{1,232} = 0.03$

Piezometry showed the vertical hydraulic gradient in the three streams to be small (0.5 – 2.5 cm) and upwelling. There was no effect of flow reduction on VHG (ANOVA: $F_{1,16} = 0.03$, $P = 0.87$). Inorganic hyporheic fine sediment (AFDM, from 20 cm depth) was similar in Kiriwhakapapa Stream and Booths Creek and greater than in Reef Creek (Fig. 1c, ANOVA: $F_{2,42} = 20.03$, $P < 0.01$). Organic hyporheic fine sediment was greatest in Kiriwhakapapa Stream, least in Reef Creek with Booths Creek intermediate (Fig. 1c, ANOVA: $F_{2,42} = 22.64$, $P < 0.01$). Flow reduction had no impact on hyporheic sediment (organic or AFDM) except for lower AFDM in the impact reach of Booths Creek (Table 1).

Hyporheic invertebrates

The macroinvertebrate communities colonising hyporheic chambers differed amongst the three streams (Fig. 3, Global $R = 0.93$, $P < 0.01$). SIMPER analysis indicated that the separation of Reef Creek communities from the other two streams resulted from the high numbers of *Acanthophlebia cruentata* at Reef Creek and high numbers of *Potamopyrgus antipodarum* and Ostracoda at Booths Creek and Kiriwhakapapa Stream. Differences between Booths Creek and Kiriwhakapapa Stream resulted from the high numbers of *Paracalliope fluviatilis* at Booths Creek and high numbers of *Deleatidium* sp., *Olinga feredayi* and *Hudsonema amabile* at Kiriwhakapapa Stream. Within Booths Creek and Kiriwhakapapa Stream, the samples taken after flow reduction (i.e. after-impact treatment), were not different to the other treatments (Global $R = 0.09$, $P = 0.12$; $R = 0.05$, $P = 0.26$ for Booths Creek and Kiriwhakapapa Stream respectively). In Reef Creek there was some separation of before and after samples (Global $R = 0.24$, $P = 0.01$) but not of flow treatments (Fig. 3).

There was no change in the depth distribution of the total number of individuals in colonisation chambers in response to flow reduction as shown by the time × treatment × depth interaction (Table 3). At Booths Creek, animals were evenly distributed through chambers in the before period but were found more in the top 10 cm of the chambers in the after period (Fig. 4a). Animals were in greater numbers in the top of chambers at Kiriwhakapapa Stream throughout the study (Fig. 4b). In Reef Creek more animals were in the top 10 cm in the before period and became more evenly distributed in the after period. There was however, an accumulation of animals at the bottom 10 cm of chambers in Reef Creek (Table 3), but this is not significant (Fig. 4c). The rarefied number of taxa at each depth tended to decrease with depth in Booths

Creek and Kiriwhakapapa Stream (Fig. 4d-e, Table 3), but not in Reef Creek (Fig. 4f). Margalef's diversity index showed a reduction in diversity with depth in Booths Creek and Kiriwhakapapa Stream while in Reef Creek there was no such trend (Table 3). Simpson's Index demonstrated a reduction in taxa evenness with depth in Booths Creek and Reef Creek and no change in Kiriwhakapapa Stream (Table 3).

The dominant taxonomic groups and taxa varied from stream to stream (Fig. 5, Table 3). Crustacea, predominantly the amphipod *P. fluviatilis* and Ostracoda dominated in Booths Creek (Fig. 5a). Kiriwhakapapa Stream was dominated by Mollusca (mainly *P. antipodarum*), Oligochaeta and Ostracoda (Fig. 5b), while Ephemeroptera, Plecoptera and Trichoptera (EPT) taxa dominated the Reef Creek hyporheic community (Fig. 5c). Flow reduction had no impact on the relative abundance of higher taxonomic groupings (Fig. 5) or on the abundance of any of the five most abundant taxa in each stream (Table 3). However, taxa did have depth preferences. Among the most abundant taxa, three depth distribution patterns were identified (Fig. 6). Taxa such as Oligochaeta in Booths Creek (Fig. 6a), Tanypodinae in Kiriwhakapapa Stream and Orthocladiinae in Reef Creek were evenly spread through the depth levels (Table 3). *P. fluviatilis*, *P. antipodarum*, Elmidae and *Deleatidium* sp. (Fig. 6b) all preferred the upper 0-10 cm benthic zone (Table 3). Ostracoda and Oligochaeta in Kiriwhakapapa Stream and the mayfly *A. cruentata* (Fig. 6c) were found in greater numbers in the lower depth levels of colonisation chambers (Table 3).

Pool invertebrates

The mean total number of animals found in pools tended to increase in the after period, especially in Booths Creek (Fig 7a-c). However, with the exception of *P. antipodarum* in Booths Creek, no taxa abundances or indices changed as a result of flow reduction (Table 4). At Booths Creek, *P. antipodarum* was much more abundant in pools of the after-impact reach (Fig. 7d). A similar but non-significant response was observed for Chironominae in Kiriwhakapapa Stream. The abundance of *A. cruentata* in Reef Creek pools was unchanged by flow reduction (Fig 7e, Table 4).

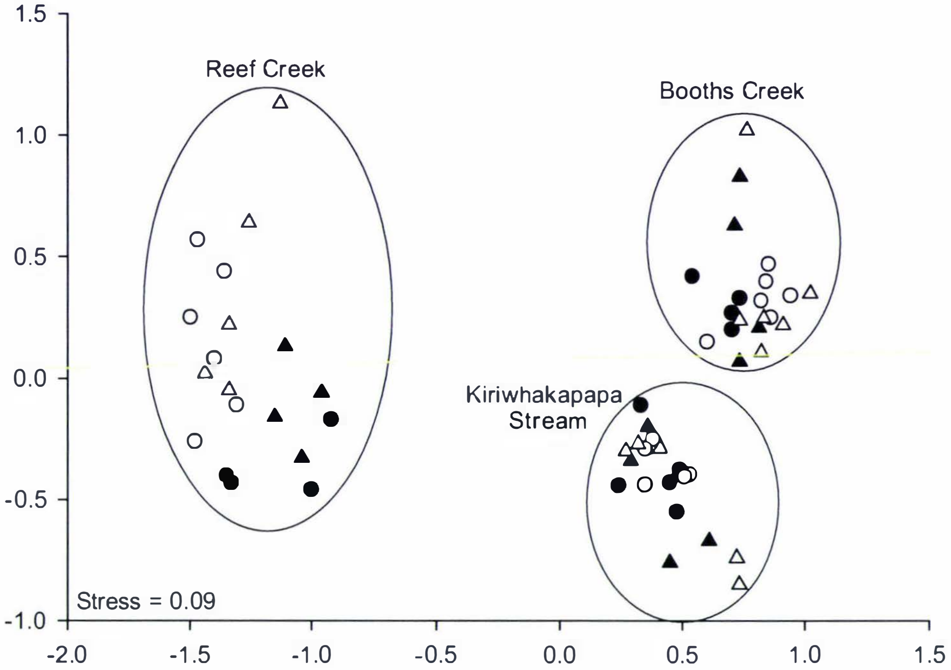

Figure 3. Two-dimensional non-metric multidimensional scaling ordination of the densities of macroinvertebrates in samples from the entire chamber in the hyporheic zone of Booths Creek, Kiriwhakapapa Stream and Reef Creek sampled between March – May 2004 and November 2004 – March 2005. Open symbols = before, closed = after, circles = control, triangles = impact. Ellipses separate sample clusters from each stream.

Table 3. *F*-test results for three factor split-plot ANOVAs of hyporheic colonisation chamber data. The whole plot factors are time (before and after) and treatment (control and impact) and the sub-plot factor is depth (0-10 cm, 10-20 cm, 20-30 cm and 30-40 cm). The dependent variables are the five most abundant taxa, number of individuals, rarefied number of taxa, and Margalef's and Simpson's indices. Sampling occurred between March – May 2004 and November 2004 – March 2005 in Booths Creek, Kiriwhakapapa Stream and Reef Creek. Only interactions of interest are shown. Results significant at the 5% level are in **bold.** *Post hoc* Tukey multiple comparison test results given in brackets where significant. df = degrees of freedom, 1 = surface-10 cm, 2 = 10-20 cm, 3 = 20-30 cm and 4 = 30-40 cm depth. Factor groups within brackets are equal, > denotes direction of difference between groups

Booths Creek	Depth (df = 3, 48)	Time × Treatment (df = 1, 48)	Time × Treatment × Depth (df = 9, 48)
Ostracoda	**10.97** (4, 3)>(3, 2)>(1)	1.07	0.87
Paracalliope fluviatilis	**37.33** (1)>(2)>(3,4)	0.07	2.12
Oligochaeta	0.97	1.00	1.09
Potamopyrgus antipodarum	**24.22** (1)>(2, 3)>(3, 4)	0.37	0.77
Elmidae	**10.80** (1)>(2, 4, 3)	5.18	0.57
Total Individuals	**6.39** (1)>(4, 2, 3)	0.07	2.08
Rarefied number of taxa	**17.76** (1)>(2, 3)>(4)	1.96	1.38
Margalef's Index	**12.02** (1)>(2, 3, 4)	0.44	0.73
Simpson's Index	**5.39** (1, 2)>(2, 3)>(3, 4)	3.08	1.67

Kiriwhakapapa Stream	Depth (df = 3, 45)	Time × Treatment (df = 1, 45)	Time × Treatment × Depth (df = 9, 45)
Potamopyrgus antipodarum	**18.70** (1)>(2, 3)>(3,4)	3.30	0.66
Oligochaeta	**6.51** (4=3)>(3, 2)>(2, 1)	0.29	1.68
Ostracoda	**7.40** (4, 3)>(3, 2)>(2, 1)	0.91	0.46
Tanypodinae	1.35	2.64	0.96
Deleatidium sp.	**36.01** (1)>(2)>(3, 4)	0.00	1.21
Total Individuals	**13.90** (1)>(2, 4, 3)	0.00	0.59
Rarefied number of taxa	**6.84** (1, 2)>(2, 3)>(3, 4)	1.41	0.56
Margalef's Index	**12.01** (1, 2)>(2, 3)>(3, 4)	1.20	0.98
Simpson's Index	1.90	1.10	1.07

Table 3 continued….

Reef Creek	Depth (df = 3, 45)	Time × Treatment (df = 1, 45)	Time × Treatment × Depth (df = 9, 45)
Orthocladiinae	2.80	0.21	0.82
Acanthophlebia cruentata	**28.43** (4, 3)>(2, 1)	0.29	1.64
Deleatidium sp.	**16.16** (1)>(2, 3, 4)	2.46	1.23
Zephlebia dentata	1.95	1.92	**2.94**
Zelandobius sp.	**6.68** (2, 1, 3)>(4)	0.00	**6.11**
Total Individuals	**4.52** (4, 1, 3)>(2)	0.37	1.87
Rarefied number of taxa	2.34	0.19	0.50
Margalef's Index	**4.35** (1, 4)>(4, 2)>(4, 3)	0.29	1.25
Simpson's Index	**7.32** (1, 2)>(4, 3)	4.11	1.11

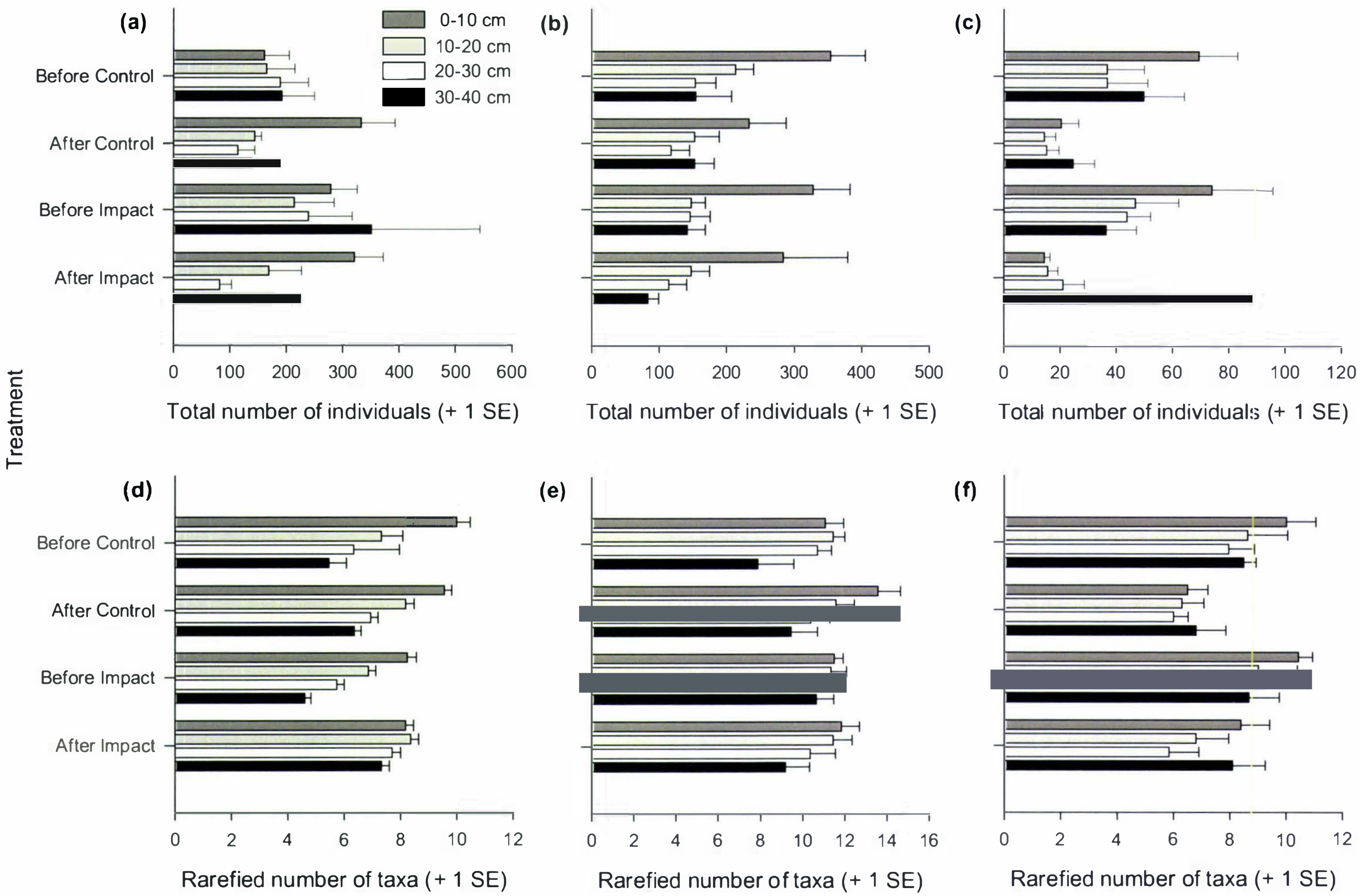

Figure 4. The mean total number of individuals (+ 1 SE) at each depth level in (a) Booths Creek, (b) Kiriwhakapapa Stream and (c) Reef Creek, and the mean number of rarefied taxa (+ 1 SE) in (d) Booths Creek, (e) Kiriwhakapapa Stream and (f) Reef Creek.

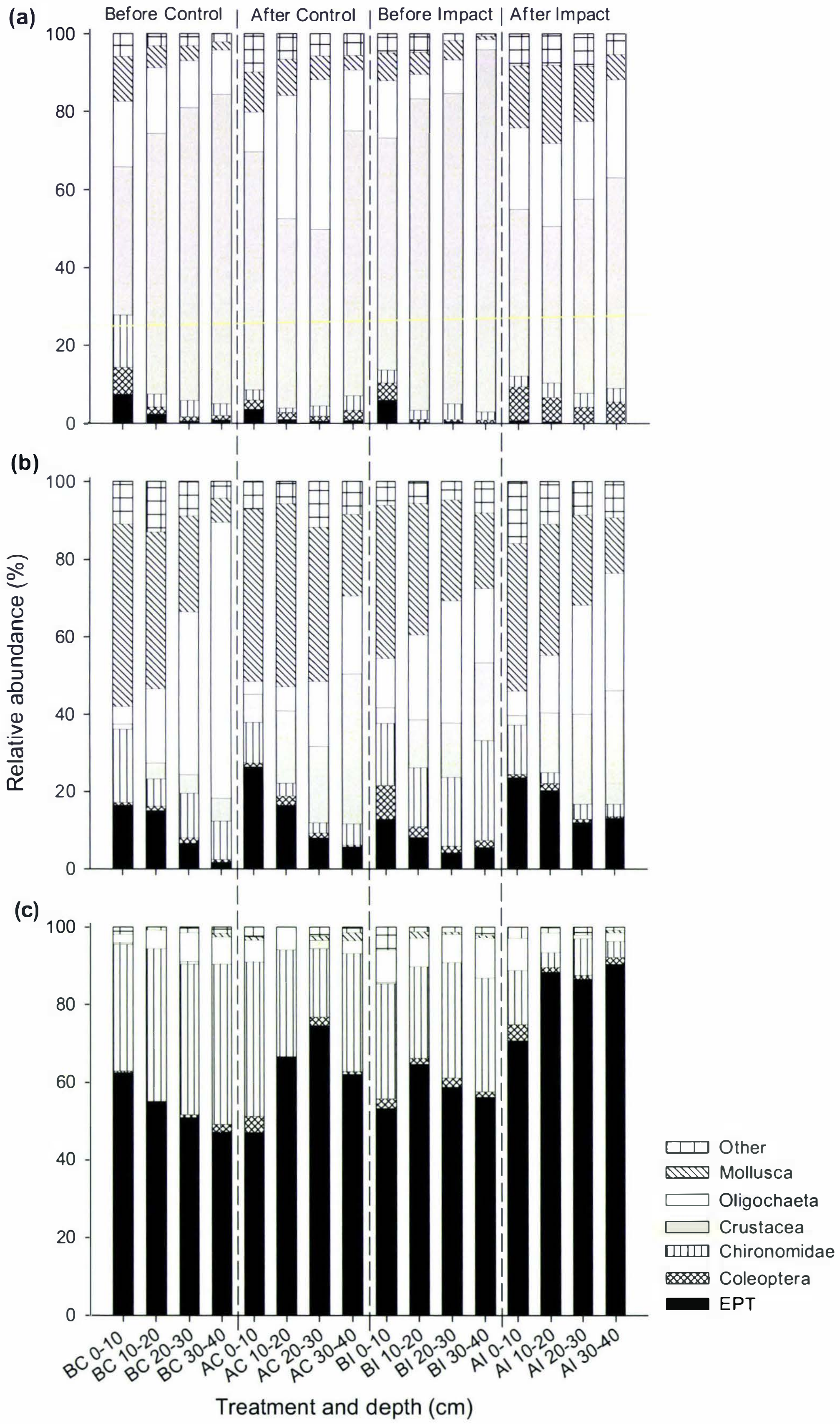

Figure 5. The relative abundance of higher taxonomic groupings at each depth level within each treatment for (a) Booths Creek, (b) Kiriwhakapapa Stream and (c) Reef Creek. BC = Before Control, AC = After Control, BI = Before Impact, AI = After Impact.

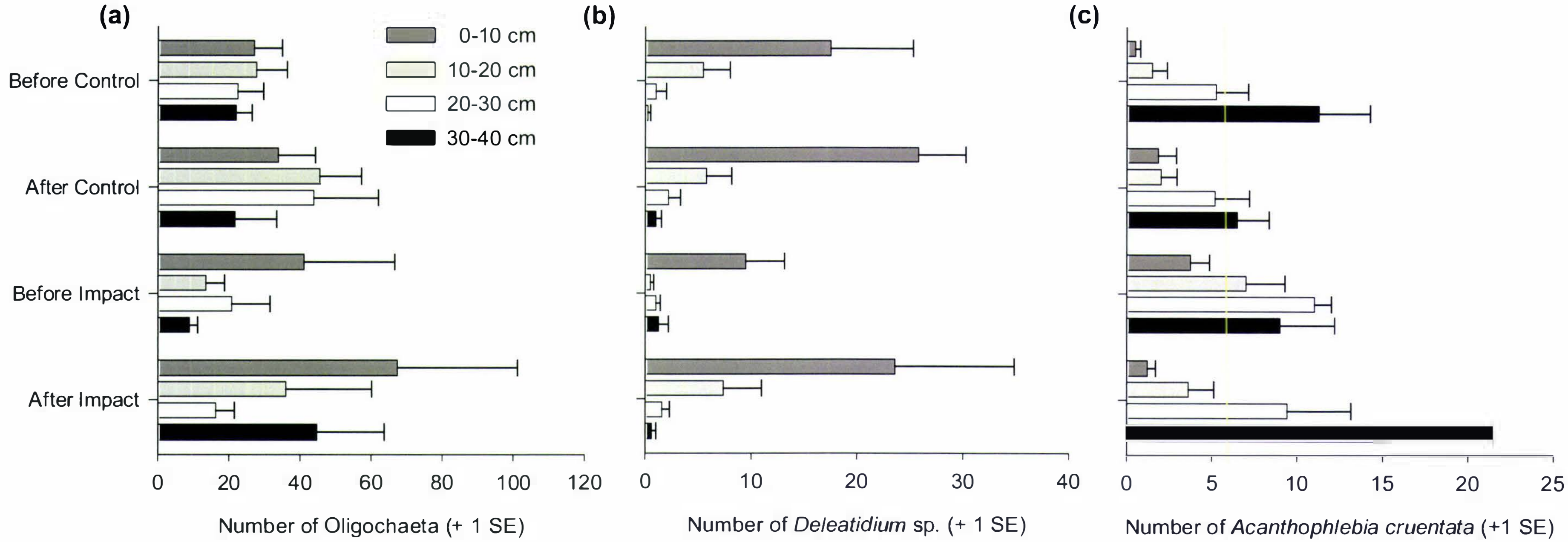

Figure 6. The mean density (+ 1 SE) in each depth level of (a) Oligochaeta at Booths Creek, (b) *Deleatidium* sp. at Kiriwhakapapa Stream and (c) *Acanthophlebia cruentata* at Reef Creek, within hyporheic colonisation chambers for each before-after, control-impact treatment.

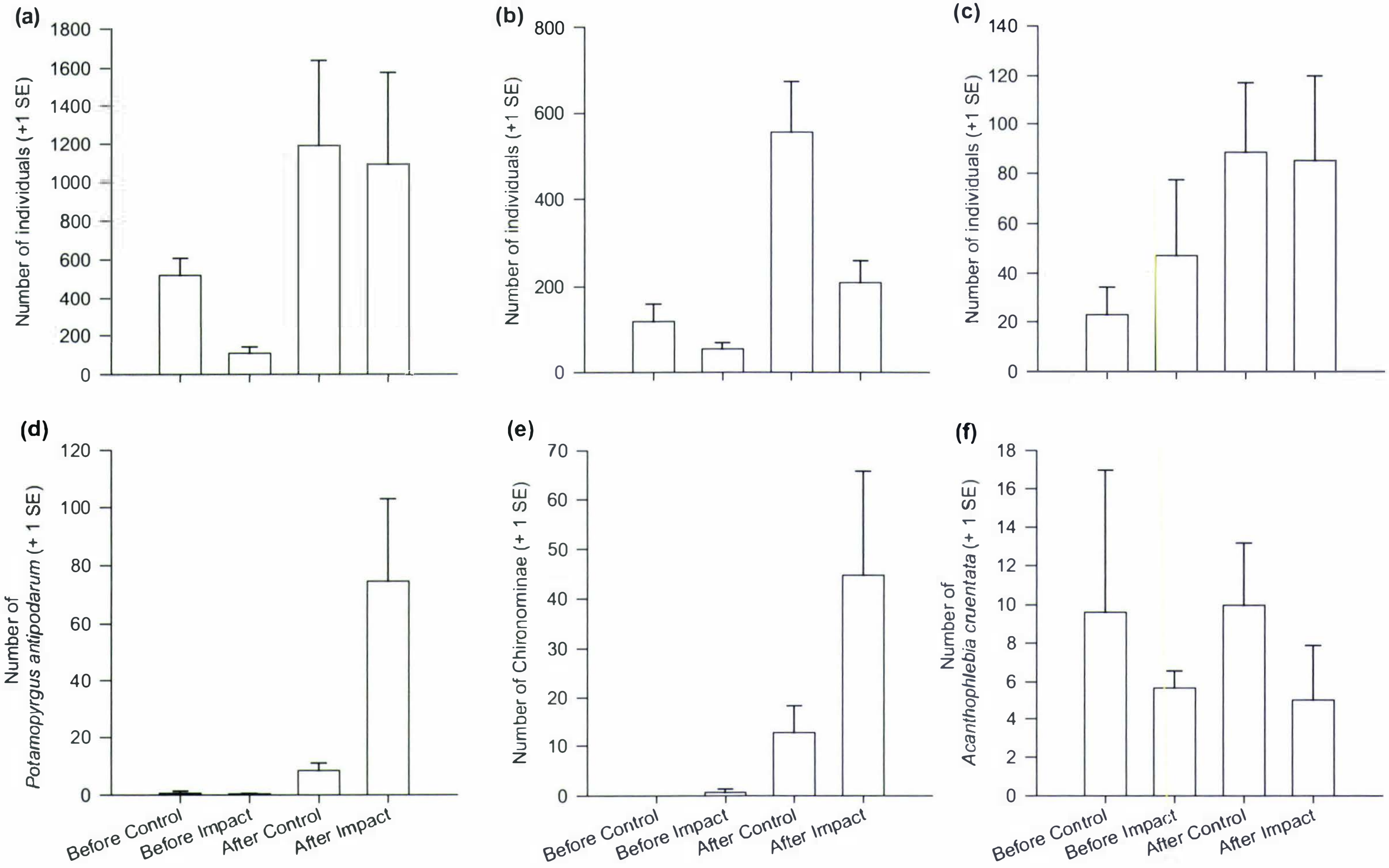

Figure 7. The mean number (+ 1 SE) of individuals per 0.1 m^2 15 second kick sample from pools in (a) Booths Creek, (b) Kiriwhakapapa Stream and (c) Reef Creek and the mean number (+ 1 SE) per 0.1 m^2 15 second kick sample from pools of (d) *Potamopyrgus antipodarum* in Booths Creek, (e) Chironominae in Kiriwhakapapa Stream and (f) *Acanthophlebia cruentata* in Reef Creek.

Table 4. F-test results for two factor ANOVAs of pool kick samples. The five most abundant taxa, number of individuals, rarefied number of taxa and Margalef's and Simpson's indices are shown. ANOVAs comprise time (before and after), and treatment (control and impact). Samples were taken in November 2004 and March 2005 in Booths Creek, Kiriwhakapapa Stream and Reef Creek. Results significant at the 5% level are in **bold.** *Post hoc* Tukey test results given in brackets where significant. df = degrees of freedom, B = before, A = after, C = control, I = impact. Factor groups within brackets are equal, > denotes direction of difference between groups

Booths Creek	Time (df= 1, 8)	Treatment (df = 1, 8)	Time × Treatment (df= 1, 8)
Paracalliope fluviatilis	**9.36** (A)>(B)	5.07	1.81
Oligochaeta	0.38	0.17	4.27
Ostracoda	**43.16** (A)>(B)	1.78	0.39
Oxyethira sp.	**15.36** (A)>(B)	0.81	0.81
Potamopyrgus antipodarum	**60.86** (A)>(B)	**6.78** (I)>(C)	**8.86** (AI)>(AC)>(BC,BI)
Total Individuals	**14.98** (A)>(B)	5.24	4.29
Rarefied number of taxa	**7.17** (A)>(B)	0.95	4.45
Margalef's Index	**7.37** (A)>(B)	0.09	1.62
Simpson's Index	0.08	3.60	0.29

Kiriwhakapapa Stream	Time (df = 1, 8)	Treatment (df= 1, 8)	Time × Treatment (df= 1, 8)
Potamopyrgus antipodarum	**67.63** (A)>(B)	3.32	0.94
Oligochaeta	0.00	1.29	0.06
Chironominae	**23.19** (A)>(B)	1.18	0.18
Hudsonema amabile	0.27	**5.99** (C)>(I)	0.33
Olinga feredayi	0.16	**10.56** (C)>(I)	2.91
Total Individuals	**18.72** (A)>(B)	**8.88** (C)>(I)	4.25
Rarefied number of taxa	0.69	3.15	0.06
Margalef's Index	0.15	3.43	0.13
Simpson's Index	0.76	0.03	1.29

Table 4 continued……….

Reef Creek	Time (df = 1, 8)	Treatment (df = 1, 8)	Time × Treatment (df = 1, 8)
Chironominae	**38.24** (A)>(B)	0.22	4.27
Austroperla cyrene	2.36	0.87	0.56
Acanthophlebia cruentata	0.00	1.11	0.01
Deleatidium sp.	4.84	1.00	0.43
Oligochaeta	0.27	0.39	3.78
Total Individuals	3.44	0.14	0.25
Rarefied number of taxa	3.24	0.06	3.98
Margalef's Index	0.77	0.06	**7.30**
Simpson's Index	1.98	0.17	0.24

Discussion

Between stream differences

The three study streams each had a distinct hyporheic macroinvertebrate community. The forested Reef Creek was dominated by EPT taxa and the two pasture streams by Crustacea (Booths Creek), Oligochaeta, and Mollusca (Kiriwhakapapa Stream). These differences in hyporheic community composition are similar to those found in other New Zealand studies comparing hyporheic community composition between forested and pasture streams. Boulton *et al.* (1997) and Scarsbrook & Halliday (2002) found pasture sites dominated by permanent hyporheic non-insect taxa (e.g. Oligochaeta, Ostracoda) and forested sites by occasional hyporheic, epigean larval insect taxa (e.g. Ephemeroptera). Other New Zealand studies conducted in relatively pristine streams have also found a hyporheos dominated by epigean insect taxa (Adkins & Winterbourn, 1999; Olsen *et al.*, 2001). The pool communities largely followed the same pattern with Crustacea and Oligochaeta dominating in Booths Creek, Mollusca and Oligochaeta at Kiriwhakapapa Stream and insect taxa at Reef Creek.

Benthic invertebrate community structure varies with catchment land use (e.g. Quinn *et al.*, 1997; Townsend *et al.*, 1997). Forested sites are typically dominated by EPT taxa and pasture sites by Diptera, Mollusca, Oligochaeta and sometimes Crustacea. It appears that many of the factors affecting benthic communities also influence hyporheic community composition. Previous studies have found silt content to be an important determinant of hyporheic invertebrate community composition and abundance (e.g. Burrell, 2001; Olsen & Townsend, 2003). Our two farmland streams had up to 3.5 times more hyporheic fine sediment than the forested Reef Creek. Increased siltation of interstitial habitats induced by land use change (conversion of forest to pasture) has been postulated as the reason for the absence of the hyporheic specialist mayfly *A. cruentata* in some streams (Boulton *et al.*, 1997; Scarsbrook & Halliday, 2002). This mayfly is common in the hyporheos of the forested Reef Creek, but absent from the nearby and similarly sized Kiriwhakapapa Stream, perhaps because of the greater amount of fine hyporheic sediment.

Vertical distribution

We observed three patterns of vertical distribution. Some taxa, such as *Deleatidium* sp. and *P. antipodarum* clearly prefer the benthic zone. Other taxa, such as Ostracoda and *A. cruentata* were more abundant deeper in the hyporheic zone, while Tanypodinae and

Orthocladiinae chironomids were more evenly spread throughout the chambers. These preferences probably result from taxa specific habitat (e.g. water velocity, low dissolved oxygen tolerance) and nutritional (e.g. algae, sediment) requirements, as well as biophysical factors (e.g. body size, shape, ability to move within substrate). Additionally, multiple factors may act together to determine the vertical distribution of animals. Given that variables such as dissolved oxygen and temperature did not vary greatly with depth in the substrate, nutritional resources and biophysical factors were probably most important in our study streams. The depth preferences observed were similar to those previously reported for most taxa (Adkins & Winterbourn, 1999; Olsen *et al.*, 2001) although there were some exceptions. Scarsbrook (1995) in a colonisation pot study found *P. antipodarum* and *O. feredayi* were uniformly distributed with depth but we found both declined in number with depth. Oligochaeta showed a uniform distribution at Booths Creek but tended to increase with depth at Kiriwhakapapa Stream. The preference of *A. cruentata* for deeper substrate supports the findings of Collier *et al.* (2004) who estimated that 76% of the annual production of this species occurs greater than 10 cm below the surface. Taxa richness measured as rarefied taxa number and Margalef's Index decreased with depth in Booths Creek and Kiriwhakapapa Stream indicating that fewer macroinvertebrate taxa are equipped to live in the hyporheic zone than at the surface of these streams. Simpson's Index showed that taxa evenness declined with depth in Kiriwhakapapa Stream and Reef Creek as a few taxa came to numerically dominate the community with increasing depth in the substrate (e.g. *A. cruentata*, Ostracoda).

The impact of flow reduction

The hyporheic zone has been proposed as a refuge for surface invertebrates from disturbances such as flood, drought, predation, extreme temperature and reduced water quality (Brunke & Gonser, 1997; Boulton *et al.*, 1998). Some studies have found invertebrates move into the hyporheic zone in response to high flow events (Poole & Stewart, 1976; Dole-Olivier *et al.*, 1997) but others have found they do not (Giberson & Hall, 1988; Palmer *et al.*, 1992; Olsen & Townsend, 2005). Intermittent streams have tended to be the focus of studies examining the potential for the hyporheic zone to act as a refuge during low flow and dewatering events. However, only Cooling & Boulton (1993) have found evidence of taxa moving into the hyporheic zone in response to dewatering, while most studies showed no response (e.g. Boulton, 1989; Clinton *et al.*, 1996; Del Rosario & Resh, 2000). Similar studies in permanent systems found that invertebrates do not move into the hyporheic zone in response to flow reduction but these studies have had no between stream replication (Gilpin & Brusven, 1976) or have sampled only shallow depths in artificial channels (Ruediger, 1980). In our study based on 60 colonisation chambers in three streams, macroinvertebrate abundance, vertical distribution and community composition were unaltered by flow reduction. Whilst *P. antipodarum* did increase in pools following flow reduction in Booths Creek, no other taxon showed evidence of moving to pools, which, if flow did cease, would be the last remaining surface water habitat.

We found no indication of animals moving to the hyporheic zone or pools in response to severe flow reduction. There are several possible reasons why benthic invertebrates may not use the hyporheic zone or pools as refugia from flow reduction. Firstly, for an invertebrate to seek a refuge it must be stressed. If the flow reduction does not create unsuitable surface conditions (i.e. high temperatures, low oxygen, overcrowding) then there is no need for a refuge. In our study streams, a severe reduction in flow decreased velocity and wetted width but had either no or small impacts on pH, dissolved oxygen, specific conductivity or daily mean and maximum temperature. Over the month of reduction, no change in benthic community composition occurred, although densities increased as the wetted habitat contracted (Dewson *et al*., 2007). Potential stressors were a reduction in surface water velocity and increased densities (possibly leading to increased competition and predation pressure) but these did not result in movement of invertebrates into the hyporheic zone.

Alternatively, if surface conditions become unfavourable, conditions in the hyporheic zone may not be any more suitable. Many taxa have preferences for particular velocities (Georgian & Thorp, 1992; Wallace & Anderson, 1996) and animals requiring higher velocities would not find these in the hyporheic zone. For algal grazing taxa and larger filter feeders (i.e. hydropsychid trichopterans), it is unlikely their nutritional requirements would be met in the hyporheic zone. Interstitial pore size, invertebrate body form, size and burrowing ability may also be incompatible (Williams & Hynes, 1974) especially if siltation and clogging of substrate occurs concurrently with flow reduction. The ability of some taxa to respire may also be compromised in the hyporheic zone as dissolved oxygen typically decreases with depth in the substrate (Williams & Hynes, 1974; Poole & Stewart, 1976). However, many hyporheic and groundwater resident taxa are tolerant of low dissolved oxygen levels (Hervant *et al*.,

1998) and we did not observe a decrease in dissolved oxygen with depth in our streams. The hyporheic zone may be a refuge from extreme surface water temperatures as temperatures are generally cooler than at the surface (Evans & Petts, 1997). However, we found surface and hyporheic mean daily temperatures to be similar, except in Booths Creek, the stream draining the most intensive agriculture. Interestingly, in Booths Creek and Kiriwhakapapa Stream, flow reduction led to an approximately 2°C reduction in daily temperature range in the surface water making the range more similar to that of the hyporheic water. This coupled with our finding that upwelling dominated, might reflect a greater influence of cooler groundwater inflows on surface water temperature when flows are low/reduced. Of course, the hyporheic zone is only going to provide a temperature refuge where surface temperatures are great enough to stress benthic taxa and our flow reductions acted to lower surface temperatures, not increase them.

Lastly, reduced flow may reduce surface – hyporheic interchange. If this is the case, movement, especially passive movement of animals into the hyporheic zone may be inhibited by reduced flows. Packman & Salehin (2003) state that the hyporheic exchange rate is generally proportional to the permeability of sediments and the square of the stream velocity. Thus, one might expect in a stream where flow reduction reduces velocity, surface-hyporheic exchange will be reduced. Furthermore, the result we observed could have been influenced by the fact that upwelling dominated in the areas where our chambers were buried. Further study is required to ascertain upwelling and downwelling zone differences in response to flow reduction.

Conclusions

We have shown that similarly sized streams in the same region can have distinct hyporheic communities. While this study lacked sufficient replication to pinpoint the exact cause of this, the distinct communities may result from between-stream differences in substrate size, altitude, slope and/or land use related changes such as fine sediment accumulation. Whilst most taxa are present at all levels within hyporheic chambers, many have clear vertical distribution preferences. Despite severe flow reduction (88-96%), there was no change to the abundance, community composition and vertical distribution of hyporheic macroinvertebrates. There was also no change in the abundance of the dominant taxa in pools. While the hyporheic zone is not a refuge that animals actively move to, significant numbers of benthic taxa are present in the hyporheic zone at any time. This provides a source of colonists should some disturbance, be it drying or scouring, denude the surface of animals.

The findings of the present study, coupled with those of Dewson *et al.* (2007) indicate that benthic and hyporheic macroinvertebrates are resistant to short periods (1 – 1.5 months) of severe flow reduction. We suspect that in many cases, natural flood and scour events are going to have a greater impact on aquatic macroinvertebrates in small streams than any short-term, seasonal water abstraction where at least some flow remains. Thus, invertebrate abundance and community structure may not be the most useful indicators of environmental stress caused by reduced flow. However, the ability of the hyporheic zone to be a passive refuge may be compromised if benthic taxa can no longer reside there because of the loss of interstitial space and reduction of surface water infiltration from sediment accumulation. In addition, important ecological services such as denitrification occur in hyporheic zones (e.g. Cirmo & McDonnell, 1997; Lefebvre *et al.*, 2004) and may be inhibited by sediment clogging. Therefore, we recommend that water managers take a greater interest in the monitoring and protection of hyporheic environments rather than simply focusing on groundwater and surface water as two distinct entities.

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Chapter 5

The response of macroinvertebrates to a gradient of flow reduction – an instream channel study in a New Zealand lowland river

Abstract

If we are to protect the biota of rivers from the ever-escalating demand for water, it is of increasing importance that environmental flow assessment results in ecologically relevant minimum flow rules. At present, the most common methods of setting minimum flow make use of flow statistics with little consideration of biological relevance.

Many aquatic animals have been shown to have distinct depth and velocity preferences, which has led to the formation of hydraulic habitat modelling methods of setting minimum flows. These methods assume hydraulic habitat is a critical parameter influencing invertebrate community composition and distribution.

We subjected instream channels to a gradient (0-98%) of flow reduction that initially only altered channel depth and velocity. Invertebrates were sampled at three levels within the substrate (0-7 cm, 8-14 cm and 15-21 cm) on three occasions (before reduction, one month and two months after reduction) with the objective of determining the effects of magnitude and duration of flow reduction on community structure and distribution within the substrate. After one month, invertebrate densities declined in rough proportion to the extent of flow reduction in all but the control and 25% flow reduction channels, but recovered to pre-reduction levels within two months. The amphipod, *Paracalliope fluviatilis* numerically dominated all channels prior to reduction, but failed to recover after two months of reduction. Instead, Ostracoda, *Oxyethira albiceps* and Cladocera increased dramatically after two months of flow reduction, especially in the lowest flow channels, often reaching densities higher than pre-reduction levels. Greater than 85% of animals were found in the upper substrate level and flow reduction had no influence on the vertical distribution of invertebrates. Of the environmental variables measured, chlorophyll-*a* concentration along with discharge best explained the community pattern observed.

We showed that the effects of increased duration and magnitude of low flows on invertebrate communities appeared to be relatively minor in that only the relative abundances of a few common taxa changed. Our results again emphasised that New Zealand invertebrate communities appear to be resistant to short-term periods of flow reduction disturbance.

Introduction

The demand for water has been growing exponentially along with human population (Postel, 1997) and as water managers and the public become more ecologically aware, greater effort is afforded to balancing instream and out of stream needs when making water allocation decisions. Environmental flow assessments attempt to determine the proportion of the original flow regime of a river that is required to maintain specified, valued features of the ecosystem (Tharme & King, 1998). In many instances, such assessments revolve around setting minimum flows, be it residual flows below a large dam, or a level at which water abstraction from natural rivers must cease. To ensure a biologically relevant flow is retained, we must understand how biological communities respond to reduced flows. Unfortunately, the most common environmental flow methodologies in use today are based on hydrological measures (Tharme, 2003). Such methods use flow statistics to derive flow indices which become the recommended environmental flow. Often this is a proportion of flow such as the seven-day mean annual low flow (Q_{7day}: Ministry for the Environment, 1998), or the flow equalled or exceeded 95% of the time (Q95: Arthington *et al.*, 2003) which are deemed a suitable 'minimum flow'. These statistical methods may have little biological relevance in maintaining ecosystem structure and functioning, but are popular as they are inexpensive and relatively easy to calculate, and do not even require a site visit.

In other cases, where either more money is available, or where there is concern over the wellbeing of biota, habitat simulation methods have been used. These methods (e.g. the PHABSIM part of the Instream Incremental Flow Methodology (IFIM)) model the quantity of the physical habitat at various levels of flow for the species of interest. Often, the requirements of a single 'important' species (often a salmonid) are catered for under the assumption that protecting that species will adequately protect the whole community. Some workers are advocating 'holistic methodologies' that define environmental flows to preserve the whole river ecosystem rather than a single target species (e.g. Arthington & Pusey, 1993; Richter *et al.*, 1996; Poff *et al.*, 1997; Arthington *et al.*, 2006).

To protect riverine ecosystems from the over-extraction of water, we require a better understanding of how macroinvertebrates respond to reduced flow. Benthic invertebrates often display specific water depth and velocity preferences from which habitat suitability curves can be derived (e.g. Statzner & Higler, 1986; Wetmore *et al.*, 1990; Collier *et al.*, 1995; Jowett, 2000). Such curves form the basis of hydraulic habitat models which can be used to aid the setting of minimum flows (Jowett & Mosley, 2004). This approach assumes hydraulic habitat is a critical parameter influencing invertebrate community composition and distribution. However, other factors such as algal dynamics, sediment deposition and temperature regime may also influence invertebrate communities and as yet are not accounted for in simple hydraulic models (e.g. Suren *et al.*, 2003 a, b). Moreover, although particular invertebrates may display 'preferences' for specific depth-velocity regimes, they may still persist in rivers where depths and velocities have been reduced to levels below their optimum as a result of water abstraction. Under such a scenario, although IFIM models may predict a loss of habitat (and by inference a reduction in invertebrate abundance), invertebrates may still persist as long as water remains in the channel.

Two types of study are commonly conducted to examine invertebrate responses to low flow; field studies during droughts and the monitoring of changes to community composition above and below water abstractions. Studies examining the responses of benthic communities to droughts (e.g. Cowx *et al.*, 1984; Wood & Petts, 1999; Caruso, 2002) are complicated by the fact that multiple variables change during such times, so that in addition to decreased water depth and velocity, there are often extreme reductions in wetted width. Moreover, other factors such as increased water temperatures may further stress invertebrate communities, confounding the effect of reduced flows on these animals. The finding that 'droughts' have potentially detrimental impacts on ecology is not particularly illuminating when it comes to making water allocation decisions, as little predictive information on the response of invertebrates to reduced depth and velocity is obtained.

Studies investigating the effects of human-induced flow reductions above and below abstraction points (e.g. Bickerton *et al.*, 1993; McIntosh *et al.*, 2002; Dewson *et al.*, 2003) are unable to look at a gradient of flow reduction in the same time or space. Additionally, these studies usually involve existing flow reductions, and are thus confounded by other changes between upstream and downstream sites. Only studies employing a before-after, control-impact (BACI) design can avoid this (e.g. Dewson *et al.*, 2007a; James *et al.*, 2007).

The potential deficiencies in monitoring the impact of reduced flows on invertebrate communities can be overcome by using experimental channels where flows can be closely manipulated without causing large alterations to other variables. In this paper, we investigated the effects of both increased magnitude and duration of reduced flows on the invertebrate community of a New Zealand lowland river using colonisation baskets in instream channels. Reduced flows usually result in concomitant decreases in wetted perimeter (Dewson *et al*., 2007b), confounding successful identification as to the effects of decreased depth and velocity, as reductions in wetted perimeter are implicated in increasing invertebrate density (e.g. Rader & Belish, 1999; Suren *et al*., 2003b; Dewson *et al*., 2007a). In our channels, wetted perimeter was unchanged by flow reduction, thus we were able to investigate the effects of depth and velocity changes on invertebrate communities without the confounding influence of changes to wetted perimeter. We hypothesised that the greater the duration and magnitude of flow reduction, the greater the degree of community change. We also expected that taxa showing a preference for slow-flowing water would increase in density, especially in the channels with the greatest reduction, while densities of taxa with a preference for faster-flowing water would decrease.

Our channel design also allowed us to investigate the impacts of flow reduction on the vertical distribution of benthic invertebrates within the substrate. It has been proposed that the hyporheic zone (the wetted interstitial zone below and alongside rivers) may be used by benthic invertebrates as a refuge from unfavourable surface conditions (Brunke & Gonser, 1997; Boulton *et al*., 1998). However, based on the findings of chapter 4 (also James *et al*., (in press)), we did not anticipate the active movement of invertebrates into the substrate or any corresponding increase in subsurface densities. We did expect most taxa to be present within the substrate, thus providing a source of colonists should some disturbance (i.e. flood or drying) denude the surface of animals.

Methods

Experimental design

Six stainless steel channels (5 m long × 50 cm wide × 40 cm deep) were installed in the Kaiapoi River at the National Institute of Water and Atmospheric Research (NIWA) Silverstream Research Facility, 40 km north of Christchurch, South Island, New Zealand (43°24´S 175°35`E). Each channel was dug 30 cm into the cobble streambed and placed on a stainless steel frame, slightly larger than the channel dimensions (Fig. 1, Plate 1). The upstream and downstream ends of each channel were made flush with the normal streambed following placement. Each channel was filled with a series of stacked stainless steel baskets (50 cm wide × 15 cm long × 7 cm deep), made from perforated steel sheets (15 mm diameter holes). Approximately 60% of the sheet area was open, so it was assumed that movement of water or animals through the basket walls would be similar to that of natural gravels. Indeed, measurements of intragravel velocity (see below for methods) showed no differences between natural gravels and gravels within baskets (A. Suren, unpublished data). Baskets were filled with gravel (30-40 mm diameter) and stacked in triplicate on top of each other. Fifteen of these stacked baskets were placed along each channel, with a 15 cm wide strip of gravel, filled flush with the surface of the channels separating each basket (Plate 2). Steel handles that were welded to the ends of the lower-most baskets protruded from the gravels and allowed the baskets to be easily removed from the channels. All baskets were deployed in December 2004 and left for one year prior to the commencement of the experiment so that the gravels would be colonised by a natural invertebrate community.

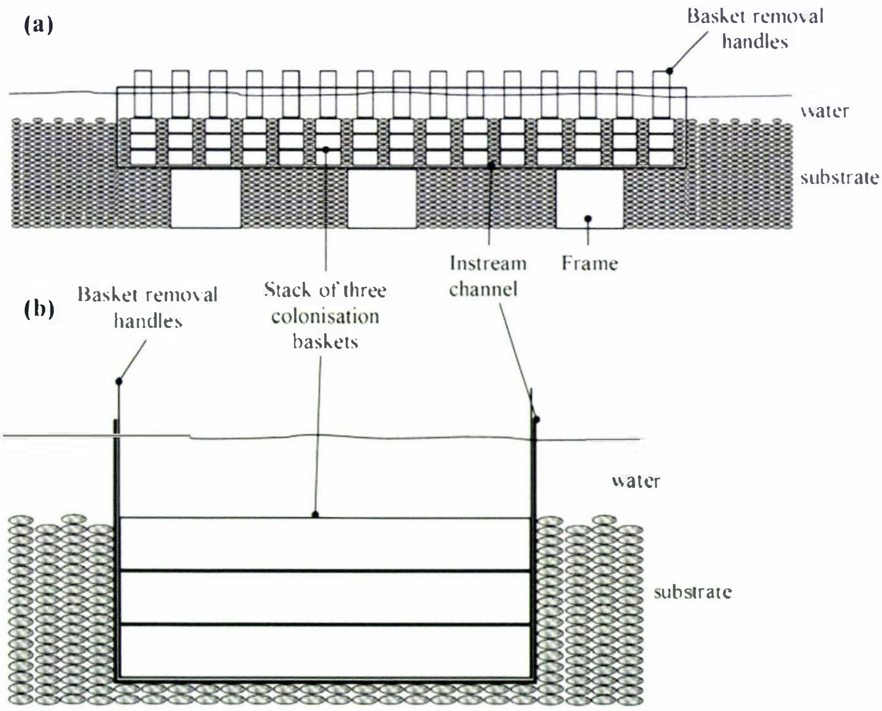

Figure 1. Diagrammatic representation of the channels viewed from the side (a) and in cross section (b).

Plate 1. The six instream channels in the Kaiapoi River facing upstream.

Plate 2. Underwater 'fish-eye' view of an instream channel. The individual basket removal handles are visible along the sides of the channel.

Physical measurements

Velocity and depth readings were taken at 2 cm intervals across the channel at the lengthwise midpoint using an acoustic doppler velocity meter (SonTek/YSI Incorporated, San Diego, USA.). Previous observations (A. Suren, unpublished data) showed little longitudinal difference in discharge or velocity. Intragravel velocities were calculated in each channel by measuring the time taken for salt solution to travel a known distance between two pairs of electrodes. One pair of electrodes was placed upstream of a randomly selected basket, while the other pair was placed downstream of the same basket (a total distance of c. 200 mm). Both electrodes were buried in the middle height stratum of each channel. A small PVC tube (2 mm diameter) was placed in front of the upstream electrode. A 12 volt current was then applied to each pair of electrodes and 25 cc of salt solution (1000 µS/cm) injected via the tube. Passage of the salt solution across the electrodes was monitored via a datalogger recording the voltage across each electrode every 0.25 seconds. Initial monitoring of conductivity showed that the small amount of salt injected into the gravels resulted in only a relatively minor increase in salinity at the downstream electrode (up to 250 µS/cm) compared to the background level of 160 µS/cm. This peak also only lasted for < 5 minutes, and was assumed to have little or no effect on any invertebrates dwelling between the electrodes.

Stream temperature was monitored by placing TidBit dataloggers (Onset Computer Corporation, Bourne, MA, USA.) in selected channels. Dataloggers were placed at heights corresponding to the middle of the upper and lower baskets. Temperature was logged every 15 minutes for the duration of the experiment.

Dissolved oxygen of the intragravel water was measured by collecting water (50 cc) using a syringe attached to the ends of the PVC tubing used for the intragravel velocity measurements. Care was taken to withdraw the water slowly from each channel, to minimise potential mixing of water from the upper layers. Oxygen content of the water was assessed by measuring absorbance at 600 nm using an Ocean Optics sensor (Ocean Optics, Dunedin, FL, USA.); the higher the oxygen content, the lower the absorbance. Absorbencies were compared to both 0% standards (obtained by adding $NaSO_4$) and 100% blank standards (obtained by bubbling air through the water for 2 hours). Oxygen content was measured over a three day period after flow reduction, with two measurements being made during the day (1200 h and 2000 h) to assess daytime productivity, and at in the morning (0700 h) to assess night time respiration. No measurements were made of intragravel oxygen before flow reduction.

Biological sampling

The experiment commenced in December 2005 and ran until April 2006. We used a before-after-control-impact (BACI) (Downes *et al*., 2002) design for the experiment, to detect changes in biological communities as a result of reduced flows. Five baskets were collected from all channels in January, after which flow was reduced in five of the channels, while flow in the sixth channel remained unchanged. Flows were reduced in randomly selected channels by placing a jack under the steel frame and jacking the troughs up over a 24 hour period. This effectively reduced water depth, velocity, and discharge in the selected channels. Channel width remained unchanged. Channels were jacked up by different amounts (190 mm, 160 mm, 120 mm, 80 mm, 40 mm and 0 mm (control)) to create a gradient of flow reduction, ranging from c. 20% to 95% of the control channel. Further invertebrate and algal samples were collected from all channels after one month and two months of flow reduction. Samples were collected by removing five randomly selected baskets from each channel. Upper, middle, and lower baskets were placed in separate containers immediately after removal of each stacked basket. All organic matter (invertebrates, periphyton and detritus) were removed from the cobbles in each basket via elutriation, and all material collected in a 250 μm mesh net and preserved immediately with isopropyl alcohol. To minimise disruption to longitudinal connectivity between the gravels in each channel, five new baskets which had been in the river for 2 months replaced the collected samples.

Invertebrate samples were rinsed through a 500 μm Endecott (Endecotts Ltd, London, UK.) sieve. For large samples, a sample splitter was employed to divide the sample into four parts. Sequential subsamples were sorted until at least 200 individuals were removed. The entirety of each subsample was processed. Vinson & Hawkins (1996) found a rapid increase in the number of taxa as the number of individuals examined increased up to 200 individuals, after which the rate of increase slowed considerably. To avoid missing rare taxa, we scanned the remainder of the sample for taxa not present in the subsample. Invertebrates were identified to the lowest possible taxonomic level using the keys of Winterbourn (1973), Chapman & Lewis (1976), Towns & Peters (1996), Winterbourn *et al*. (2000) and Smith (2003). Chironomidae were identified to sub-family level and Oligochaeta to class.

Following counting and removal of all invertebrates from each sample, remaining organic matter was dried (60°C, 24 hours), and ashed (550°C, 12 hours) to determine the ash free dry weight (AFDW) of organic material in each basket.

Periphyton samples were collected from three randomly selected stones in the top of each basket, prior to the elutriation process. Care was taken to ensure that all invertebrates attached to stones were removed and added to the invertebrate samples. All stones were frozen (-18°C) pending analysis. Upon thawing, all material was scraped from each stone using a fine scrubbing brush, and collected. The *x, y* and *z* dimensions of each stone were then measured and the surface area calculated (Biggs & Kilroy, 2000). Chlorophyll-*a* was determined for each sample using the spectrophotometric ethanol method and the AFDW of the periphyton samples was measured by drying, weighing, ashing (400°C for 4 hours) and reweighing (Biggs & Kilroy, 2000).

Data Analysis

Measured water depth and velocity, and channel width were used to calculate discharge in the channels over time. All hydraulic parameters (discharge, velocity, depth and intragravel velocity) were analysed by two-way ANOVA (using channel and time as factors) to see whether these parameters differed between channels and before and after flow reduction, and how flow reduction changed these parameters (the channel × time interaction term). Where significant time effects were observed, a one-way ANOVA was used to see which channels differed in their hydraulic parameters. A two-way ANOVA was also used on oxygen data to show how this differed between channels and between observations taken day and night.

From the invertebrate data, we calculated total abundance, total taxa richness, the percent EPT individuals, the Macroinvertebrate Community Index (MCI) and its quantitative variant (QMCI) (Stark, 1985). The MCI and QMCI were originally designed to detect organic pollution but are used extensively by water managers in New Zealand to show overall changes to invertebrate communities. Furthermore, it has been suggested that there may be a correlation between low MCI values and extended low flow periods (Boothroyd & Stark, 2000).

One-way ANCOVA (main factor = time, covariate = velocity) was used to assess the effect of time on algal biomass (chlorophyll-*a* and AFDW), total basket (all levels summed) invertebrate abundance, taxon richness, MCI, QMCI, EPT % individuals, and density of the seven most abundant taxa. Velocity was chosen as the covariate as it seemed more relevant to invertebrates and was closely related to discharge (see Fig. 2).

For the organic matter and invertebrate data from the three basket levels, we used two-way split-plot ANCOVA to test for Time and Level differences. Time was the main plot variable, Basket Level the sub-plot variable, Basket the replication variable and velocity the covariate. A split-plot method was used as the three levels within each basket were considered to not be independent, i.e. what was encountered in the lower levels was potentially strongly related to what was in the upper level. Time was tested against the Basket(Time) mean square while Level and all terms including Level were tested against the residual mean square using Statistix 8.1 (Analytical Software, Tallahassee, FL, USA.). The Tukey multiple comparison test evaluated significant treatment differences while the covariate (velocity) coefficients indicated the direction of the covariate relationship (e.g. a negative coefficient was indicative of a dependent variable decreasing as velocity increased). Data were $\log_{10}$, square or fourth root transformed where necessary to improve normality and ensure homogeneity of variances.

Similarities using Bray-Curtis distances of both total basket and basket level invertebrate assemblages were used to construct two dimensional projections using non-metric multi-dimensional scaling (MDS) in PRIMER 6 (PRIMER-E Ltd., Plymouth, UK.). Data were fourth root transformed to down-weight the influence of abundant taxa (Clarke & Warwick, 2001). Analysis of similarities (ANOSIM) was used to investigate any differences with time and basket level, while similarity percentages (SIMPER) indicated which taxa were responsible for any observed assemblage differences with time, basket level and flow reduction.

The Euclidian distance of total basket AFDW, periphyton biomass (as chlorophyll-*a* and AFDW), discharge and velocity were used to create an environmental MDS which could then be compared to that of the total basket invertebrate assemblage. The RELATE procedure of PRIMER 6 was used to test the hypothesis that there was no relationship between the multivariate pattern from two sets of samples, in our case, the invertebrate and environmental resemblance matrices. The BEST procedure was then used to test which environmental variables best explained the observed invertebrate community pattern.

Results

Physical changes

As expected, there were significant differences in velocity and depth between the six channels ($F_{(5, 54)}$ = 8.58 and 56.38 respectively, $P < 0.01$), and between channels before and after flow reduction ($F_{(1, 54)}$ = 128.91 and 322.06 respectively, $P < 0.01$). The significant channel × time interaction term ($F_{(5, 54)}$ = 7.28 and 54.59 respectively) showed that flows differed between the channels during the different times. One-way ANOVA and post-hoc tests showed that velocity and depth were similar in all channels prior to flow reduction ($F_{(5, 42)}$ = 0.49 and 1.07 respectively, $P > 0.05$), but that velocities and depths differed greatly between the 6 channels after flow reduction ($F_{(5, 12)}$ = 16.65 and 94.15 respectively, $P < 0.01$). As expected, jacking up the channels resulted in marked reductions in velocity and discharge (Fig. 2), ranging from c. 98% to 25% reduction. There were significant correlations between depth, velocity and discharge (R^2 ranging from 0.75 to 0.96). Therefore, only velocity was considered further.

Average intragravel velocities were slow (mean = 1.7 mm/s), and variable (ranges from 0.9 – 2.5 mm/s). Unexpectedly, intragravel velocities differed between channels prior to flow reduction ($F_{(5, 49)}$ = 22.64, $P < 0.01$: Fig. 3), even though water velocity did not. Jacking up the channels resulted in significantly reduced intragravel velocities ($F_{(5, 49)}$ = 60.64, $P < 0.01$) in all channels except the control. Intragravel velocities were reduced from 17% to 51%, while velocities in the control decreased by 3%. Regression analysis showed that there was a significant negative relationship between the percentage reduction in channel velocity and the percentage reduction in intragravel velocity ($R^2 = 0.82$, $P < 0.01$).

Mean water temperature was 14.5°C, and temperatures ranged from 11.2°C to 19.6°C throughout the study. As expected, daily minima occurred during the night (average 11.8°C), and daily maxima during the day, with the highest daily temperatures (19°C) observed in January and February. There were no significant differences between observed temperature regimes in any of the channels before or after flow reduction. Dissolved oxygen levels were generally high (mean = 94% saturation), but variable (ranges from 50 – 145%). There was no difference in dissolved oxygen between channels after flow reduction ($F_{(5, 95)}$ = 1.64, $P > 0.05$) despite the different velocities in each channel, and no differences between water withdrawn from the upper and lower baskets. There were significant temporal differences in oxygen content ($F_{(1,}$

$_{95)} = 41.11, P < 0.01$), with mean daytime levels being higher (mean = 103%) than mean night time levels (mean = 76%).

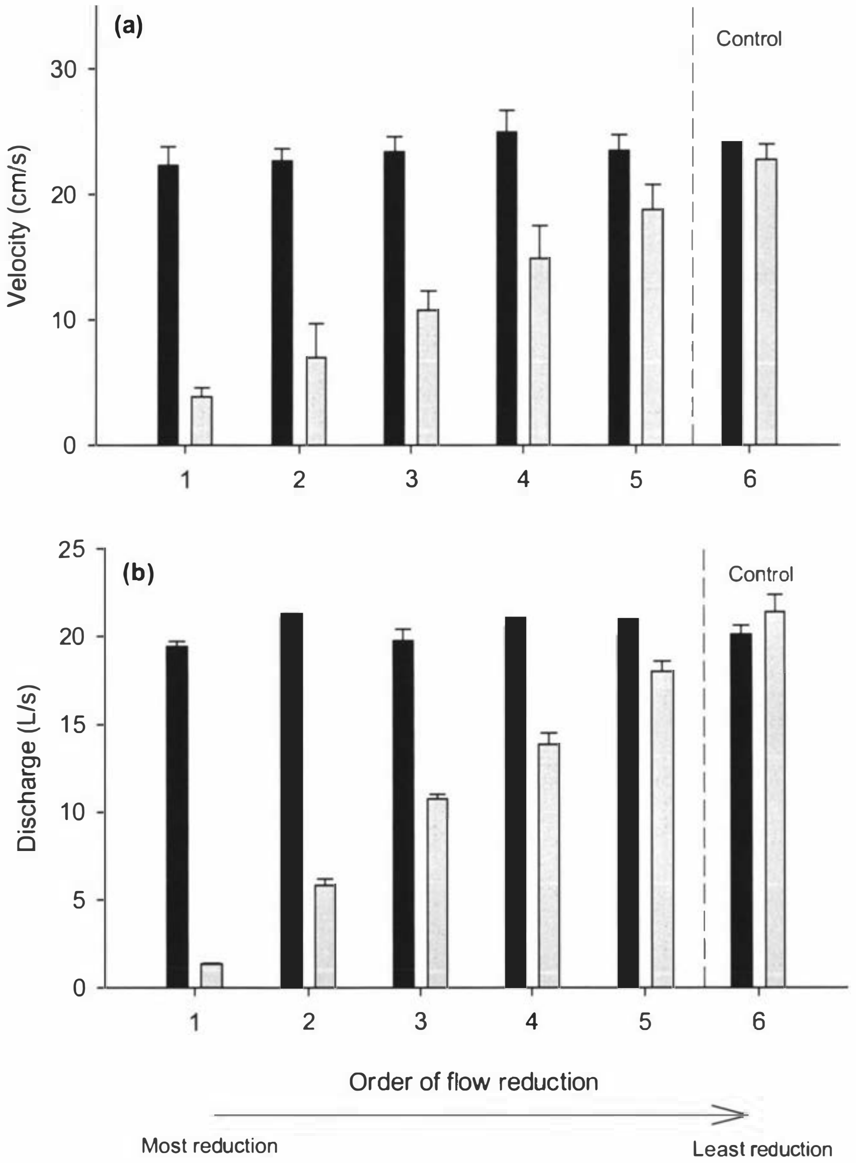

Figure 2. Mean channel velocity (a) and discharge (b) ($n = 10$, +1 SD) in the six experimental channels before (black bars) and after flows were reduced (grey bars) by jacking up each channel.

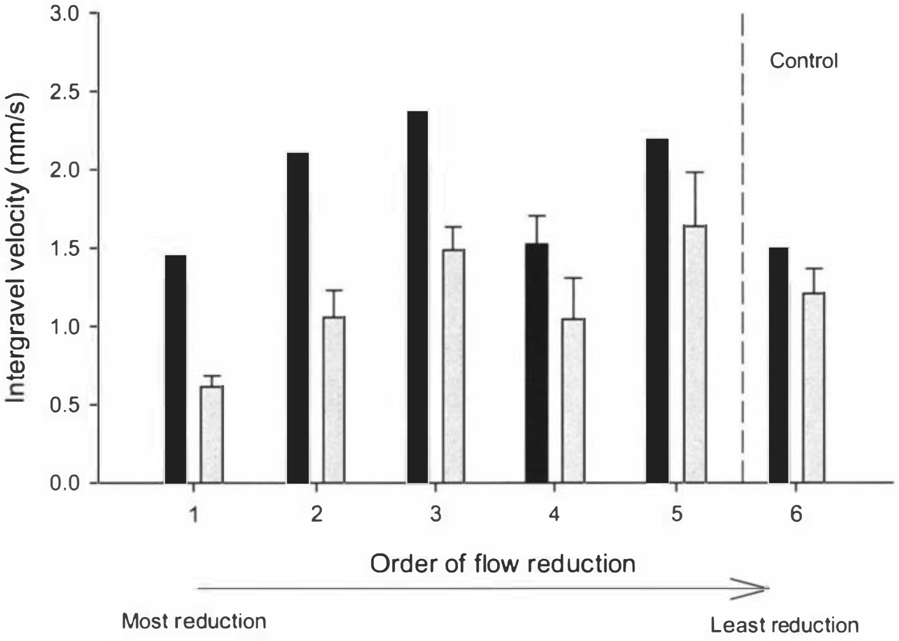

Figure 3. Mean intragravel velocity, (n = 3, + 1 SD) in the six experimental channels before (black bars) and after flows were reduced (grey bars) by jacking up each channel.

Biological changes

Chlorophyll-*a* and AFDW of periphyton increased with time (Table 1). These variables displayed a positive trend (albeit statistically non-significant) with velocity after one month of reduction. After two months of flow reduction, this trend reversed with higher chlorophyll and AFDW biomass in lower velocity channels 2 months following flow reduction (Fig. 4). AFDW of organic matter in the baskets (all levels combined) did not change with time (Table 1). AFDW was significantly higher in channels with lower velocities (Tables 1 and 2, Fig. 5). Organic matter was concentrated in the upper basket, with the mid and lower levels having equitable and lower amounts (Table 2, Fig. 5). There was no observed relationship between AFDW and velocity in the different basket levels.

Table 1. Results of ANCOVA showing the effects of time (main factor) and velocity (covariate) on top basket (chlorophyll-*a* and AFDW1) and all basket levels combined (AFDW2, total abundance, taxa, MCI, QMCI, EPT percentage individuals, seven most abundant taxa) variables in experimental channels during the experiment. AFDW1 = periphyton biomass from cobbles taken from top basket, AFDW2 = values from invertebrate samples (after invertebrates removed). Tukey multiple comparisons (0 = before, 1 = one month after and 2 = two months after reduction) and covariate coefficients in brackets where significant. Table continued on next page.

Variable	Source	df	Sum-of-Squares	Mean-Square	*F* ratio	*P* value	Tukey result / covariate coefficient
Chlorophyll-*a*	Time	2	0.51	0.25	8.83	**<0.01**	(2=1>0)
	Velocity	1	<0.01	<0.01	<0.01	0.96	
	Error	86	2.47	0.03			
AFDW1 (periphyton biomass)	Time	2	95.80	47.90	5.43	**<0.01**	(2=1>0)
	Velocity	1	6.91	6.91	0.78	0.38	
	Error	86	758.00	8.81			
AFDW 2 (interstitial material + periphyton)	Time	2	0.01	0.01	0.67	0.51	
	Velocity	1	0.04	0.04	5.36	**0.02**	(-4.1×10^4)
	Error	86	0.64	0.01			
Total abundance	Time	2	2.23×10^7	1.11×10^7	15.62	**<0.01**	(2=0>1)
	Velocity	1	3695135	3695135	5.18	**0.03**	(3.98)
	Error	86	6.14×10^7	713407			
Total taxa	Time	2	134.33	67.17	9.99	**<0.01**	(2>1=0)
	Velocity	1	21.95	21.95	3.26	0.07	
	Error	86	578.49	6.73			
MCI	Time	2	45.47	22.74	1.06	0.35	
	Velocity	1	82.38	82.38	3.83	0.05	
	Error	86	1849.13	21.50			
QMCI	Time	2	2.52	1.26	28.60	**<0.01**	(1=0>3)
	Velocity	1	0.20	0.20	4.47	**0.04**	(-9.2×10^4)
	Error	86	3.80	0.04			
EPT % individuals	Time	2	2.61	1.30	67.41	**<0.01**	(2>1>0)
	Velocity	1	0.01	0.01	0.68	0.41	
	Error	86	1.66	0.02			
Paracalliope fluviatilis	Time	2	0.32	0.16	2.88	0.06	
	Velocity	1	0.85	0.85	15.23	**<0.01**	(0.002)
	Error	86	4.81	0.06			
Ostracoda	Time	2	0.73	0.37	7.33	**<0.01**	(2>1=0)
	Velocity	1	0.01	0.01	0.22	0.64	
	Error	86	4.29	0.05			

Table 1 continued...........

Variable	Source	df	Sum-of-Squares	Mean-Square	*F* ratio	*P* value	Tukey result / covariate coefficient
Orthocladiinae	Time	2	82.64	41.32	2.11	0.13	
	Velocity	1	21.15	21.15	1.08	0.30	
	Error	86	1684.89	19.59			
Oxyethira albiceps	Time	2	10.37	5.19	86.72	**<0.01**	(2>1=0)
	Velocity	1	2.25	2.25	37.57	**<0.01**	(0.003)
	Error	86	5.14	0.06			
Cladocera	Time	2	12.35	6.18	9.06	**<0.01**	(2>1=0)
	Velocity	1	0.39	0.39	0.57	0.45	
	Error	86	58.60	0.68			
Polyplectropus sp.	Time	2	127807	63903.40	10.04	**<0.01**	(2=1>0)
	Velocity	1	3243	3243	0.51	0.48	
	Error	86	547621	6367.70			
Chironominae - Tanytarsini	Time	2	57.20	28.60	50.43	**<0.01**	(0>2>1)
	Velocity	1	7.60	7.60	13.40	**<0.01**	(0.006)
	Error	86	48.77	0.57			

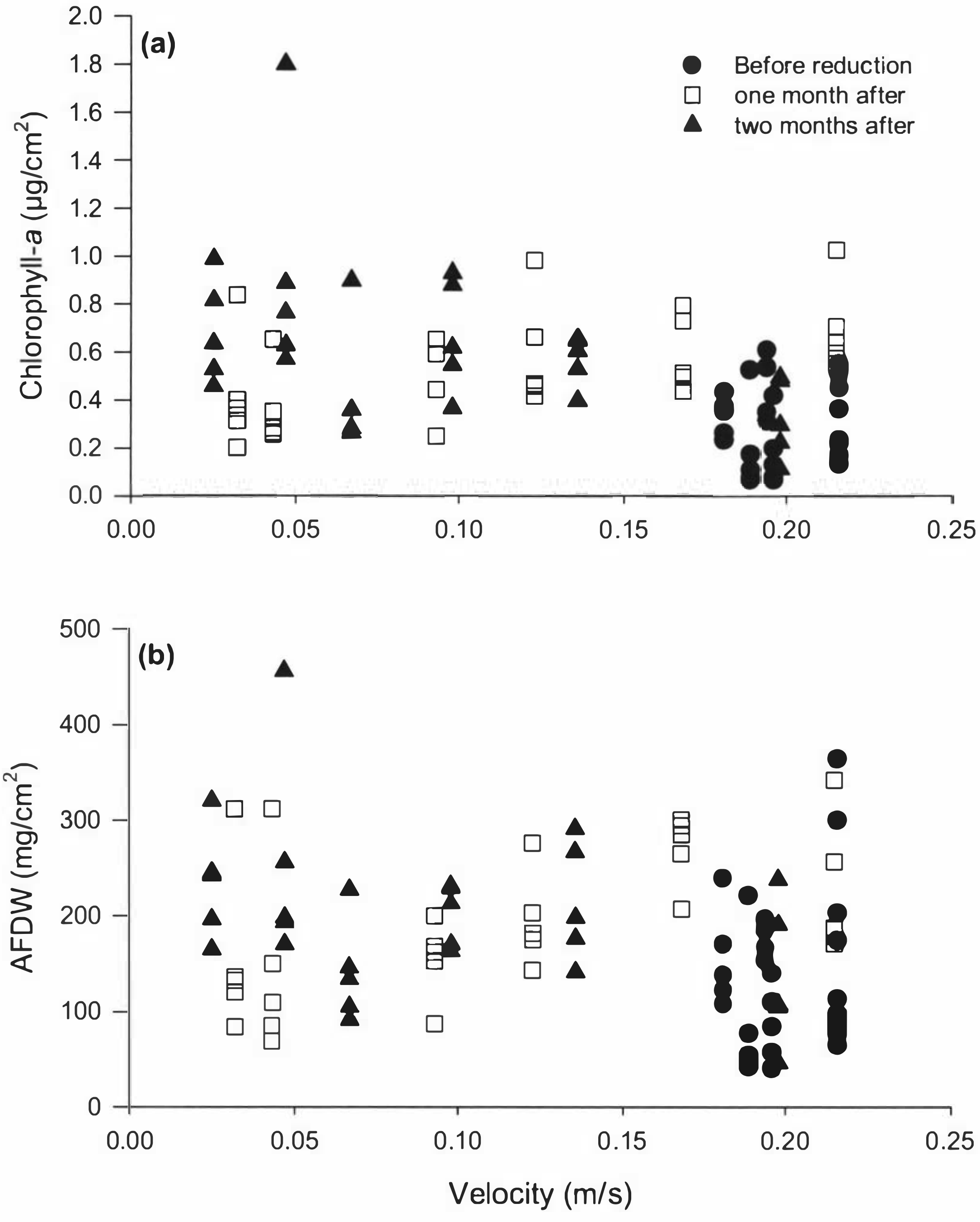

Figure 4. Periphyton biomass as a) chlorophyll-*a* concentration and b) AFDW showing the effect of velocity measured before (closed circles), after one month (open squares) and after two months (closed triangles) of flow being reduced by jacking up each channel. Each symbol represents one basket sample.

Table 2. Results of two-way split-plot ANCOVA showing the effects of time, basket level and velocity (covariate) on total AFDW, total macroinvertebrate abundance, total taxa, and the abundance of the seven most common taxa during the experiment. Tukey multiple comparisons (Time: 0 = before, 1 = one month after and 2 = two months after reduction; Level: 1 = upper, 2 = mid, 3 = lower) and covariate coefficients in brackets where significant. Table continued on next page.

Variable	Source	df	Sum-of-Squares	Mean-Square	F-ratio	P value	Tukey result / covariate coefficient
AFDW	Time	2	0.005	0.003	0.44	0.66	
	Level	2	6.95	3.47	782.78	**<0.01**	(1>2=3)
	Time × Level	4	0.03	0.01	1.57	0.18	
	Velocity	1	0.05	0.05	11.07	**<0.01**	(-2.7×10^{4})
	Error	247	1.10	0.004			
Total abundance	Time	2	1.66	0.83	43.17	**<0.01**	(2=0>1)
	Level	2	81.23	40.61	1931.70	**<0.01**	(1>3>2)
	Time × Level	4	0.30	0.08	3.62	**0.01**	
	Velocity	1	0.36	0.36	17.25	**<0.01**	(7.2×10^{4})
	Error	247	5.19	0.02			
Total taxa	Time	2	325.35	162.67	34.92	**<0.01**	(2>1=0)
	Level	2	607.20	303.60	53.60	**<0.01**	(1>3>2)
	Time × Level	4	35.87	8.97	1.58	0.18	
	Velocity	1	88.25	88.25	15.58	**<0.01**	(0.01)
	Error	247	1399.03	5.66			
Paracalliope fluviatilis	Time	2	1.15	0.57	8.93	**<0.01**	(0>2=1)
	Level	2	75.37	37.69	694.06	**<0.01**	(1>3>2)
	Time × Level	4	0.12	0.03	0.27	0.69	
	Velocity	1	2.44	2.44	45.02	**<0.01**	(0.002)
	Error	247	13.41	0.05			
Ostracoda	Time	2	2.49	1.24	10.09	**<0.01**	(2>1=0)
	Level	2	86.84	43.42	776.30	**<0.01**	(1>3>2)
	Time × Level	4	0.28	0.07	1.26	0.29	
	Velocity	1	0.004	0.004	0.06	0.80	
	Error	247	13.82	0.06			

Table 2 continued.............

Variable	Source	df	Sum-of-Squares	Mean-Square	F-ratio	P value	Tukey result / covariate coefficient
Orthocladiinae	Time	2	1.127	0.61	4.23	0.06	
	Level	2	120.73	60.36	826.90	**<0.01**	(1>3>2)
	Time × Level	4	0.33	0.08	1.14	0.34	
	Velocity	1	0.71	0.71	9.77	**<0.01**	(0.001)
	Error	247	18.03	0.07			
Oxyethira albiceps	Time	2	18.32	9.16	167.36	**<0.01**	(2>1=0)
	Level	2	119.71	59.85	745.07	**<0.01**	(1>3>2)
	Time × Level	4	1.88	0.47	5.84	**<0.01**	
	Velocity	1	5.93	5.93	73.49	**<0.01**	(0.0030)
	Error	247	19.92	0.08			
Cladocera	Time	2	8.39	4.19	17.47	**<0.01**	(2>0=1)
	Level	2	131.66	65.83	405.06	**<0.01**	(1>3=2)
	Time × Level	4	0.24	0.06	0.37	0.83	
	Velocity	1	0.29	0.29	1.79	0.18	
	Error	247	40.14	0.16			
Polyplectropus sp.	Time	2	2.72	1.36	10.19	**0.01**	(2=1>0)
	Level	2	50.79	25.39	575.37	**<0.01**	(1>2>3)
	Time × Level	4	0.20	0.05	1.11	0.35	
	Velocity	1	0.17	0.17	3.84	0.05	
	Error	247	10.90	0.04			
Chironominae - Tanytarsini	Time	2	29.81	14.90	227.10	**<0.01**	(0>2>1)
	Level	2	76.43	38.21	258.65	**<0.01**	(1>3>2)
	Time × Level	4	6.63	1.66	11.22	**<0.01**	
	Velocity	1	3.41	3.41	23.11	**<0.01**	(0.002)
	Error	247	36.49	0.15			

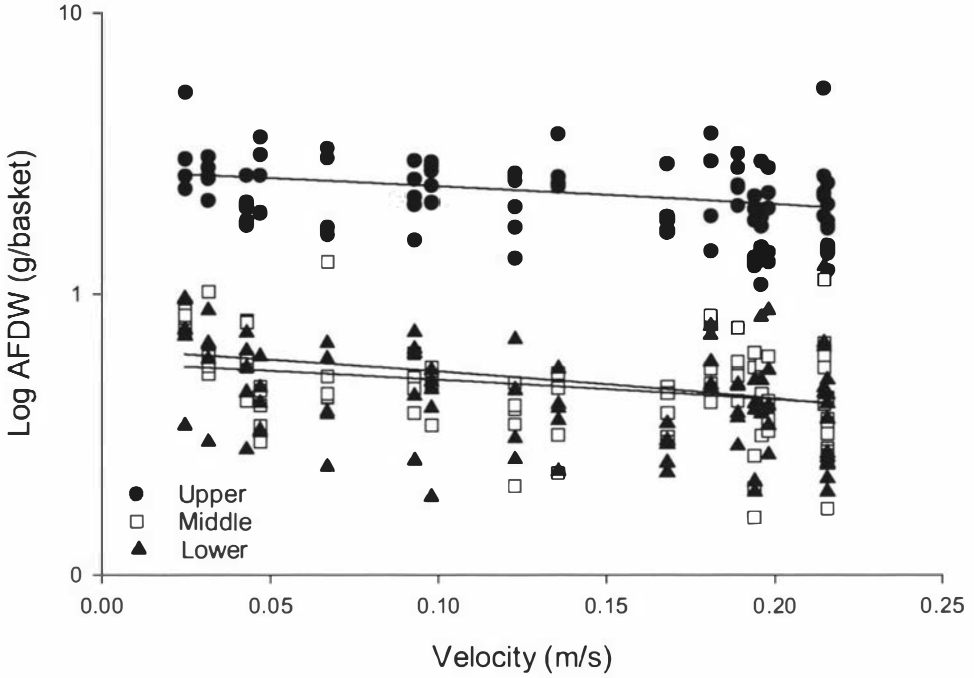

Figure 5. AFDW of organic matter found in each of the upper (closed circles), middle (open squares) and lower (closed triangles) colonisation baskets showing the differences in AFDW between layers, and the significant negative relationships between AFDW and velocity.

Total invertebrate abundance differed significantly over time (Table 1), and decreased one month after flow reduction, before increasing again to pre-reduction densities (Fig 6a). The magnitude of this initial reduction was much higher in the channels with the greatest flow reduction (Fig. 6a). Taxonomic richness and EPT percentage individuals increased over time irrespective of flow reduction (Table 1, Fig. 6b-c). Calculated MCI scores were relatively low (mean ± SE = 80.66 ± 4.82), and were unchanged by velocity or time (Fig. 6d). QMCI scores were also moderately low (mean ± SE = 4.02 ± 0.03) but declined with decreasing velocity and increasing time (Fig. 6e). This reflected the fact that densities of a number of low-scoring taxa such as Ostracoda and *Oxyethira albiceps* increased dramatically after two months.

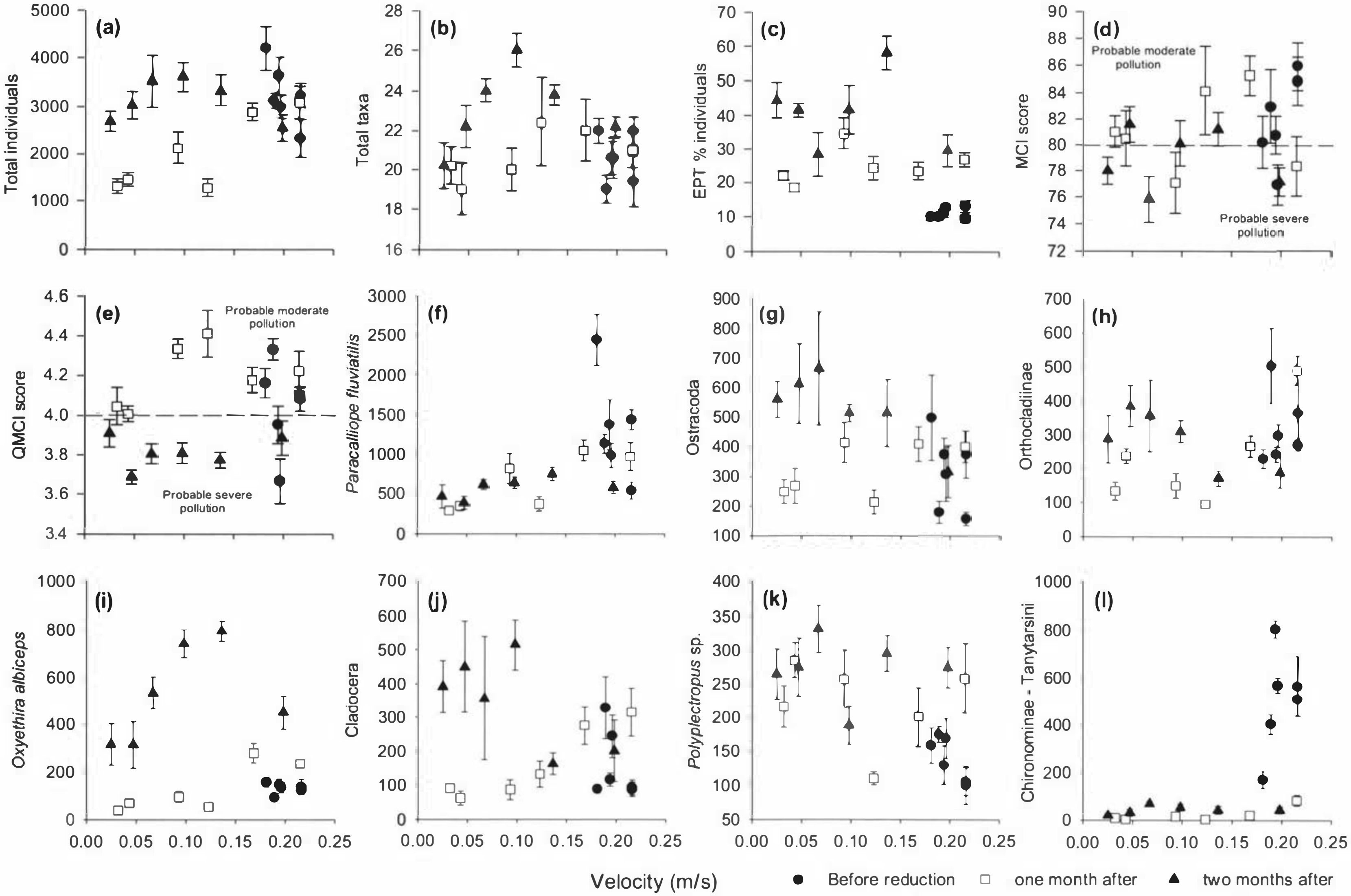

Figure 6. The effect of velocity on the mean ($n = 5, \pm 1$ SE), total basket values of community metrics and abundance of the seven most common taxa before, after one month and after two months of flow being reduced by jacking up each channel. Circle = before reduction, square = one month after and triangle = two months after reduction.

The seven dominant taxa selected for analysis accounted for 80% of total invertebrate abundance. These taxa displayed varying responses to time and velocity (Table 1, Fig. 6f-l). The amphipod *Paracalliope fluviatilis* was most abundant before flow reduction, then declined with reductions in velocity after both one and two months. In contrast, densities of three taxa (Ostracoda, Cladocera, and the hydroptilid caddisfly *O. albiceps*) remained unchanged before and after flow reduction for one month, but then increased markedly after two months, especially in the lower velocity channels. Orthocladiinae midges showed a similar, albeit weaker response, while densities of *Polyplectropus* sp. increased and densities of Chironominae decreased over the experimental period, irrespective of velocity (Figures 6g-l).

MDS ordination of invertebrate data from all basket levels combined showed a clear temporal trend in changes to the invertebrate community (Fig 7), with samples from each sampling occasion forming relatively discrete groups (Fig. 7, global $R = 0.79$, $P < 0.01$). The SIMPER analysis indicated that separation of samples collected before and one month following flow reduction reflected mostly decreases in densities of Chironominae, *Paracalliope fluviatilis*, *Pycnocentrodes* sp. and Tanypodinae, and increases in the density of Ceratopogonidae and Nemertea. After flows had been reduced, densities of *Oxyethira albiceps*, *Psilochorema* sp., Nemertea, Ceratopogonidae, Acari and Cladocera increased, while densities of Tanypodinae decreased. These changes were responsible for the observed separation between samples collected one month and two months after flow reduction. Samples collected before flow reduction, and those collected two months after were well separated along axis 1, but showed little variation along axis 2. A similar pattern was observed for samples collected from the control channels. However, a large difference in axis 2 scores was visible in samples collected one month after flow reduction, with the greatest deviation in scores coming from samples with the greatest flow reduction (Fig. 7). SIMPER analysis indicated that during this time, densities of taxa such as Chironominae, *Psilochorema* sp., Ceratopogonidae, *P. fluviatilis, O. albiceps* and Orthocladiinae decreased in channels with reduced flow, whereas densities of these taxa in the control and 25% reduced flow channels were similar, so these samples clustered together on axis 2. This was further illustrated by a decrease in total invertebrate density in the low velocity channels after one month, whereas densities in the control and 25% channels remained at pre-reduction levels (Fig. 6a). After 2 months of flow reduction, faunal composition of samples from all channels clustered tightly together (Fig. 7) and the total abundance in the low velocity channels had recovered to pre-reduction levels (Fig. 6a).

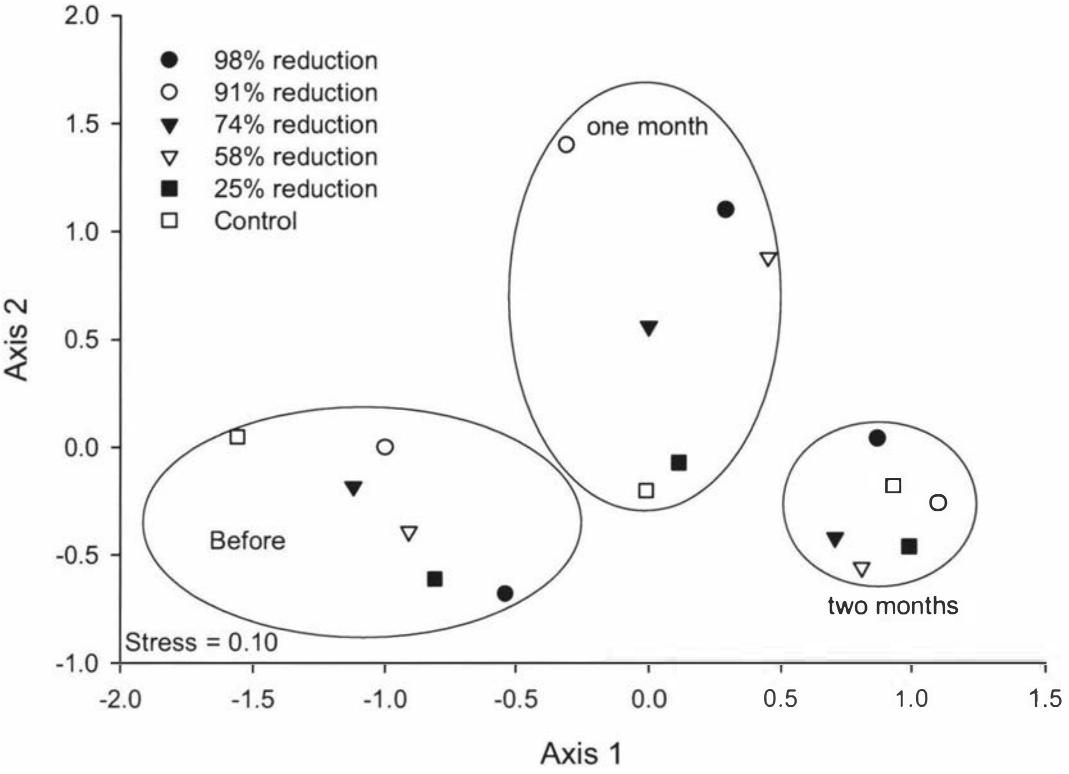

Figure 7. Non-metric multidimensional scaling ordination of the mean ($n = 5$) total basket (all depth levels combined) community from each channel before, after one month and after two months of flow being reduced by jacking up each channel.

Total invertebrate abundance, taxon richness, and densities of the 7 dominant taxa were all greater in the upper than in the mid and lower basket levels (Table 2). A MDS of basket level data showed a strong separation along axis 1 of upper baskets from mid and lower baskets (Fig. 8, ANOSIM: $R = 0.72$, $P < 0.01$). Samples collected before flow reduction also had higher axis 2 scores than those collected both one and two months after flow reduction (Fig. 8). SIMPER analysis suggested that most of the sample segregation based on basket level reflected the lower densities of all common taxa (e.g. *P. fluviatilis*, Orthocladiinae and Cladocera) in the lower baskets. As with the total basket MDS (Fig. 7), there was a progression with time along axis 2 in all basket levels (Fig. 8, ANOSIM: $R = 0.22$, $P < 0.01$).

No relationships were found between total invertebrate density, or densities of common hyporheic inhabitants (Ostracoda and *Polyplectropus* sp.) in all levels with velocity or time (Fig. 9). The observed decrease in total density in the lower velocity channels after one month of reduction, and subsequent recovery after two months only occurred in the upper level (Fig. 9a).

The RELATE procedure of PRIMER 6 found the measured environmental data and biotic community data (all basket levels summed) to be strongly related (Rho = 0.35, $P < 0.01$). The BEST procedure found that of the five environmental variables included (total AFDM, periphyton AFDM, chlorophyll-*a*, discharge, velocity), chlorophyll-*a* and discharge best explained the observed community patterns (Rho = 0.42, $P < 0.01$).

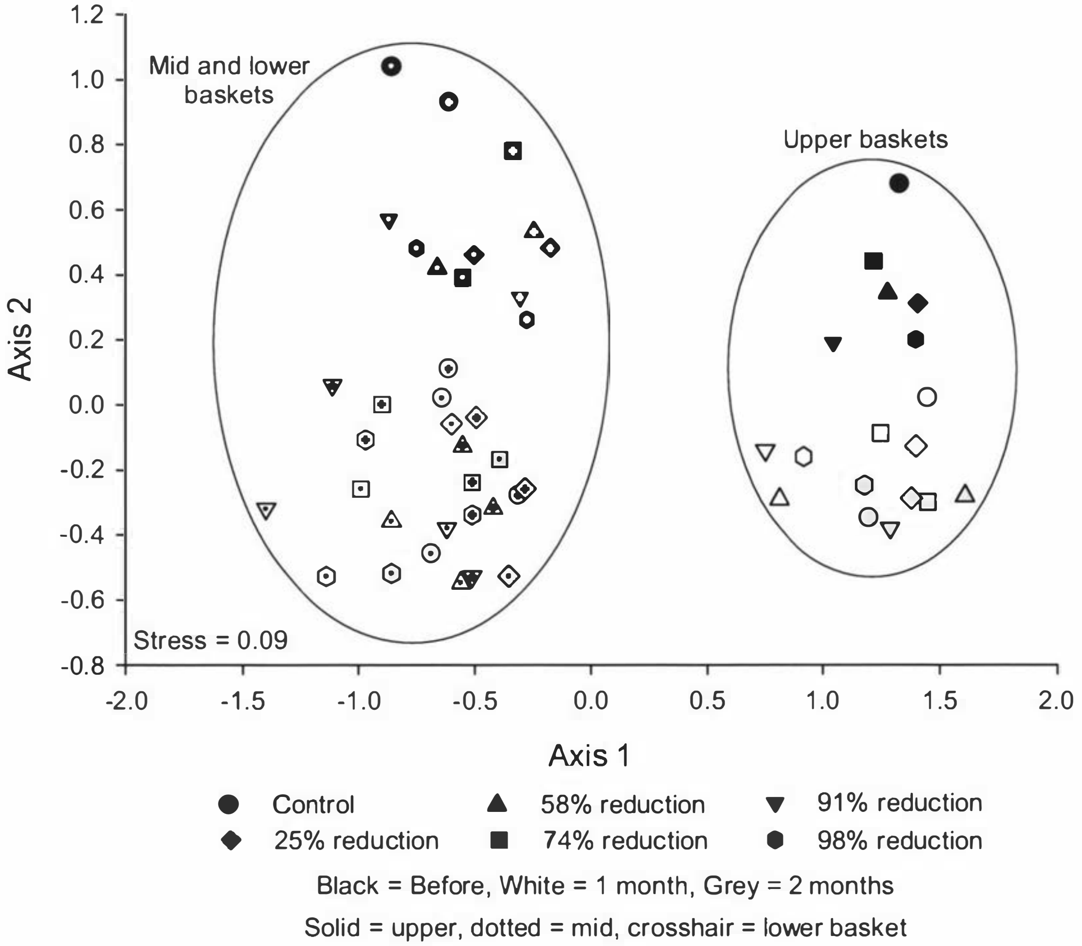

Figure 8. Non-metric multidimensional scaling ordination of the mean ($n = 5$) upper (solid), mid (dotted) and lower (crosshair) basket communities from each channel before (black), after one month (white) and after two months (grey) of flow being reduced by jacking up each channel.

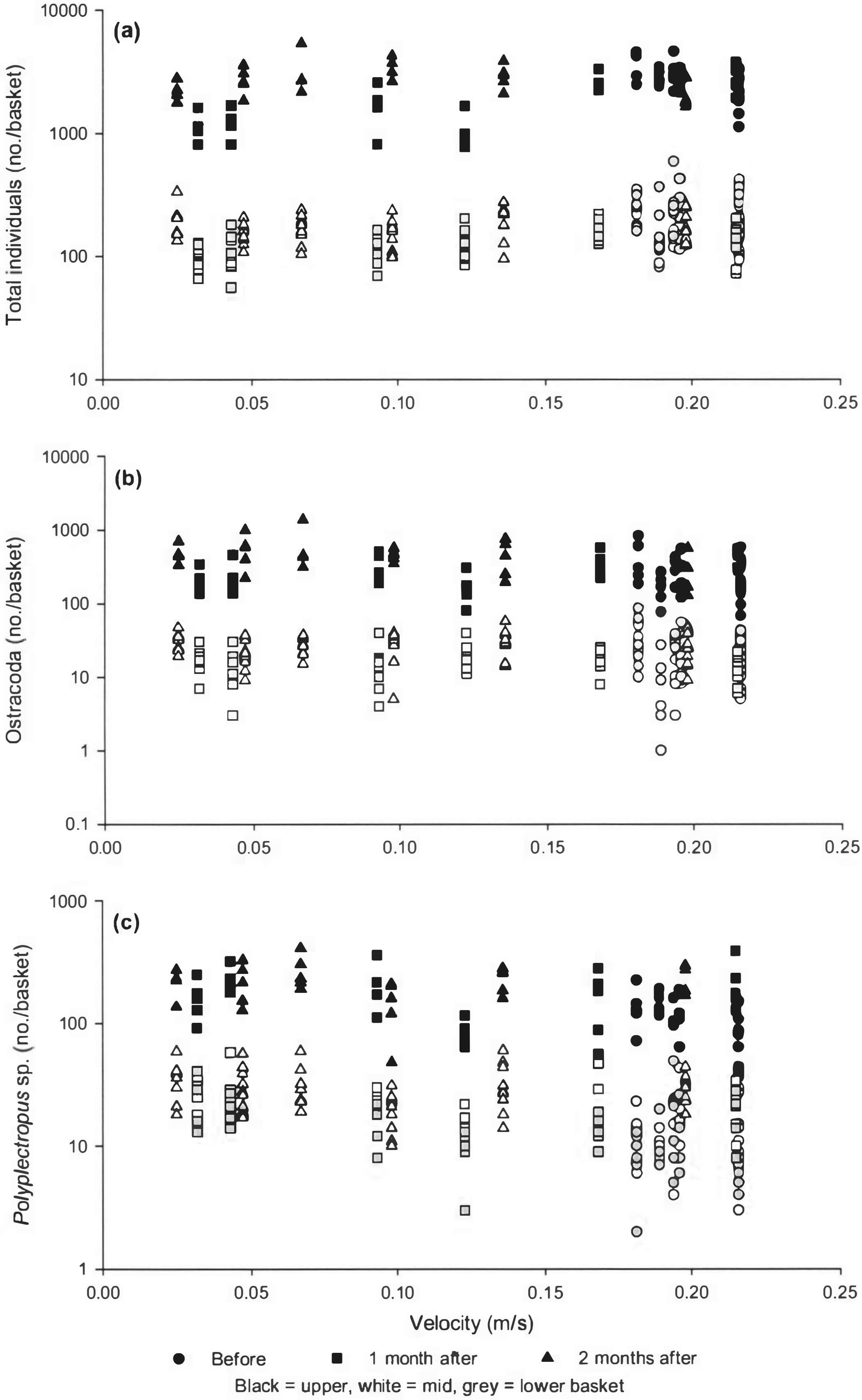

Figure 9. The a) total individuals, b) Ostracoda abundance and c) *Polyplectropus* sp. abundance in upper (black), mid (white) and lower (grey) baskets, before (circles), after one month (squares) and after two months (triangles) of flow being reduced by jacking up each channel.

Discussion

Effects of flow reduction

Our experimental manipulations reduced flows in the instream channels by up to 98%, and we monitored changes to invertebrate communities over a two-month period. We felt that the two-month duration of our study represented a long enough period for the invertebrate communities to respond and was representative of the length of low flow periods in New Zealand rivers. Analysis of hydrographs of 20 rivers of a similar River Environment Classification (REC) class (sensu Snelder *et al.*, 2005) as the Kaiapoi River (i.e. cool-dry climate, lowland source of flow, and alluvial geology) showed that the average maximum duration of low flows ($< Q_{7day}$) was 99 days; 30 days longer than our study. However, the average duration of such low flows was only 29 days; half as long as our study. This suggests that the temporal duration of the flow reductions in our channels were within the range of the duration of low flows naturally observed. Moreover, we suggest that our flow reduction of 98% in one of the channels was representative of a more severe low flow event than a Q_{7day} flow.

After a one-month period, flow reductions greater than 25% decreased invertebrate densities in the experimental channels, whereas densities increased to pre-reduction levels after two months. In this regard, the effect of increased duration of flow reduction on invertebrate densities was equivocal. Previous studies also show an inconsistent response to flow reduction, with some workers (e.g. Wright & Berrie, 1987; Dewson *et al.*, 2007a) reporting an increase in density after flow reduction, while others (e.g. Cowx *et al.*, 1984; McIntosh *et al.*, 2002) reported a decrease. Finally, other studies (e.g. Cortes *et al.*, 2002; Suren *et al.*, 2003b; Suren & Jowett 2006) reported no change in invertebrate density when flows were reduced. Such inconsistency likely results from differences in the invertebrate communities examined in each study, the magnitude and duration of reduced flows, as well as changes to other variables such as wetted perimeter and habitat area. The effects of these have recently been reviewed (see Chapter 1 and Dewson *et al.*, 2007b). Despite the lack of a strong temporal response to flow reduction, there was a demonstrable response to the magnitude of flow reduction. There was no change to invertebrate density in the control and 25% reduction channels, but density declined in the channels subject to higher reductions (58 – 98%). The few studies that have examined gradients of flow reduction have also found that the magnitude of flow reduction determines the response. Rader & Belish (1999) found that minor flow diversions had minimal effects on invertebrate densities, but severe flow diversions (i.e. nearly 100%) decreased invertebrate densities by half. Similarly, Wills *et al.* (2006) found flow diversions of 90% decreased densities of EPT taxa to a greater extent than diversions of 50% or base flow conditions.

It is difficult to directly compare our results with previous studies, as most of these have looked at systems where diversions have been operating for decades (e.g. Petts & Bickerton, 1994; Rader & Belish, 1999) and invertebrate communities tolerant of reduced flows have formed and persisted for considerable periods of time. Only a few studies have investigated flow reductions on a time scale that quantifies the short-term responses of invertebrate communities to reduced flows (but see Suren *et al.*, 2003a, b; Suren & Jowett 2006; Dewson *et al.*, 2007a).

Our study highlighted interesting behavioural differences between different invertebrate taxa with flow reduction. For example, densities of *P. fluviatilis* declined with reductions in velocity whereas densities of Ostracoda, Cladocera, and *O. albiceps* increased after two months, especially in the channels with the greatest flow reductions / lowest velocities. Ostracoda have previously been observed to be tolerant of low flow conditions. Suren *et al.* (2003b) and Suren & Jowett (2006) observed an increase in their density during low flow events in the Waipara River and attributed this to an increase in the amount of filamentous green algae that was available as a habitat for these animals. We found no major increase of filamentous green algae in our channels, but periphyton biomass did increase over time and this may have represented good habitat to Ostracoda, as well as to Cladocera and *O. albiceps*.

Our results showed that flow reduction had relatively minor effects on invertebrate communities. This was surprising, especially when considering the extent to which velocities had been reduced (up to 98%). If invertebrates were responding to changes in velocity according to their hydraulic habitat preferences, we would have expected a greater change. Unfortunately, detailed velocity preferences for most of the taxa encountered in this study are lacking, but Jowett (2000) presents optimum velocity preferences for four taxa common in this study: 0.18 m/s for Tanytarsini, ~0.35 m/s for *O. albiceps* and *P. fluviatilis*, and 0.61 m/s for Orthocladiinae. Velocities in the six channels prior to reduction were ~ 0.23 m/s, below the "optimal" velocity for three of these taxa, but velocities were reduced to as low as 0.039 m/s, well below these published optimal velocities. Densities of both *P. fluviatilis* and Tanytarsini had declined after one month, possibly in response to the reduced velocities, and their densities remained lowered throughout the study. However, densities of the other two taxa either did not change, or increased after two months. The lack of change in Orthocladiinae densities was particularly surprising, considering that channel velocities had been reduced from 3× less than optimal to 16× less than optimal. A lack of consistent change according to optimal preferences in velocity suggests that these taxa were responding to factors other than simple hydraulic parameters. Given this, the importance of using an IFIM based approach to predict the responses of invertebrate communities to loss of habitat as a result of flow reduction may not be particularly clear-cut.

Six of the 12 metrics examined showed no demonstrable effect of reduced velocities on invertebrate communities, whereas densities of only the microcrustacea and *O. albiceps* were higher in the reduced flow channels. Our results suggest that effects of both the magnitude and duration of flow reduction are negligible on the invertebrate community within the Kaiapoi River. This observation is similar to findings of other studies examining the effects of low flows on New Zealand invertebrate communities (Collier, 1995; Caruso, 2002; Suren *et al.*, 2003b; Suren & Jowett, 2006) that also found that invertebrate communities were unaffected by low flow conditions. Apart from changes in the dominant taxa (e.g. an increase in microcrustacea in some studies), no taxa were lost from the community. Recent work by Dewson *et al.* (2007a) found the invertebrate community response to severe (>90%) flow reduction can vary among streams and is probably dependent on the taxa that are present. For example, an impacted lowland stream dominated by *P. fluviatilis* showed no community response to flow reduction, while in a small pristine forested stream, total density and percentage of EPT individuals decreased. However, they did not observe a loss of taxa, nor a shift in community composition to one dominated by worms, snails and Chironomidae as popular perception might have one expect (e.g. Ministry for the Environment, 1998; Jowett, 2000).

Our experimental manipulation was done in the Kaiapoi River, typical of many slow-flowing lowland streams affected by agricultural activity and draining the Canterbury Plains. The invertebrate community here was dominated by taxa with low MCI tolerance scores and is thus indicative of a 'probable moderate' to 'probable severe' level of organic pollution (Boothroyd & Stark, 2000). Such pollution tolerant biota may be tolerant of reduced flows, suggesting that these indices are insensitive to flow reduction. The subtle effects of flow reduction on the invertebrate community we observed suggest that the biota of these lowland rivers are unaffected by reduced flows and similar to the findings of Dewson *et al.* (in press) who found that severe flow reduction (>90%) had no effect on the invertebrate community of an agriculturally impacted stream. We therefore suggest that water abstraction from small agricultural streams is unlikely to have a major impact on invertebrate communities.

Wetted perimeter (and thus total habitat area), dissolved oxygen and water temperature remained unchanged by flow reductions in our channels, so we attributed the observed minor changes to the invertebrate community to the experimental decrease in velocity and depth. Changes to depth and velocity can influence other variables, such as rates of sediment deposition and benthic algal biomass. Although increased fine sediment deposition was expected with a decrease in velocity, this was not observed in this study, as there was only a slight increase in the amount of deposited inorganic material in the low flow channels. Chlorophyll-*a* biomass, combined with discharge data best explained changes to the invertebrate community patterns. Of interest was the observation that chlorophyll-*a* concentrations showed a similar, although weak trend which paralleled that of a number of dominant taxa (e.g. Ostracoda, *O. albiceps*, Cladocera), as biomass decreased with velocity after one month of flow reduction then increased after two months. A change in periphyton quantity/quality resulting from reduced velocity probably contributed to the observed change to the invertebrate community (a bottom-up effect).

Use of the hyporheic refuge

As chapter 4 (also James *et al*., (in press)) found in natural stream channels, the vertical distribution of invertebrates in our experimental channels was unaffected by decreased velocities resulting from flow reduction. Throughout the experiment, greater than 85% of total invertebrate abundance was found in the upper basket level (top 7 cm) irrespective of the level of flow reduction. This is high compared to other New Zealand studies that have found only 29-41% in the top 9 cm, 64% in the top 11 cm and 70% in the top 10 cm of sediment samples (Scarsbrook, 1995; Montgomerie, 1997; Adkins & Winterbourn, 1999, respectively) and may reflect channel design, since these other studies were all conducted in natural streambeds. Moreover, any truly hyporheic animals would have been incapable of colonising the channels with their solid bottoms, despite the one year colonisation period. Subsurface conditions were similar throughout the experiment, with temperatures equivalent to those at the surface. Intragravel oxygen levels were also not significantly different between the upper and lowermost baskets.

Previous studies have found silt content to be an important determinant of hyporheic invertebrate community composition and abundance (e.g. Burrell, 2001; Olsen & Townsend, 2003), however, sedimentation of the mid and lower basket levels was not increased by reduced surface velocities. The main observed change to the hyporheic zone was reduced intragravel velocities. This, coupled with the finding of Packman & Salehin (2003) who state that the hyporheic exchange rate is generally proportional to the permeability of sediments and the square of the stream velocity, indicates reduced surface velocities probably resulted in reduced exchange between the upper and lower basket levels in our channels. Thus, the ability of animals to be actively and passively transported to the lower baskets may have declined along with surface velocity. With resources (e.g. periphyton) being concentrated in the upper basket level, surface conditions would need to be dire for invertebrates to seek refuge in the lower baskets. Even though water movement in the 98% reduction channel was barely perceptible, the invertebrates present in our channels preferred the surface where they were able to persist at pre-reduction densities.

Conclusions

While flow reduction appeared to disturb the invertebrate community by initially reducing overall density and causing shifts in the relative abundance of some common taxa, the community as a whole appeared resistant to the effects of even severe flow reduction.

Given this result and that a number of other studies (e.g. Collier, 1995; Caruso, 2002; Suren *et al.*, 2003b; Suren & Jowett 2006; Dewson *et al.*, 2007a) consistently show that New Zealand aquatic invertebrate communities are resistant to the effects of reduced flow, we suggest that setting minimum flows in small rivers on the basis of perceived hydraulic habitat preferences by invertebrates may not be particularly useful. Invertebrates appear to be able to tolerate conditions far below their known hydraulic habitat preferences and can persist through relatively long periods of low flow.

Other factors such as land use and hydrological regime (especially streambed movement) will dictate the nature of the invertebrate community within a stream. Reduced flow in small streams will, at worst, merely result in abundance changes among the common taxa but is unlikely to result in gross changes to community composition (e.g. change from EPT dominated to snail, worm and Chironomidae dominated). However, this assertion is made on the basis of this relatively short-term study in a degraded lowland stream. Our experimental flow reductions represented only what we regard as a relatively harsh summer flow reduction and not a permanent reduction in flow as would occur below a dam or permanent abstraction point. We still strongly advocate the importance of flushing flows to "reset" or cleanse the streambed, and bed-moving flows to help distribute substrate materials throughout a channel. Nevertheless, existing literature is still relatively sparse on this subject and more studies that include multiple components of the biota (i.e. algae, invertebrates, and vertebrates), pre-reduction data, gradients of flow reduction, and contrast different stream types are desperately needed if we are to ensure environmental flow requirements are ecologically relevant and not just calculated by a hydrologist in an office.

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Synthesis

The aim of this thesis was to investigate the impact of severe flow reduction (but not complete drying) on instream habitat condition, macroinvertebrate drift behaviour and usage of the hyporheic zone by benthic macroinvertebrates. This was investigated experimentally in natural stream channels and instream experimental channels. In reviewing the literature (Chapter 1), it became clear that most flow reduction studies were observational and lacked adequate coverage of changes in habitat condition associated with changes in discharge. While obvious and relatively easy to measure variables such as depth, velocity and wetted width were generally well examined in the literature, others such as temperature regime, dissolved oxygen fluctuation and sediment deposition are often neglected. For that reason, there is a clear need for experimental flow reduction studies that involve both a before-after, control-impact (BACI) design and that measure a full suite of habitat condition variables. Previous studies investigating flow reduction impacts on benthic macroinvertebrates often concentrate on density and community composition. Few workers have focussed on behavioural responses such as drift or hyporheic zone usage in the context of a BACI experimental flow reduction.

Severe flow reductions in the natural channels of three small New Zealand streams clearly altered habitat condition (Chapter 2). Along with the predictable decreases of velocity, depth and wetted width, to the best of my knowledge this is the first study showing that flow reduction can lead to reduced dissolved oxygen minima. In addition, contrary to popular belief, flow reduction had minimal effect on water temperature.

These changes to instream habitat condition resulted in behavioural responses by several macroinvertebrate taxa. Immediately after flow reduction, the numbers of some taxa drifting in the water column increased markedly (Chapter 3). This response was greatest in the days immediately following flow reduction, although many taxa displayed some level of elevated drift throughout the reduced flow period. Given the common drift response in all three study streams, it seems that animals enter the drift in response to physical changes as they attempt to redistribute themselves to more suitable microhabitats. It is unclear if animals actively enter the drift or if elevated drift occurs passively, simply because animals are moving around more on the substrate. Additionally, the distance travelled by individuals in the drift is generally less than 5 metres, even in the non-reduced reaches of the study streams. Thus, drift is unlikely to be a successful means of moving significant distances downstream to escape reduced flow conditions in small streams. The observation that flow reduction induces invertebrate drift suggests that benthic macroinvertebrates detect and respond to physical changes in the instream environment.

The hypothesis that invertebrates move deeper into the substrate to avoid unfavourable surface conditions has scarcely been tested, especially in relation to reduced flows in permanently flowing streams. I found no evidence of any change in the abundance or distribution of invertebrates within the hyporheic zone of natural stream channels (Chapter 4) or in the subsurface layers in experimental instream channels (Chapter 5). Furthermore, there was little evidence that animals move to other instream refugia such as pools in response to severe flow reduction (Chapter 4). However, a proportion of the population of many taxa appear to be present within the substrate at any time, providing a source of colonists should some extreme event (i.e. major flood or dry period) denude the surface of animals.

Experimental flow reductions in natural stream channels provide a realistic setting to investigate the impacts of reduced flow on habitat condition and macroinvertebrates. However, it did not allow the effects of flow reduction magnitude to be examined. To this end, a separate experiment in instream channels enabled the effects of flow reduction magnitude to be tested (Chapter 5). The initial focus of this research was on the use of the subsurface layers in response to flow reduction, but as in the natural stream experiment described above, invertebrates showed no inclination to move vertically within the substrate. Thus, I shifted my focus to the impacts of flow reduction duration and magnitude on the total population of animals within the channels. Despite reductions of up to 98%, the only invertebrate changes observed in response to flow reduction were shifts in the relative abundance of some common taxa. In conjunction with other studies, this led to the conclusion that New Zealand stream invertebrates are both resistant and resilient to the impacts of flow reduction.

Flow reduction is an area of increasing importance to water managers. This thesis extends current knowledge in this area by presenting the first BACI examination of the response of habitat condition and aquatic macroinvertebrate behaviour to severe flow reduction in natural stream channels. It also includes one of the few BACI studies investigating the effect of flow reduction magnitude and duration on aquatic invertebrates.