Small stream ecosystems and irrigation: An ecological assessment of water abstraction impacts

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Abstract

Small streams are often used for small-scale water abstractions, but the effects of these water abstractions on the instream environment, invertebrate communities and ecosystem functioning of small permanent streams is poorly understood. This research extends current knowledge by surveying existing water abstractions and completing flow manipulation experiments in the field. Reduced discharge often decreases water velocity, water depth, and wetted channel width and can increase sedimentation, modify the thermal regime and alter water chemistry. In a survey of sites upstream and downstream of existing water abstractions, I found that downstream sites had higher densities of invertebrates, but fewer taxa sensitive to low water quality compared with upstream sites. There were greater differences in physicochemical characteristics such as velocity and conductivity and in invertebrate communities between upstream and downstream sites on streams where a larger proportion of total discharge was abstracted. Using before-after, control-impact (BACI) designed experiments, weirs and diversions were created to experimentally decrease discharge by over 85% in each of three small streams, ranging from pristine to low water quality. The response of invertebrates to short-term (one-month) discharge reduction was to accumulate in the decreased available area, increasing local invertebrate density. After a year of reduced flow, the density of invertebrates and percentage of mayflies, stoneflies and caddisflies decreased at the pristine site, whereas only taxonomic richness decreased at the mildly polluted stream. Reduced discharge had no affect on the invertebrate community at the stream with the lowest water quality. Reduced discharge had little influence on leaf decomposition rates, but distances travelled by released coarse particulate organic matter (CPOM) increased with increasing discharge. The effects of reduced discharge on primary production were not consistent between streams. Overall, the severity (magnitude/duration) of flow reduction appeared to influence invertebrate responses to water abstraction although the outcomes of water abstraction were dependent on the invertebrate assemblage present in each stream.

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This project was possible because of the generosity of the landowners at Kiriwhakapapa Stream and Booths Creek, who allowed weirs and diversions to be installed on their properties, and assisted with the resource consent process. Also, the technical and financial support provided by the Department of Conservation (DOC) and Greater Wellington Regional Council (GW), especially Lindsay Chadderton (DOC) who arranged funding and Matt Rowland (GW) who assisted with the resource consent process and built weirs and diversions for the flow reduction experiments.

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Arrangement of this thesis and note on authorship

The chapters in this thesis were written as manuscripts for publication in refereed journals. This has led to some repetition among the chapters, particularly for the methods. In addition, the numbering of figures, tables and photographic plates restarts for each chapter. Manuscripts are co-authored to acknowledge the contribution of others as appropriate. In particular, the input of my principal supervisor, Russell Death, who contributed to developing the project concept, editing manuscripts, administering project funding and generally discussing the ongoing developments in the project. Also, the contribution of Alex James, fellow PhD student, who simultaneously studied aspects of invertebrate behavioural responses to experimental flow reduction, and so had significant input into the development of the flow reduction experiment. Alex and Russell worked with me to combine two separate literature reviews of individual and population (AJ) and community (ZD) responses to reduced flow into a manuscript suitable for publication. For each of the data chapters, my input was the greatest, I planned the research, undertook fieldwork, analysed data and wrote the manuscripts. The invertebrate drift and refugia usage data used in Chapters 3, 4 and 7 was collected by Alex James and included in these chapters to make them more complete for publication purposes.

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General Introduction

There is an increasing awareness that small stream ecosystems have water requirements (e.g., Baron *et al.* 2002, Richter *et al.* 2003), although there is a shortage of scientific data describing the quantity and timing of water required to protect these ecosystems (Richter 1993). Not only is it necessary to sustain stream ecosystems for ecological reasons, but the maintenance of adequate water quality and quantity ensures the ongoing usefulness of water resources for out of stream uses. However, the increasing size and urbanisation of the human population, along with a continually expanding area of irrigated land are among the factors leading to an increasing global demand for water resources (Postel 1997, Arnell 1999). Increased demand alone would make it more difficult to balance the needs of human society with the requirements of freshwater ecosystems, but changes to climate are expected to complicate matters further. Recent predictions suggest that as well as lowering summer flows, climate change may extend the duration of low flows (Gibson *et al.* 2005), and increase the competition between in and out of stream uses for water (Meyer *et al.* 1999). To manage increasing demands on water resources, we need to improve our understanding of the water requirements of stream ecosystems and the environmental, social and economic costs of water losses from them.

Even in New Zealand, where freshwater availability is among the highest in the world (United Nations 2003), river flow regimes are "one of the most contentious water management issues" (Ministry for the Environment 1998). As well as water withdrawals from large rivers for hydroelectricity and major irrigation schemes, there are many water abstractions from smaller streams for purposes such as domestic water supply and small-scale irrigation. These small-scale water abstractions tend to receive less media attention than major water projects. However, the ecological value of small streams can be high and information about the impacts of flow reduction is particularly scarce for these small streams (Ministry for the Environment 1998). The stress of water abstraction is likely to be greatest during the summer period in New Zealand for several reasons. Many small water abstractions are utilised only through the summer season for irrigation, elevated water temperatures and algal proliferations are more likely at this time, and permitted abstractions can be relatively high as a percentage of total discharge during low flow periods.

Flow influences stream invertebrates by controlling characteristics of the physical habitat (Hart & Finelli 1999, Bunn & Arthington 2002). Water abstraction can alter many aspects of the instream environment, including water velocity and depth (e.g., Minshall & Winger 1968, McIntosh *et al.* 2002), wetted width (e.g., Gore 1977, Cowx *et al.* 1984), sedimentation (e.g., Castella *et al.* 1995, Wood & Armitage 1999), and water temperatures (e.g., Mosley 1983, Rader & Belish 1999). Consequently, flow reduction might initiate changes to the invertebrate community by altering the availability and suitability of habitat for invertebrates. Changes to the instream environment and invertebrate communities with flow reduction might also affect ecosystem functioning. For example, water velocity, sedimentation and water temperature can influence leaf breakdown rates (Webster & Benfield 1986, Royer & Minshall 2003).

To address the lack of information about the impacts of water abstractions on small streams, the goal of this thesis was to investigate the effects of flow reduction (not complete drying) on the instream environment, invertebrate communities and ecosystem functioning in small permanent streams (Table 1). I hypothesised that water abstractions would decrease habitat availability and suitability for invertebrates, resulting in changes to the composition of invertebrate communities to reflect the slower flowing conditions. I also predicted that changes to the physicochemical characteristics of the instream environment would alter the rate of ecosystem processes downstream of these water abstractions. The objectives of this research were to:

- Examine the responses of invertebrate communities to existing water abstractions in an observational study (Chapter 2).
- Create whole stream flow reductions to gain more control over the volume and timing of water abstraction and enable the collection of before and after data at control and impact sites in order to:
    - Assess changes to environmental characteristics and the invertebrate community in response to both short-term flow reduction (Chapter 3), and one year of flow reduction (Chapter 4).
    - Test the effects of reduced flows on ecosystem functioning (Chapter 5).
- Individually assess the effects of decreased water velocity and increased filamentous algae on invertebrates in a small-scale instream channel experiment (Chapter 6).

- Synthesise the findings of this study into an article that communicates the main outcomes of the research to a management audience (Chapter 7).

Table 1. Timeline of research undertaken for this thesis

Timing	**Research activities**
Early to Mid 2003	Observational study of invertebrate communities at sites upstream and downstream of existing water abstractions
Late 2003 to Early 2004	**Short-term (1 month) experimental flow reductions** Pre-diversion sampling: December 2003-March 2004 1 month flow reduction: between March and May 2004 Weirs removed, normal flow restored: May 2004
Late 2004 to Early 2006	**Longer-term (1 year) experimental flow reductions** Pre-diversion sampling: November 2004-January 2005 1 year flow reduction: January 2005-January 2006 Weirs remain in place
Early 2006	Instream channel experiments completed between February and May 2006

References

Arnell N.W. (1999) Climate change and global water resources. *Global Environmental Change*, **9**, S31-S49.

Baron J.S., Poff N.L., Angermeier P.L., Dahm C.N., Gleick P.H., Hairston N.G., Jackson R.B., Johnston C.A., Richter B.D. & Steinman A.D. (2002) Meeting ecological and societal needs for freshwater. *Ecological Applications*, **12**, 1247-1260.

Bunn S.E. & Arthington A.H. (2002) Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, **30**, 492-507.

Castella E., Bickerton M., Armitage P.D. & Petts G.E. (1995) The effects of water abstractions on invertebrate communities in U.K. streams. *Hydrobiologia*, **308**, 167-182.

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

Gibson C.A., Meyer J.L., Poff N.L., Hay L.E. & Georgakakos A. (2005) Flow regime alterations under changing climate in two river basins: implications for freshwater ecosystems. *River Research and Applications*, **21**, 849-864.

Gore J.A. (1977) Reservoir manipulations and benthic macroinvertebrates in a prairie river. *Hydrobiologia*, **55**, 113-123.

Hart D.D. & Finelli C.M. (1999) Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms. *Annual Review of Ecology and Systematics*, **30**, 363-395.

McIntosh M.D., Benbow M.E. & Burky A.J. (2002) Effects of stream diversion on riffle macroinvertebrate communities in a Maui, Hawaii, stream. *River Research and Applications*, **18**, 569-581.

Meyer J.L., Sale M.J., Mulholland P.J. & Poff N.L. (1999) Impacts of climate change on aquatic ecosystem functioning and health. *Journal of the American Water Resources Association*, **35**, 1373-1386.

Ministry for the Environment (1998). *Flow Guidelines for Instream Values. Volume A.* Ministry for the Environment, Wellington, New Zealand.

Minshall G.W. & Winger P.V. (1968) The effect of reduction in stream flow on invertebrate drift. *Ecology*, **49**, 580-582.

Mosley M.P. (1983) Variability of water temperatures in the braided Ashley and Rakaia rivers. *New Zealand Journal of Marine and Freshwater Research*, **17**, 331-342.

Postel S.L. (1997) *Last Oasis.* W.W. Norton & Company, New York, U.S.A.

Rader R.B. & Belish T.A. (1999) Influence of mild to severe flow alterations on invertebrates in three mountain streams. *Regulated Rivers: Research and Management*, **15**, 353-363.

Richter B.D. (1993) Ecosystem-level conservation at the nature conservancy: growing needs for applied research in conservation biology. *Journal of the North American Benthological Society*, **12**, 197-200.

Richter B.D., Mathews R., Harrison D.L. & Wigington R. (2003) Ecologically sustainable water management: managing river flows for ecological integrity. *Ecological Applications*, **13**, 206-224.

Royer T.V. & Minshall G.W. (2003) Controls on leaf processing in streams from spatial-scaling and hierarchical perspectives. *Journal of the North American Benthological Society*, **22**, 352-358.

United Nations/World Water Assessment Programme (2003) *The United Nations World Water Development Report: Water for People, Water for Life.* UNESCO Publishing and Berghahn Books, Paris, New York and Oxford.

Webster J.R. & Benfield E.F. (1986) Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics*, **17**, 567-594.

Wood P.J. & Armitage P.D. (1999) Sediment deposition in a small lowland stream-management implications. *Regulated Rivers: Research and Management*, **15**, 199-210.

CHAPTER 1

The influence of reduced flows on stream invertebrates: a review of the effects on individuals, populations and communities

This chapter has been accepted by the Journal of the North American Benthological Society:

Dewson Z.S., James A.B.W. & Death R.G. (in press) The influence of reduced flows on stream invertebrates: a review of the effects on individuals, populations and communities.

Abstract

Although there have been several reviews of drought effects on stream invertebrates, there has been no similar review of artificially reduced flows. We reviewed the literature on the effects of reduced flows to address this knowledge gap by first considering the effects of reduced water volume on habitat conditions, and then the effects on invertebrate individuals, populations, and communities. Reduced discharge usually results in decreased water velocity, water depth, and wetted channel width. Reduced discharge can also increase sedimentation and modify the thermal regime and water chemistry. Invertebrates differ in their environmental tolerances and requirements, and any loss of habitat area or alteration of food resources with reduced flow can influence invertebrate behaviour and biotic interactions. Invertebrate drift often increases immediately after flow reduction, although some taxa are more responsive to changes in flow than others. Invertebrate abundance increases or decreases in response to reduced flow, whereas invertebrate taxonomic richness commonly decreases along with habitat diversity. Increased sedimentation is often cited as an important habitat change. Natural and artificial flow reductions have similar effects on invertebrates, but the severity (magnitude/duration) of flow reduction influences invertebrate responses. Certain invertebrate taxa are especially sensitive to flow reduction and might be useful indicators of reduced flow impairment or measures of flow restoration success.

Introduction

The sustainable management of rivers and streams to maintain biological integrity in the face of increasing demands for water extraction is becoming increasingly difficult (Baron *et al.* 2002, Poff *et al.* 2003a, Richter *et al.* 2003). There will be even greater challenges for water resource management in the future, as the global distribution of fresh water resources is altered by climate change (Jackson *et al.* 2001). The maintenance of natural flow regimes is often touted as a mechanism for the sustainable management of river ecosystems (Poff *et al.* 1997, Baron *et al.* 2002). Natural flows span a wide range, including periods of low flow resulting from precipitation deficits. Low flows are often seasonal, occurring at a similar time each year (Smakhtin 2001), but human activities may artificially create or extend low flows, causing major deviations from the natural flow regime. The demand for water often peaks during dry periods of the year, when stream flows are naturally low, such 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 indirectly affects them by influencing substrate composition, water chemistry, and the delivery rate of nutrients and food particles (Statzner *et al.* 1988, Alan 1995, Hart & Finelli 1999, Crowder & Diplas 2000). In this way, flow affects habitat availability and suitability for benthic invertebrates (Statzner & Higler 1986, Hart & Finelli 1999).

Assessing how much water a river needs to prevent adverse affects on the environment, while still allowing water abstraction is a task many water resource managers face. However, it remains difficult to predict how the biota will respond to altered flow regimes (Bunn & Arthington 2002). The instream flow incremental method (IFIM) has been used successfully for salmonids, but its application for invertebrates and other fish remains limited (Gore *et al.* 1998, 2001).

Boulton (2003) and Lake (2003) have reviewed the effects of drought on stream invertebrates and fish, highlighting a paucity of information. 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 reduced flows on instream habitat and invertebrates. We adopted a hierarchical approach for this review (Fig. 1), by first considering the effects of reduced water volume on habitat conditions, then the effects of habitat conditions on invertebrates, and finally, how these changes manifest themselves in patterns of benthic community structure.

Our goal was to determine if there are consistent abiotic or biotic changes resulting from natural and artificial flow reductions. We identified features of flow reductions and streams that could influence invertebrate responses to reduced flow (Table 1). We hypothesized that impacts on the invertebrate community would be greatest for continuous, severe artificial flow reductions, because these would alter instream conditions the most and allow little time for recovery between low flows. We expected that some stream types would be more vulnerable to flow reduction than others. For example, streams of higher water quality would be most at risk, because of the predominance of sensitive taxa. We have considered both natural and artificially reduced flows in this review (Table 2), but have excluded studies where the stream channel dried completely, or where the stream is naturally intermittent, since these would have different consequences for invertebrates. Although we did not exclude large rivers and large dams from this review, there is a bias toward smaller streams, because we only included studies where the effects of reduced discharge itself are the focus, rather than other aspects of the altered flow regime.

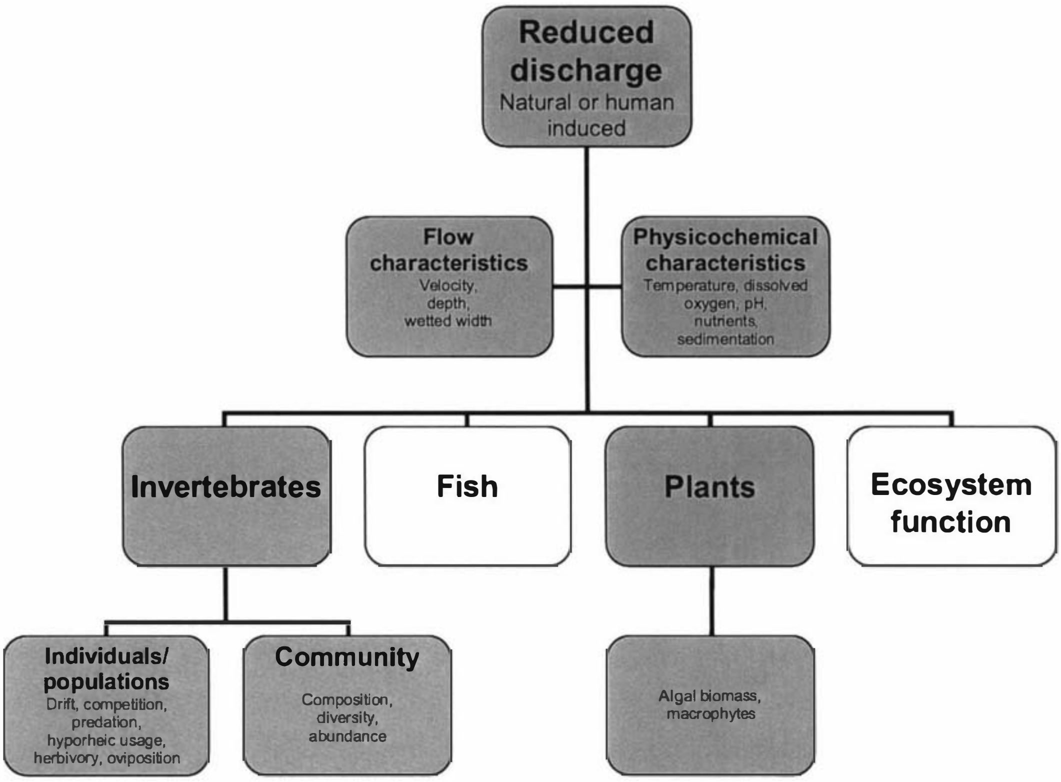

Figure 1. An overview of the factors influenced by flow reductions. Aspects included in this review are shaded grey.

Table 1. Features of flow reduction and stream characteristics predicted to influence the impact of flow reduction on invertebrates.

		Lowest impact	**Highest impact**
Features of flow reduction	Severity	minor	severe (100%)
	Duration and timing	short-term, seasonal	long-term, continuous
	Cause	natural	artificial
Stream characteristics	Habitat diversity	low	high
	Water quality	low	high
	Size	large	small
	Invertebrate assemblage	tolerant taxa	sensitive taxa

Table 2. Summary of the magnitude and duration of low flows investigated using both natural and human-induced flow reductions. Available descriptions of stream size are included for each stream and a range given where more than one stream is studied. Table continued on following page.

	Authors	Stream size or order	Size of discharge reduction	Duration of flow reduction
Natural flow reductions	Caruso 2002	12 streams with mean annual low flow: 0.2-5.5 m^3/s	Various	Four to six month drought
	Cowx *et al.* 1984	Width: 8 m	60% reduction	Three month drought
	Dahm *et al.* 2003	1st order <0.001 m^3/s during drought	Various	Analysis of droughts from long term flow records
	Delucchi 1989	Permanent stream summer discharge: 4-81 L/s	Up to 94% reduction	Summer flow recession
	Extence 1981	Not stated	Not stated	Three month drought
	Suren *et al.* 2003a,b.	Two streams with median discharge: 3.1-4.6 m^3/s	83-89% reduction	Six week summer flow recession
	Wood & Petts 1994 Wood & Petts 1999 Wood *et al.* 2000 Wood & Armitage 2004	Mean discharge: 0.73 m^3/s Width: 1.5-8 m	Various	Long-term studies of drought in a chalk stream
	Wright & Berrie 1987 Wright & Symes 1999 Ham *et al.* 1981	Discharge: 0.5-3.6 m^3/s Width: 7-10 m	Various	Nine year study including a minor and major drought

Table 2 (continued). Summary of the magnitude and duration of low flows investigated using both natural and human-induced flow reductions. Available descriptions of stream size are included for each stream and a range given where more than one stream is studied. Table continued on following page.

	Authors	Stream size or order	Size of discharge reduction	Duration of flow reduction
Human induced flow reductions	Armitage & Petts 1992 Castella *et al.* 1995	22 streams with discharge: 0.13-15 m^3/s Width: 1-40 m	Various	Many years, ongoing
	Bickerton *et al.* 1993	Three streams with discharge: 0.01-0.39 m^3/s Width: 7-10 m	55-100% reduction	Many years, ongoing
	Cazaubon & Giudicelli 1999	Mean discharge: 80-190 m^3/s Width: 33 m	~60% reduction	Many years, ongoing
	Cortes *et al.* 2002	Width: 6-33 m	Various	Many years, ongoing
	Dewson *et al.* 2003	Four streams with mean annual low flow: 0.06-0.24 m^3/s	22-81% reduction	Many years, ongoing
	Gore 1977	Mean discharge: 12.7 m^3/s Width: 30 m	60-87% reduction	Six weeks of reduced flow
	Kinzie *et al.* 2006	2nd-3rd order	Average 83% reduction, but up to 100%	Many years, ongoing
	Malmqvist & Englund 1996 Englund & Malmqvist 1996	52 streams with discharge: 0.5-258 m^3/s	92-99.5% reduction	Many years, ongoing
	McIntosh *et al.* 2002	2nd order	92-97% reduction	Many years, ongoing
	Petts & Bickerton 1994	Width: 1-7 m	100% of glacial meltwater	Dam completed in 1961
	Rader & Belish 1999	Three streams: 2nd-3rd order	Mild: ~25% reduction Severe: nearly 100% reduction	Dammed and diverted since 1957

Table 2 (continued). Summary of the magnitude and duration of low flows investigated using both natural and human-induced flow reductions. Available descriptions of stream size are included for each stream and a range given where more than one stream is studied.

	Authors	Stream size or order	Size of discharge reduction	Duration of flow reduction
Experimental flow reductions	Corrarino & Brusven 1983	Artificial channel width: 6 m	50-95% reduction	Four weeks
	Hinckley & Kennedy 1972 Hooper & Ottey 1988	Base flow: 0.23-0.5 m^3/s Width: 2-3.4 m	30-80% reduction	Weirs and diversions manipulate flow over one week
	Kraft 1972	Summer discharge: ~1 m^3/s	Up to 90% reduction	Three months
	Minshall & Winger 1968	1st order Width: 0.5 m	63-100% reduction	Four days
	Poff & Ward 1991 Poff *et al.* 1991	Autumn discharge: 0.51-0.62 m^3/s	Not stated	Two days
	Ruediger 1980	Artificial channel width: 6 m	50-95% reduction	One to two weeks
	Rutledge *et al.* 1992	Artificial channel width: 3 m	To baseflow of 0.11 m^3/s	Five months

The impact of reduced stream flow on habitat condition

Velocity, depth and wetted width

Reduced discharge typically results in decreases in water velocity, depth and wetted width (Table 3), although there is considerable variation between and within streams, caused by differences in the cross sectional shape of the channel (Larimore *et al.* 1959, Stanley *et al.* 1997, Gippel & Stewardson 1998, Jowett 1998). For example, reduced discharge decreases wetted width in streams with high width to depth ratios, whereas depth decreases in streams with lower width to depth ratios. Reduced water velocity, depth and wetted width result from natural and artificial discharge reductions, including groundwater abstraction (Bickerton *et al.* 1993), water diversion (Minshall & Winger 1968, McIntosh *et al.* 2002, Brasher 2003, Kinzie *et al.* 2006), dam closure (Gore 1977) and drought (Extence 1981, Cowx *et al.* 1984).

Water velocity, depth and wetted width do not always decrease with discharge. Whilst this might often go unreported, several authors have specifically mentioned a lack of change in wetted width, because of its relationship with habitat size. For example, wetted width was unchanged below diversions in headwater streams in the central Rocky Mountains, U.S.A. (Rader & Belish 1999), in an English chalk stream during a major drought (Wright & Symes 1999), and between sites upstream and downstream of water abstractions in New Zealand (Dewson *et al.* 2003).

Decreases in velocity, depth and wetted width tend to develop gradually with the onset of natural low flows, whereas changes can be sudden when damming or water diversions artificially create low flows. For example, Gore (1977) found that the width of the river below the Tongue River Reservoir Dam was reduced from an average of 30 m to just 7 m when the dam was closed, reducing discharge by around 32%. In all cases, a 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 contracts the ecosystem (Stanley *et al.* 1997). The effects of artificial discharge reductions on invertebrate communities could be severe in comparison to natural flow reductions, because of their sudden onset.

Changes to velocity, depth and wetted width could influence invertebrates in a number of ways. These include reducing the available habitat (wetted width), decreasing the delivery rate of dissolved oxygen or suspended material for filter feeders (velocity), or indirectly by altering food resources such as periphyton and coarse particulate organic matter (velocity and depth).

Temperature

The sun, wind, and groundwater are expected to have a greater influence on surface water temperatures at lower discharges. Several researchers suggest that low flows result in increased water temperatures (Riggs 1980, Everard 1996), but few provide empirical evidence. Studies of natural droughts usually find water temperatures increase as discharge decreases (e.g., Cowx *et al.* 1984), but these increases might be confounded by increasing air temperatures. Artificial flow reductions allow temperatures to be measured simultaneously in reduced and unreduced flow reaches, showing that higher temperatures occur in reduced flow reaches of large rivers (Cazaubon & Giudicelli 1999) and small streams (Petts & Bickerton 1994, Rader & Belish 1999). A model by Meier *et al.* (2003) predicted a temperature increase downstream of a diversion in a small Swiss alpine stream. In contrast, some streams become cooler during low flows, reflecting a greater influence of groundwater (Grant 1977, Mosley 1983, Kinzie *et al.* 2006). This effect can be particularly strong in small streams where groundwater contributes a high proportion to total discharge (Grant 1977, Mosley 1983).

Chemical characteristics

The photosynthesis and respiration of algae and macrophytes causes dissolved oxygen concentrations to increase during daylight and decrease at night. Since most measurements of dissolved oxygen are made during the day, minimum oxygen levels that might stress stream biota are rarely recorded. We found no evidence of reduced flow changing dissolved oxygen concentrations in streams (Cazaubon & Giudicelli 1999, Rader & Belish 1999, Caruso 2002) (Table 3).

In rain-fed streams, natural low flows are caused by periods of low precipitation. In an acidic U.K. stream, reduced rainfall was implicated in raising the pH of stream water, because there was less runoff from the surrounding acidic landscape (Woodward *et al.* 2002). Similarly, Caruso (2002) explained lower nutrient levels in New Zealand streams by a lack of storms and runoff during a low flow period. Groundwater can have a greater influence at low flows (natural or artificial) and explains some of the variation found between streams. Dahm *et al.* (2003) attributed decreased nutrient levels to the greater contribution of low nutrient deep groundwater to surface flow. In contrast, greater inputs of solute rich groundwater can lead to increased electrical conductivity (Rader & Belish 1999, Caruso 2002).

Chemical characteristics can directly (e.g., insufficient oxygen) and indirectly (e.g., nutrient affect on periphyton food supply) influence invertebrates during low flows. Therefore, we suggest that the chemical consequences of reduced flow deserve more attention.

Sedimentation

Increased sedimentation is often a consequence of reduced flow (Table 3), because lower velocities allow more sediment to settle out of suspension. Substrate size generally increases with water velocity (Jowett 1992), although within the confines of catchment geology. As stream flow decreases, more suspended fine sediment is deposited over underlying larger substrates (Wright & Berrie 1987, Wood & Petts 1994, Castella *et al.* 1995, Wood & Armitage 1999). As flow recedes with the onset of drought, fine sediment deposition occurs on stream margins, the streambed, and within interstitial spaces (Wood & Petts 1999). If high or flushing flows do not occur, these accumulated fine sediments remain (Bickerton *et al.* 1993, Wood & Petts 1999). Ham *et al.* (1981) found that at low flows, sediment that accumulated within *Ranunculus* beds remained when these macrophyte beds receded. Reduced flow can also decrease sedimentation (Wright & Symes 1999), because suspended sediment levels may decrease (Caruso 2002, Bond 2004). In the absence of storms that would induce runoff and erosion, Caruso (2002) found lower turbidity and sediment supply in southern New Zealand streams during low flow.

Algae and macrophytes

We have considered algae and macrophytes as a habitat and food resource for invertebrates in this review, since invertebrates are our main focus. The flow regime is an important determinant of periphyton development in gravel-bed rivers (Biggs & Close 1989). Water velocity can affect the colonisation, production and loss of periphyton (Biggs & Close 1989, Jowett & Biggs 1997). There is evidence for both positive and negative relationships between velocity and periphyton (McIntire 1966, Poff *et al.* 1990, Biggs & Hickey 1994, Jowett & Biggs 1997). However, these contrasts are probably because of differences between periphyton growth forms in rivers. For instance, dense periphyton can increase with velocity by taking advantage of increased nutrients, whereas filamentous algae will decrease as the sloughing of filaments increases with water velocity (Biggs *et al.* 1998).

The periphyton community typically changes from a low biomass diatom assemblage to a high biomass filamentous green algal community during reduced flows. This is a response to increased temperatures, higher nutrient concentrations, and reduced current velocity (McIntire 1966, Poff *et al.* 1990, Suren *et al.* 2003a) (Table 3). High flows generally scour periphyton, whereas it can proliferate under reduced flow conditions (Biggs 1985, Biggs *et al.* 2005). However, Suren *et al.* (2003a) found that the responses of periphyton to reduced flow differed in rivers of contrasting nutrient enrichment. They measured substantial increases in filamentous algae in a nutrient enriched river, while low biomass diatoms remained dominant during low flows in an un-enriched river. When flow reduction is especially severe, benthic algal biomass can decrease (Kinzie *et al.* 2006).

The accumulation of epiphytic algae on macrophytes in an English chalk stream was responsible for retarding macrophyte growth during low discharge (Ham *et al.* 1981). The effects of reduced flow on macrophytes deserve much more attention, because they are an important habitat for invertebrates.

Table 3. Summary of effects reported for reduced stream flow on habitat condition. Table continued on following page.

	Increase	**No change**	**Decrease**
Velocity			Minshall & Winger 1968 Kraft 1972 Ham *et al.* 1981 Wright & Berrie 1987 Malmqvist & Englund 1996 Bickerton *et al.* 1993 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 and Bickerton 1994 Cazaubon and Giudicelli 1999 Rader and Belish 1999 Meier *et al.* 2003	Kraft 1972 McIntosh *et al.* 2002	Grant 1977 Mosley 1983 Kinzie *et al.* 2006
Dissolved oxygen		Rader and Belish 1999 Cazaubon and Giudicelli 1999 Caruso 2002	
pH	Close and Davis-Colley 1990 Woodward *et al.* 2002	Rader and 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		

Table 3 (continued). Summary of effects reported for reduced stream flow on habitat condition.

	Increase	No change	Decrease
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.* 2003a Biggs *et al.* 2005	Suren *et al.* 2003a	Kinzie *et al.* 2006

Individual and population responses to reduced flows

Invertebrate 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 (Brittain & Eikeland 1988) and may occur actively or passively. During periods of reduced flow, lower water velocities will decrease passive drift, but active drift can increase in response to artificial flow reductions in regulated rivers (Pearson & Franklin 1968, Radford & Hartland-Rowe 1971, Gore 1977) and experimental flow reductions in both natural (Minshall & Winger 1968, Hooper & Ottey 1988, Poff & Ward 1991, Poff *et al.* 1991) and artificial channels (Ruediger 1980, Corrarino & Brusven 1983, Rutledge *et al.* 1992) (Table 4). Invertebrates may drift at low water velocities because flow is insufficient to meet their nutritional or physiological needs (Walton 1980a, Vinikour 1981, Kohler 1985), or to avoid pools (Leudtke & Brusven 1976, Dudgeon 1983, Brittain & Eikeland 1988). Active drift can also result from predator avoidance, which may be enhanced at low flows (Peckarsky 1980, Walton 1980b, Malmqvist & Sjostrom 1987, Kratz 1996).

Invertebrate drift responses to reduced flows differ among taxa. For example, Poff & Ward (1991) observed that reduced flow increased active drift by some taxa (*Baetis* spp., *Epeorus longimanus*, Simuliidae, *Brachycentrus americanus*) and decreased it by other taxa (*Paraleptophlebia heteronea*, *Ephemerella infrequens*, *Triznaka signata*, *Lepidostoma ormea*). They also found that some taxa drift passively, increasing drift densities with flow increases and decreasing at reduced flows. Hooper & Ottey (1988) found that the drift rates of many taxa (*Simulium* sp. in particular) increased when they experimentally decreased discharge at night. Similarly, when there was a sudden reduction in discharge following the closure of the Tongue River Dam (Montana, U.S.A.), invertebrate drift increased ten-fold (Gore 1977). The propensity for *Rhithrogena hageni* to drift in response to this flow reduction prompted Gore (1977) to recommend this mayfly as an indicator of adequate stream flow conditions.

Refugia use

The hyporheic zone (the interface between surface and ground waters) can be a refuge for benthic fauna when surface conditions become unfavourable (e.g., Williams & Hynes 1974, Boulton *et al.* 1998). For example, taxa may actively move into the hyporheic zone if it provides a thermal refuge under low flow conditions. Hyporheic water is often cooler than surface water because of the high groundwater content and the insulative properties of the substrate (Evans & Petts 1997). However, Gilpin & Brusven (1976) found no difference in the abundance of invertebrates colonising hyporheic chambers between sections of a stream with either normal or reduced flow. Ruediger (1980) also found that the vertical distribution of benthic invertebrates within experimental channels was unaffected by surface flow reductions, and Delucchi (1989) found little vertical movement of invertebrates in the substrate of a permanent stream as flow decreased. These studies suggest that the hyporheic zone is not used as an invertebrate refuge in permanent streams (Table 4).

There is considerable literature on the use of pools and the hyporheic zone as refuges in response to flow reduction, but these studies predominantly consider intermittent or temporary streams (e.g., Boulton 1989, Delucchi 1989). Clearly, the importance of these habitats as refugia will increase if streams dry completely. However, more studies of permanent streams are required to determine whether pools and the hyporheic zone provide an escape from harsh conditions during low flows.

Oviposition behaviour

Recent studies have shown 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). Therefore, reduced flow may increase the availability of oviposition sites (Table 4), although the influence of reduced flow will depend on species-specific oviposition preferences. A decrease in suitable oviposition sites was probably responsible for decreases in insect abundance following a drought in a Welsh stream (Cowx *et al.* 1984). The impact of changes in oviposition behaviour caused by reduced flow on invertebrate dispersal and population dynamics is unknown. As well as changing the availability of oviposition sites, reduced flow can alter sedimentation, dissolved oxygen levels, and temperature regimes. The effects of these changes on oviposition behaviour and egg survival are also unknown. The effect of flow reduction on oviposition has long-term implications for invertebrate populations and deserves more attention.

Predation and competition

The contraction of wetted width with flow reduction can result in increased densities of invertebrates and could lead to greater predation and competition (Table 4). Extence (1981) found increased predator numbers following a severe drought and thought that this was the result of increased prey density. Where the velocity preferences of prey and predators differ, reduced velocities could also remove velocity mediated predation refugia. Prey densities have been shown to decrease when the hydraulic regime was favourable to the predator (Peckarsky *et al.* 1990). Larval black flies (*Simulium vittatum*) and predatory triclad flatworms (*Dugesia dorotocephala*) have contrasting current velocity preferences (Hansen *et al.* 1991). The majority of encounters between the flatworms and their larvae prey occurred in slower regions of laboratory flow chambers where predation efficiency was greatest. The authors attributed this phenomenon to hydro-mechanical constraints on prey handling ability. The black fly (*Simulium ornatum*) appears to select microhabitats with high current velocities despite a reduction in feeding efficiency to ease stonefly predation (Malmqvist & Sackmann 1996). Zhang *et al.* (1998) found that simuliid larvae have greater species richness and abundance than predicted at low flow sites and attributed this to lower densities of predators and less competition.

Water velocity controls the rate of food delivery for filter feeders (Nowell & Jumars 1984). For this reason, hydropsychid caddisfly larvae tend to aggregate in high velocity water, where feeding rates are higher (Georgian & Thorp 1992). Larvae may react to flow reduction by moving to zones of more rapid flow (Edington 1965), thereby increasing densities, and hence competition for space and food. At low velocities, individuals of *Hydropsyche morosa* are less tolerant of conspecifics, possibly because of reduced food delivery rates (Matczak & Mackay 1990). Reduced flow can increase or decrease the relative importance of biotic interactions for stream invertebrates, depending on the life histories and habitat preferences of the taxa involved.

Grazer-periphyton interactions

The use of algal resources by grazers is constrained by water velocity (Poff & Ward 1992). Water velocity can influence the foraging efficiency of grazers, and their role in structuring algal assemblages. For example, in a Michigan stream, *Cladophora* (macroalgae) is only present at water velocities > 50 cm/s, because the foraging of the crayfish *Orconectes propinquus* (a major herbivore) is impaired at those velocities (Hart 1992). Similarly, at low velocities, *Agapetus boulderensis* (grazing caddisfly) lowers periphyton biomass and alters the structure of the algal assemblage, but at higher velocities, they only decrease algal biomass (Poff & Ward 1995). The effect that water velocity has on grazing efficiency is species specific. Poff *et al.* (2003b) showed that a caddisfly (*Glossosoma verdona*) was a more effective grazer at higher velocities, whereas the grazing 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, the drift of *Helicopsyche borealis* is greater when periphyton levels are low, whereas at high velocities, there is no relationship between drift and the level of periphyton (Vaughn 1986).

Table 4. Summary of effects reported for reduced stream flow on invertebrate individuals and populations.

	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	
Oviposition opportunities	Peckarsky *et al.* 2000 Reich 2004		Cowx *et al.* 1984
Predation	Extence 1981 Malmqvist & Sackmann 1996		Zhang *et al.* 1998
Competition	Matczak & Mackay 1990		Zhang *et al.* 1998

Community responses to reduced flows

Invertebrate taxonomic richness

Reduced flows often result in reduced taxonomic richness in permanent streams (Table 5). Some studies attribute these losses of richness to a loss of habitat types during reduced flows (Cazaubon & Giudicelli 1999, McIntosh *et al.* 2002). If habitat diversity is retained under extreme low flow conditions then the reduction in species richness may be modest (Wood & Petts 1999). In a comparison of macroinvertebrate communities above and below a diversion in a Hawaiian stream, McIntosh *et al.* (2002) found a reduction in the number of taxa when downstream flow was reduced by 92-97% during summer. In particular, taxa preferring fast flowing cascade habitats were lost because these habitats were lost downstream of the diversion. In a large regulated river in France, Cazaubon & Giudicelli (1999) found that benthic invertebrate communities had fewer taxa than similar unregulated rivers. They concluded that the loss of braided channel habitats was responsible. The importance of habitat diversity is reinforced by studies comparing multiple streams. Armitage & Petts (1992) found that water abstraction generally degraded the fauna of upland streams in the U.K. less than small lowland streams. They attributed this difference to the retention of a diverse range of suitable microhabitats in the reduced channel area of upland streams following water abstraction and the abundance of tributaries to facilitate recolonisation. The effects of flow reduction can also vary between habitats. In a perennial section of a U.K. 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 the instream environment, such as increased water temperature, increased sedimentation, and altered periphyton assemblages may be responsible for changes in taxonomic richness with reduced flow. For example, Cazaubon & Giudicelli (1999) suggest that higher summer water temperatures and annual temperature ranges contribute to lower invertebrate richness. Wood & Armitage (1999) suggested that their study site had low richness compared to other English lowland streams because sediments gradually covered gravel surfaces as flow declined in the small gravel bed stream. In the same stream, Wood *et al.* (2000) found that species richness generally increased with increased flow over a six-year period. During this time, taxa with preferences for lower flow velocities and fine sediments characterized sites during drought years, whereas taxa with preferences for high velocities and gravel substrate characterized sites during years without drought. In a comparative study, Englund & Malmqvist (1996) concluded that reduced food supply for grazing invertebrates at sites with reduced flow was responsible for lower species richness.

Changes to invertebrate taxonomic richness with reduced flow can often be explained by either changes in habitat diversity or changes in instream conditions. Consequently, channel morphology can have a major influence on invertebrate community responses to flow reduction. A uniform section of stream probably maintains its range of habitats during extreme flow reductions, while sections that are more diverse are likely to lose a greater proportion of the habitat types that are available during higher flows (Wood & Petts 1994). In addition, the severity of flow reduction will influence invertebrate responses, because it affects both the amount of habitat lost and the magnitude of change in instream conditions. In severely diverted (almost 100% of flow diverted for 10-11 months) headwater streams of the central Rocky Mountains, U.S.A., Rader & Belish (1999) found reduced invertebrate richness; but in similar streams with only mild flow alteration (25% of flow diverted for 5 months) they observed no change in richness. Similarly, Castella *et al.* (1995) found that minor abstractions generally had less effect on biota than major abstractions.

Invertebrate density

Decreased invertebrate densities can result from both natural and artificially reduced flows (Table 5). For example, reduced flow sites on large regulated rivers had low invertebrate densities in comparison to 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 decreased density was a result of changes in competition and predation, because habitat area decreased and food quality and quantity were altered by flow reduction. Decreased habitat area might also be responsible for decreased invertebrate densities during natural low flows in small streams (Cowx *et al.* 1984, Wood *et al.* 2000).

Benthic invertebrate density can also increase when flows reduce (Table 5). Reduced wetted area can sometimes explain these increases in density, because individuals are concentrated into a smaller area (Gore 1977, Wright & Berrie 1987). Other studies suggest that changes in habitat suitability or food resources are responsible for increased densities, because in these studies, wetted width does not decrease with discharge (Wright & Symes 1999, Dewson *et al.* 2003).

Studies that report contrasting responses to flow reduction provide some insight into the factors influencing invertebrate responses to flow reduction (e.g., Armitage & Petts 1992, Rader & Belish 1999, Suren *et al.* 2003). Food resources such as algae and organic matter might be especially influential on invertebrate density (Hart & Finelli 1999, Smakhtin 2001). Suren *et al.* (2003a) illustrate this in a comparison of invertebrate densities in two New Zealand rivers of contrasting nutrient enrichment. With increases in filamentous green algae in the high enrichment river, there were significant increases in invertebrate density during summer low flows. In contrast, a diatom dominated periphyton assemblage in the low enrichment river supported a stable invertebrate community (Suren *et al.* 2003a). The composition of the invertebrate community will also have an influence on changes in density, because changes in habitat suitability affect each taxon differently. For example, when fine sediments accumulated in a small English chalk stream during a drought, the density of *Sialis* *lutaria* (alder fly larvae) increased, while the density of *Gammarus pulex* (amphipod) decreased (Wood & Petts 1994). Again, the severity of flow reduction influences invertebrate density responses to flow reduction. Rader & Belish (1999) observed that mean invertebrate densities increased by 57% downstream of mild diversions, whereas there was a 50% reduction in invertebrate density where diversions were severe.

Invertebrate community composition

Invertebrate community composition often changes in response to flow reduction (Table 6). These changes probably result from increases in habitat suitability for some species, and decreased suitability for others (Gore *et al.* 2001). Reduced flows should favour taxa that prefer slower water velocities (Jowett 1997). For instance, Cortes *et al.* (2002) found that invertebrate assemblages at regulated sites were generally more tolerant to stresses such as oxygen depletion, preferred slower flowing water, and had shorter life cycles compared to assemblages at unregulated sites. Sediment accumulation also influences habitat suitability for invertebrates. Wright & Berrie (1987) found that increased sedimentation and a loss of macrophytes were responsible for changes in macroinvertebrate community composition during a drought. Castella *et al.* (1995) also identified reduced macrophyte cover and increased sedimentation as important factors contributing to invertebrate community changes with water abstraction. In a Hawaiian stream, even though taxa preferring fast flowing cascade habitats were lost downstream of a diversion, the relative abundances of other taxa were unchanged, because all dominant taxa decreased in density (McIntosh *et al.* 2002).

Table 5. Summary of effects reported for reduced stream flow on invertebrate taxonomic richness and density.

	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
Density	Gore 1977 Extence 1981 Wright & Berrie 1987 Rader & Belish 1999 Wright & Symes 1999 Dewson *et al.* 2003 Suren *et al.* 2003b	Cortes *et al.* 2002 Suren *et al.* 2003b	Cowx *et al.* 1984 Hooper & Ottey 1988 Wood & Petts 1994 Englund & Malmqvist 1996 Malmqvist & Englund 1996 Cazaubon & Giudicelli 1999 Rader & Belish 1999 Wood & Petts 1999 Wood *et al.* 2000 McIntosh *et al.* 2002 Wood & Armitage 2004 Kinzie *et al.* 2006

Table 6. Summary of studies that have reported changes to invertebrate community species composition in response to reduced stream flow.

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

Conclusion

Periods of reduced flow are an integral part of the natural flow regime (Humphries & Baldwin 2003) and may be important in the maintenance of freshwater ecosystem diversity (Wood *et al.* 2000, Humphries & Baldwin 2003). However, increasing water resource development may seriously impact river ecosystems, especially when it coincides with natural low flow periods (Wood *et al.* 2000).

In completing this review, it became apparent that while the literature explaining the definition of, potential problems associated with, and expected responses of streams to reduced flows is voluminous, there are relatively few empirical studies of the influence of reduced flows on abiotic and biotic factors in permanent streams. Most studies show that velocity, depth and wetted width decrease with flow reduction, whereas sedimentation and filamentous algal biomass typically increase with reduced flows. Changes to temperature and water chemistry tend to be variable and reflect the relative contribution of groundwater and runoff into streams. We found no evidence that dissolved oxygen decreases with reduced flow, although studies of reduced flow frequently omit this variable. In our opinion, dissolved oxygen responses to reduced flows require more consideration.

Invertebrate drift consistently increased immediately after flow reduction, although some taxa are clearly more responsive to changes in flow than others. Literature on the use of refugia by invertebrates during low flow in permanent streams and the importance of biotic interactions with flow reduction is scarce. However, it appears that benthic invertebrates do not use the hyporheic zone as a refuge during low flow in permanent streams.

Decreases in invertebrate taxonomic richness with flow reduction are common, and often related to decreases in habitat diversity at reduced flow sites. Increased sedimentation has an important influence in many cases. Invertebrate abundance can increase or decrease in response to reduced flow. The direction of this response might rely on changes in periphyton, sedimentation, and wetted width within the stream, but the severity of flow reduction seems to have an overriding influence on both invertebrate abundance and richness.

The responses of certain invertebrate taxa to flow reduction suggest that invertebrates might be useful as indicators in assessments of reduced flow impacts or as a measure of the success of flow restoration. Furthermore, it should be possible to identify taxa that are sensitive to flow reduction. For example, those that drift when flow changes, those that are affected by sedimentation, or those that have specific velocity requirements.

The evaluation of our predictions (Table 1) against the published literature highlights areas where more research is needed. Natural and artificial flow reductions appear not to have markedly different effects on invertebrates, whereas the severity of the flow reduction has an important influence on invertebrate responses by determining the magnitude of changes to important features of the environment such as habitat diversity, sedimentation, and periphyton food supply. Flow reduction has more impact on streams where habitat diversity is lost and where habitat conditions change the most. There are significant gaps remaining in our knowledge, including:

1. the effects of duration and timing of flow reductions; e.g., do longer flow reductions have more impact on invertebrates than short-term flow reductions?
2. how water quality and land use alter responses to flow reduction. Comparative studies are required and should include detailed measurements of habitat characteristics such as dissolved oxygen and periphyton community.
3. whether stream size and morphology influence responses to flow reduction; e.g., does taking 80% of discharge from a 1 m^3/s river differ from taking 80% from a 100 m^3/s river?

We suggest that experimental manipulations of flow, or studies comparing different flow reduction regimes could address these gaps.

References

Allan J.D. (1995) *Stream Ecology: Structure and Function of Running Waters.* 1st edn. Chapman & Hall, London.

Armitage P.D. & Petts G.E. (1992) Biotic score and prediction to assess the effects of water abstractions on river macroinvertebrates for conservation purposes. *Aquatic Conservation: Marine and Freshwater Ecosystems,* **2,** 1-17.

Baron J.S., Poff N.L., Angermeier P.L., Dahm C.N., Gleick P.H., Hairston N.G.J., Jackson R.B., Johnston C.A., Richter B.D. & Steinman A.D. (2002) Meeting ecological and societal needs for freshwater. *Ecological Applications,* **12,** 1247-1260.

Bickerton M., Petts G.E., Armitage P.D. & Castella E. (1993) Assessing the ecological effects of groundwater abstraction on chalk streams: three examples from eastern England. *Regulated Rivers: Research and Management*, **8,** 121-134.

Biggs B.J.F. (1985) Algae - a blooming nuisance in rivers. *Soil and Water,* **2,** 27-31.

Biggs B.J.F. & Close M.E. (1989) Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients. *Freshwater Biology,* **22,** 209-231.

Biggs B.J.F. & Hickey C.W. (1994) Periphyton responses to a hydraulic gradient in a regulated river in New Zealand. *Freshwater Biology*, **32**, 49-59.

Biggs B.J.F., Goring D.G. & Nikora V.I. (1998) Subsidy and stress responses of stream periphyton to gradients in water velocity as a function of community growth form. *Journal of Phycology,* **34,** 598-607.

Biggs B.J.F., Nikora V.I. & Snelder T.H. (2005) Linking scales of flow variability to lotic ecosystem structure and function. *River Research and Applications,* **21,** 283-298.

Bond N.R. (2004) Spatial variation in fine sediment transport in small upland streams: the effects of flow regulation and catchment geology. *River Research and Applications,* **20,** 705-717.

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

Boulton A.J. (2003) Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. *Freshwater Biology,* **48,** 1173-1185.

Boulton A.J., Findlay S., Marmonier P., Stanley E.H. & Valett H.M. (1998) The functional significance of the hyporheic zone in stream and rivers. *Annual Review of Ecology and Systematics,* **29,** 59-81.

Brasher A.M.D. (2003) Impacts of human disturbances on biotic communities in Hawaiian streams. *BioScience,* **53,** 1052-1060.

Brittain J.E. & Eikeland T.J. (1988) Invertebrate drift - a review. *Hydrobiologia,* **166,** 77-93.

Bunn S.E. & Arthington A.H. (2002) Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management,* **30,** 492-507.

Caruso B.S. (2002) Temporal and spatial patterns of extreme low flows and effects on stream ecosystems in Otago, New Zealand. *Journal of Hydrology,* **257,** 115-133.

Castella E., Bickerton M., Armitage P.D. & Petts G.E. (1995) The effects of water abstractions on invertebrate communities in UK streams. *Hydrobiologia,* **308,** 167-182.

Cazaubon A. & Giudicelli J. (1999) Impact of the residual flow on the physical characteristics and benthic community (algae, invertebrates) of a regulated Mediterranean river: the Durance, France. *Regulated Rivers: Research and Management,* **15,** 441-461.

Close M.E. & Davies-Colley R.J. (1990) Baseflow water chemistry in New Zealand rivers 2. Influence of environmental factors. *New Zealand Journal of Marine and Freshwater Research,* **24,** 343-356.

Corrarino C.A. & Brusven M.A. (1983) The effects of reduced stream discharge on insect drift and stranding of near shore insects. *Freshwater Invertebrate Biology,* **2,** 88-98.

Cortes R.M.V., Ferreira M.T., Oliveira S.V. & Oliveira D. (2002) Macroinvertebrate community structure in a regulated river segment with different flow conditions. *River Research and Applications,* **18,** 367-382.

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

Crowder D.W. & Diplas P. (2000) Using two-dimensional hydrodynamic models at scales of ecological importance. *Journal of Hydrology,* **230,** 172-191.

Dahm C.D., Baker M.A., Moore D.I. & Thibault J.R. (2003) Coupled biogeochemical and hydrological responses of streams and rivers to drought. *Freshwater Biology,* **48,** 1219-1231.

Delucchi C.M. (1989) Movement patterns of invertebrates in temporary and permanent streams. *Oecologia,* **78,** 199-207.

Dewson Z.S., Death R.G. & James A.B.W. (2003) The effect of water abstractions on invertebrate communities in four small North Island streams. *New Zealand Natural Sciences,* **28,** 51-65.

Dudgeon D. (1983) An investigation of the drift of aquatic insects in Tai Po Kau forest stream, New Territories, Hong Kong. *Archiv für Hydrobiologie,* **96,** 434-447.

Edington J.M. (1965) The effect of water flow on populations of net-spinning Trichoptera. *Mitteilungen Internationale Vereinigung für Theoretische und Angewandte Limnologie,* **13,** 40-48.

Englund G. & Malmqvist B. (1996) Effects of flow regulation, habitat area and isolation on the macroinvertebrate fauna of rapids in north Swedish rivers. *Regulated Rivers: Research and Management,* **12,** 433-445.

Evans E.C. & Petts G.E. (1997) Hyporheic temperature patterns within riffles. *Hydrological Sciences - Journal - des Sciences Hydrologiques,* **42,** 199-213.

Everard M. (1996) The importance of periodic droughts for maintaining diversity in the freshwater environment. *Freshwater Forum,* **7,** 33-50.

Extence C.A. (1981) The effect of drought on benthic invertebrate communities in a lowland river. *Hydrobiologia,* **83,** 217-224.

Gasith A. & Resh V.H. (1999) Streams in Mediterranean climate regions: abiotic influences and biotic responses to predictable seasonal events. *Annual Review of Ecology and Systematics,* **30,** 51-81.

Georgian T. & Thorp J.H. (1992) Effects of microhabitat selections on feeding rates of net-spinning caddisfly larvae. *Ecology,* **73,** 229-240.

Gilpin B.R. & Brusven M.A. (1976) Subsurface sampler for determining the vertical distribution of stream-bed benthos. *The Progressive Fish-Culturist,* **38,** 192-194.

Gippel C.J. & Stewardson M.J. (1998) Use of wetted perimeter in defining minimum environmental flows. *Regulated Rivers: Research and Management,* **14,** 53-67.

Gore J.A. (1977) Reservoir manipulations and benthic macroinvertebrates in a prairie river. *Hydrobiologia,* **55,** 113-123.

Gore J.A., Crawford D.J. & Addison D.S. (1998) An analysis of artificial riffles and enhancement of benthic community diversity by physical habitat simulation (PHABSIM) and direct observation. *Regulated Rivers: Research and Management,* **14,** 69-77.

Gore J.A., Layzer J.B. & Mead J. (2001) Macroinvertebrate instream flow studies after 20 years: a role in stream management and restoration. *Regulated Rivers: Research and Management,* **17,** 527-542.

Grant P.J. (1977) Water temperatures of the Ngaruroro River at three stations. *Journal of Hydrology (N.Z),* **16,**148-157.

Ham S.F., Wright J.F. & Berrie A.D. (1981) Growth and recession of aquatic macrophytes on an unshaded section of the River Lambourn, England, from 1971 to 1976. *Freshwater Biology,* **11,** 381-390.

Hansen R.A., Hart D.D. & Merz R.A. (1991) Flow mediates predator-prey interactions between triclad flatworms and larval black flies. *Oikos,* **60,** 187-196.

Hart D.D. (1992) Community organization in streams: the importance of species interactions, physical factors and chance. *Oecologia,* **91,** 220-228.

Hart D.D. & Finelli C.M. (1999) Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms. *Annual Review of Ecology and Systematics,* **30,** 363-395.

Hinckley T.M. & Kennedy H.D. (1972) Fluctuations of aquatic and terrestrial invertebrates in drift samples from Convict Creek, California. *Northwest Science,* **46,** 270-276.

Hooper F.F. & Ottey D.R. (1988) Responses of macroinvertebrates of two headwater streams to discharge fluctuations. *Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie,* **23,** 1159-1166.

Humphries P. & Baldwin D.S. (2003) Drought and aquatic ecosystems: an introduction. *Freshwater Biology,* **48,** 1141-1146.

Jackson R.B., Carpenter S.R., Dahm C.N., McKnight D.M., Naiman R.J., Postel S.L. & Running S.W. (2001) Water in a changing world. *Ecological Applications,* **11,** 1027-1045.

Jowett I.G. (1992) River hydraulics and instream habitat modeling for river biota. In: *Waters of New Zealand* (Ed M.P. Mosley), pp. 249-263. New Zealand Hydrological Society, The Caxton Press, Christchurch, New Zealand.

Jowett I.G. (1997) Environmental effects of extreme flows. In: *Floods and Droughts: the New Zealand Experience.* (Eds M.P. Mosley & C.P. Pearson), pp. 104-116. The Caxton Press, Christchurch, New Zealand.

Jowett I.G. (1998) Hydraulic geometry of New Zealand rivers and its use as a preliminary method of habitat assessment. *Regulated Rivers: Research and Management,* **14,** 451-466.

Jowett I.G. & Biggs B.J.F. (1997) Flood and velocity effects on periphyton and silt accumulation in two New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research,* **31,** 287-300.

Kinzie R.A.I., Chong C., Devrell J., Lindstrom D. & Wolff R. (2006) Effects of water removal on a Hawaiian stream ecosystem. *Pacific Science,* **60,** 1-47.

Kohler S.L. (1985) Identification of stream drift mechanisms: an experimental and observational approach. *Ecology,* **66,** 1749-1761.

Kraft M.E. (1972) Effects of controlled flow reduction on a trout stream. *Journal of the Fisheries Research Board of Canada,* **29,** 1405-1411.

Kratz K.W. (1996) Effects of stoneflies on local prey populations: mechanisms of impact across prey density. *Ecology,* **77,** 1573-1585.

Lake P.S. (2003) Ecological effects of perturbation by drought in flowing waters. *Freshwater Biology,* **48,** 1161-1172.

Larimore R.W., Childers W.F. & Heckrotte C. (1959) Destruction and re-establishment of stream fish and invertebrates affected by drought. *Transactions of the American Fisheries Society,* **88,** 261-285.

Luedtke R.J. & Brusven M.A. (1976) Effects of sand sedimentation on colonization of stream insects. *Journal of the Fisheries Research Board of Canada,* **33,** 1881-1886.

Malmqvist B. & Englund G. (1996) Effects of hydropower-induced flow perturbations on mayfly (Ephemeroptera) richness and abundance in north Swedish river rapids. *Hydrobiologia,* **341,** 145-158.

Malmqvist B. & Sackmann G. (1996) Changing risk of predation for a filter-feeding insect along a current velocity gradient. *Oecologia,* **108,** 450-458.

Malmqvist B. & Sjostrom P. (1987) Stream drift as a consequence of disturbance by invertebrate predators - field and laboratory experiments. *Oecologia,* **74,** 396-403.

Matczak T.D. & Mackay R.J. (1990) Territoriality in filter-feeding caddisfly larvae: laboratory experiments. *Journal of the North American Benthological Society,* **9,** 26-34.

McIntire C.D. (1966) Some effects of current velocity on periphyton communities in laboratory streams. *Hydrobiologia,* **27,** 559-570.

McIntosh M.D., Benbow M.E. & Burky A.J. (2002) Effects of stream diversion on riffle macroinvertebrate communities in a Maui, Hawaii, stream. *River Research and Applications,* **18,** 569-581.

Meier W., Bonjour C., Wüest A. & Reichert P. (2003) Modeling the effect of water diversion on the temperature of mountain streams. *Journal of Environmental Engineering,* **129,** 755-764.

Minshall G.W. & Winger P.V. (1968) The effect of reduction in stream flow on invertebrate drift. *Ecology,* **49,** 580-582.

Mosley M.P. (1983) Variability of water temperatures in the braided Ashley and Rakaia rivers. *New Zealand Journal of Marine and Freshwater Research,* **17,** 331-342.

Nowell A.R.M. & Jumars P.A. (1984) Flow environments of aquatic benthos. *Annual Review of Ecology and Systematics,* **15,** 303-328.

Pearson W.D. & Franklin D.R. (1968) Some factors affecting drift rates of *Baetis* and Simuliidae in a large river. *Ecology,* **49,** 75-81.

Peckarsky B.L. (1980) Predator-prey interactions between stoneflies and mayflies: behavioral observations. *Ecology,* **61,** 932-943.

Peckarsky B.L., Horn S.C. & Statzner B. (1990) Stonefly predation along a hydraulic gradient: a field test of the harsh-benign hypothesis. *Freshwater Biology,* **24,** 181-191.

Peckarsky B.L., Taylor B.W. & Caudill C.C. (2000) Hydrologic and behavioural constraints on oviposition of stream insects: implications for adult dispersal. *Oecologia,* **125,** 186-200.

Petts G.E. & Bickerton M.A. (1994) Influence of water abstraction on the macroinvertebrate community gradient within a glacial stream system: La Borgne d'Arolla, Valais, Switzerland. *Freshwater Biology,* **32,** 375-386.

Poff N.L., Allan J.D., Bain M.B., Karr J.R., Prestegaard K.L., Richter B.D., Sparks R.E. & Stromberg J.C. (1997) The natural flow regime - a paradigm for river conservation and restoration. *BioScience,* **47,** 769-784.

Poff N.L., Allan J.D., Palmer M.A., Hart D.D., Richter B.D., Arthington A.H., Rogers K.H., Meyer J.L. & Stanford J.A. (2003a) River flows and water wars: emerging science for environmental decision making. *Frontiers in Ecology and the Environment,* **1,** 298-306.

Poff N.L., DeCino R.D. & Ward J.V. (1991) Size-dependent drift responses of mayflies to experimental hydrologic variation: active predator avoidance or passive hydrodynamic displacement? *Oecologia,* **88,** 577-586.

Poff N.L., Voelz N.J., Ward J.V. & Lee R.E. (1990) Algal colonization under four experimentally-controlled current regimes in a high mountain stream. *Journal of the North American Benthological Society,* **9,** 303-318.

Poff N.L. & Ward J.V. (1991) Drift responses of benthic invertebrates to experimental streamflow variation in a hydrologically stable stream. *Canadian Journal of Fisheries and Aquatic Sciences,* **48,** 1926-1936.

Poff N.L. & Ward J.V. (1992) Heterogenous currents and algal resources mediate in situ foraging activity of a mobile stream grazer. *Oikos,* **65,** 465-478.

Poff N.L. & Ward J.V. (1995) Herbivory under different flow regimes: a field experiment and test of a model with a benthic stream insect. *Oikos,* **71,** 179-188.

Poff N.L., Wellnitz T. & Monroe J.B. (2003b) Redundancy among three herbivorous insects across an experimental current velocity gradient. *Oecologia,* **134,** 262-269.

Rader R.B. & Belish T.A. (1999) Influence of mild to severe flow alterations on invertebrates in three mountain streams. *Regulated Rivers: Research and Management,* **15,** 353-363.

Radford D.S. & Hartland-Rowe R. (1971) A preliminary investigation of bottom fauna and invertebrate drift in an unregulated and a regulated stream in Alberta. *Journal of Applied Ecology,* **8,** 883-903.

Reich P. (2004) Patterns of composition and abundance in macroinvertebrate egg masses from temperate Australian streams. *Marine and Freshwater Research,* **55,** 39-56.

Richter B.D., Mathews R., Harrison D.L. & Wigington R. (2003) Ecologically sustainable water management: managing river flows for ecological integrity. *Ecological Applications,* **13,** 206-224.

Riggs H.C. (1980) Characteristics of low flows. *Journal of Hydrologic Engineering,* **106,** 717-731.

Ruediger R.A. (1980) *Response of Aquatic Macroinvertebrates to Increments of Reduced Stream Discharge.* MSc thesis, University of Idaho, U.S.A.

Rutledge M.J., Graybill J.P., Kilpatrick J.F. & Kelso J.R.M. (1992) *Effect of Artificial Freshes in Experimental Channels on Benthic Macroinvertebrate Density and Drift and on Quinnat Salmon Growth.* New Zealand Freshwater Research Report No.1., Freshwater Division, NIWAR, Christchurch, New Zealand.

Smakhtin V.U. (2001) Low flow hydrology: a review. *Journal of Hydrology,* **240,** 147-186.

Stanley E.H., Fisher S.G. & Grimm N.B. (1997) Ecosystem expansion and contraction in streams - desert streams vary in both space and time and fluctuate dramatically in size. *BioScience,* **47,** 427-435.

Statzner B., Gore J.A. & Resh V.H. (1988) Hydraulic stream ecology - observed patterns and potential applications. *Journal of the North American Benthological Society,* **7,** 307-360.

Statzner B. & Higler B. (1986) Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. *Freshwater Biology,* **16,** 127-139.

Suren A.M., Biggs B.J.F., Kilroy C. & Bergey L. (2003a) Benthic community dynamics during summer low-flows in two rivers of contrasting enrichment 1. Periphyton. *New Zealand Journal of Marine and Freshwater Research,* **37,** 53-70.

Suren A.M., Biggs B.J.F., Duncan M.J. & Bergey L. (2003b) Benthic community dynamics during summer low-flows in two rivers of contrasting enrichment 2. Invertebrates. *New Zealand Journal of Marine and Freshwater Research,* **37,** 71-83.

Vaughn C.C. (1986) The role of periphyton abundance and quality in the microdistribution of a stream grazer, *Helicopsyche borealis* (Trichoptera: Helicopsychidae). *Freshwater Biology,* **16,** 485-493.

Vinikour W.S. (1981) Aquatic insect drift through a final-cut strip mine pit, with emphasis on drift distances. *Hydrobiologia,* **77,** 225-232.

Walton O.E. (1980a) Active entry of stream benthic macroinvertebrates into the water column. *Hydrobiologia,* **74,** 129-139.

Walton O.E. (1980b) Invertebrate drift from predator-prey associations. *Ecology,* **61,** 1486-1497.

Williams D.D. & Hynes H.B.N. (1974) The occurrence of benthos deep in the substratum of a stream. *Freshwater Biology,* **4,** 233-256.

Wood P.J., Agnew M.D. & Petts G.E. (2000) Flow variations and macroinvertebrate community responses in a small groundwater-dominated stream in south-east England. *Hydrological Processes,* **14,** 3133-3147.

Wood P.J. & Armitage P.D. (1999) Sediment deposition in a small lowland stream-management implications. *Regulated Rivers: Research and Management,* **15,** 199-210.

Wood P.J. & Armitage P.D. (2004) The response of the macroinvertebrate community to low-flow variability and supra-seasonal drought within a groundwater dominated stream. *Archiv für Hydrobiologie,* **161,** 1-20.

Wood P.J. & Petts G.E. (1994) Low flows and recovery of macroinvertebrates in a small regulated chalk stream. *Regulated Rivers: Research and Management,* **9,** 303-316.

Wood P.J. & Petts G.E. (1999) The influence of drought on chalk stream macroinvertebrates. *Hydrological Processes,* **13,** 387-399.

Woodward G., Jones J.I. & Hildrew A.G. (2002) Community persistence in Broadstone Stream (UK) over three decades. *Freshwater Biology,* **47,** 1419-1435.

Wright J.F. & Berrie A.D. (1987) Ecological effects of groundwater pumping and a natural drought on the upper reaches of a chalk stream. *Regulated Rivers: Research and Management,* **1,** 145-160.

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

Zhang Y., Malmqvist B. & Englund G. (1998) Ecological processes affecting community structure of blackfly larvae in regulated and unregulated rivers: a regional study. *Journal of Applied Ecology,* **35,** 673-686.

CHAPTER 2

The effects of water abstraction on invertebrate communities in small streams: a survey of existing water abstractions

Abstract

Many small streams are the source of small-scale water abstractions that can alter hydrology and potentially have negative consequences for the biota. We examined the influence of water abstractions on the invertebrate communities of three small permanent streams by sampling benthic invertebrates and environmental characteristics of sites upstream and downstream of existing water abstractions during the Austral summer of 2003. The percentage of median discharge permitted for abstraction was between 28 and 57% for each of the streams. There tended to be greater differences in physicochemical characteristics and invertebrate communities between upstream and downstream sites on streams where a larger proportion of total discharge was abstracted. Decreases in mean velocity and depth were small on all streams, and there were no downstream decreases in channel width. However, conductivity, temperature and periphyton biomass were generally higher at downstream sites. Upstream and downstream sites on the two streams with the highest proportion of water abstracted had the most distinctive invertebrate communities. In general, there were higher densities of invertebrates downstream of water abstractions, but relatively fewer of these were the more sensitive mayfly, stonefly and caddisfly taxa. It appears that the greater the proportion of water abstracted from a stream or river, the greater the associated change to physicochemical characteristics and the invertebrate community.

Introduction

Water abstractions can substantially alter the flow regime, causing hydrological changes with potentially negative consequences for aquatic life and water quality (Jackson *et al.* 2001). Hence, there must be limits to the quantity of water that can be withdrawn before waterways become severely degraded (Richter *et al.* 2003). Much of what is known about invertebrate community responses to reduced discharge comes from studies of large rivers, whose waters may already be heavily utilised or highly regulated (e.g., Gore 1977, Englund & Malmqvist 1996, Cazaubon & Giudicelli 1999, Cortes *et al.* 2002). Studies of droughts also provide some indication of potential responses to water abstraction (e.g., Wright & Berrie 1987, Wood & Petts 1999).

The physical effects of water abstraction can include reduced wetted width (e.g., Cowx *et al.* 1984, Stanley *et al.* 1997, Brasher 2003), lower velocities (e.g., Bickerton *et al.* 1993, McIntosh *et al.* 2002, Brasher 2003) and decreased depths (e.g., Minshall & Winger 1968, Gore 1977, Cowx *et al.* 1984). Since hydraulic variables influence the availability of instream habitat (Statzner & Higler 1986), changes to flow can affect invertebrate community diversity. This is the basis of the Instream Flow Incremental Methodology (IFIM) (Bovee 1982), which has been widely used to assess river flow requirements. It operates by quantifying how habitat suitability for a target species varies with discharge (Jowett 2000). Changes to nutrient concentrations (e.g., Ladle & Bass 1981, Rader & Belish 1999), increased water temperatures (e.g., Everard 1996, Rader & Belish 1999) and lowered dissolved oxygen levels (Everard 1996, Jowett 1997) can also occur with reduced discharge, and these changes could further influence the invertebrate community.

Reduced flows often result in reduced taxonomic richness if habitat diversity decreases with decreasing discharge (e.g., Cazaubon & Giudicelli 1999, McIntosh *et al.* 2002), or if there are changes in the condition of the habitat (Wood and Armitage 1999, Wood *et al.* 2000). Invertebrate densities can also decline during low discharge periods (e.g., Englund & Malmqvist 1996, Cazaubon & Giudicelli 1999, McIntosh *et al.* 2002). However, densities can increase if individuals become concentrated into a reduced wetted area (e.g., Gore 1977, Wright & Berrie 1987), and some studies have noted that invertebrate responses to water abstractions vary between streams (Armitage & Petts 1992, Castella *et al.* 1995, Rader & Belish 1999, Suren *et al.* 2003a).

Predicted changes to the global distribution of fresh water with climate change (Jackson *et al.* 2001), and continually increasing demands for water resources (Postel

1997) mean that water from smaller streams could increasingly be utilised as larger river systems become over exploited. Although water abstractions for small irrigation schemes and domestic water supply might remove low volumes of water compared to larger projects, the proportionate decrease in discharge is high in these small streams and the effects on ecosystem health are not well known. Water abstractions on small streams have received relatively little attention (Rader & Belish 1999, McIntosh *et al.* 2002), other than by inclusion in studies of water abstractions on multiple streams of varying sizes (Petts & Bickerton 1994, Castella *et al.* 1995, Englund & Malmqvist 1996).

Our aim was to assess the influence of substantial water abstractions on the invertebrate communities of three small permanent streams. We sampled sites upstream and downstream of existing water abstractions, concentrating on the low flow period of summer, when many small water abstractions are utilised and any water abstraction will have the greatest effect on stream discharge. We hypothesised that downstream of water abstractions, there would be lower water velocity and depth, and decreased wetted channel width compared to upstream. We expected that such changes to flow characteristics would decrease habitat availability and suitability, resulting in lower benthic invertebrate densities and taxonomic richness at downstream sites.

Methods

Study sites

To assess the influence of water abstractions, we chose pairs of sites, upstream and downstream of water abstractions on three New Zealand streams, with mean annual low flows (MALF) of between 0.055 and 0.235 m^3/s. Raparapawai Stream (Tararua) (Plates 1, 2), Tamaki River (Tararua) (Plates 3, 4), and Mangatarere Stream (Wairarapa) (Plates 5, 6) were between 2 and 15 m wide, with average velocities between 0.03 and 0.61 m/s. The conductivity of the water in these streams was between 70 and 133 $\mu S/cm$, and they were all small, riffle-pool streams, running through predominantly agricultural and horticultural land. Channels were largely unshaded at all sampling sites. There was between 43 and 98% of MALF allocated for out of stream use in these streams, with abstractions either operated continuously throughout the year, for potable water supply and stock water, or predominantly over the summer period, for irrigation (Table 1).

Plate 1. Upstream of water abstraction, Raparapawai Stream, Tararua.

Plate 2. Downstream of water abstraction, Raparapawai Stream, Tararua.

Plate 3. Upstream of water abstraction, Tamaki River, Tararua.

Plate 4. Downstream of water abstraction, Tamaki River, Tararua.

Plate 5. Upstream of water abstraction, Mangatarere Stream, Wairarapa.

Plate 6. Downstream of water abstraction, Mangatarere Stream, Wairarapa.

Table 1. Characteristics of sampling sites and water abstractions from the Raparapawai Stream, Mangatarere Stream, and Tamaki River during summer 2003.

Stream	Maximum permitted rate of abstraction (L/s)	Permitted abstraction as % of MALF	Abstraction as % of median discharge over summer study period	Distance from abstraction to downstream site (km)	Purpose of abstraction
Raparapawai Stream	54	98%	57%	3.3	Dairy farm irrigation, summer usage only
Mangatarere Stream	113	67%	45%	1.0	Water race/stock water, continuous usage
Tamaki River	100	43%	28%	2.0	Potable water supply, continuous usage

One drawback of surveying the effects of water abstractions on the instream environment and invertebrate communities, is that affected sites must necessarily be located downstream of the impact, with control sites upstream. This complicates the results, since changes unrelated to the water abstraction could also occur between sites. To minimise such changes in this study, upstream and downstream sites were matched as closely as possible for land usage, substrate size, and riparian vegetation. Land use, geology, rainfall, and climate variables from New Zealand's River Environment Classification (REC) (Snelder & Biggs 2002), were used in a Principle Components Analysis (PCA) to assess the similarity between upstream and downstream sites on each stream (Fig. 1). PC1 explained 69.9% of the variation and PC2 a further 18.6% of the variation in the data. One-way analysis of similarities (ANOSIM) showed that there was no overall difference in these habitat characteristics between upstream and downstream sites (ANOSIM global R = -0.30, P = 0.80).

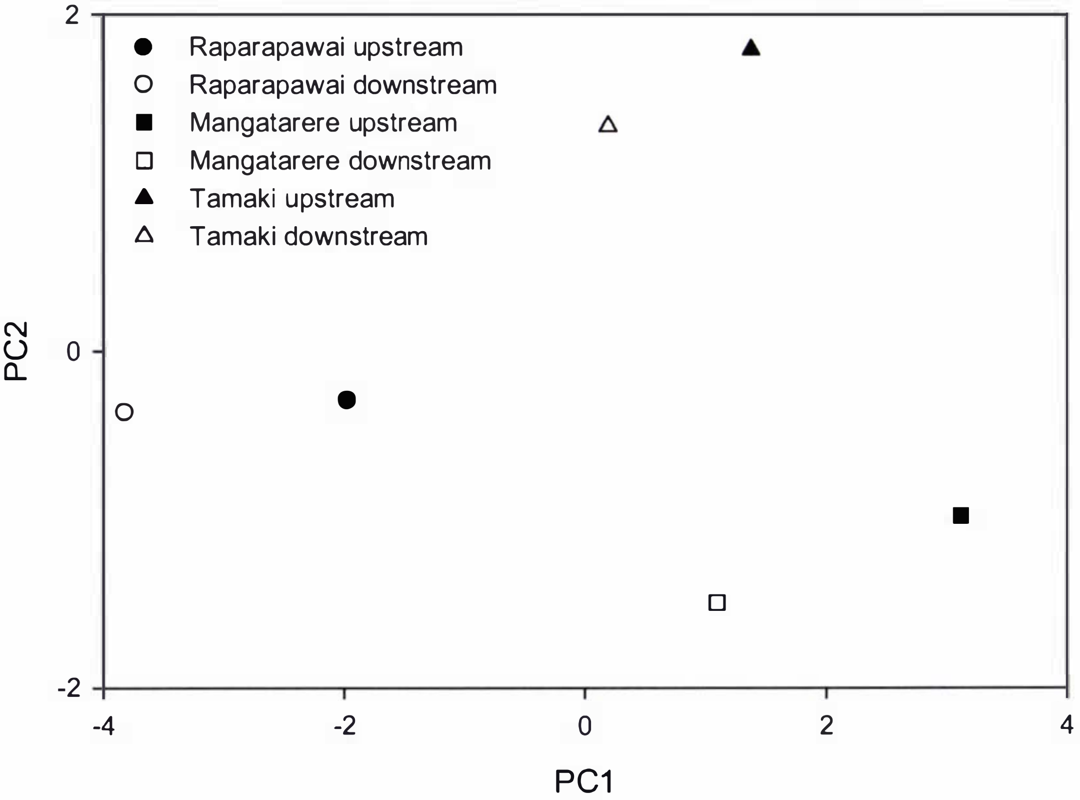

Figure 1. Axes 1 and 2 of a PCA based on land use, geology, rainfall, and climate variables from the River Environment Classification (REC) for upstream and downstream sites on Raparapawai Stream, Mangatarere Stream, and Tamaki River.

Survey design

We sampled each site on five occasions, at 14-day intervals between February and April 2003 (Austral summer and autumn). We also sampled once in July, when winter flows were similar at upstream and downstream sites. Samples were collected within three 20 m long riffles at each site, with at least 20 m between each riffle.

Physicochemical characteristics

Discharge was gauged using one transect per riffle, by measuring depth and velocity at 0.4 × depth from the bed. Velocity was measured at approximately 20 equidistant intervals across the stream using a Marsh McBirney Inc. Model 2000 Portable Flowmeter (accuracy 0.01 m/s). We focused on riffles, as they were the dominant habitat type in these streams. We expected that this habitat type would be most sensitive to water abstraction, since at very low flows, riffles may dry completely, leaving a series of isolated pools (Gordon *et al.* 2004). We measured temperature and conductivity at each site with an Orion 122 conductivity meter and pH with a pHTestr 2. Temperature was also recorded at 30 minute intervals between February and April using Onset Hobo® H8 temperature loggers for each site. We obtained hydrographs for the three streams from local authorities.

Across the gauging transect, the percentage algal cover (filamentous algae, diatom, bare rock) and percentage occupied by each substrate size class (boulder, large cobble, small cobble, gravel, sand, mud) were visually estimated by one person within 20 equidistant quadrats.

Invertebrate sampling protocol

Within each sampled riffle, three Surber samples (250-µm mesh, area = 0.1 m^2) were collected at random and preserved with 10% formalin until required. Samples were rinsed through a 500 µm Endecott sieve and sub-sampled. Since there was a large range in total invertebrate abundances among samples from different sites, we attempted to equalise the sampling effort among samples by sub-sampling. A sample splitter was used to divide each sample into four parts and either an entire 25% of the sample was sorted or further quarters were sorted until at least 200 individuals were counted (each successive 25% was fully counted). To avoid missing rare taxa, we scanned the remainder of the sample for taxa not present in the sub-sample. We identified invertebrates to the lowest possible taxonomic level using the keys of Winterbourn

(1973), Winterbourn *et al.* (2000) and Smith (2003). Chironomids were identified to sub-family level.

Periphyton sampling protocol

We collected one stone (< 60 mm, *a*-axis) adjacent to each Surber sample for periphyton biomass analysis. Samples were transported on ice in the dark and stored at - 20°C until analysis. Photosynthetic pigments were extracted from cobbles by submerging them in 90% acetone for 24 hours at 5°C. Absorbance was read at 750, 665 and 664 nm on a Varian Cary 50 Conc. UV-Visible spectrophotometer™ before and after 0.1M HCl was added. The amount of chlorophyll *a* ($\mu g/cm^2$) was calculated for 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).

Data analysis

We calculated the total number of individuals, expected number of taxa from 200 individuals, Berger-Parker dominance index (Berger & Parker 1970), Simpson's index (Simpson 1949) and the percentage of Ephemeroptera, Plecoptera and Trichoptera (% EPT) individuals and taxa (Lenat 1988) for each sample to describe the invertebrate communities. The New Zealand equivalent of the Hilsenhoff Biotic Index (Hilsenhoff 1987), the Macroinvertebrate Community Index (MCI) (Stark 1985) and its quantitative variant the QMCI were also calculated for each sample. We also calculated site averages for discharge, width, depth, velocity, conductivity, temperature and chlorophyll *a* measurements from each sampling occasion.

Two-way analysis of variance (ANOVA) was used to examine differences in these measures between upstream and downstream sites using SAS (2004). As there were substantial between stream differences, ANOVA was performed on data from each stream separately. Furthermore, since the winter samples were only taken for comparative purposes, they were excluded from this analysis. Treatment factors were upstream/downstream of abstraction (abstraction) and sampling occasion (time). All factors were treated as fixed effects, since sites and times were chosen, not a random selection of all possible options. We used each of the three riffles within each abstraction site as a replicate in the analysis, but averaged the three samples taken from each riffle for this analysis.

We calculated the average abundance of each invertebrate taxon on each sampling occasion for the three streams. These data were fourth root transformed to reduce the importance of abundant taxa. Non-metric multi-dimensional scaling (MDS) was carried out using the Bray Curtis similarity measure and we used one-way analysis of similarities (ANOSIM) to test the differences between upstream and downstream groups over all sampling occasions for each stream using PRIMER (Clarke & Gorley 2006). The contributions of individual species to the difference between communities at control and impact sites were examined separately for each stream with the similarity percentages (SIMPER) routine in PRIMER. We also tested the difference between the three streams and ran a two-way nested ANOSIM on data from the three streams to examine whether there was a difference between upstream and downstream groups nested within sites. Using the Bray Curtis similarities, we calculated classification strengths for upstream and downstream groupings on each stream, as well as for the three stream groups. Calculating classification strength is a method of comparing similarities within classes, with those between classes, since in a strong classification, there will be greater similarity within, than between classes (Van Sickle & Hughes 2000). Classification strength (M) was calculated as the mean of all between class similarities (B), divided by the weighted mean of within class similarities (W) (Van Sickle & Hughes 2000). Classification strength (M) is a value between 0 and 1, that decreases as the strength of the classification increases (Van Sickle & Hughes 2000).

For each site on each occasion, average velocity, depth, discharge, width, conductivity, chlorophyll *a*, and the percentage cover of filamentous algae/diatoms/bare rock were entered into an environmental matrix, transformed where necessary and normalised. Since the percentage cover of boulders/large cobbles/small cobbles/gravel/sand/mud did not change over time, these were not included. The relationship between the environmental data and the observed pattern in the invertebrate community for each stream was explored using Spearman rank correlations in the BIOENV procedure in PRIMER. A permutation test was used to evaluate significance (Clarke & Warwick 2001).

Results

Physicochemical characteristics and periphyton biomass

As a percentage of median discharge over the summer of 2003, permitted abstractions were 57%, 45% and 28% for Raparapawai Stream, Mangatarere Stream and Tamaki

River respectively (Table 1). When measured during sampling, discharges were on average 32%, 9% and 14% lower at downstream sites on these streams (Table 2). However, as a percentage of average daily discharge, permitted abstractions varied considerably over time, and greater downstream decreases in discharge tended to occur at lower flows (Fig. 2). The percentage decreases in discharge between upstream and downstream declined over summer and discharge increased downstream in all streams in winter (Fig. 2). Each of the streams was at, or below MALF at some point over the sampling period, and minimum discharges of 149, 128 and 9 L/s were recorded for Mangatarere Stream, Tamaki River and Raparapawai Stream respectively during mid-late February.

Differences in velocity and depth between upstream and downstream sites tended to be small (Table 2). However, velocity was an average of 0.09 m/s lower at the downstream site on Raparapawai Stream and for Tamaki River, water depth was greater upstream (Table 2). Wetted channel width did not decrease downstream for any of the streams (Table 2). Conductivity increased by 27.7 μS/cm between upstream and downstream sites on Raparapawai Stream and by 8.7 μS/cm on Mangatarere Stream, but there was no increase in the Tamaki River (Table 2).

During the month of April, mean daily temperatures were greater (by < 1 °C) at downstream sites on both Mangatarere Stream ($F_{1,52} = 4.22$, $P = 0.05$) and Tamaki River ($F_{1,46} = 6.91$, $P = 0.01$), compared to upstream, but there was no difference for Raparapawai Stream ($F_{1,50} = 1.12$, $P = 0.29$). The daily temperature range was also 2.5 °C higher for the downstream site at the Mangatarere Stream ($F_{1,52} = 74.03$, $P < 0.01$). However, the upstream site had a greater daily temperature range (by < 1 °C) for Raparapawai Stream ($F_{1,50} = 6.97$, $P = 0.01$) and there was no difference between the sites on the Tamaki River ($F_{1,46} = 2.77$, $P = 0.10$).

Mean chlorophyll *a* concentration was higher downstream of abstractions on the Mangatarere Stream ($F_{1,20} = 5.61$, $P = 0.03$) and Raparapawai Stream ($F_{1,20} = 20.22$, $P < 0.01$), but lower downstream for Tamaki River ($F_{1,20} = 7.43$, $P = 0.01$) (Fig. 3). Chlorophyll *a* concentrations changed over time for Mangatarere Stream ($F_{4,20} = 20.35$, $P < 0.01$), Tamaki River ($F_{4,20} = 38.22$, $P < 0.01$) and Raparapawai Stream ($F_{4,20} = 43.32$, $P < 0.01$). Chlorophyll *a* concentrations generally increased during stable discharge and decreased following high discharge events (Fig. 3).

Table 2. Mean (± 1 S.E., *n* = 15) physicochemical characteristics of sites upstream and downstream of water abstraction on five occasions between February and April 2003. Changes significant at the 5% level are indicated in bold.

Site	Discharge (m^3/s)	Width (m)	Velocity (m/s)	Depth (m)	Conductivity (µS/cm)
Raparapawai upstream	0.19 ± 0.02	5.11 ± 0.23	0.28 ± 0.02	0.10 ± 0.00	86.5 ± 0.7
Raparapawai downstream	0.13 ● 0.02	5.44 ● 0.51	0.19 ± 0.03	0.09 ± 0.01	114.2 ± 3.4
% change	**-31.6%**	+6.5%	**-32.1%**	-10.0%	**+32.0%**
Mangatarere upstream	0.34 ± 0.02	7.55 ± 0.66	0.27 ± 0.03	0.13 ± 0.01	74.4 ± 0.6
Mangatarere downstream	0.31 ± 0.03	6.95 ± 0.18	0.24 ± 0.02	0.13 ± 0.01	83.1 ± 1.0
% change	-8.8%	-7.9%	-11.1%	0.0%	**+11.7%**
Tamaki upstream	0.50 ± 0.03	5.81 ● 0.14	0.37 ± 0.02	0.16 ± 0.01	72.5 ± 0.4
Tamaki downstream	0.43 ± 0.04	7.00 ± 0.26	0.36 ± 0.02	0.13 ± 0.01	75.4 ± 0.9
% change	**-14.0%**	**+20.5%**	-2.7%	**-18.8%**	+4.0%

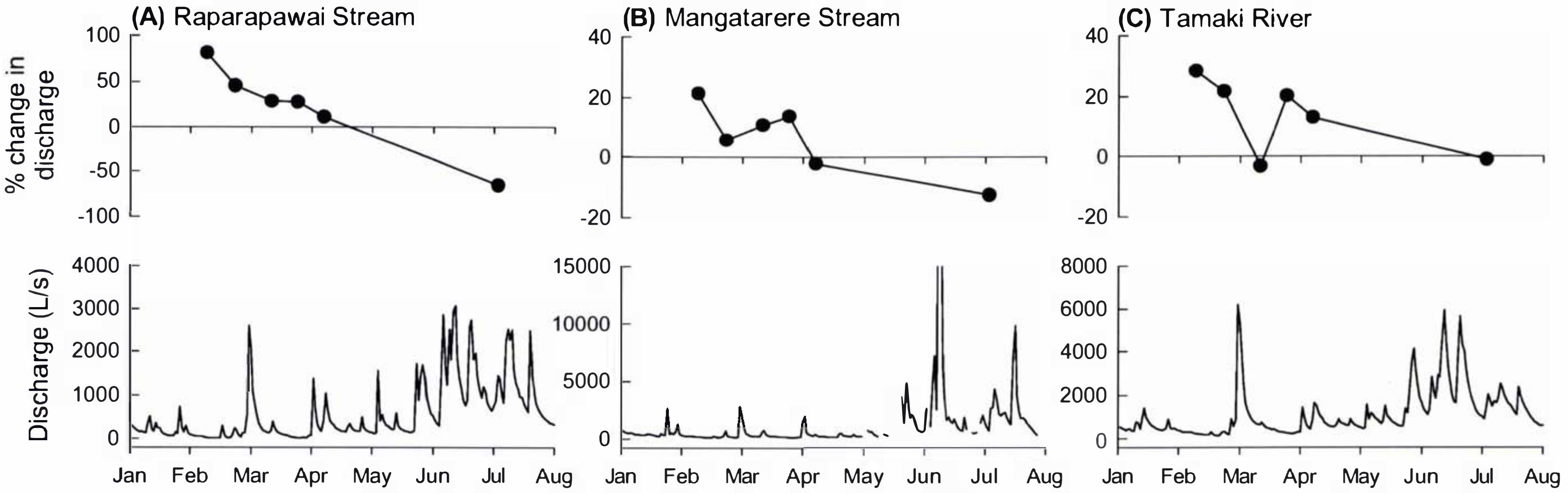

Figure 2. Percentage reduction in discharge between upstream and downstream sites during sampling on six occasions between February and July 2003 and the mean daily discharge between January and August 2003 for (A) Raparapawai Stream, (B) Mangatarere Stream and (C) Tamaki River.

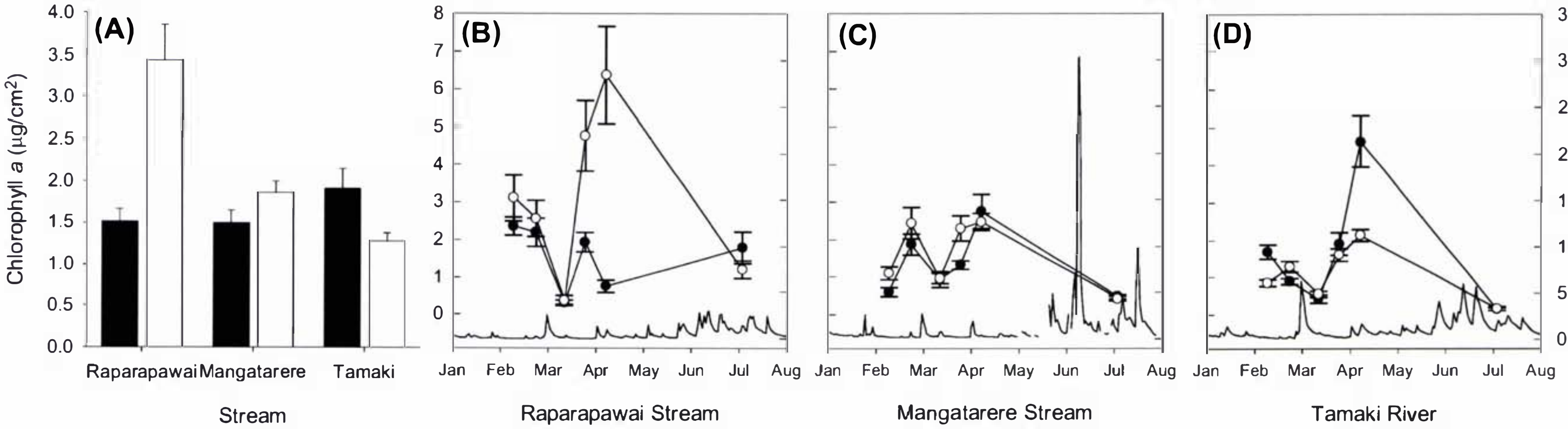

Figure 3. Mean chlorophyll *a* concentration (± 1 S.E.) on cobbles from sites upstream (black symbols) and downstream (open symbols) of water abstractions on each sampling occasion between February and July 2003 (left axis). (A) summary bar chart, mean of five summer sampling occasions (+ 1 S.E.), (B) Raparapawai Stream, (C) Mangatarere Stream and (D) Tamaki River. Mean daily discharge (L/s) between January and August for each stream is represented by the lower solid line (right axis).

Invertebrate community diversity

Invertebrate densities were higher at downstream sites for Mangatarere and Raparapawai streams (Table 3), but densities were more different over time than between upstream and downstream sites (Fig. 4A). Mangatarere Stream had consistently higher rarefied numbers of taxa upstream over the study period, but the opposite was true for Raparapawai Stream (Fig. 4B). Invertebrate densities and numbers of taxa at upstream and downstream sites at the Tamaki River were similar, but a lower percentage of individuals were Ephemeroptera, Plecoptera, or Trichoptera (EPT) at the downstream site (Table 3, Fig. 4C). The percentages of EPT individuals and taxa were also lower at the downstream site on Raparapawai Stream (Table 3). At Mangatarere Stream, there was an increase in dominance (Berger Parker) and decrease in species evenness (Simpson) in the downstream direction, whereas on Tamaki River, dominance decreased downstream (Table 3). The QMCI of upstream and downstream sites did not differ for any of the streams.

Table 3. ANOVA results for mean community metrics at sites upstream and downstream of water abstraction in the Raparapawai Stream, Mangatarere Stream, and Tamaki River on five occasions between February and April 2003. Degrees of freedom (d. f.) and *F* values are given for all main effects and their interactions. Values significant at the 5% level are indicated in bold.

Stream		d. f.	Number of individuals	Rarefied number of taxa	% EPT individuals	% EPT taxa	Berger Parker index	Simpson's index	QMCI
Raparapawai Stream	Abstraction	1, 20	**8.98**	**8.24**	**5.33**	**18.86**	1.15	2.64	2.01
	Time	4, 20	**7.03**	**2.87**	**5.54**	0.44	0.54	0.55	0.40
	Abstraction * Time	4, 20	**6.44**	1.07	2.73	2.01	0.65	0.77	**6.88**
Mangatarere Stream	Abstraction	1, 20	**6.70**	**47.16**	0.99	0.03	**11.12**	**22.43**	0.22
	Time	4, 20	**12.54**	**9.39**	**4.43**	1.94	0.46	0.94	0.95
	Abstraction * Time	4, 20	1.39	1.72	2.30	0.34	2.29	1.97	0.94
Tamaki River	Abstraction	1, 20	1.32	0.66	**18.21**	0.16	**4.87**	0.74	0.62
	Time	4, 20	**13.78**	2.71	**5.31**	2.30	**7.60**	**7.36**	0.76
	Abstraction * Time	4, 20	1.13	1.77	**5.13**	**4.42**	**3.75**	**4.54**	0.91

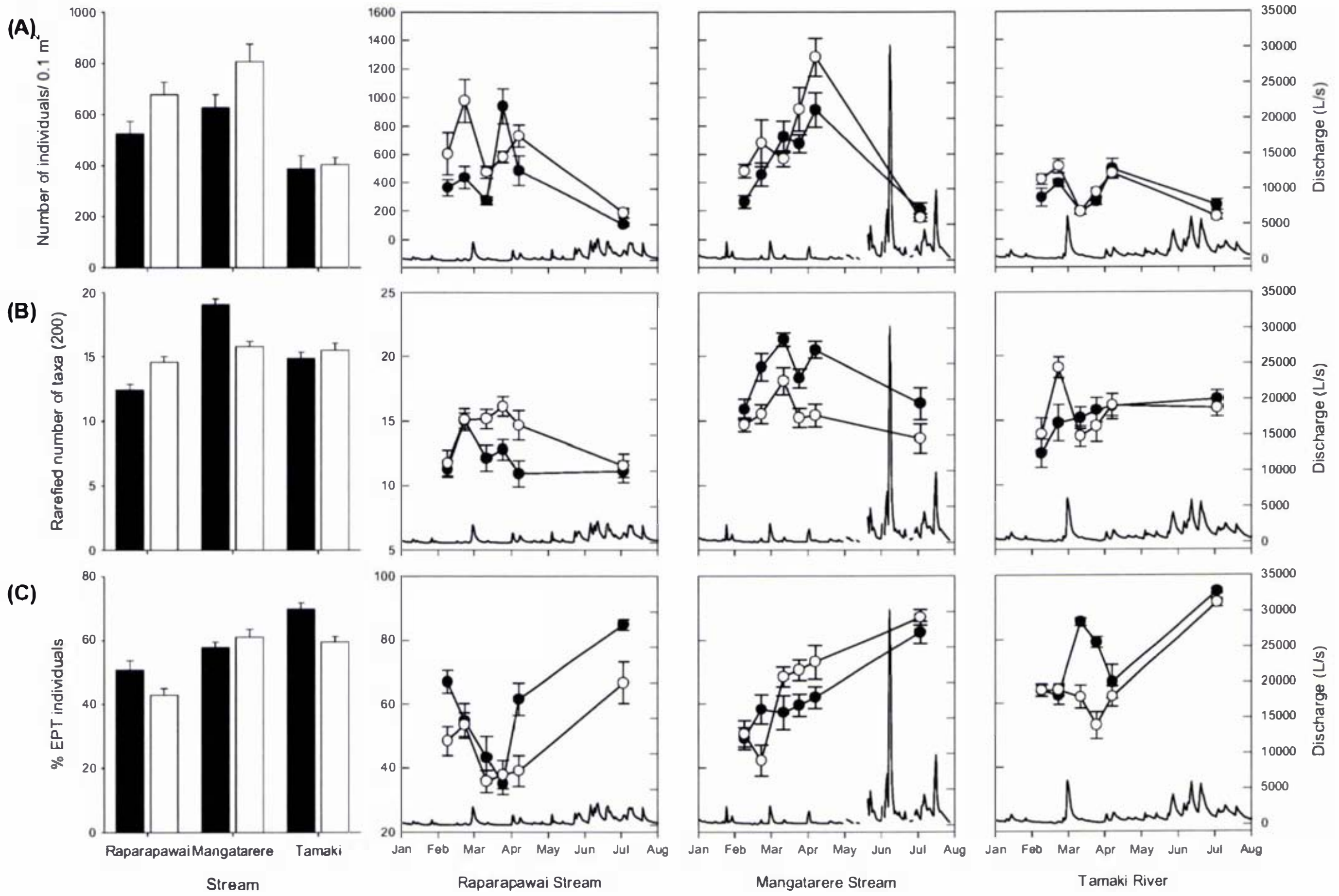

Figure 4. Mean daily discharge (L/s) between January and August (right axis) and (A) number of individuals per 0.1 m^2, (B) rarefied number of taxa, and (C) % EPT individuals (mean ± 1 S.E.) (left axis) at upstream (black symbols) and downstream (open symbols) sites on Mangatarere Stream, Tamaki River and Raparapawai Stream over six sampling occasions between February and July 2003. Summary bar charts display the means of the five summer sampling occasions for each metric (+ 1 S.E.).

Invertebrate community composition

There were distinct invertebrate communities in the three streams in this study (Table 4, Fig. 5A). Classification strength for the three streams in the study was greater than for upstream and downstream sites on each stream (Table 4). Even so, invertebrate communities at sites upstream and downstream of water abstractions were distinct for Raparapawai Stream (Fig. 5B) and Mangatarere Stream (Fig. 5C). The separation between upstream and downstream was not as clear for Tamaki River (Fig. 5D), and this stream had the weakest classification (Table 4). On all streams, increases in Elmidae and *Deleatidium* sp. made large contributions to the community differences between upstream and downstream sites (SIMPER). Other important community differences included an increase in the abundance of *Pycnocentrodes* sp. and decreases in the abundance of *Coloburiscus humeralis* and *Austrosimulium* sp. between upstream and downstream sites on Mangatarere Stream, as well as a higher abundance of *Potamopyrgus antipodarum* for the downstream site at Raparapawai Stream. A two-way ANOSIM testing the difference between upstream and downstream sites nested within streams showed that over all streams, there were significant differences between upstream and downstream sites (ANOSIM global $R = 0.49$, $P < 0.01$).

Table 4. Classification strengths (Van Sickle & Hughes 2000) and results of ANOSIM testing the null hypothesis that there are no differences between stream groups or between upstream and downstream sites within each stream for Raparapawai Stream, Mangatarere Stream, and Tamaki River between February and April 2003. M = classification strength, calculated as the mean of all between class similarities (B) divided by the weighted mean of within class similarities (W), decreases as the strength of the classification increases. ANOSIM values significant at the 5% level are indicated in bold.

	No. of classes	B	W	M	ANOSIM global *R*
All streams	3	68.4	77.7	0.88	**0.76**
Raparapawai Stream	2	77.0	80.8	0.93	**0.71**
Mangatarere Stream	2	76.2	78.5	0.95	**0.47**
Tamaki River	2	74.7	80.0	0.97	0.29

Of the environmental variables measured, the downstream increase in conductivity consistently provided the best explanation for invertebrate community patterns over the five sampling occasions using the BIOENV procedure in PRIMER.

Increased conductivity and diatom cover, along with decreased pH between upstream and downstream, followed the invertebrate differences between upstream and downstream on the Mangatarere Stream. Although not significant, downstream increases in conductivity also provided some explanation for invertebrate community patterns at Tamaki River and Raparapawai Stream (Table 5).

Table 5. Environmental variables providing the best explanation for invertebrate community composition between sites upstream and downstream of water abstractions using the BIOENV procedure in PRIMER (Clarke & Gorley, 2006). Values significant at the 5% level are indicated in bold.

Stream	Best correlated environmental variables	Correlation *R* statistic
Raparapawai Stream	Conductivity % diatom cover	0.44
Mangatarere Stream	Conductivity pH % diatom cover	**0.66**
Tamaki River	Conductivity	0.30

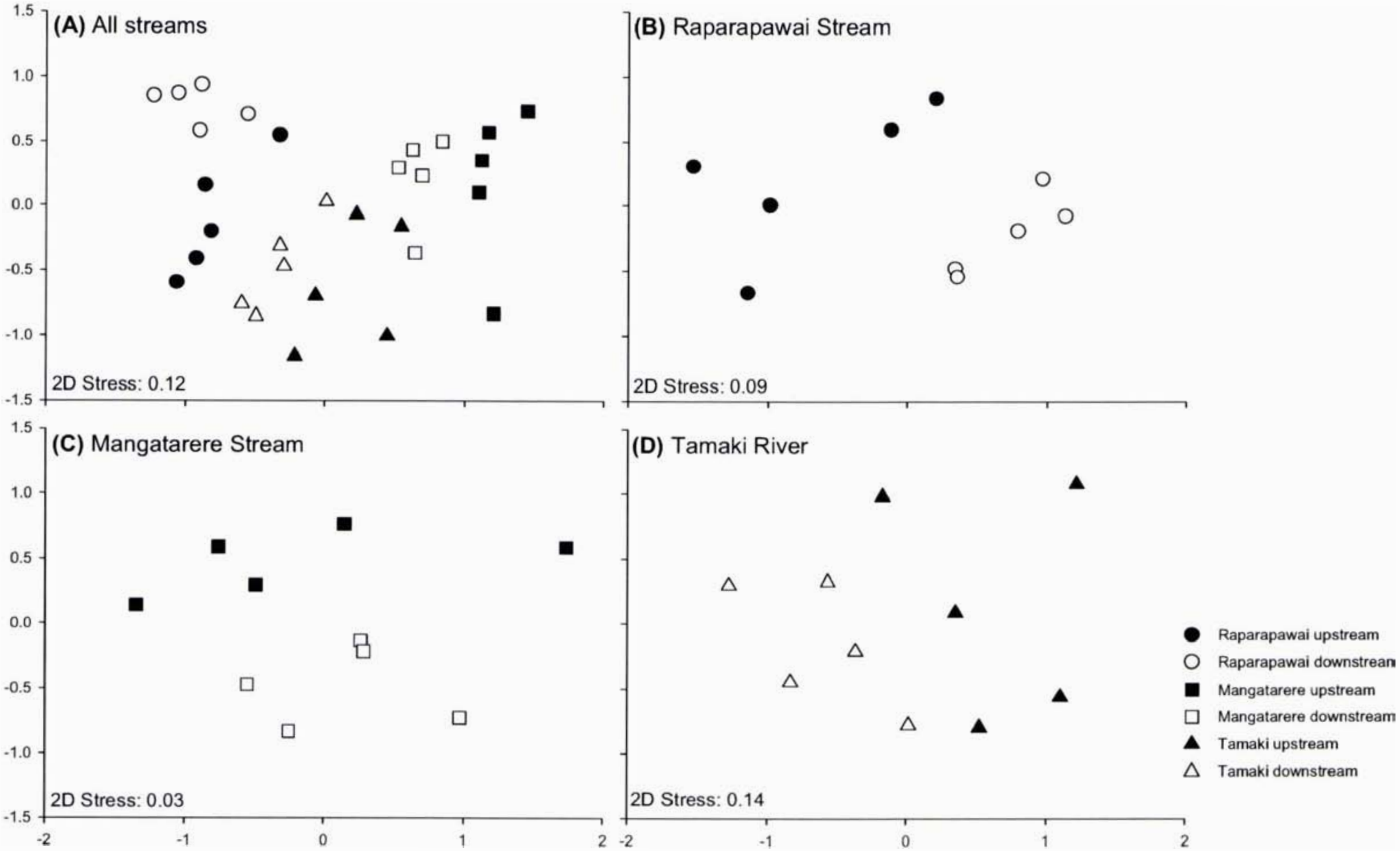

Figure 5. MDS of mean invertebrate community from each of five summer sampling occasions upstream and downstream of water abstractions for Raparapawai Stream, Mangatarere Stream, and Tamaki River between February and April 2003.

Discussion

During the summer of 2003, the percentage of median discharge abstracted was highest for Raparapawai Stream (57%), followed by Mangatarere Stream (45%) and Tamaki River (28%). The magnitude of differences in physicochemical characteristics and invertebrate communities between upstream and downstream sites tended to reflect the percentage of water abstracted. Responses to water abstraction in the literature are often highly variable between streams (e.g., Armitage & Petts 1992, Bickerton *et al.* 1993, Chapter 1), and based on what we found, this variability may relate to differences in the proportion of water abstracted between streams (Castella *et al.* 1995, Rader & Belish 1999).

Water velocity was lower at the downstream site only at the Raparapawai Stream, probably because the proportionate reduction in discharge was greatest for this site. There was a decrease in depth at Tamaki River, but no loss of wetted width for any of the streams in our study. Water velocity often decreases downstream of water removals (e.g., Bickerton *et al.* 1993, McIntosh *et al.* 2002, Brasher 2003), as does depth (e.g., Minshall & Winger 1968, Gore 1977, Kinzie *et al.* 2006) and wetted width (e.g., Cowx *et al.* 1984, Stanley *et al.* 1997, Brasher 2003). However, the responses of these variables to changes in discharge depend on the cross sectional shape of the channel (Gordon *et al.* 2004). The U shaped channels at these sites meant that the outcomes of decreased discharges were decreases in velocity or depth, rather than wetted width.

Sites downstream of water abstractions on Mangatarere Stream and Tamaki River were warmer than upstream sites, and daily temperature range was greater at the downstream site on Mangatarere Stream. Increased water temperatures can result from high air temperatures and reduced water volumes during low flow periods (Everard 1996, Jowett 1997), and small water volumes might be responsible for greater diurnal temperature fluctuations (Cowx *et al.* 1984, Smakhtin 2001). However, the addition of cool groundwater can be particularly influential on surface water temperatures in small streams (Mosley 1983), and this probably explains the smaller daily temperature range for the downstream site at Raparapawai Stream. Raparapawai Stream had the greatest increase in conductivity and periphyton biomass between upstream and downstream sites in this study, followed by Mangatarere Stream. Tamaki River had no increase in conductivity or periphyton biomass, again reflecting the reduced volume of water abstracted at this site. Increased concentrations of nutrients can result from low stream flow (Boulton & Lake 1990, Stanley *et al.* 1997), either by reduced dilution (Ladle & Bass 1981) or by the increased contribution of deeper groundwater during dry periods (Dahm *et al.* 2003). This in combination with increased temperatures and reduced current velocity, are likely causes of the increased algal biomass below the abstractions (McIntire 1966, Biggs 1985, Poff *et al.* 1990, Suren *et al.* 2003b).

When investigating the effects of water abstractions, affected sites must necessarily be located downstream of the impact, with control sites upstream. This could confound the results, since changes unrelated to the water abstraction might also occur between sites. However, in this study, sites were chosen so that differences in land usage, geology, rainfall, and climate between upstream and downstream were minimal (Fig. 1). Thus, except for water abstraction, invertebrate communities should be similar at upstream and downstream sites. The sampling in winter clearly shows how discharge would naturally increase downstream in each of the streams (Fig. 2), and that invertebrate communities are very similar at upstream and downstream sites on each of the streams when flows are not reduced (Fig. 4). Furthermore, the QMCI (an index of organic enrichment) values do not change between upstream and downstream, indicating that land use impacts on the stream have not changed as you move downstream. Therefore, there is strong evidence that the changes observed in this study are the result of water abstraction and not an artefact of the downstream location of impact sites.

Invertebrate community diversity differed most between sites upstream and downstream of water abstractions on the streams with the highest proportion of water allocated for abstraction. This reflects the greater relative change in physicochemical characteristics with increased abstraction. In ordination space, upstream and downstream invertebrate communities were distinct for Raparapawai Stream and Mangatarere Stream, but not Tamaki River. The strength of these upstream-downstream groupings was also greatest for Raparapawai Stream, followed by Mangatarere Stream and Tamaki River (Table 4), corresponding to both the magnitude of permitted abstraction in these streams and the degree of change created by the abstractions on the physicochemical habitat. Of the physicochemical changes responding to water abstraction, conductivity was the most reliable explanation of invertebrate community patterns, although the relatively small changes to conductivity that we observed were probably not affecting invertebrates directly.

The downstream site on Raparapawai Stream had higher invertebrate density and more taxa than the upstream site, but a lower percentage of these individuals and taxa were from the more sensitive Ephemeroptera, Plecoptera, or Trichoptera (EPT) groups. Mangatarere Stream also had higher invertebrate density downstream of the water abstraction, but there were fewer taxa and a decrease in species evenness. There was no difference to numbers of individuals or taxa between upstream and downstream at the Tamaki River. However, the percentage of EPT individuals was lower at the downstream site. This is in contrast with most previous studies, where reduced flows often resulted in reduced abundances of benthic invertebrates (e.g., Englund & Malmqvist 1996, Cazaubon & Giudicelli 1999, McIntosh *et al.* 2002). Since wetted width was unaffected by reduced flow in the streams, the increased densities cannot be a result of reduced wetted area (Gore 1977, Wright & Berrie 1987, Gasith & Resh 1999). Perhaps the invertebrate communities are simply responding to the higher periphyton levels at downstream sites.

There was no consistent loss of diversity among the streams in this study. Reduced flows often result in losses of diversity because of a loss of habitat types (e.g., Cazaubon & Giudicelli 1999, McIntosh *et al.* 2002), but there was no evidence for this in our streams. Even so, there was a tendency for the relative abundance of sensitive EPT taxa to decline downstream. Perhaps this was a consequence of individual species preferences for flow or changes in algal abundance (Hart & Finelli 1999, Smakhtin 2001). It seems that changes in habitat condition (Wood and Armitage 1999, Wood *et al.* 2000) provide a reasonable explanation for invertebrate community responses to reduced flow in these streams. Differences between sites tended to develop during periods of relatively stable flow, whereas high flow events were responsible for nullifying differences in invertebrate communities and periphyton biomass at upstream and downstream sites (Fig. 4). This is a further indication that algal biomass is influencing invertebrate community responses to flow.

In conclusion, there were differences in the invertebrate communities upstream and downstream of these water abstractions during summer. There were greater differences between upstream and downstream sites on streams where a larger proportion of total discharge was abstracted. Furthermore, since variables such as wetted width, velocity and depth changed little between sites, it seems that increased nutrients and periphyton offer the best explanation for the observed changes.

References

Armitage P.D. & Petts G.E. (1992) Biotic score and prediction to assess the effects of water abstractions on river macroinvertebrates for conservation purposes. *Aquatic Conservation: Marine and Freshwater Ecosystems,* **2,** 1-17.

Berger W.H. & Parker F.L. (1970) Diversity of planktonic Foraminifera in deep sea sediments. *Science,* **168,** 1345-1347.

Bickerton M., Petts G.E., Armitage P.D. & Castella E. (1993) Assessing the ecological effects of groundwater abstraction on chalk streams: three examples from eastern England. *Regulated Rivers: Research and Management,* **8,** 121-134.

Biggs B.J.F. (1985) Algae - a blooming nuisance in rivers. *Soil and Water,* **2,** 27-31.

Boulton A.J. & Lake P.S. (1990) The ecology of two intermittent streams in Victoria, Australia. I. Multivariate analyses of physicochemical features. *Freshwater Biology,* **24,** 123-141.

Bovee K.D. (1982) A guide to stream habitat analysis using the instream flow incremental methodology. *Instream Flow Information Paper (US Fish and Wildlife Service, Fort Collins, Colorado),* **12.**

Brasher A.M.D. (2003) Impacts of human disturbances on biotic communities in Hawaiian streams. *BioScience,* **53(11),** 1052-1060.

Castella E., Bickerton M., Armitage P.D. & Petts G.E. (1995) The effects of water abstractions on invertebrate communities in U.K. streams. *Hydrobiologia,* **308,** 167-182.

Cazaubon A. & Giudicelli J. (1999) Impact of the residual flow on the physical characteristics and benthic community (algae, invertebrates) of a regulated Mediterranean river: the Durance, France. *Regulated Rivers: Research and Management,* **15,** 441-461.

Clarke K.R. & Gorley R.N. (2006) *PRIMER v6: User Manual/Tutorial.* PRIMER-E: Plymouth.

Clarke K.R. & Warwick R.M. (2001) *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation.* 2nd edn. PRIMER-E: Plymouth.

Cortes R.M.V., Ferreira M.T., Oliveira S.V. & Oliveira D. (2002) Macroinvertebrate community structure in a regulated river segment with different flow conditions. *River Research and Applications,* **18,** 367-382.

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

Dahm C.D., Baker M.A., Moore D.I. & Thibault J.R. (2003) Coupled biogeochemical and hydrological responses of streams and rivers to drought. *Freshwater Biology,* **48,** 1219-1231.

Englund G. & Malmqvist B. (1996) Effects of flow regulation, habitat area and isolation on the macroinvertebrate fauna of rapids in north Swedish rivers. *Regulated Rivers: Research and Management,* **12,** 433-445.

Everard M. (1996) The importance of periodic droughts for maintaining diversity in the freshwater environment. *Freshwater Forum,* **7,** 33-50.

Gasith A. & Resh V.H. (1999) Streams in Mediterranean climate regions: abiotic influences and biotic responses to predictable seasonal events. *Annual Review of Ecology and Systematics,* **30,** 51-81.

Gordon N.D., McMahon T.A., Finlayson B.L., Gippel C.J. & Nathan R.J. (2004) *Stream Hydrology: An Introduction for Ecologists.* 2nd edn. John Wiley & Sons Ltd., West Sussex, England.

Gore J.A. (1977) Reservoir manipulations and benthic macroinvertebrates in a prairie river. *Hydrobiologia,* **55,** 113-123.

Graham A.A., McCaughan D.J. & McKee F.S. (1988) Measurement of surface area of stones. *Hydrobiologia,* **157,** 85-87.

Hart D.D. & Finelli C.M. (1999) Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms. *Annual Review of Ecology and Systematics,* **30,** 363-395.

Hilsenhoff W.L. (1987) An improved biotic index of organic stream pollution. *Great Lakes Entomologist,* **20(1),** 31-39.

Jackson R.B., Carpenter S.R., Dahm C.N., McKnight D.M., Naiman R.J., Postel S.L. & Running S.W. (2001) Water in a changing world. *Ecological Applications,* **11(4),** 1027-1045.

Jowett I.G. (1997) Environmental effects of extreme flows. In: *Floods and Droughts: the New Zealand Experience* (Eds M.P. Mosley & C.P. Pearson), pp. 104-116. The Caxton Press, Christchurch, New Zealand.

Jowett I.G. (2000) Flow management. In: *New Zealand Stream Invertebrates: Ecology and Implications for Management* (Eds K.J. Collier & M.J. Winterbourn), pp. 289-312. New Zealand Limnological Society, Christchurch, New Zealand.

Kinzie R.A.I., Chong C., Devrell J., Lindstrom D. & Wolff R. (2006) Effects of water removal on a Hawaiian stream ecosystem. *Pacific Science,* **60,** 1-47.

Ladle M. & Bass J.A.B. (1981) The ecology of a small chalk stream and its responses to drying during drought conditions. *Archiv für Hydrobiologie,* **90,** 448-466.

Lenat D.R. (1988) Water quality assessment using a qualitative method for benthic macroinvertebrates. *Journal of the North American Benthological Society,* **7,** 222-233.

McIntire C.D. (1966) Some effects of current velocity on periphyton communities in laboratory streams. *Hydrobiologia,* **27,** 559-570.

McIntosh M.D., Benbow M.E. & Burky A.J. (2002) Effects of stream diversion on riffle macroinvertebrate communities in a Maui, Hawaii, stream. *River Research and Applications,* **18,** 569-581.

Minshall G.W. & Winger P.V. (1968) The effect of reduction in stream flow on invertebrate drift. *Ecology,* **49(3),** 580-582.

Mosley M.P. (1983) Variability of water temperatures in the braided Ashley and Rakaia rivers. *New Zealand Journal of Marine and Freshwater Research,* **17,** 331-342.

Petts G.E. & Bickerton M.A. (1994) Influence of water abstraction on the macroinvertebrate community gradient within a glacial stream system: La Borgne d'Arolla, Valais, Switzerland. *Freshwater Biology,* **32,** 375-386.

Poff N.L., Voelz N.J., Ward J.V. & Lee R.E. (1990) Algal colonization under four experimentally-controlled current regimes in a high mountain stream. *Journal of the North American Benthological Society,* **9,** 303-318.

Postel S. (1997) *Last Oasis.* W.W. Norton & Company Inc., New York.

Rader R.B. & Belish T.A. (1999) Influence of mild to severe flow alterations on invertebrates in three mountain streams. *Regulated Rivers: Research and Management,* **15,** 353-363.

Richter B.D., Mathews R., Harrison D.L. & Wigington R. (2003) Ecologically sustainable water management: managing river flows for ecological integrity. *Ecological Applications,* **13(1),** 206-224.

SAS Institute Inc. (2004) *The SAS System for Windows.* SAS Institute Inc., Cary, North Carolina.

Simpson E.H. (1949) Measurement of diversity. *Nature,* **163,** 688.

Smakhtin V.U. (2001) Low flow hydrology: a review. *Journal of Hydrology,* **240,** 147-186.

Smith B.J. (2003) *Quick Guide to the MCI Invertebrates.* National Institute of Water and Atmospheric Research, Hamilton, New Zealand.

Snelder T.H. & Biggs B.J.F. (2002) Multi-scale river environment classification for water resources management. *Journal of the American Water Resources Association,* **38,** 1225-1240.

Stanley E.H., Fisher S.G. & Grimm N.B. (1997) Ecosystem expansion and contraction in streams - desert streams vary in both space and time and fluctuate dramatically in size. *BioScience,* **47,** 427-435.

Stark J.D. (1985) *A Macroinvertebrate Community Index of Water Quality for Stony Streams.* National Water and Soil Conservation Authority, Wellington, New Zealand.

Statzner B. & Higler B. (1986) Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. *Freshwater Biology,* **16,** 127-139.

Steinman A.D. & Lamberti G.A. (1996) Biomass and pigments of benthic algae. In: *Methods in Stream Ecology* (Eds F.R. Hauer & G.A. Lamberti), pp. 295-313. Academic Press Inc., U.S.A.

Suren A.M., Biggs B.J.F., Duncan M.J. & Bergey L. (2003a). Benthic community dynamics during summer low-flows in two rivers of contrasting enrichment 2. Invertebrates. *New Zealand Journal of Marine and Freshwater Research,* **37,** 71-83.

Suren A.M., Biggs B.J.F., Kilroy C. & Bergey L. (2003b). Benthic community dynamics during summer low-flows in two rivers of contrasting enrichment 1. Periphyton. *New Zealand Journal of Marine and Freshwater Research,* **37,** 53-70.

Van Sickle J. & Hughes R.M. (2000) Classification strengths of ecoregions, catchments and geographic clusters for aquatic vertebrates in Oregon. *Journal of the North American Benthological Society,* **19,** 370-384.

Winterbourn M.J. (1973) A guide to the freshwater Mollusca of New Zealand. *Tuatara,* **20,** 141-159.

Winterbourn M.J., Gregson K.L.D. & Dolphin C.H. (2000) Guide to the aquatic insects of New Zealand. *Bulletin of the Entomological Society of New Zealand,* **13.**

Wood P.J., Agnew M.D. & Petts G.E. (2000) Flow variations and macroinvertebrate community responses in a small groundwater-dominated stream in south-east England. *Hydrological Processes,* **14,** 3133-3147.

Wood P.J. & Armitage P.D. (1999) Sediment deposition in a small lowland stream-management implications. *Regulated Rivers: Research and Management,* **15,** 199-210.

Wood P.J. & Petts G.E. (1999) The influence of drought on chalk stream macroinvertebrates. *Hydrological Processes,* **13,** 387-399.

Wright J.F. & Berrie A.D. (1987) Ecological effects of groundwater pumping and a natural drought on the upper reaches of a chalk stream. *Regulated Rivers: Research and Management,* **1,** 145-160.

CHAPTER 3

Invertebrate responses to short-term water abstraction in small streams

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Abstract

Small permanent streams are coming under increasing pressure for water abstraction. Although these abstractions might only be required on a short-term basis (e.g., summer time irrigation), the highest demand for water often coincides with seasonal low flows. We constructed weirs and diversions that reduced discharge in three small streams (< 4 m width) to test the hypotheses that short-term water abstractions would decrease habitat availability and suitability for invertebrates, resulting in increased invertebrate drift, reduced taxonomic richness and decreased benthic invertebrate densities. We sampled benthic invertebrates, invertebrate drift and periphyton at control (upstream) and impact (downstream) sites on each stream before and during one month of discharge reduction. Discharge decreased by an average of 89 to 98% at impact sites and wetted width decreased by 24 to 30%. Water depth decreased by 28 to 64% while velocity decreased by 50 to 62%. Water conductivity, temperature and dissolved oxygen showed varying responses to flow reduction among the three streams, whereas algal biomass and pH were unaffected in all streams. The densities of invertebrate taxa tended to increase in the impact reaches of these streams even though invertebrate drift increased at impact sites in the first few days following discharge reduction. There was a higher proportion of mayflies, stoneflies and caddisflies at the impact site on one stream after flow reduction. There were no changes to the number of taxa or species evenness at impact sites. Our results suggest that for these small streams, the response of invertebrates to short-term discharge reduction was to accumulate in the decreased available area, increasing local invertebrate density.

Introduction

There has been an exponential rise in water usage over the last century (Postel 1997, Jackson *et al.* 2001) and a corresponding rise in the area of irrigated land (Jackson *et al.* 2001). Future challenges include adapting to predicted alterations in the global distribution of fresh water resources with climate change (Jackson *et al.* 2001). Meanwhile, the difficulty of expanding accessible supplies of water has increased, as have the costs of large irrigation projects (Postel 1997). As a result, more attention has focused on smaller scale projects that are potentially more cost effective (Postel 1997). Therefore, we expect that there will be a disproportionate increase in the usage of water from smaller streams (< 500 L/s) for purposes such as irrigation, as larger river systems become over exploited. Although such abstractions might only be required on a short-term basis, the highest demand for water often coincides with seasonal low flows. There is a shortage of robust scientific data describing the quantity and timing of water required to protect stream ecosystems of any size (Richter 1993, Chapter 1). The effects of short-term abstractions on the invertebrate communities of small permanent streams are to the best of our knowledge, largely unknown.

Invertebrate community changes following reduced discharge are probably a result of changes to the instream environment. Statzner & Higler (1986) have shown that hydraulic variables can influence the availability of instream habitat. With decreasing discharge there is commonly a loss of wetted area (e.g., Gore 1977, Cowx *et al.* 1984, Brasher 2003), and reduced water velocity and depth (e.g., Minshall & Winger 1968, Ham *et al.* 1981, McIntosh *et al.* 2002a). Changes to nutrient concentrations (e.g., Ladle & Bass 1981, Rader & Belish 1999), increased water temperatures (e.g., Everard 1996, Rader & Belish 1999) and lowered dissolved oxygen levels (Everard 1996, Jowett 1997) have also been reported as responses to discharge reduction in permanent streams. Reduced discharge can both reduce (e.g., Englund & Malmqvist 1996, Rader & Belish 1999, Wood & Petts 1999, McIntosh *et al.* 2002a) and increase (e.g., Gore 1977, Wright & Berrie 1987, Wright & Symes 1999) invertebrate abundance in different situations. However, taxonomic richness usually declines with discharge (e.g., Wood & Armitage 1999, Wood *et al.* 2000) and several previous studies have implicated reduced discharge in increasing active drift (Minshall & Winger 1968, Radford & Hartland-Rowe 1971, Gore 1977).

Some studies have examined the response of invertebrate communities in small streams to drought (e.g., Cowx *et al.* 1984, Wright & Symes 1999, Wood *et al.* 2000), or seasonal low flows (Suren *et al.* 2003). Sites upstream and downstream of water abstractions have been compared (e.g., Castella *et al.* 1995, McIntosh *et al.* 2002a, Dewson *et al.* 2003), and several studies have investigated the effects of altered flow regimes from dams, although mostly on large rivers (e.g., Gore 1977, Englund & Malmqvist 1996, Cortes *et al.* 2002). However, such observational studies lack pre-impact data or the appropriate reference sites to identify reduced flow as the only cause of the observed effects (Boulton 2003). Experimental flow manipulations in replicate streams are an ideal mechanism for investigating the effects of low flows on benthic invertebrate communities, since they allow the collection of appropriate before and after data. However, published accounts of experimental flow reductions are scarce and tend to focus on invertebrate drift responses (e.g., Hinckley & Kennedy 1972, Corrarino & Brusven 1983, Poff & Ward 1991) or small-scale manipulations of velocity in artificial channels (e.g., Poff *et al.* 1990, Poff *et al.* 2003).

The aim of our study was to experimentally manipulate flows in uniform lengths of three natural stream channels, in a robust before-after, control-impact (BACI) design to eliminate the potential confounding influences inherent in observational studies. To decrease discharge, we used weirs and diversions in three small streams; a technique often employed in small New Zealand streams to provide water for irrigation and town drinking supplies. We hypothesised that changes to flow characteristics following discharge reduction would decrease habitat availability and suitability for invertebrates, resulting in increased invertebrate drift, reduced taxonomic richness and decreased benthic invertebrate densities. We also expected that periphyton would proliferate under reduced flow conditions.

Methods

Study sites

This discharge reduction experiment was conducted on three small streams in the Wairarapa Region of the lower North Island, New Zealand: Booths Creek and un-named tributaries of Kiriwhakapapa Stream and Reef Creek. The three perennial, runoff fed streams represent different levels of water quality and range in discharge from 27 to 250 L/s (mean summer discharge). Water quality is classified as moderately polluted at Booths Creek using the Macroinvertebrate Community Index (MCI) (Stark 1985), whereas the Kiriwhakapapa Stream tributary is mildly polluted and Reef Creek has clean water. Water quality in these streams reflects the intensity of agricultural land use in their catchments.

Booths Creek (41° 04 40.29'S 175° 31 58.53'E) is a small (250 L/s), low gradient, meandering stream, with pool-riffle morphology and gravel-cobble substrate (Plates 1, 2, 3). Inflows from stock watering channels increase the discharge of this stream. Cropping land surrounds Booths Creek at the study site, with patches of willow (*Salix* spp.) in the riparian zone.

The Kiriwhakapapa Stream tributary is a small (110 L/s), moderately modified stream in the foothills of the Tararua Ranges (40° 49 07.10'S 175° 34 21.04'E) (Plates 4, 5, 6). This meandering stream also has a pool-riffle morphology and gravel-cobble substrate, with fine sediments contributed by bank erosion. The study site on the Kiriwhakapapa Stream tributary is within an extensive sheep and beef farm where stock has access to the stream and the channel has little shading in the study reaches.

The Reef Creek tributary is a relatively pristine, headwater stream (27 L/s) within a native forest catchment (40° 48 34.46'S 175° 32 21.84'E) (Plates 7, 8). The high gradient channel of this stream is characterised by pool, step and riffle sequences and gravel-boulder substrate with outcropping bedrock. The study site on the Reef Creek tributary is in a V-shaped valley, with the forest canopy providing almost complete shade to the channel in the study reaches.

Low flows occur during summer in these streams and higher flows occur frequently throughout the rest of the year. There are no historical flow records for these streams and no history of water abstraction at the study sites. We will subsequently refer to un-named tributaries by the names of the streams they feed.

Plate 1. Weir and culvert leading to diversion channel, Booths Creek, Wairarapa.

Plate 2. Diversion channel (left) and original channel (right) at Booths Creek.

Plate 3. Filamentous green algae exposed as water receded at Booths Creek.

Plate 4. Weir and culvert leading to diversion channel, Kiriwhakapapa Stream, Wairarapa.

Plate 5. Downstream reach of experiment at Kiriwhakapapa Stream.

Plate 6. Weir and diversion channel (right of picture) at Kiriwhakapapa Stream.

Plate 7. Weir and diversion pipe used for flow reduction experiments, Reef Creek, Wairarapa.

Plate 8. Reduced flow reach during experiment at Reef Creek.

Experimental design

We constructed weirs and diversions on three streams to reduce stream discharge for a distance of approximately 100 m. This distance provided enough area for invertebrate sampling and was not long enough for flow to be restored by groundwater inflow. Weirs extended across the entire stream, with no overflow during the period of the study. The wooden board weirs were not completely sealed so that a proportion of the flow could move through, under and around these weirs, whilst the majority of the flow was diverted out of the experimental reaches through open diversion channels (Booths Creek and Kiriwhakapapa Stream) or pipes (Reef Creek). By removing a high proportion of the discharge in this way, we have created a barrier to invertebrate drift into downstream reaches. However, this approach is consistent with the type of water abstraction that occurs from streams of this size. Study reaches were identified upstream (control) and downstream (impact) of weirs on each stream. Each reach was sampled on three occasions prior to diversion (December 2003-March 2004) and on either two (Booths Creek) or four occasions (Reef Creek and Kiriwhakapapa Stream) during experimental discharge reduction. This type of design is a before-after, control-impact design with samples paired in time (BACIP) (Downes *et al.* 2002). We delayed the start of the diversion for Booths Creek because of an extended period of high discharge following flooding that occurred just before the diversions started. Discharge reductions were maintained for one month during March and April 2004 (Reef Creek and Kiriwhakapapa Stream) or April and May 2004 (Booths Creek). For each stream, we sampled control and impact sites on the same day. Samplings were spread throughout the month to provide an indication of the timing of responses to water abstraction. Reef Creek and Kiriwhakapapa Stream sites were sampled 3, 10, 17 and 31 days after the diversion started, while Booths Creek was sampled after 3 and 17 days (fewer samplings because of flooding delays).

Flow related and physicochemical characteristics

At each study site, we established fixed locations with U shaped cross sections to measure discharge on each sampling occasion. Discharge was calculated by measuring depth and velocity at 0.4 of the depth from the streambed for at least ten equidistant intervals across the stream using a Marsh McBirney Inc. Model 2000 Portable

Flowmeter to an accuracy of 0.01 m/s. The minimum depth for these velocity measurements was 4 cm. Average measurements of conductivity (± 1 µS/cm), dissolved oxygen (± 0.2 mg/L) and pH (± 0.2 units) were recorded on each occasion from approximately an hour of logging at one-minute intervals using a YSI Incorporated multi-probe system instrument (YSI 556 MPS). Logging was completed over two consecutive hours at control and impact sites on each stream around midday. Temperature was recorded at 30 minute intervals from December 2003 to May 2004 using Onset Hobo® H8 temperature loggers. We measured the wetted width of the channel at 14 fixed locations at five metre intervals along the study reach at each sampling. We used regular intervals for these measurements to get an idea of the overall loss of wetted width in the stream, rather than the loss of specific habitat types.

Invertebrate sampling protocol

At each site, we collected benthic invertebrates from within riffle habitats using five Surber samples (area = 0.1 m^2, 250-µm mesh), and preserved the samples in 10% formalin. We expected that this habitat type would change the most after we reduced the discharge, since at very low flows, riffles may dry completely, leaving a series of isolated pools (Gordon *et al.* 2004). Depth and velocity were recorded for each Surber sample location and locations were marked to avoid repeat sampling on subsequent visits. Prior to benthic sampling on each occasion, we collected drift samples. These were installed mid afternoon and remained in the stream overnight (for approximately 18-20 hours). Drift samples were collected in two nets (105 mm × 55 mm mouth, 250-µm mesh), positioned just below the water surface, side by side at the downstream end of each control and impact reach. Invertebrate samples were rinsed through a 500-µm Endecott sieve and sub-sampled. We used a sample splitter to divide the sample into four parts and sorted sequential sub-samples until at least 200 individuals were removed. The entirety of each sub-sample 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. However, to avoid missing rare taxa, we scanned the remainder of the sample for taxa not present in the sub-sample. Invertebrates were identified to genus or species level where possible, except for oligochaetes (class) and chironomids (sub-family).

Periphyton sampling protocol

Adjacent to each Surber sample, a stone (< 60 mm, *a*-axis) was selected for periphyton biomass analysis. Stones were transported on ice in the dark and stored at -20°C. Photosynthetic pigments were extracted from stones by submerging them in 90% acetone for 24 hours at 5°C. Absorbance was read at 750, 665 and 664 nm on a Varian Cary 50 Conc. UV-Visible spectrophotometer™ 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 (upper half) calculated using length, width and depth of each cobble following Graham *et al.* (1988).

Data analysis

Invertebrate density, taxonomic richness, Berger-Parker dominance index (Berger & Parker 1970), Simpson's index (Simpson 1949) and the percentage of Ephemeroptera, Plecoptera and Trichoptera (EPT) individuals and taxa (Lenat 1988) were calculated for each benthic sample to describe the invertebrate communities. For all indices, we calculated a mean value for each site on each sampling occasion. Since *Oxyethira albiceps* (McLachlan) is a particularly pollution tolerant taxon compared to other Trichoptera (Boothroyd & Stark 2000), it was excluded from % EPT calculations, but included for all other analyses. Although not designed to detect the effects of discharge reductions, the New Zealand equivalent of the Hilsenhoff Biotic Index (Hilsenhoff 1987), the Macroinvertebrate Community Index (MCI) (Stark 1985) and its quantitative variant the QMCI (Stark 1985) were also calculated for each sample. We thought that these indices might be affected by reduced discharge since Boothroyd & Stark (2000) suggest that there may be a correlation between low MCI values and extended low flow periods. We calculated drift densities (per m^3) by correcting for discharge through each net, based on the velocity at net entrances. From this, we calculated drift propensity (drift density/benthic density) to ensure that drift densities did not simply reflect changes to benthic density (McIntosh *et al.* 2002b).

Mean values of physicochemical variables, invertebrate community indices and the densities of the five most common taxa in each stream were used as dependent variables for a three factor (control-impact (CI), before-after (BA), and times) analysis of variance (ANOVA) in SAS (2004). Downes *et al.* (2002) suggested this model for the BACIP design. We transformed data using $\log_{10}$ or square root when necessary to reduce heteroscedasticity. The test for the impact of flow reduction is the BA*CI interaction term in this model.

Similarities between assemblages of mean invertebrate densities for each stream (after fourth root transformation) were presented in two dimensions using non-metric multi-dimensional scaling (MDS) in PRIMER (Clarke & Gorley 2006). We used a one-way ANOSIM to test the null hypothesis that there were no differences between the four treatments (control before, impact before, control after, impact after). ANOSIM computes a test statistic that contrasts the differences between sites with those within sites using ranked similarities and then calculates statistical significance by permutation (Clarke & Warwick 2001). We used pairwise tests to compare control and impact sites within the before and after time periods and the contributions of individual species to the difference between communities at control and impact sites were examined separately for each stream with the similarity percentages (SIMPER) routine in PRIMER.

Results

Flow related and physicochemical changes

Weirs and diversions reduced discharge in all streams. When diversions were in operation, the discharge was 89 to 98% lower at impact sites and velocity decreased by an average of 57% at impact sites compared to controls (Table 1, Fig. 1). Impact sites also lost an average 24 to 30% of their wetted width following discharge reduction (Table 1, Fig. 2). Discharge reduction decreased mean depth by an average of 41%, although the decrease in depth was not significant at Booths Creek (Table 1, Fig. 2).

After diversion, conductivity increased by 13 μS/cm between control and impact sites on Kiriwhakapapa Stream, while there was no change for the other two streams (Table 1). Flow reduction had no effect on pH, but dissolved oxygen decreased at impact sites on Booths Creek and Reef Creek (Table 1, Fig. 2).

Table 1. Mean (± 1 S.E.) values of physicochemical variables at control and impact sites after discharge reduction in Booths Creek, Kiriwhakapapa Stream and Reef Creek between March and May 2004 (discharge reduction period). Percentage changes are from control to impact sites during experimental discharge reduction. *F* values for before-after × control-impact (BA*CI) interactions are included as a test for the impacts of flow reduction. Values significant at the 5% level are indicated in bold. This table continues on the following page.

Stream	**Booths Creek**	**Kiriwhakapapa Stream**	**Reef Creek**
Discharge control (L/s)	258.8 ± 23.1	60.6 ± 11.7	13.7 ± 4.0
Discharge impact (L/s)	6.2 ± 1.6	6.7 ± 3.6	1.3 ± 0.2
BA*CI interaction	**$F_{1,3}$ = 223.06**	**$F_{1,5}$ = 33.43**	**$F_{1,5}$ = 20.29**
% change discharge	-97.6%	-88.9%	-90.5%
Wetted width control (m)	3.40 ± 0.05	2.17 ± 0.03	2.24 ± 0.16
Wetted width impact (m)	2.60 ± 0.01	1.52 ± 0.02	1.70 ± 0.05
BA*CI interaction	**$F_{1,3}$ = 151.71**	**$F_{1,5}$ = 178.40**	**$F_{1,5}$ = 21.86**
% change wetted width	-23.6%	-30.0%	-24.1%
Depth control (cm)	16.3 ± 1.5	11.9 ± 0.8	9.1 ± 0.6
Depth impact (cm)	5.8 ± 0.4	8.2 ± 0.6	6.6 ± 0.7
BA*CI interaction	$F_{1,3}$ = 0.90	**$F_{1,5}$ = 35.54**	**$F_{1,5}$ = 21.86**
% change depth	-64.4%	-31.1%	-27.5%
Velocity control (m/s)	0.58 ± 0.06	0.57 ± 0.04	0.28 ± 0.04
Velocity impact (m/s)	0.22 ± 0.04	0.24 ± 0.03	0.14 ± 0.02
BA*CI interaction	**$F_{1,3}$ = 19.42**	**$F_{1,5}$ = 6.55**	**$F_{1,5}$ = 9.38**
% change velocity	-62.1%	-57.9%	-50.0%
Conductivity control (μS/cm)	176.1 ± 1.0	67.9 ± 0.6	52.9 ± 1.0
Conductivity impact (μS/cm)	175.8 ± 0.0	81.1 ± 2.0	53.2 ± 2.4
BA*CI interaction	$F_{1,3}$ = 0.45	**$F_{1,5}$ = 15.82**	$F_{1,5}$ = 0.00
% change conductivity	-0.2%	+19.4%	+0.5%

Table 1 (continued). Mean (± 1 S.E.) values of physicochemical variables at control and impact sites after discharge reduction in Booths Creek, Kiriwhakapapa Stream and Reef Creek between March and May 2004 (discharge reduction period). Percentage changes are from control to impact sites during experimental discharge reduction. *F* values for before-after × control-impact (BA*CI) interactions are included as a test for the impacts of flow reduction. Values significant at the 5% level are indicated in bold.

Stream	**Booths Creek**	**Kiriwhakapapa Stream**	**Reef Creek**
pH control	8.1 ± 0.3	7.2 ± 0.1	6.7 ± 0.1
pH impact	7.2 ● 0.1	7.1 ± 0.0	6.8 ± 0.1
BA*CI interaction	$F_{1,3}$ = 3.88	$F_{1,5}$ = 0.17	$F_{1,5}$ = 0.02
% change pH	-11.1%	-1.0%	+1.0%
Dissolved oxygen control (%)	111.3 ± 3.2	98.0 ± 0.9	92.9 ± 0.9
Dissolved oxygen impact (%)	85.3 ± 1.8	90.9 ± 2.5	85.5 ± 1.6
BA*CI interaction	**$F_{1,2}$ = 17.38**	$F_{1,4}$ = 4.98	**$F_{1,4}$ = 22.71**
% change dissolved oxygen	-23.4%	-7.2%	-7.9%
Max daily temperature control (°C)	14.5 ± 0.2	14.4 ± 0.3	10.0 ± 0.2
Max daily temperature impact (°C)	14.1 ± 0.2	14.9 ± 0.3	9.9 ± 0.2
BA*CI interaction	$F_{1,3}$ = 3.08	**$F_{1,5}$ = 6.38**	Missing data, no test
% change max daily temperature	-3.2%	+3.4%	-0.2%
Daily temperature range control (°C)	3.0 ± 0.3	3.6 ± 0.2	0.8 ± 0.1
Daily temperature range impact (°C)	2.4 ± 0.2	4.4 ± 0.3	0.7 ± 0.0
BA*CI interaction	$F_{1,3}$ = 1.32	**$F_{1,5}$ = 12.62**	Missing data, no test
% change daily temperature range	-19.5%	+20.9%	-6.4%

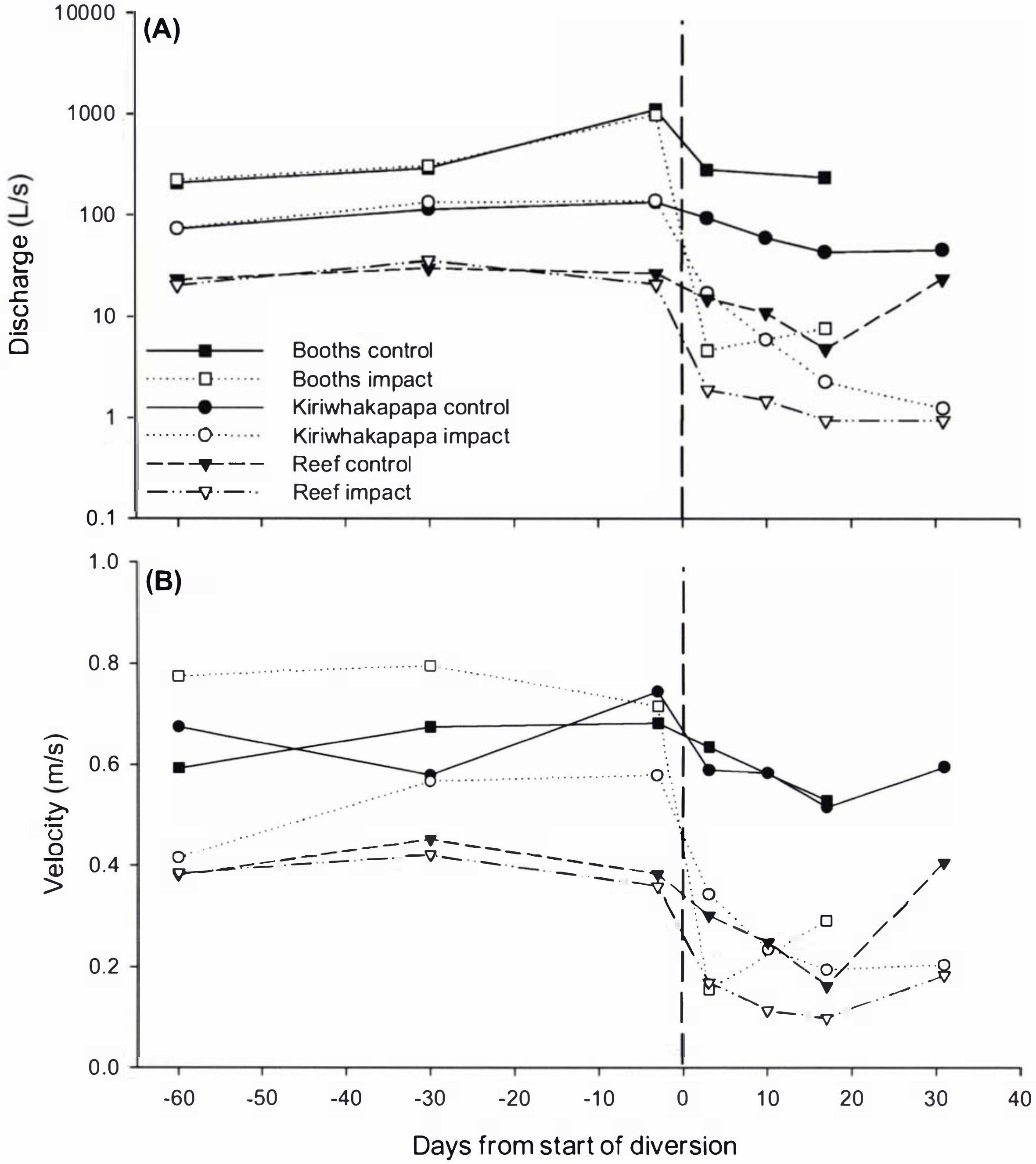

Figure 1. (A) Gauged discharge and (B) mean velocity for control and impact study sites at Booths Creek, Kiriwhakapapa Stream and Reef Creek before (December 2003-March 2004) and after (March-May 2004) discharge reduction began. Vertical dashed lines indicate the start of diversions.

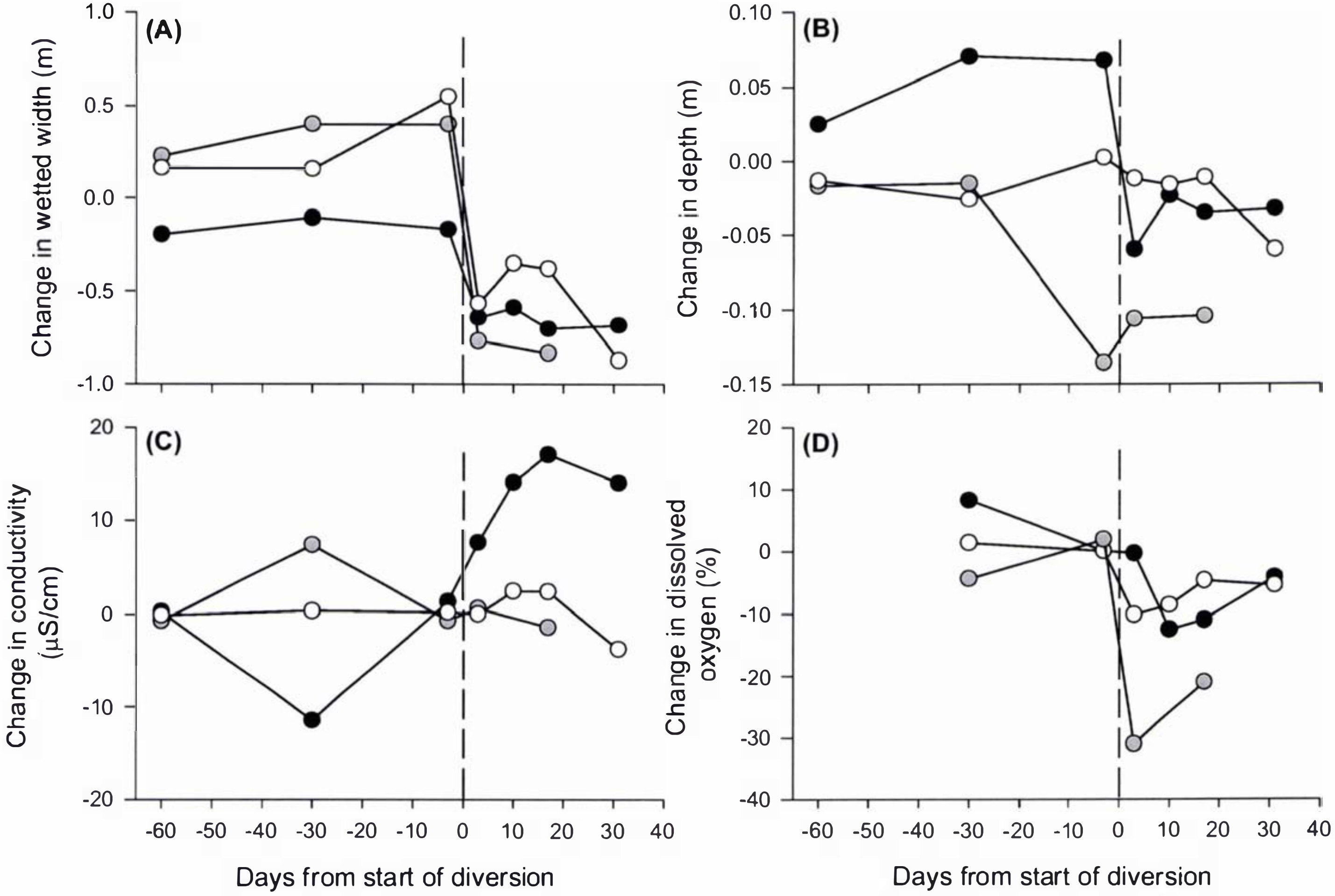

Figure 2. Change in (A) wetted width, (B) depth, (C) conductivity and (D) dissolved oxygen between control and impact sites on Booths Creek (grey symbols), Kiriwhakapapa Stream (black symbols) and Reef Creek (open symbols) before (December 2003-March 2004) and after (March-May 2004) discharge reduction began. Vertical dashed lines indicate the start of diversions.

Water temperature at the forested Reef Creek study site was considerably lower than the other study streams throughout the sampling period (Table 1). There were no differences in maximum daily temperature or daily temperature range between control and impact sites on Booths Creek, but maximum daily temperature and daily temperature range increased at the impact site after flow reduction on Kiriwhakapapa Stream (Table 1). We were unable to test for temperature changes at Reef Creek because the before-impact temperature logger was lost.

Periphyton

Flow reduction had no effect on periphyton biomass at Booths Creek ($F_{1,3} = 1.34$, $P = 0.37$), Kiriwhakapapa Stream ($F_{1,4} = 2.19$, $P = 0.21$) or Reef Creek ($F_{1,4} = 0.31$, $P = 0.61$) (Fig. 3).

Invertebrate community

Total invertebrate densities were higher in samples from impact sites compared with controls after diversion (Fig. 4). However, these increases in total density were not significant for any of the streams (Table 2). The five most common taxa in each stream increased in density between control and impact sites after diversion (Table 3). There were significant increases in Oligochaeta (Booths Creek and Kiriwhakapapa Stream), and for the leptophlebiid mayflies *Austroclima sepia* (Booths Creek), *Deleatidium* sp. (Kiriwhakapapa Stream), and *Zephlebia dentata* (Reef Creek) (Table 3). The largest percentage increases in density in each stream came from *Austroclima sepia* in Booths Creek (+851%), Orthocladiinae chironomids in Kiriwhakapapa Stream (+297%) and *Coloburiscus humeralis* (Family Coloburiscidae) in Reef Creek (+77%).

Taxonomic richness, percentage of EPT taxa, Berger Parker index, Simpson's index and QMCI were unchanged by flow reduction in all streams (Table 2, Table 4). There was an increase in the percentage of EPT individuals at Booths Creek, and the impact site at Kiriwhakapapa Stream had a lower value for the MCI than the control after diversions were started (Table 2, Table 4).

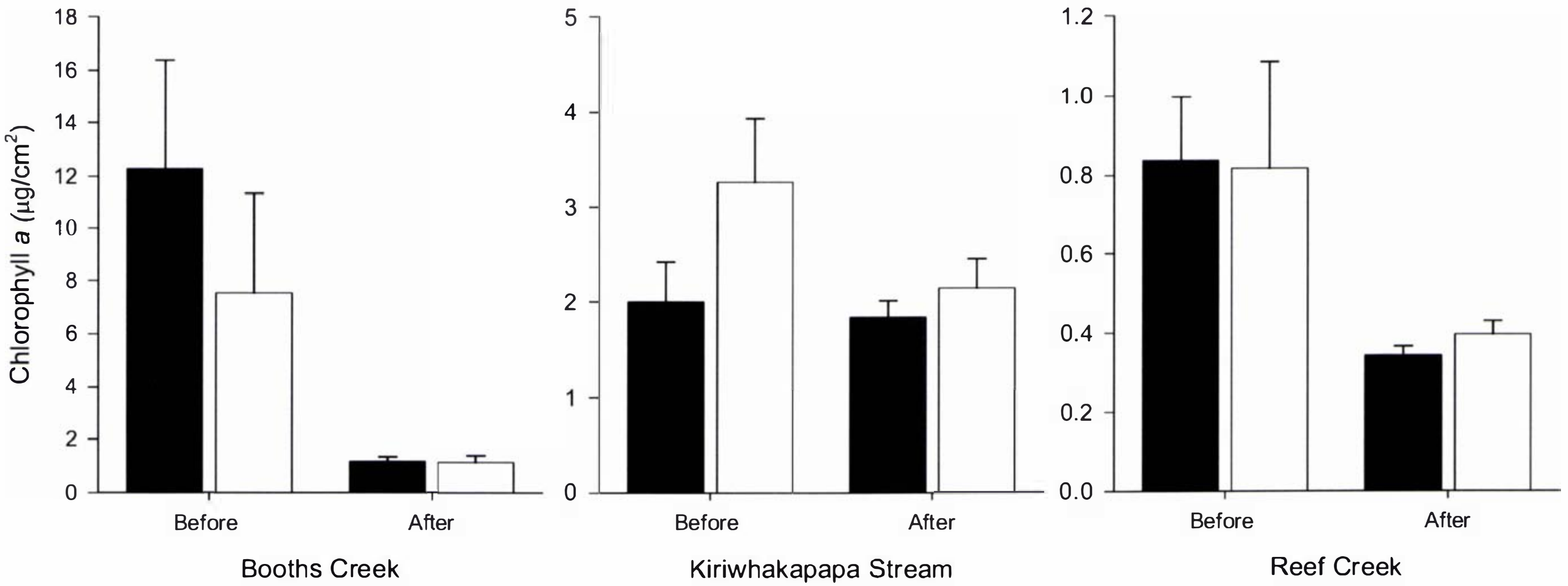

Figure 3. Mean chlorophyll *a* concentration (+ 1 S.E.) on cobbles from control (black bars) and impact (open bars) study sites before (December 2003-March 2004) and after (March-May 2004) discharge reduction began.

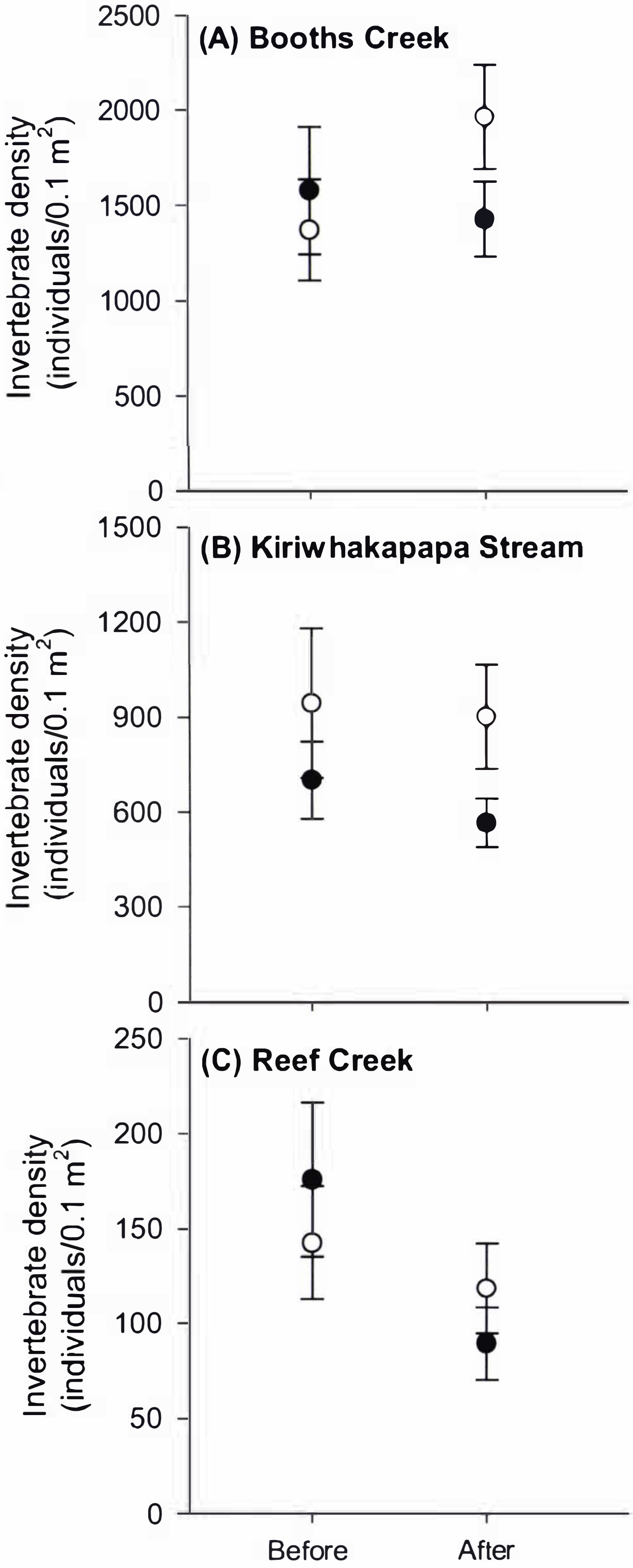

Figure 4. Mean (± 1 S.E.) invertebrate densities of control (black symbols) and impact (open symbols) sites before and after discharge reductions began at (A) Booths Creek, (B) Kiriwhakapapa Stream and (C) Reef Creek.

Table 2. *F* values for three factor ANOVA testing for the impacts of flow reduction on invertebrate community metrics at Booths Creek, Kiriwhakapapa Stream and Reef Creek between December 2003 and May 2004. The before-after × control-impact (BA*CI) interactions are the tests of interest in this model. Values significant at the 5% level are indicated in bold.

Stream	**Source of variation**	**d. f.**	**Invertebrate density**	**Number of taxa**	**% EPT individuals**	**% EPT taxa**	**Berger Parker index**	**Simpson's index**	**MCI**	**QMCI**
Booths Creek	Control-Impact (CI)	1, 3	0.14	0.11	9.01	0.38	2.18	1.39	0.50	0.00
	Before-After (BA)	1, 3	0.07	0.40	5.93	2.75	0.97	0.63	0.84	0.82
	Time within BA	3, 3	**11.29**	1.28	3.75	5.34	5.38	6.18	4.80	5.87
	BA*CI	1, 3	2.18	0.03	**18.36**	3.57	1.29	2.36	0.32	0.15
Kiriwhakapapa Stream	Control-Impact (CI)	1, 5	2.09	0.14	0.06	1.51	1.42	1.33	1.05	1.28
	Before-After (BA)	1, 5	0.01	1.83	2.00	2.65	0.05	0.01	**7.43**	3.84
	Time within BA	5, 5	3.40	2.96	**5.23**	4.37	0.63	0.60	**10.94**	**6.30**
	BA*CI	1, 5	0.18	0.65	0.35	0.02	0.09	0.01	**7.29**	0.00
Reef Creek	Control-Impact (CI)	1, 5	0.34	0.81	0.04	0.02	0.01	0.01	0.46	3.68
	Before-After (BA)	1, 5	0.34	2.08	5.27	**7.53**	3.67	5.18	0.42	5.04
	Time within BA	5, 5	4.02	4.75	**8.65**	4.29	3.64	3.14	1.88	3.43
	BA*CI	1, 5	0.82	0.45	2.48	0.25	0.72	0.39	0.04	2.76

Table 3. Mean density of invertebrates / 0.1 m^2 (± 1 S.E.) after discharge reduction at impact sites and the percentage increase in abundance between control and impact sites. Total densities and the five most common taxa in Booths Creek, Kiriwhakapapa Stream and Reef Creek during the after discharge reduction period are listed. *F* values for before-after × control-impact (BA*CI) interactions are included as a test for the impacts of flow reduction. Values significant at the 5% level are indicated in bold.

Stream	**Taxa**	**Classification**	**Mean density after impact (/ 0.1 m^2)**	**% increase control - impact**	**BA*CI interaction**
Booths Creek	Total number of individuals		1966 ± 274	37.0 %	$F_{1,3} = 2.18$
	Paracalliope fluviatilis	Amphipoda	1087 ± 169	6.0 %	$F_{1,3} = 0.42$
	Oligochaeta	Oligochaeta	304 ± 102	138.6 %	**$F_{1,3} = 12.26$**
	Elmidae	Coleoptera	231 ± 64	240.4 %	$F_{1,3} = 3.60$
	Potamopyrgus antipodarum	Gastropoda	154 ± 23	99.5 %	$F_{1,3} = 0.24$
	Austroclima sepia	Ephemeroptera	70 ± 15	851.4 %	**$F_{1,3} = 18.32$**
Kiriwhakapapa Stream	Total number of individuals		903 ± 165	59.0 %	$F_{1,5} = 0.18$
	Potamopyrgus antipodarum	Gastropoda	245 ● 85	10.6 %	$F_{1,5} = 0.78$
	Deleatidium sp.	Ephemeroptera	150 ± 33	91.8 %	**$F_{1,5} = 67.20$**
	Oligochaeta	Oligochaeta	82 ● 26	165.4 %	**$F_{1,5} = 13.60$**
	Orthocladiinae	Diptera	77 ± 39	297.2 %	$F_{1,5} = 0.27$
	Elmidae	Coleoptera	44 ± 9	12.0 %	$F_{1,5} = 1.38$
Reef Creek	Total number of individuals		119 ± 24	33.0 %	$F_{1,5} = 0.82$
	Deleatidium sp.	Ephemeroptera	53 ± 11	26.5 %	$F_{1,5} = 0.92$
	Zelandobius sp.	Plecoptera	13 ± 4	14.9 %	$F_{1,5} = 0.94$
	Coloburiscus humeralis	Ephemeroptera	14 ± 6	76.9 %	$F_{1,5} = 0.27$
	Zephlebia dentata	Ephemeroptera	10 ± 2	42.8 %	**$F_{1,5} = 6.35$**
	Orthopsyche thomasi	Trichoptera	6 ± 2	21.3 %	$F_{1,5} = 0.09$

Table 4. Mean (± 1 S.E.) values of invertebrate community metrics for control and impact sites at Booths Creek, Kiriwhakapapa Stream and Reef Creek between March and May 2004 (discharge reduction period).

Stream	**Treatment**	**Number of taxa**	**% EPT individuals**	**% EPT taxa**	**Berger Parker index**	**Simpson's index**	**MCI**	**QMCI**
Booths Creek	Control	14.0 ± 0.2	2.6 ± 0.1	30.1 ● 0.2	0.72 ± 0.05	0.54 ± 0.06	81.9 ± 2.1	4.5 ± 0.2
	Impact	15.2 ± 0.2	6.7 ± 1.2	37.5 ± 0.5	0.57 ± 0.00	0.39 ± 0.00	85.1 ● 1.3	4.5 ± 0.0
Kiriwhakapapa Stream	Control	21.5 ± 0.4	38.3 ± 2.1	55.9 ± 1.1	0.38 ± 0.02	0.21 ± 0.01	110.8 ● 0.9	5.1 ± 0.1
	Impact	21.2 ± 0.9	40.8 ± 4.2	53.8 ± 0.7	0.32 ● 0.06	0.17 ± 0.04	107.4 ± 1.1	4.9 ± 0.3
Reef Creek	Control	11.4 ± 0.5	89.5 ± 3.0	73.4 ± 1.4	0.50 ± 0.01	0.31 ± 0.01	137.7 ± 2.6	7.2 ± 0.1
	Impact	13.3 ± 1.1	87.4 ± 2.7	72.9 ± 2.9	0.47 ± 0.04	0.29 ± 0.04	139.8 ± 4.1	7.3 ± 0.2

Invertebrate drift propensity increased immediately after diversions started for impact sites at Booths Creek and Reef Creek (Fig. 5). A smaller increase in drift was observed at Kiriwhakapapa Stream. Drift propensities returned to control levels within a week of flow reduction at Kiriwhakapapa Stream and Reef Creek, but remained higher than control levels for the entire sampling period at Booths Creek (17 days).

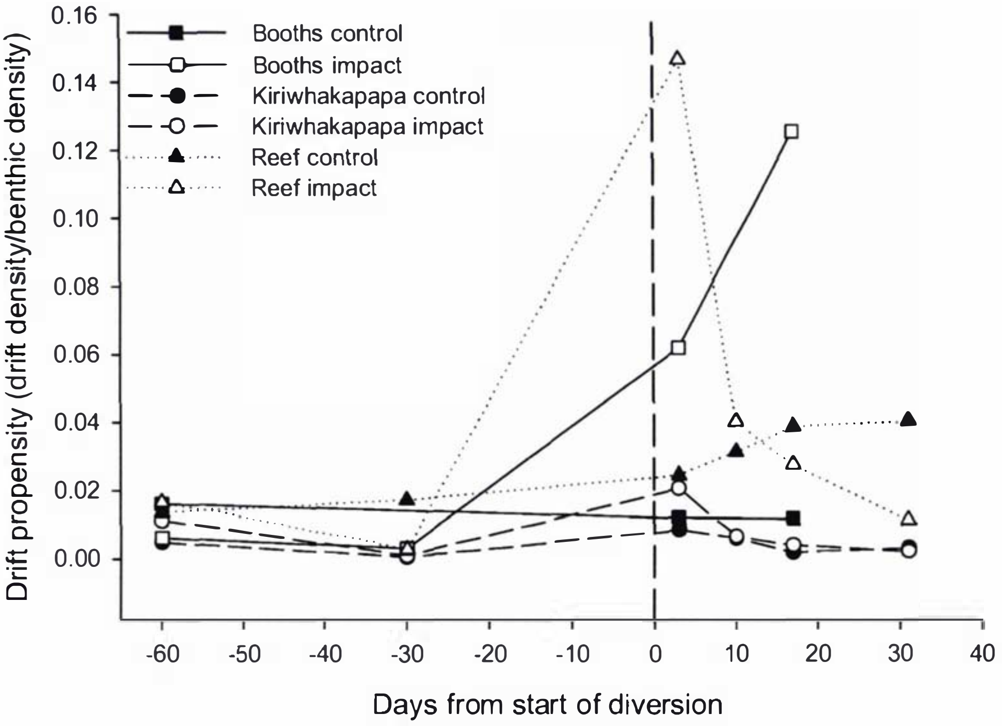

Figure 5. Mean invertebrate drift propensity over time for control and impact study sites at Booths Creek, Kiriwhakapapa Stream and Reef Creek before (December 2003-March 2004) and after (March-May 2004) discharge reduction began. The vertical dashed line indicates the start of diversions.

Analysis of similarity showed that there were no differences in invertebrate community structure between the four treatments (before control, before impact, after control, after impact) at Booths Creek (ANOSIM global $R = -0.18$, $P = 0.84$) or Reef Creek (ANOSIM global $R = 0.15$, $P = 0.14$) (Fig. 6). However, at Kiriwhakapapa Stream, there were differences among the treatments (ANOSIM global $R = 0.44$, $P < 0.01$). Although there was no difference between the control and impact sites before flow reduction (ANOSIM $R = -0.44$, $P = 1.00$), the invertebrate communities at these sites were significantly different after the diversion (ANOSIM $R = 0.46$, $P = 0.03$). At Kiriwhakapapa Stream, increases in the density of *Potamopyrgus antipodarum,* *Deleatidium* sp., Orthocladiinae, Oligochaeta and Chironominae after flow reduction were the main contributors to this community difference (SIMPER). The stress values of between 0.06 and 0.13 for these ordinations indicated that the two-dimensional pictures provided a good representation of the similarity data (Clarke & Warwick 2001).

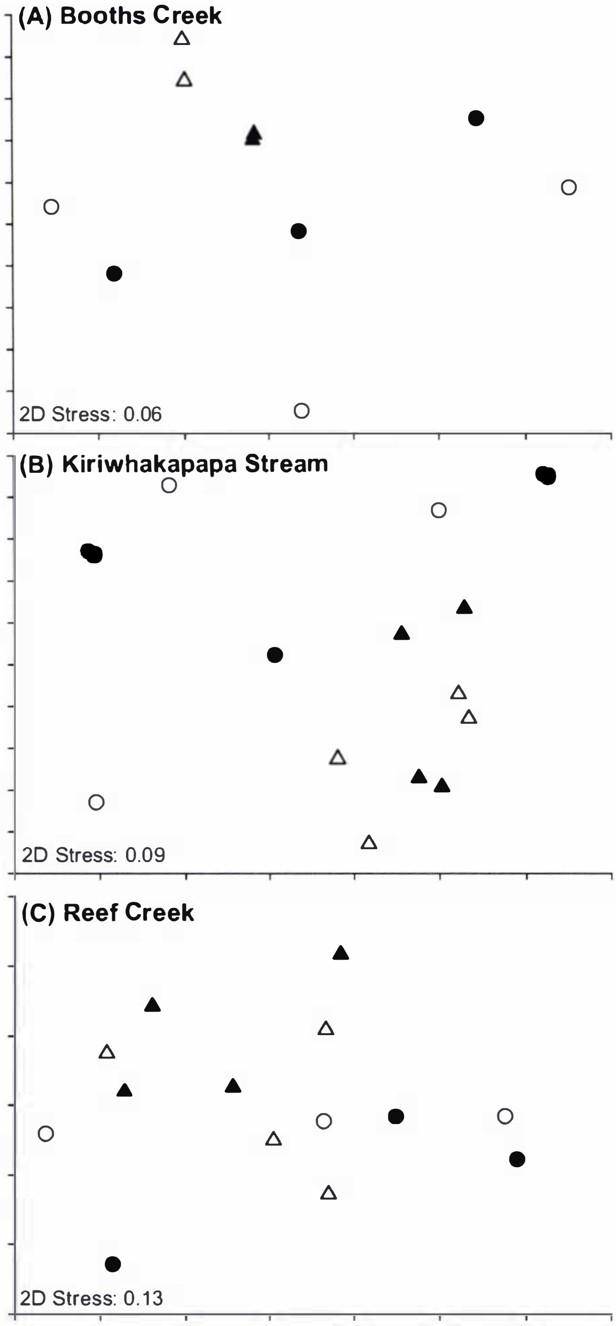

Figure 6. Non-metric multi-dimensional scaling (MDS) ordinations of mean invertebrate densities from each site on each sampling occasion before (circles) and after (triangles) flow reduction for control (black symbols) and impact (open symbols) sites at (A) Booths Creek, (B) Kiriwhakapapa Stream and (C) Reef Creek.

Discussion

In this study, we used weirs and diversions to reduce the discharge of three small streams in a controlled experimental test of the effects of water abstractions on instream habitat and invertebrate communities in a realistic setting. For these streams, short-term discharge reductions resulted in increased local invertebrate densities. We suggest that these increased invertebrate densities resulted from the concentration of invertebrates into the reduced wetted area.

Several previous studies have also reported increased benthic densities at sites with reduced discharge (e.g., Gore 1977, Rader & Belish 1999, Dewson *et al.* 2003, Suren *et al.* 2003). However, changes in wetted width often do not explain these increases, probably because increased invertebrate densities are a short-term response to reduced discharge. Following the closure of the Tongue River Reservoir Dam, Gore (1977) found large increases in drift and a threefold increase in benthic density downstream as wetted width decreased suddenly by 77% (23 m). In contrast, Rader & Belish (1999) found that invertebrate densities were 57% higher downstream of a mild diversion despite no corresponding loss of wetted perimeter. This diversion had been operating for many years and they suggested that the increased densities might be the result of increased fecundity and food availability because of higher temperatures downstream of the diversion. Dewson *et al.* (2003) also found increased densities of invertebrates at sites downstream of existing water abstractions with no decrease in wetted width or increase in temperature.

Observed increases of invertebrate drift during flow manipulations in several studies (Minshall & Winger 1968, Radford & Hartland-Rowe 1971, Gore 1977) suggest that invertebrate densities should decrease after discharge reduction. Invertebrate drift in this study peaked at impact sites relative to controls in the first few days following discharge reduction. However, since drifting invertebrates are a relatively small proportion of total benthic abundance, this did not reduce benthic densities. In fact, invertebrate densities actually increased at impact sites, probably because of a loss of habitat (wetted width) following discharge reduction. Increases in invertebrate density between control and impact sites varied for Booths Creek (+37%), Kiriwhakapapa Stream (+59%) and Reef Creek (+33%), even though the percentage of wetted width lost was similar (between 24-30%) for all streams. It is likely that the respective increases in density reflect the proportionate loss in riffle habitat at each site since our invertebrate sampling was concentrated in riffles, which should lose proportionally more width than pools or runs when discharge decreases. Our wetted width measurements included riffles, pools and runs; therefore, they underestimate the loss of riffle habitat.

Short-term discharge reductions had some effect on invertebrate community composition in Kiriwhakapapa Stream. Increased densities of many invertebrate taxa were largely responsible for these changes since there were no changes to taxonomic richness or evenness after the discharge reduction and no common taxa were eliminated by the altered conditions. Armitage & Petts (1992) also suggested that faunal abundance is more sensitive to discharge reductions than number of taxa, but still recognise the importance of looking at overall community change.

We hypothesised that our experimental flow manipulations would alter habitat availability and suitability, resulting in changes to the invertebrate community. There was a loss of wetted area, and reduced water velocity and depth, but no marked changes to water conductivity, water temperatures or dissolved oxygen levels. Periphyton biomass also remained unchanged. We had anticipated a decline in taxonomic richness and decreased benthic invertebrate densities if habitat suitability declined with flow reduction. However, the most obvious invertebrate community response to short-term discharge reduction in these streams was increased local invertebrate densities. Even with extreme discharge reductions (89-98%), our impact sites retained some areas with suitable habitat and water velocities for invertebrates. Mean velocities at sample sites in our impact reaches were between 0.14 and 0.24 m/s after discharge reduction. These velocities are not especially low, and the lack of change to invertebrate communities in these streams indicates that conditions were probably not too stressful. If discharge decreased for a longer period, we might expect more substantial changes to community composition since these might influence subsequent generations of invertebrates. Furthermore, adjustments to the temperature regime, dissolved oxygen levels, nutrient concentrations and sedimentation might become more important over time, as might the influence of biotic interactions within the community, especially where invertebrate densities increase.

We suggest that it is important to consider the duration of proposed water removal activities in making water allocation decisions. The timing and severity of the water abstraction are also important considerations, and these require further study. We found that the severe short-term water abstractions simulated in this study had minimal effect on invertebrate communities, other than increasing invertebrate density. If water abstractions are seasonal and separated by periods of high discharge (such as annual floods), then any changes in the distribution of invertebrates caused by short-term water abstraction are likely to be reset by high discharges that swamp the physical capacity of water collecting apparatus. In this regard, short-term water abstractions from small streams can be markedly different from those on larger waterways where substantial permanent structures (e.g., dams) are involved.

References

Armitage P.D. & Petts G.E. (1992) Biotic score and prediction to assess the effects of water abstractions on river macroinvertebrates for conservation purposes. *Aquatic Conservation: Marine and Freshwater Ecosystems,* **2,** 1-17.

Berger W.H. & Parker F.L. (1970) Diversity of planktonic Foraminifera in deep sea sediments. *Science,* **168,** 1345-1347.

Boothroyd I. & Stark J. (2000) Use of invertebrates in monitoring. In: *New Zealand Stream Invertebrates: Ecology and Implications for Management* (Eds K.J. Collier & M.J. Winterbourn), pp. 344-373. New Zealand Limnological Society, Christchurch, New Zealand.

Boulton A.J. (2003) Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. *Freshwater Biology,* **48,** 1173-1185.

Brasher A.M.D. (2003) Impacts of human disturbances on biotic communities in Hawaiian streams. *BioScience,* **53,** 1052-1060.

Castella E., Bickerton M., Armitage P.D. & Petts G.E. (1995) The effects of water abstractions on invertebrate communities in U.K. streams. *Hydrobiologia,* **308,** 167-182.

Clarke K.R. & Gorley R.N. (2006) *PRIMER v6: User Manual/Tutorial.* PRIMER-E: Plymouth.

Clarke K.R. & Warwick R.M. (2001) *Change to Marine Communities: An Approach to Statistical Analysis and Interpretation.* 2nd edn. PRIMER-E: Plymouth.

Corrarino C.A. & Brusven M.A. (1983) The effects of reduced stream discharge on insect drift and stranding of near shore insects. *Freshwater Invertebrate Biology,* **2**, 88-98.

Cortes R.M.V., Ferreira M.T., Oliveira S.V. & Oliveira D. (2002) Macroinvertebrate community structure in a regulated river segment with different flow conditions. *River Research and Applications,* **18**, 367-382.

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

Dewson Z.S., Death R.G. & James A.B.W. (2003) The effect of water abstractions on invertebrate communities in four small North Island streams. *New Zealand Natural Sciences,* **28,** 51-65.

Downes B.J., Barmuta L.A., Fairweather P.G., Faith D.P., Keough M.J., Lake P.S., Mapstone B.D. & Quinn G.P. (2002) Monitoring Ecological Impacts - Concepts and Practice in Flowing Waters. Cambridge University Press, Cambridge.

Englund G. & Malmqvist B. (1996) Effects of flow regulation, habitat area and isolation on the macroinvertebrate fauna of rapids in north Swedish rivers. *Regulated Rivers: Research and Management,* **12,** 433-445.

Everard M. (1996) The importance of periodic droughts for maintaining diversity in the freshwater environment. *Freshwater Forum,* **7,** 33-50.

Gordon N.D., McMahon T.A., Finlayson B.L., Gippel C.J. & Nathan R.J. (2004) *Stream Hydrology: An Introduction for Ecologists.* 2nd edn. John Wiley & Sons Ltd., West Sussex, England.

Gore J.A. (1977) Reservoir manipulations and benthic macroinvertebrates in a prairie river. *Hydrobiologia,* **55,** 113-123.

Graham A.A., McCaughan D.J. & McKee F.S. (1988) Measurement of surface area of stones. *Hydrobiologia,* **157,** 85-87.

Ham S.F., Wright J.F. & Berrie A.D. (1981) Growth and recession of aquatic macrophytes on an unshaded section of the River Lambourn, England, from 1971 to 1976. *Freshwater Biology,* **11,** 381-390.

Hilsenhoff W.L. (1987) An improved biotic index of organic stream pollution. *Great Lakes Entomologist,* **20,** 31-39.

Hinckley T.M. & Kennedy H.D. (1972) Fluctuations of aquatic and terrestrial invertebrates in drift samples from Convict Creek, California. *Northwest Science,* **46,** 270-276.

Jackson R.B., Carpenter S.R., Dahm C.N., McKnight D.M., Naiman R.J., Postel S.L. & Running S.W. (2001) Water in a changing world. *Ecological Applications,* **11,** 1027-1045.

Jowett I.G. (1997) Environmental effects of extreme flows. In: *Floods and Droughts: the New Zealand Experience* (Eds M.P. Mosley & C. P. Pearson), pp. 104-116. The Caxton Press, Christchurch, New Zealand.

Ladle M. & Bass J.A.B. (1981) The ecology of a small chalk stream and its responses to drying during drought conditions. *Archiv für Hydrobiologie,* **90,** 448-466.

Lenat D.R. (1988) Water quality assessment using a qualitative method for benthic macroinvertebrates. *Journal of the North American Benthological Society,* **7,** 222-233.

McIntosh M.D., Benbow M.E. & Burky A.J. (2002a) Effects of stream diversion on riffle macroinvertebrate communities in a Maui, Hawaii, stream. *River Research and Applications,* **18,** 569-581.

McIntosh A.R., Peckarsky B.L. & Taylor B.W. (2002b) The influence of predatory fish on mayfly drift: extrapolating from experiments to nature. *Freshwater Biology,* **47,** 1497-1513.

Minshall G.W. & Winger P.V. (1968) The effect of reduction in stream flow on invertebrate drift. *Ecology,* **49,** 580-582.

Poff N.L., Voelz N.J., Ward J.V. and Lee R.E. (1990) Algal colonization under four experimentally-controlled current regimes in a high mountain stream. *Journal of the North American Benthological Society,* **9,** 303-318.

Poff N.L. & Ward J.V. (1991) Drift responses of benthic invertebrates to experimental streamflow variation in a hydrologically stable stream. *Canadian Journal of Fisheries and Aquatic Science,* **48,** 1926-1936.

Poff N.L., Wellnitz T. & Monroe J.B. (2003) Redundancy among three herbivorous insects across an experimental current velocity gradient. *Oecologia,* **134,** 262-269.

Postel S.L. (1997) *Last Oasis.* W. W. Norton & Company, New York, N. Y., U.S.A.

Rader R.B. & Belish T.A. (1999) Influence of mild to severe flow alterations on invertebrates in three mountain streams. *Regulated Rivers: Research and Management,* **15,** 353-363.

Radford D.S. & Hartland-Rowe R. (1971) A preliminary investigation of bottom fauna and invertebrate drift in an unregulated and a regulated stream in Alberta. *Journal of Applied Ecology,* **8,** 883-903.

Richter B. (1993) Ecosystem level conservation at the nature conservancy: growing needs for applied research in conservation biology. *Journal of the North American Benthological Society,* **12,** 197-200.

SAS Institute Inc. (2004) *The SAS System for Windows.* SAS Institute Inc., Cary, North Carolina, U.S.A.

Simpson E.H. (1949) Measurement of diversity. *Nature,* **163,** 688.

Stark J.D. (1985) *A Macroinvertebrate Community Index of Water Quality for Stony Streams.* National Water and Soil Conservation Authority, Wellington, New Zealand.

Statzner B. & Higler B. (1986) Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. *Freshwater Biology,* **16,** 127-139.

Steinman A.D. & Lamberti G.A. (1996) Biomass and pigments of benthic algae. In: *Methods in Stream Ecology* (Eds F.R. Hauer & G. A. Lamberti), pp. 295-313. Academic Press, Inc., U.S.A.

Suren A.M., Biggs B.J.F., Duncan M.J. & Bergey L. (2003) Benthic community dynamics during summer low-flows in two rivers of contrasting enrichment 2. Invertebrates. *New Zealand Journal of Marine and Freshwater Research,* **37,** 71-83.

Vinson M.R. & Hawkins C.P. (1996) Effects of sampling area and subsampling procedure on comparisons of taxa richness among streams. *Journal of the North American Benthological Society*, **15,** 392-399.

Wood P.J. & Armitage P.D. (1999) Sediment deposition in a small lowland stream-management implications. *Regulated Rivers: Research and Management,* **15,** 199-210.

Wood P.J. & Petts G.E. (1999) The influence of drought on chalk stream macroinvertebrates. *Hydrological Processes,* **13,** 387-399.

Wood P.J., Agnew M.D. & Petts G.E. (2000) Flow variations and macroinvertebrate community responses in a small groundwater-dominated stream in south-east England. *Hydrological Processes,* **14,** 3133-3147.

Wright J.F. & Berrie A.D. (1987) Ecological effects of groundwater pumping and a natural drought on the upper reaches of a chalk stream. *Regulated Rivers: Research and Management,* **1,** 145-160.

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

CHAPTER 4

Invertebrate community responses to experimentally reduced discharge in small streams of different water quality

This chapter is under review for the Journal of the North American Benthological Society:
Dewson Z.S., James A.B.W. & Death R.G. Invertebrate community responses to experimentally reduced discharge in small streams of different water quality.

Abstract

Water abstraction can alter invertebrate community composition by changing the availability or suitability of habitat for invertebrates. Studies of drought and existing water abstractions provide much of the current knowledge on the influence of flow reduction on invertebrate communities. There are several published accounts of experimental flow reductions, but these tend to focus on invertebrate drift responses to changes in flow or are restricted to small-scale manipulations of velocity in artificial channels. It is unclear from previous studies what the outcomes of water abstraction are for the physical habitat and invertebrate communities of small permanent streams. To clarify these outcomes, we performed whole channel flow manipulations to imitate real water abstractions. We used weirs and diversions to reduce discharge by greater than 85% in three small New Zealand streams (11 to 84 L/s), ranging in water quality from pristine to moderately polluted. We sampled benthic invertebrates and periphyton at control and impact sites on each stream before and during two months of reduced discharge during summer 2005, and then left the diversions in operation throughout the following year to sample invertebrates again after 9 and 12 months of flow reduction. During the experiment, wetted width decreased by 24 to 34% at impact sites. At the same time, there were decreases in water velocity and depth but only small changes to conductivity, pH, dissolved oxygen and temperature at impact sites in these streams. At the pristine site, the density of invertebrates and percentage of EPT individuals decreased in response to reduced flows. Only taxonomic richness decreased at the mildly polluted stream, and reduced discharge had no affect on the invertebrate community at the stream with the lowest water quality. Overall community structure also changed in response to flow reduction at all but the lowest quality stream. Changes in community composition involved changes in the abundance of common taxa and the collection of fewer rare taxa per sample. Our results indicate that the impacts of water abstraction on invertebrate communities differ between streams that vary in water quality, probably because of the relative sensitivity of invertebrate assemblages to changes in the physical habitat of these streams.

Introduction

With an increasing global demand for water resources and the likelihood of climate change modifying the availability of that water, an understanding of the impacts of reduced flows on stream ecosystems is crucial to the effective management of streams. The increasing size and urbanisation of the human population, along with a continually expanding area of irrigated land are among many factors leading to increased worldwide water usage (Postel 1997, Arnell 1999). Meanwhile, numerous climate change scenarios provide conflicting views on the expected direction and magnitude of changes to precipitation (Arnell & Reynard 1996, Christensen *et al.* 2004). In any case, changes to the global distribution of fresh water (Jackson *et al.* 2001) will make it even more difficult to balance the needs of human society with the requirements of freshwater ecosystems in many parts of the world.

There is a shortage of scientific data describing the quantity and timing of water required to protect stream ecosystems of any size (Richter 1993, Chapter 1). Small streams are not exempt from the rising pressure on water resources. In fact, with many larger waterways already over exploited, we expect that usage of water from smaller streams for purposes such as irrigation will only increase. There has already been a five-fold increase in irrigated land over the last century (Postel 1997), and agricultural irrigation is the largest global user of water (Arnell 1999).

Hydrological changes that result from water abstraction can alter the availability and suitability of instream habitat for invertebrates. This can potentially alter invertebrate community composition. Wetted width often decreases with flow reduction (e.g., Gore 1977, Cowx *et al.* 1984, Brasher 2003), reducing habitat availability. The suitability of the remaining habitat can be altered by decreased water velocities and depths (e.g., Minshall & Winger 1968, Ham *et al.* 1981, McIntosh *et al.* 2002a), increased sedimentation (e.g., Wright & Berrie 1987, Wood & Petts 1994, Castella *et al.* 1995, Wood & Armitage 1999), changes to nutrient concentrations (e.g., Ladle & Bass 1981, Rader & Belish 1999), increased water temperatures (e.g., Everard 1996, Rader & Belish 1999) and lowered dissolved oxygen levels (Everard 1996, Jowett 1997). As a consequence, flow reductions often decrease invertebrate diversity (e.g., Rader & Belish 1999, Wright & Symes 1999, Wood & Armitage 1999) and either increase (e.g., Wright & Berrie 1987, Rader & Belish 1999, Suren *et al.* 2003) or decrease invertebrate abundance (e.g., Englund & Malmqvist 1996, Cazaubon & Giudicelli 1999, Wood *et al.* 2000).

Changes to invertebrate community composition with decreasing flow might depend on the species present. Many species have specific water velocity requirements, while others have rather general requirements (Jowett 1992). Therefore, changes in habitat with flow reduction can affect species differently. In this way, the initial composition of the invertebrate community controls the invertebrate community response to flow reduction. The habitat changes generated by water abstraction vary widely, depending on characteristics such as channel morphology, stability, enrichment, stream size, and temperature regime. Not surprisingly then, outcomes from studies of invertebrate responses to reduced discharge are highly variable (e.g., Bickerton *et al.* 1993, Castella *et al.* 1995, Dewson *et al.* 2003).

Much of the current knowledge of invertebrate community responses to reduced flows comes from investigations of droughts and existing water abstractions (e.g., Castella *et al.* 1995, Wright & Symes 1999, McIntosh *et al.* 2002a). Often, these observational studies lack pre-impact data or the appropriate reference sites to identify reduced flow as the only cause of the observed effects (Boulton 2003). This complication can be overcome by using experimental flow manipulations. There are several published accounts of experimental flow reductions, but these tend to focus on invertebrate drift responses to changing flow (e.g., Hinckley & Kennedy 1972, Corrarino & Brusven 1983, Poff & Ward 1991), or involve small-scale manipulations of velocity in artificial channels (e.g., Poff *et al.* 1990, Poff *et al.* 2003). It is unclear from previous studies what the outcomes of water abstraction are for the physical habitat and invertebrate communities of small permanent streams. To clarify these outcomes, we performed whole channel flow manipulations to imitate real water abstractions, using weirs and diversions to remove water from the natural channels of three small streams for one month (Dewson *et al.* 2007). Streams in this study ranged in water quality from pristine to highly modified. The following summer we reinstalled weirs on these streams to create longer-term flow reductions for the current study. We were able to control the magnitude of flow reduction and gather before and after data at upstream (control) and downstream (impact) sites. We hypothesized that reduced discharge would favour the increase of taxa with preferences for lower velocity conditions, and lead to a decline of more sensitive taxa and those with highly specific habitat preferences. We expected that decreasing discharge in these streams would decrease habitat availability and suitability for invertebrates by altering flow characteristics, causing periphyton to proliferate, and increasing sedimentation. Consequently, we anticipated increased invertebrate drift, decreased benthic invertebrate densities and reduced taxonomic richness at impact sites relative to controls.

Methods

Study sites

This discharge reduction experiment was conducted on three small streams in the Wairarapa Region of the lower North Island, New Zealand: Booths Creek and unnamed tributaries of Kiriwhakapapa Stream and Reef Creek. The three perennial, runoff fed streams range in discharge from 27 to 250 L/s (mean summer discharge) and represent differing levels of water quality. Water quality is classified as moderately polluted at Booths Creek using the Macroinvertebrate Community Index (MCI) (Stark 1985), whereas the Kiriwhakapapa Stream tributary is mildly polluted and Reef Creek has clean water. Water quality in these streams reflects the intensity of agricultural landuse in their catchments.

Booths Creek (41° 04 40.29'S 175° 31 58.53'E) is a small (250 L/s), low gradient, meandering stream, with pool-riffle morphology and gravel-cobble substrate. Flood flows generally produce a narrow, peaked hydrograph for this stream, but flood recession is sometimes slower, depending on the inflow received from the stock watering channels that influence its flow regime. Cropping land surrounds Booths Creek at the study site, with patches of willow (*Salix* spp.) in the riparian zone.

The Kiriwhakapapa Stream tributary is a small (110 L/s) stream in the foothills of the Tararua Ranges (40° 49 07.10'S 175° 34 21.04'E). This meandering stream also has a pool-riffle morphology and gravel-cobble substrate, with fine sediments contributed by bank erosion. Flood flows produce a narrow, peaked hydrograph for this stream. The study site on the Kiriwhakapapa Stream tributary is within an extensive sheep and beef farm where stock has access to the stream and the channel has little shading in the study reaches.

The Reef Creek tributary is a relatively pristine, headwater stream (27 L/s) within a native forest catchment (40° 48 34.46'S 175° 32 21.84'E). The high gradient channel of this stream is characterized by pool, step and riffle sequences and gravel-boulder substrate with outcropping bedrock. Of the three study streams, the Reef Creek tributary is the flashiest, with flood flows producing very narrow, peaked hydrographs. The study site on the Reef Creek tributary is in a V shaped valley, with the forest canopy providing almost complete shade to the channel in the study reaches.

Low flows occur during the Austral summer in these streams and higher flows occur frequently throughout the rest of the year. There are no historical flow records for these streams and no history of water abstraction at the study sites. We will subsequently refer to unnamed tributaries by the names of the streams they feed.

Experimental design

We constructed weirs and diversions on three streams to reduce stream discharge for a distance of approximately 100 m. This distance provided enough area for invertebrate sampling and was not long enough for flow to be restored by groundwater inflow. Weirs extended across the entire stream, with overflow only occurring during flood flows. The wooden board weirs were not completely sealed so that a proportion of the flow and invertebrates could move through, under and around these weirs, whilst the majority of the flow was diverted out of the experimental reaches through open diversion channels (Booths Creek and Kiriwhakapapa Stream) or diversion pipes (Reef Creek). By removing a high proportion of the discharge in this way, we have created a barrier to invertebrate drift into downstream reaches. However, this approach is consistent with the type of water abstraction that occurs from streams of this size. Study reaches were identified upstream (control) and downstream (impact) of weirs on each stream. Each reach was sampled on three occasions prior to discharge reduction (monthly between November 2004 and January 2005) and two occasions while discharge reduction was in operation during summer (after one month and two months), between January and March 2005. Diversions remained in place for the rest of the year, although high flow overtopped weirs on several occasions during winter. We returned to sample each site 9 and 12 months after the diversions began, in October 2005 and January 2006. For each stream, we sampled control and impact sites on the same day. This type of design is a before-after, control-impact design with samples paired in time (BACIP) (Downes *et al.* 2002).

Flow related and physicochemical characteristics

Throughout the experiment, we recorded water height at intervals of 20 minutes using TruTrack WT-HR 1000 Water Height Data Loggers with an accuracy of ±1%. We calculated discharge on each sampling occasion by measuring depth and velocity at 0.4 × depth from the bed for at least ten equidistant intervals across the stream using a Marsh McBirney Inc. Model 2000 Portable Flowmeter to an accuracy of 0.01 m/s. The relationship between water height and discharge was described using a power function ($y = cx^b$, where c and b are constants) so that discharge could be calculated from the water height records (Gordon *et al.* 2004). Average measurements of conductivity (± 1 μS/cm), dissolved oxygen (± 0.2 mg/L) and pH (± 0.2 units) were recorded on each invertebrate sampling occasion from approximately an hour of logging at intervals of one minute using a YSI Incorporated multi-probe system instrument (YSI 556 MPS). Logging was completed over two consecutive hours at control and impact sites on each stream around midday. Temperature was recorded every 30 minutes throughout the study using Onset Hobo® H8 temperature loggers. Wetted width of the channel was measured at 14 fixed locations at five metre intervals along the study reach at each sampling. The coverage of fine sediment on the substrate was visually estimated by one person at 15 randomly selected transects at each study site on three occasions while diversions were operating (after > 8 months of flow reduction). At each transect, we estimated the percentage of substrate covered by fine sediment within a 300 mm wide strip across the width of the stream. From these measurements, we calculated the average percentage cover of fine sediment for each site and time.

Invertebrate sampling protocol

At each site, five Surber samples (area = 0.1 m^2) were collected from within riffle habitat and preserved in 10% formalin. We expected that this habitat type would change the most after we reduced the discharge, since at very low flows, riffles may dry completely, leaving a series of isolated pools (Gordon *et al.* 2004). Depth and velocity were recorded at each Surber sample location and sample locations were marked to avoid repeat sampling on subsequent visits. Prior to benthic sampling on each occasion, we collected drift samples. These were installed mid afternoon and remained in the stream overnight (for approximately 18-20 hours). Drift samples were collected in two nets (105 mm × 55 mm mouth, 250-μm mesh), positioned just below the water surface, side by side at the downstream end of each control and impact reach. Invertebrate samples were rinsed through a 500 μm Endecott sieve and sub-sampled. We used a sample splitter to divide the sample into four parts and sorted sequential sub-samples until at least 200 individuals were removed. The entirety of each sub-sample was processed. Vinson & Hawkins (1996) found a rapid increase in the number of taxa found as the number of individuals examined increased up to 200 individuals, after which the rate of increase slowed considerably. However, to avoid missing rare taxa, we scanned the remainder of the sample for taxa not present in the sub-sample. Invertebrates were identified to genus or species level where possible using the keys of Winterbourn (1973), Chapman & Lewis (1976), Winterbourn *et al.* (2000) and Smith (2003), except for oligochaetes (class) and chironomids (sub-family).

Periphyton sampling protocol

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

Data analysis

We calculated the total number of individuals, expected number of taxa from 200 individuals, the percentage of Ephemeroptera, Plecoptera, and Trichoptera (EPT) individuals (Lenat 1988) and Simpson's index (Simpson 1949) for each sample to describe the invertebrate communities. Since *Oxyethira albiceps* is a particularly pollution tolerant taxon compared to other Trichoptera (Boothroyd & Stark 2000), it was excluded from percentage EPT calculations, but included for all other analyses. Although not designed to detect the effects of discharge reductions, the New Zealand equivalent of the Hilsenhoff Biotic Index (Hilsenhoff 1987), the Macroinvertebrate Community Index (MCI) (Stark 1985) and its quantitative variant the QMCI (Stark 1985) were also calculated for each sample. We calculated drift densities (per m^3) by correcting for discharge through each net, based on the velocity at net entrances. From this, we calculated drift propensity (drift density/benthic density) to ensure that drift densities did not simply reflect changes to benthic density (McIntosh *et al.* 2002b).

Data from each stream were analysed separately because there were substantial differences in invertebrate communities between the streams. For all indices, we calculated a mean value for each site on each sampling occasion. We also calculated site averages for depth, velocity, conductivity, pH, dissolved oxygen, chlorophyll *a* and temperature measurements from each sampling occasion. These physical characteristics, as well as invertebrate community indices and the densities of the five most common taxa in each stream were used as dependent variables for three factor (control-impact (CI), before-after (BA), and times) analysis of variance (ANOVA) in SAS (2004). Downes *et al.* (2002) suggested this model for the BACIP design, with the test for impact being the BA*CI interaction term. For all invertebrate measures, we used this model to test whether the discharge reduction was having an effect during the initial two months of summer flow reduction and after one year of reduced flow. We transformed data using $\log_{10}$ or square root when necessary to reduce heteroscedasticity. In order to test the difference in discharge between control and impact sites using mean daily discharge data, we used a one-way ANOVA to test the H_0: mean daily discharge at control = mean daily discharge at impact, since discharge was not recorded at the impact site before flow reduction began. We excluded daily discharge data between April and October 2005 because invertebrates were not sampled during this winter period. Sediment cover data were also tested with one-way ANOVA because we only measured this after flow reduction began.

Similarities between assemblages of mean invertebrate densities for each stream (after fourth root transformation) were presented in two dimensions using non-metric multi-dimensional scaling (MDS) in PRIMER (Clarke & Gorley 2006) and the trajectory of data points over time superimposed. We used a one-way analysis of similarity (ANOSIM) to test the null hypothesis that there were no differences between the four treatments (control before, impact before, control after, impact after) within the two months summer discharge reduction. We repeated the test, with samples from 9 and 12 months included with the after treatments. ANOSIM computes a test statistic that contrasts the differences between sites with those within sites using ranked similarities and then calculates statistical significance by permutation (Clarke & Warwick 2001). Pairwise tests were used to compare control and impact sites within the before and after time periods and the contributions of individual species to the difference between communities at control and impact sites were examined separately for each stream with the similarity percentages (SIMPER) routine in PRIMER.

Results

Effects of discharge reduction on habitat characteristics and periphyton biomass

During the Austral summer, our weirs and diversions decreased discharge by an average of 94, 89 and 91% in Booths Creek, Kiriwhakapapa Stream and Reef Creek respectively

(Table 1). Maximum discharge reductions were greater than 97% for each of the streams at some time during the experiment (based on water heights recorded at intervals of 20 minutes). Water did not spill over the weirs within the initial two months of sampling, but throughout the year, we recorded heightened flows at impact sites several times and observed overflowing weirs on all streams (Fig. 1).

After discharge reduction began, wetted width decreased at impact sites by 22, 38 and 31% of control widths on Booths Creek, Kiriwhakapapa Stream and Reef Creek (Table 1). Water depth only decreased significantly at Kiriwhakapapa Stream. Velocities decreased by 52% to 0.22 ± 0.05 m/s at Booths Creek, by 89% to 0.07 ± 0.02 m/s at Kiriwhakapapa Stream and by 84% to 0.05 ± 0.02 m/s at Reef Creek compared to controls (Table 1).

Conductivity, pH, dissolved oxygen, and chlorophyll *a*, were largely unaltered by discharge reduction in these streams (Table 1). Even when statistically significant, differences to these variables between control and impact sites following discharge reduction were very small. There was an increase in conductivity (5.3 μS/cm) and decrease in dissolved oxygen (1.02 mg/L) at the impact site on Reef Creek (Table 1). Although the difference in periphyton biomass between control and impact sites on Booths Creek appears large, it is not statistically significant (Table 1). In contrast, the small (0.60 $\mu g/cm^2$) decrease in chlorophyll *a* concentration between control and impact sites on Reef Creek was significant (Table 1).

Mean daily temperatures were lower at impact sites after discharge reduction for Booths Creek ($F_{1, 127} = 83.7$, $P < 0.01$) and Kiriwhakapapa Stream ($F_{1, 127} = 58.0$, $P < 0.01$) over the initial two months of flow reduction. The decrease in mean daily temperature for the impact site at Reef Creek was not significant ($F_{1, 127} = 1.4$, $P = 0.23$). However, the differences in means were on average less than 1°C, with control means of 19°C, 18°C and 13°C for Booths Creek, Kiriwhakapapa Stream, and Reef Creek respectively. Maximum daily temperatures were also lower at impact sites on each stream (Booths Creek, $F_{1, 127} = 143.8$, $P < 0.01$; Kiriwhakapapa Stream, $F_{1, 127} = 56.2$, $P < 0.01$; Reef Creek, $F_{1, 127} = 11.9$, $P < 0.01$). The highest temperatures recorded during the first summer of the experiment were at control sites on each stream and these maximum temperatures were between 0.4 and 1.2°C higher than at corresponding impact sites. The maximum temperature recorded at the impact site on Booths Creek during the experiment was 26.0°C, Kiriwhakapapa Stream reached 27.9°C, and Reef Creek a maximum of 14.9°C.

Table 1. Mean (± 1 S.E.) values of physicochemical variables at control and impact sites at each sampling after discharge reduction in Booths Creek, Kiriwhakapapa Stream and Reef Creek between January 2005 and January 2006. Percentage changes are from control to impact sites during experimental discharge reduction. *F* values for before-after × control-impact interactions (BA*CI) are included as a test for impacts of flow reduction. In the case of discharge, we test the H_0: mean daily discharge at control = mean daily discharge at impact (during sampling period), since discharge was not recorded at the impact site before flow reduction. Values significant at the 5% level are indicated in bold. This table continues on the following page.

Stream	**Booths Creek**	**Kiriwhakapapa Stream**	**Reef Creek**
Discharge control (L/s)	229.5 ± 20.0	47.8 ± 6.6	36.9 ± 11.5
Discharge impact (L/s)	13.4 ± 1.4	5.2 ± 0.8	3.4 ± 0.9
BA*CI	**$F_{1,232} = 276.22$**	**$F_{1,276} = 271.27$**	**$F_{1,273} = 37.45$**
% change discharge	-94.2%	-89.2%	-90.8%
Wetted width control (m)	3.93 ± 0.39	2.25 ± 0.03	1.96 ± 0.16
Wetted width impact (m)	3.05 ± 0.41	1.39 ± 0.07	1.35 ± 0.02
BA*CI	**$F_{1,4} = 39.73$**	**$F_{1,5} = 23.25$**	**$F_{1,4} = 11.86$**
% change wetted width	-22.4%	-38.2%	-31.1%
Depth control (m)	0.17 ± 0.02	0.11 ± 0.01	0.08 ± 0.01
Depth impact (m)	0.10 ± 0.02	0.05 ± 0.01	0.07 ± 0.00
BA*CI	$F_{1,5} = 3.02$	**$F_{1,5} = 8.44$**	$F_{1,5} = 5.08$
% change depth	-41.2%	-54.5%	-12.5%
Velocity control (m/s)	0.46 ± 0.04	0.63 ± 0.04	0.31 ± 0.11
Velocity impact (m/s)	0.22 ± 0.05	0.07 ± 0.02	0.05 ± 0.02
BA*CI	**$F_{1,5} = 7.73$**	**$F_{1,5} = 44.09$**	**$F_{1,5} = 6.67$**
% change velocity	-52.2%	-88.9%	-83.9%

Table 1 (continued). Mean (± 1 S.E.) values of physicochemical variables at control and impact sites at each sampling after discharge reduction in Booths Creek, Kiriwhakapapa Stream and Reef Creek between January 2005 and January 2006. Percentage changes are from control to impact sites during experimental discharge reduction. F values for before-after × control-impact interactions (BA*CI) are included as a test for impacts of flow reduction. Values significant at the 5% level are indicated in bold.

Stream	**Booths Creek**	**Kiriwhakapapa Stream**	**Reef Creek**
Conductivity control (µS/cm)	152.5 ± 6.1	85.8 ± 6.8	55.6● 1.8
Conductivity impact (µS/cm)	144.7 ± 12.9	81.3 ± 3.3	60.9 ± 1.2
BA*CI	$F_{1,5} = 0.82$	$F_{1,5} = 0.55$	**$F_{1,5} = 36.37$**
% change conductivity	-5.1%	-5.2%	+9.5%
pH control	8.0 ± 0.5	8.1 ± 0.4	7.1 ± 0.1
pH impact	7.7 ± 0.4	7.1 ± 0.1	7.3 ± 0.1
BA*CI	$F_{1,5} = 1.23$	$F_{1,5} = 6.20$	$F_{1,5} = 1.78$
% change pH	-3.4%	-12.1%	+1.7%
Dissolved oxygen control (mg/L)	8.6 ± 1.2	9.7 ± 0.3	10.1 ± 0.5
Dissolved oxygen impact (mg/L)	7.9 ± 1.0	8.8 ± 0.6	9.0 ± 0.4
BA*CI	$F_{1,5} = 0.72$	$F_{1,5} = 1.19$	**$F_{1,5} = 6.79$**
% change dissolved oxygen	-7.6%	-9.6%	-10.2%
Chlorophyll *a* control (µg/cm^2)	6.1 ± 3.3	3.9 ± 0.7	1.6 ± 0.2
Chlorophyll *a* impact (µg/cm^2)	2.1 ± 0.5	3.5 ± 0.6	1.0 ± 0.1
BA*CI	$F_{1,5} = 1.67$	$F_{1,5} = 1.34$	**$F_{1,5} = 9.81$**
% change chlorophyll *a*	-65.0%	-11.0%	-37.5%

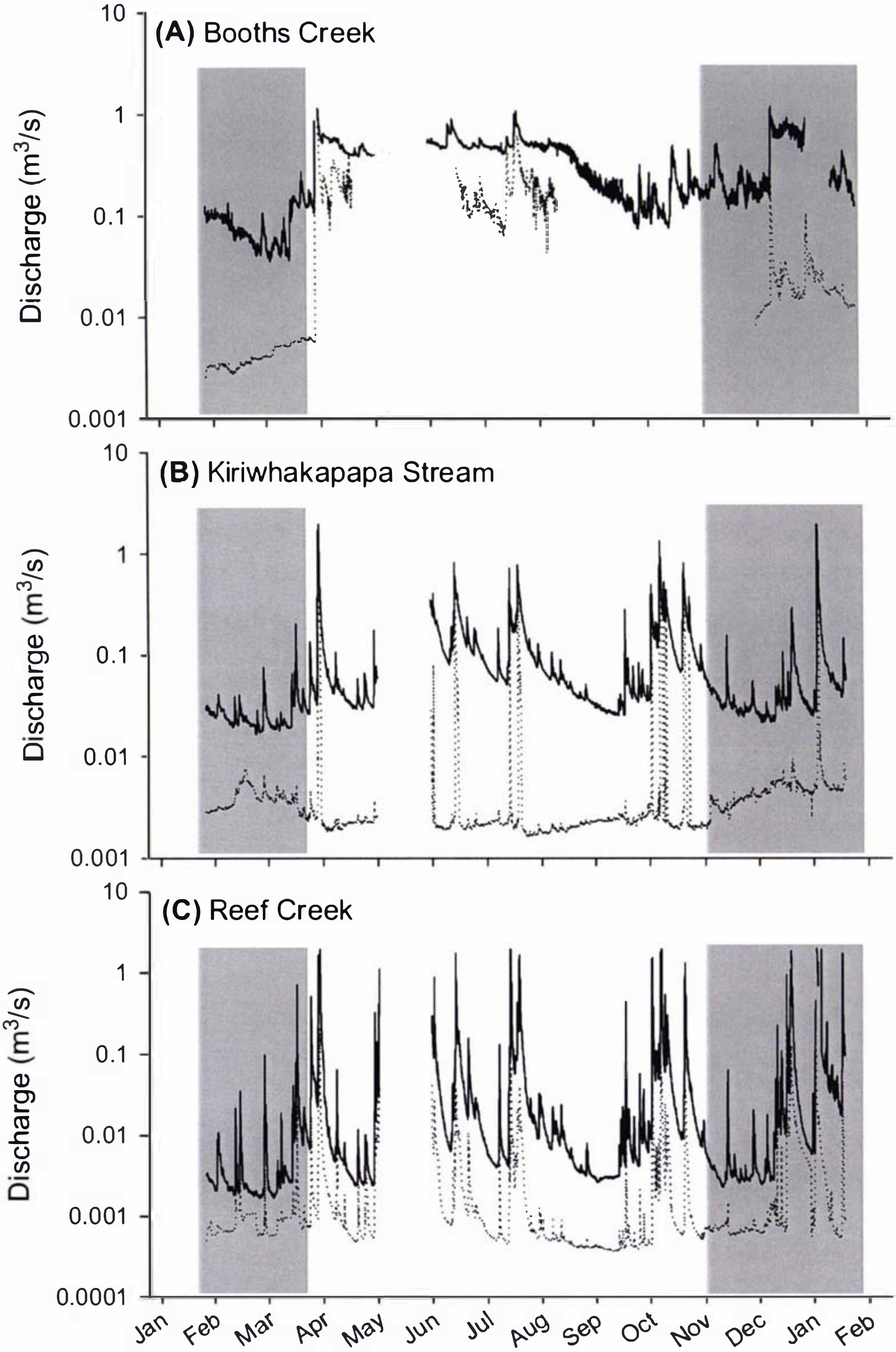

Figure 1. Calculated discharge (log scale) over time since discharge reduction began for control (upper line) and impact (lower dotted line) sites on (A) Booths Creek, (B) Kiriwhakapapa Stream and (C) Reef Creek between January 2005 and January 2006. Sampling occurred within grey shaded areas of the hydrograph.

After flow reduction, fine sediments covered a significantly greater percentage of the substrate at impact sites on Booths Creek (control = 9.2%, impact = 46.4%) ($F_{1,88}$ = 74.1, $P < 0.01$), and Kiriwhakapapa Stream (control = 43.0%, impact = 81.2%) ($F_{1,88}$ = 66.5, $P < 0.01$). There was no difference in sediment cover between control and impact sites on Reef Creek ($F_{1,88} = 0.3$, $P = 0.58$), with an average of 11.9% cover overall.

Effects of discharge reduction on invertebrate community diversity

During the second month of discharge reduction, the density of invertebrates decreased at the impact site on Reef Creek (Table 2, Fig. 2) as did the percentage of EPT individuals present and the QMCI value. At the same time, the number of taxa was unchanged relative to the control site (Table 2). These differences persisted after one year of flow reduction at this stream (Table 2). Initially, only taxonomic richness decreased after discharge reduction on Kiriwhakapapa Stream, although after one year, QMCI was also lower for the impact site at this stream (Table 2). Neither density nor taxonomic richness altered after discharge reduction in Booths Creek (Table 2, Fig. 3). Values of Simpson's index for impact sites did not change relative to controls after the discharge reduction for any of the streams (Table 2).

The five most common taxa at Booths Creek made up 90% of total invertebrate abundance, with Amphipoda: *Paracalliope fluviatilis* dominating the community (*Paracalliope fluviatilis* (68%), Oligochaeta (10%), Elmidae (6%), Orthocladiinae (3%) and Leptophlebiidae: *Austroclima sepia* (3%)). The abundances of these taxa did not change after diversion (Table 2).

In contrast, the five most common taxa at Kiriwhakapapa Stream made up 72% of invertebrate abundance and a single taxon was not especially dominant (Orthocladiinae (21%), Chironominae (19%), Gastropoda: *Potamopyrgus antipodarum* (16%), Oligochaeta (11%), and Leptophlebiidae: *Deleatidium* sp. (5%)). Of these, both *Potamopyrgus antipodarum* (Fig. 4A) and *Deleatidium* sp. (Fig. 4B) decreased in abundance at the impact site relative to control during the second month of discharge reduction, but the difference in *Potamopyrgus antipodarum* abundance was not maintained over the year of flow reduction (Table 2).

Table 2. Percentage change between control and impact sites after flow reduction for invertebrate community metrics and the densities of the five most abundant taxa at Booths Creek, Kiriwhakapapa Stream and Reef Creek between January and March 2005 (initial 2 months of flow reduction). *F* values for before-after × control-impact interactions (BA*CI) are included as the test of impact after two months (January to March 2005) and one year (January 2005 to January 2006) of flow reduction. Values significant at the 5% level are indicated in bold.

Stream	**Booths Creek**			**Kiriwhakapapa Stream**			**Reef Creek**		
	%	2 months $F_{1,3}$	1 year $F_{1,5}$	%	2 months $F_{1,3}$	1 year $F_{1,5}$	%	2 months $F_{1,3}$	1 year $F_{1,5}$
Number of individuals	+76%	1.09	0.90	-44%	3.85	6.24	**-57%**	**122.56**	**23.13**
Number of taxa	-13%	1.31	1.04	**-19%**	**9.58**	**11.41**	+3%	1.17	3.49
% EPT individuals	-56%	0.40	0.24	+9%	0.36	0.06	**-26%**	**18.49**	**14.93**
Simpson's index	+36%	1.39	0.53	+16%	1.80	5.87	-26%	0.04	0.02
QMCI	+15%	6.54	2.45	-15%	2.45	**6.71**	**-15%**	**18.50**	**10.28**
Paracalliope fluviatilis	+143%	2.01	1.17						
Elmidae	+105%	1.36	2.24						
Austroclima sepia	-56%	0.03	0.06						
Oligochaeta	-18%	0.04	0.11	+95%	1.25	0.98			
Potamopyrgus antipodarum				**-87%**	**29.45**	5.52			
Chironominae				-80%	2.01	6.00	-58%	1.89	1.41
Deleatidium sp.				**-85%**	**397.83**	**28.63**	**-78%**	**23.60**	**15.84**
Orthopsyche sp.							**-84%**	**19.05**	**18.17**
Zelandobius sp.							**-59%**	**35.71**	4.74
Orthocladiinae	+5%	0.07	0.38	+10%	0.08	0.93	+87%	0.20	0.01

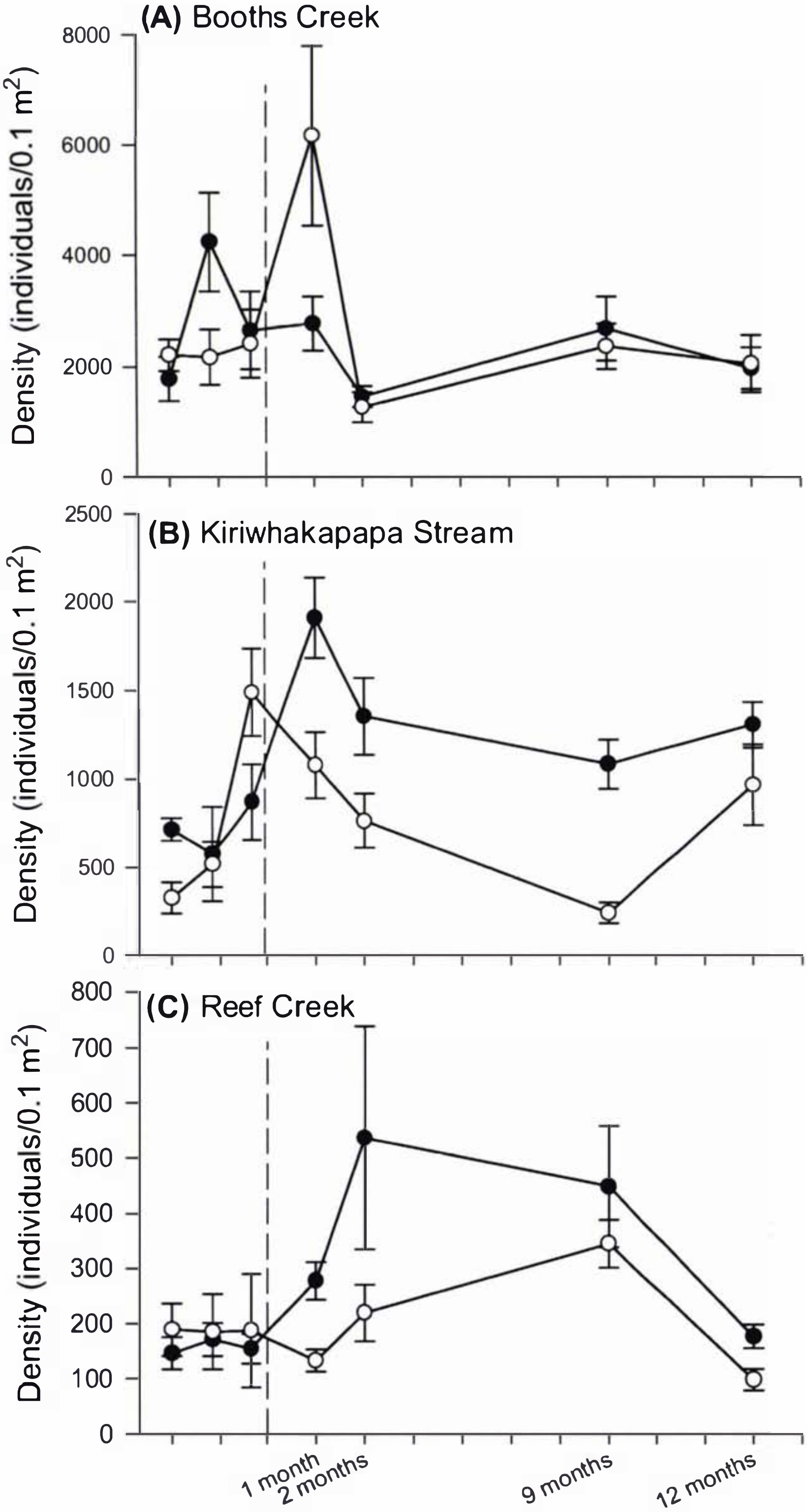

Figure 2. Mean density of individuals per 0.1 m^2 (± 1 S.E.), on three sampling occasions before discharge reduction and 1 month, 2 months, 9 months and 12 months after discharge reduction began for control (black symbols) and impact (open symbols) sites on (A) Booths Creek, (B) Kiriwhakapapa Stream and (C) Reef Creek between November 2004 and January 2006. Vertical dashed lines indicate the start of diversions.

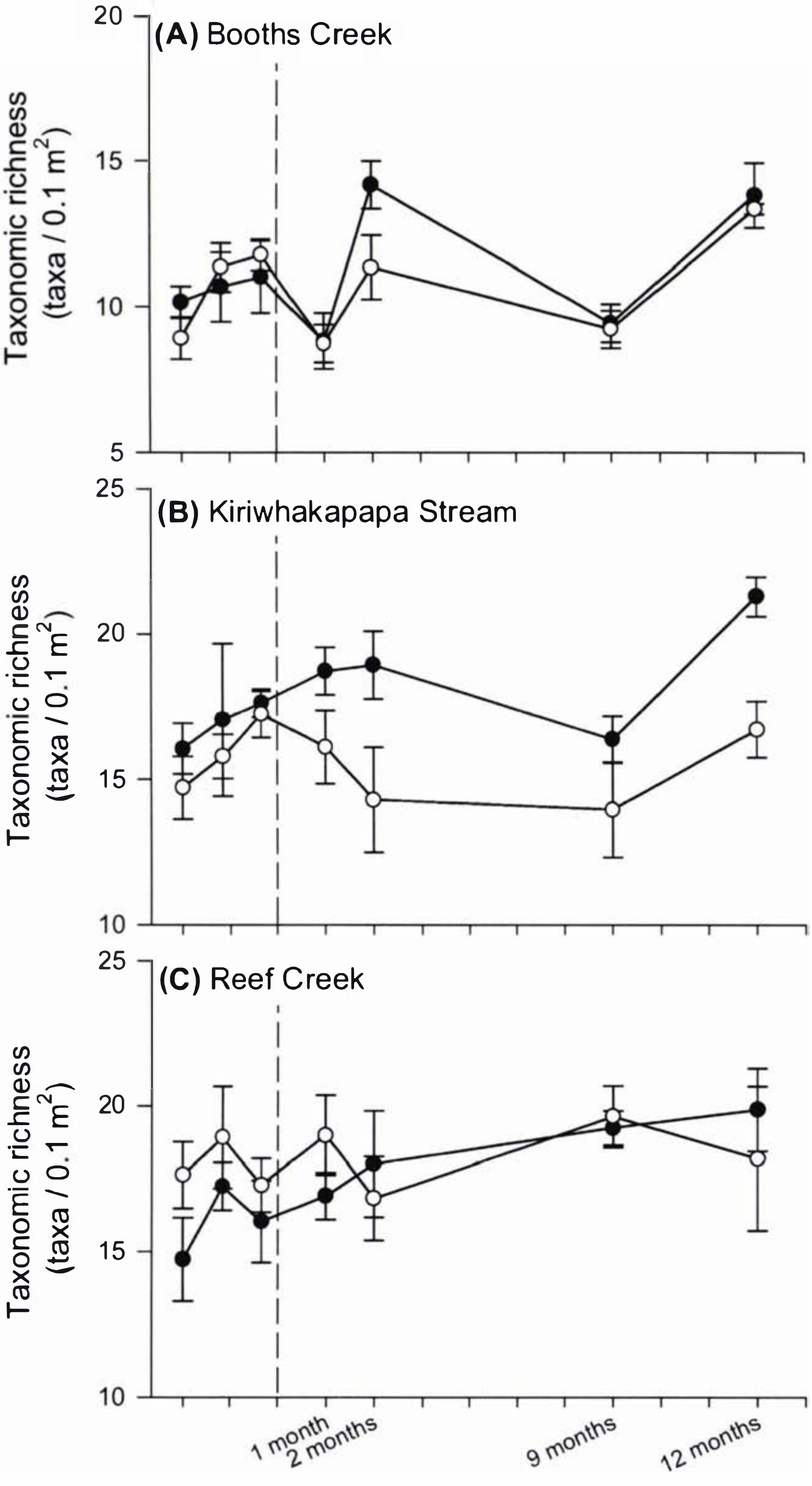

Figure 3. Mean rarefied taxonomic richness per 0.1 m^2 (± 1 S.E.), on three sampling occasions before discharge reduction and 1 month, 2 months, 9 months and 12 months after discharge reduction began for control (black symbols) and impact (open symbols) sites on (A) Booths Creek, (B) Kiriwhakapapa Stream and (C) Reef Creek between November 2004 and January 2006. Vertical dashed lines indicate the start of diversions.

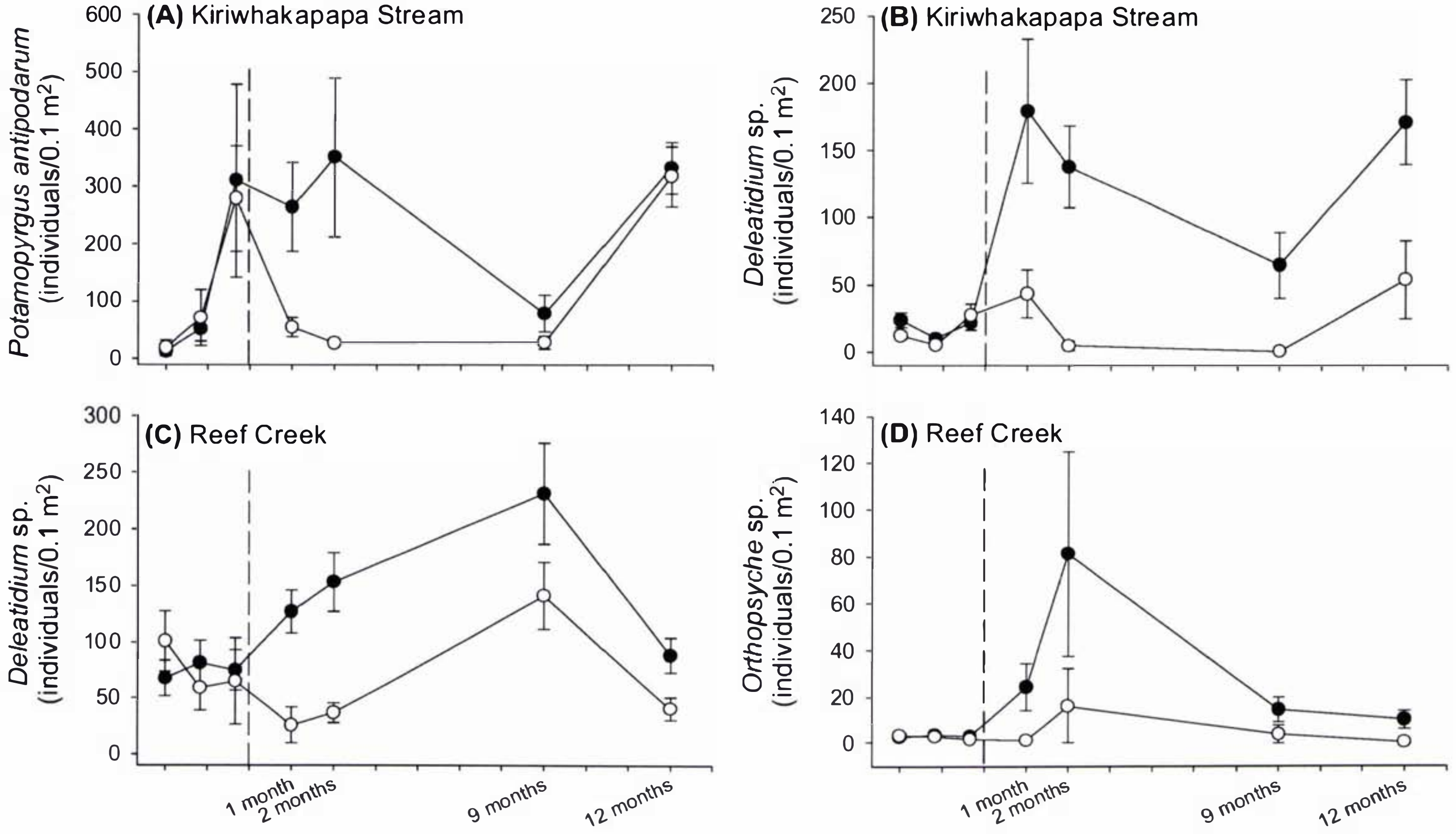

Figure 4. Mean density of individuals per 0.1 m^2 (± 1 S.E.) for common taxa that showed significant changes in density following discharge reduction, on three sampling occasions before discharge reduction and 1 month, 2 months, 9 months and 12 months after discharge reduction began for control (black symbols) and impact (open symbols) sites between November 2004 and January 2006. (A) *Potamopyrgus antipodarum* at Kiriwhakapapa Stream, (B) *Deleatidium* sp. at Kiriwhakapapa Stream, (C) *Deleatidium* sp. at Reef Creek, (D) *Orthopsyche* sp. at Reef Creek. The vertical dashed line indicates the start of diversions.

At Reef Creek, the five most common taxa made up 66% of invertebrate abundance and *Deleatidium* sp. was dominant (*Deleatidium* sp. (36%), Chironominae (8%), Orthocladiinae (8%), Plecoptera: *Zelandobius* sp. (7%), and Hydropsychidae: *Orthopsyche* sp. (7%)). At this stream, *Deleatidium* sp. (Fig. 4C), *Orthopsyche* sp. (Fig. 4D), and *Zelandobius* sp. decreased in abundance at the impact site relative to control during the second month of discharge reduction, although the difference in *Zelandobius* sp. abundance was not maintained over the year of flow reduction (Table 2).

For the few taxa that were common in more than one of the study streams, we found that they responded consistently to discharge reduction (Table 2). Oligochaeta, Chironominae, and Orthocladiinae showed no change in abundance with discharge reduction in any of the streams where they were common, whereas *Deleatidium* sp. decreased after discharge reduction in both Kiriwhakapapa Stream and Reef Creek.

Invertebrate drift propensity increased markedly at impact sites on each stream for at least three days after the diversions started (Fig. 5). There was a much smaller increase in drift propensity at Kiriwhakapapa Stream than at Booths Creek and Reef Creek. Drift propensities were still declining after one week of flow reduction, but after one month, drift propensities had returned to control levels (Fig. 5).

Effects of discharge reduction on invertebrate community composition

One-way ANOSIM showed that invertebrate communities were very different between the three streams in this study (ANOSIM global $R = 0.99$, $P < 0.01$). Mean invertebrate communities from control and impact sites were generally closer in ordination space before than after discharge reduction for Booths Creek (Fig. 6A), Kiriwhakapapa Stream (Fig. 6B), and Reef Creek (Fig. 6C). Analysis of similarity showed that there were no differences in invertebrate community structure between control and impact sites before discharge reduction for any of the streams (Table 3). At Booths Creek, there was still no difference between control and impact sites after flow reduction. Differences between control and impact sites tended to increase over time for Kiriwhakapapa Stream and Reef Creek so that after two months of discharge reduction, invertebrate communities at control and impact sites were distinct for Kiriwhakapapa Stream (ANOSIM $R = 0.75$) and Reef Creek (ANOSIM $R = 1.0$) (Table 3). However, the low group sizes for these pairwise comparisons meant that there were not enough possible permutations to obtain a statistically significant result (Clarke and Warwick 2001).

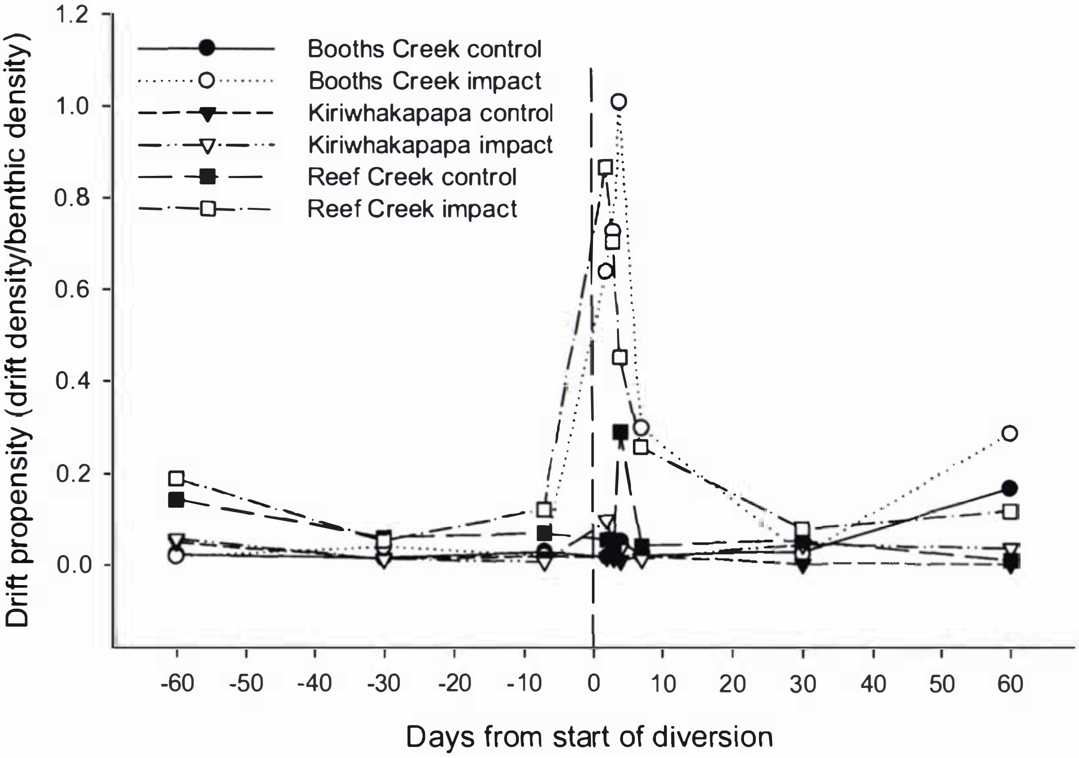

Figure 5. Mean invertebrate drift propensity over time for control and impact study sites at Booths Creek, Kiriwhakapapa Stream and Reef Creek before (November 2004-January 2005) and after (January-March 2005) discharge reductions began. The vertical dashed line indicates the start of diversions.

After a year of flow reduction, there was still no difference between invertebrate communities at control and impact sites on Booths Creek (ANOSIM R = -0.14, P = 0.71), but there were differences between control and impact communities at Kiriwhakapapa Stream (ANOSIM R = 0.71, P = 0.03) and Reef Creek (ANOSIM R = 0.65, P = 0.03) (Table 3). At Kiriwhakapapa Stream, decreases in the density of Chironominae, *Potamopyrgus antipodarum,* Orthocladiinae and *Deleatidium* sp. were the main contributors to this community difference, whereas decreases in *Deleatidium* sp., *Coloburiscus humeralis* and *Orthopsyche* sp. were primarily responsible for the differences between the control and impact communities on Reef Creek (SIMPER).

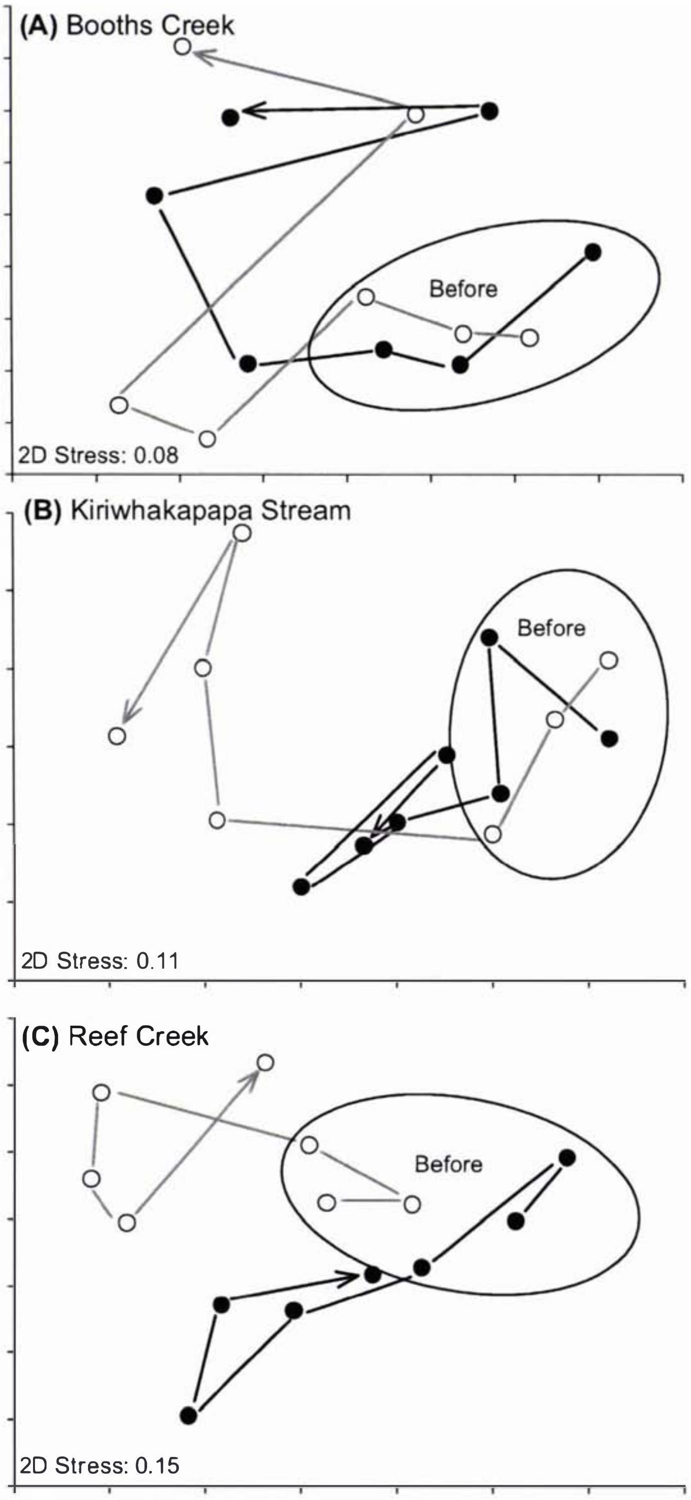

Figure 6. Non-metric multi-dimensional scaling (MDS) of mean invertebrate communities from each of the seven sampling occasions. The trajectory through time is marked for control (black symbols) and impact (open symbols) sites on (A) Booths Creek, (B) Kiriwhakapapa Stream and (C) Reef Creek between November 2004 and January 2006. Sampling occasions before diversions started are within ellipses.

Table 3. One-way ANOSIM testing the H_O: no differences between the four treatments (control before, impact before, control after, impact after) on fourth root transformed abundance data for Booths Creek, Kiriwhakapapa Stream, and Reef Creek (ANOSIM global *R* test statistic) collected during two months of summer flow reduction and after one year of flow reduction. Selected pairwise comparisons are presented to compare control and impact sites within the before and after time periods. Values significant at the 5% level are indicated in bold.

Test	**Global *R***	**Pairwise tests control vs. impact**	***R***
2 months			
Booths Creek	**0.49**	Before	-0.22
		After	-0.50
Kiriwhakapapa Stream	**0.52**	Before	-0.30
		After	0.75
Reef Creek	**0.58**	Before	-0.11
		After	1.00
1 year			
Booths Creek	0.21	After	-0.14
Kiriwhakapapa Stream	**0.52**	After	**0.71**
Reef Creek	**0.51**	After	**0.65**

Discussion

The highest demand for water often coincides with seasonal low flows, when water is required for purposes such as irrigation. At this time, any abstraction represents a higher proportion of total stream discharge. Invertebrate community responses to experimental flow reductions differed between the three streams in this study and varied over time. At the pristine site, invertebrate densities decreased and there were fewer EPT individuals after flow decreased. This was largely a result of changes in the abundance of common taxa. Taxonomic richness decreased at the mildly polluted stream in this study, as fewer rare taxa were collected. Reduced discharge had no affect on the invertebrate community at the most polluted stream. This was probably because the invertebrate assemblage at this site was less sensitive to the environmental changes brought about by flow reduction.

There were lower water temperatures at the impact sites on our study streams. This was unexpected, since at low flows, the sun can warm surface water more quickly, and many studies find that surface water temperatures are higher at reduced flows (e.g., Petts & Bickerton 1994, Cazaubon & Giudicelli 1999, Rader & Belish 1999). However, in our streams, the cooling influence of groundwater explains the temperature decreases. Groundwater is contributing a high proportion of surface flow downstream of diversions and this counteracts the increased influence of the sun at low flows. Several previous studies have also found that groundwater decreases water temperatures as discharge decreases (Grant 1977, Mosley 1983, Kinzie *et al.* 2006). Furthermore, Mosley (1983) found that the contribution of cooler groundwater was particularly important for the temperature of smaller streams (< 0.5 m^3/s) at low flow. Increased temperatures at reduced flow were not responsible for the invertebrate community changes observed in this study. However, in the absence of cooling groundwater, water abstraction might increase water temperatures and have a greater impact on invertebrates. Changes to conductivity, pH, and dissolved oxygen with discharge reduction were negligible in these streams. As for temperature, groundwater may be an overriding influence on surface water chemistry, especially since runoff was low throughout the summer sampling period. However, dissolved oxygen differences would have been apparent if we had considered night time measurements (James *et al.* in prep).

There were substantial decreases to velocity, depth and wetted width after flow reduction, and considerable increases in sediment cover in all but the pristine stream. We suggest that these changes were directly or indirectly responsible for the invertebrate community differences between control and impact sites during our experiment. Numerous studies have shown that changes in velocity can account for changes in the abundance of invertebrates (e.g., Rabeni & Minshall 1977, Georgian & Thorp 1992, Hart *et al.* 1996, Doisy & Rabeni 2001). Velocity can affect invertebrates through its influence on their dispersal and the acquisition of resources, by altering characteristics of their habitat, or by its influence on competition and predation (Hart & Finelli 1999). Therefore, the influence of reduced flow on invertebrates differs among taxa, depending on their mode of feeding and habitat requirements.

After flow reduction, invertebrate communities at Kiriwhakapapa Stream and Reef Creek changed to reflect decreased velocity conditions. Densities of *Deleatidium* sp., *Potamopyrgus antipodarum, Zelandobius* sp. and *Orthopsyche* sp. decreased over two months in response to flow reduction in these streams (Table 2, Fig. 4). Clearly, water velocity is crucial for filter feeders such as *Orthopsyche* sp. and the decrease in velocity was probably responsible for its decline in abundance. Water velocity can control the distribution of filter feeders such as Hydropsychidae (Georgian & Thorp 1992), since it determines the rate of food delivery (Nowell & Jumars 1984, Hart & Finelli 1999). Less clear is the reason for decreased abundances of *Deleatidium* sp. Although *Deleatidium* sp. generally prefers swifter water (Jowett 2000), their decrease in abundance might be a response to decreased food quality, increased sedimentation or a slower delivery rate of dissolved oxygen. In contrast, *Potamopyrgus antipodarum* and *Zelandobius furcillatus* generally prefer slower velocities (Jowett 1997, 2000), so their decline was unexpected. A reduction in the surface area available for grazing, deteriorating algal resources, or increases in predation during reduced discharge might have contributed to their decreased densities. However, after one year of flow reduction, differences in the densities of both *Potamopyrgus antipodarum* and *Zelandobius* sp. were no longer evident in these streams. This finding suggests that after the initial adjustment period, reduced flow conditions did not reduce habitat suitability for these taxa.

Invertebrate drift increased dramatically as flow reductions began, indicating that that for many invertebrates, the change in velocity could initiate this drift behaviour. Previous studies have also observed increases in invertebrate drift after decreases in flow (e.g., Minshall & Winger 1968, Radford & Hartland-Rowe 1971, Hooper & Ottey 1988), suggesting that invertebrate densities should decrease after discharge reduction. However, drift propensity returned to normal levels within a week, whereas benthic invertebrate community differences increased over time (Figs. 2, 3, 4, 6). Therefore, we concluded that environmental changes caused by decreased velocity, such as decreased habitat area and increased sedimentation were probably an important influence on invertebrate communities in the longer term.

Water quality, and thus the sensitivity of the existing invertebrate community, could be influencing invertebrate community responses to flow reduction. We concluded that water abstraction was not affecting the invertebrate community in Booths Creek. The degraded nature of the stream seems to be the most likely explanation for this. Many of the common taxa in this stream prefer lower to moderate velocities (*Paracalliope fluviatilis*, Elmidae, Oligochaeta, Orthocladiinae) (Jowett 1997, 2000). Therefore, reduced flow was unlikely to stress these invertebrates. The abundance of the only common mayfly in this stream (*Austroclima sepia*) did decrease after flow reduction. However, the decrease was not significant because there was high variation between samplings. We had expected flow reduction to have the greatest impact on Reef Creek, as it contained more sensitive species than the other streams. Our results support this hypothesis, because Reef Creek was the only stream where overall invertebrate density decreased after flow reduction. Bickerton *et al.* (1993) previously suggested that regional differences in water quality might mask the local impacts of water abstraction, since the diversity of macroinvertebrate communities make it difficult to identify consistent changes with water abstraction. Similarly, differences between stream types can influence invertebrate community responses to water abstractions (Castella *et al.* 1995).

Responses to water abstraction vary when the initial composition of the invertebrate communities is different. Therefore, classic biomonitoring techniques (e.g., biotic indices) might not be sensitive to the changes caused by water abstraction. As an alternative, it might be possible to identify taxa that are responsive to decreases in flow and use these as indicators of the impact of water abstraction. Our results suggest that factors affecting invertebrate community composition, such as water quality and stream type, are an important consideration for managing water allocation.

References

Arnell N.W. (1999) Climate change and global water resources. *Global Environmental Change,* **9,** S31-S49.

Arnell N.W. & Reynard N.S. (1996) The effects of climate change due to global warming on river flows in Great Britain. *Journal of Hydrology,* **183,** 397-424.

Bickerton M., Petts G., Armitage P. & Castella E. (1993) Assessing the ecological effects of groundwater abstraction on chalk streams: three examples from eastern England. *Regulated Rivers: Research and Management,* **8,** 121-134.

Boothroyd I. & Stark J. (2000) Use of invertebrates in monitoring. In: *New Zealand Stream Invertebrates: Ecology and Implications for Management* (Eds K.J. Collier & M. J. Winterbourn), pp. 344-373. New Zealand Limnological Society, Christchurch, New Zealand.

Boulton A.J. (2003) Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. *Freshwater Biology,* **48,** 1173-1185.

Brasher A.M.D. (2003) Impacts of human disturbances on biotic communities in Hawaiian streams. *BioScience,* **53,** 1052-1060.

Castella E., Bickerton M., Armitage P.D. & Petts G.E. (1995) The effects of water abstractions on invertebrate communities in UK streams. *Hydrobiologia,* **308,** 167-182.

Cazaubon A. & Giudicelli J. (1999) Impact of the residual flow on the physical characteristics and benthic community (algae, invertebrates) of a regulated Mediterranean river: the Durance, France. *Regulated Rivers: Research and Management,* **15,** 441-461.

Chapman M.A. & Lewis M.H. (1976) *An Introduction to the Freshwater Crustacea of New Zealand.* Collins, Auckland, New Zealand.

Christensen N.S., Wood A.W., Voisin N., Lettenmaier D.P. & Palmer R.N. (2004) The effects of climate change on the hydrology and water resources of the Colorado River basin. *Climatic Change,* **62(1-3),** 337-363.

Clarke K.R. & Gorley R.N. (2006) *PRIMER v6: User Manual/Tutorial.* PRIMER-E: Plymouth.

Clarke K.R. & Warwick R.M. (2001) *Change to Marine Communities: An Approach to Statistical Analysis and Interpretation.* 2nd edn. PRIMER-E: Plymouth.

Corrarino C.A. & Brusven M.A. (1983) The effects of reduced stream discharge on insect drift and stranding of near shore insects. *Freshwater Invertebrate Biology,* **2,** 88-98.

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

Dewson Z.S., Death R.G. & James A.B.W. (2003) The effect of water abstractions on invertebrate communities in four small North Island streams. *New Zealand Natural Sciences,* **28,** 51-65.

Dewson Z.S., James A.B.W. & Death R.G. (2007) Invertebrate responses to short-term water abstraction in small New Zealand streams. *Freshwater Biology,* **52,** 357-369.

Doisy K.E. & Rabeni C.F. (2001) Flow conditions, benthic food resources, and invertebrate community composition in a low-gradient stream in Missouri. *Journal of the North American Benthological Society,* **20(1),** 17-32.

Downes B.J., Barmuta L.A., Fairweather P.G., Faith D.P., Keough M.J., Lake P.S., Mapstone B.D. & Quinn G.P. (2002) *Monitoring Ecological Impacts - Concepts and Practice in Flowing Waters.* Cambridge University Press, Cambridge.

Englund G. & Malmqvist B. (1996) Effects of flow regulation, habitat area and isolation on the macroinvertebrate fauna of rapids in north Swedish rivers. *Regulated Rivers: Research and Management,* **12,** 433-445.

Everard M. (1996) The importance of periodic droughts for maintaining diversity in the freshwater environment. *Freshwater Forum,* **7,** 33-50.

Georgian T. & Thorp J.H. (1992) Effects of microhabitat selections on feeding rates of net-spinning caddisfly larvae. *Ecology,* **73(1),** 229-240.

Gordon N.D., McMahon T.A., Finlayson B.L., Gippel C.J. & Nathan R.J. (2004) *Stream Hydrology: An Introduction for Ecologists.* 2nd edn. John Wiley & Sons Ltd., West Sussex, England.

Gore J.A. (1977) Reservoir manipulations and benthic macroinvertebrates in a prairie river. *Hydrobiologia,* **55,** 113-123.

Graham A.A., McCaughan D.J. & McKee F.S. (1988) Measurement of surface area of stones. *Hydrobiologia,* **157,** 85-87.

Grant P.J. (1977) Water temperatures of the Ngaruroro River at three stations. *Journal of Hydrology (N.Z.),* **16,** 148-157.

Ham S.F., Wright J.F. & Berrie A.D. (1981) Growth and recession of aquatic macrophytes on an unshaded section of the River Lambourn, England, from 1971 to 1976. *Freshwater Biology,* **11,** 381-390.

Hart D.D., Clark B.D. & Jasentuliyana A. (1996) Fine-scale field measurements of benthic flow environments inhabited by stream invertebrates. *Limnology and Oceanography,* **41(2),** 297-308.

Hart D.D. & Finelli C.M. (1999) Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms. *Annual Review of Ecology and Systematics,* **30,** 363-395.

Hilsenhoff W.L. (1987) An improved biotic index of organic stream pollution. *Great Lakes Entomologist,* **20,** 31-39.

Hinckley T.M. & Kennedy H.D. (1972) Fluctuations of aquatic and terrestrial invertebrates in drift samples from Convict Creek, California. *Northwest Science,* **46,** 270-276.

Hooper F.F. & Ottey D.R. (1988) Responses of macroinvertebrates of two headwater streams to discharge fluctuations. *Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie,* **23,** 1159-1166.

Jackson R.B., Carpenter S.R., Dahm C.N., McKnight D.M., Naiman R.J., Postel S.L. & Running S.W. (2001) Water in a changing world. *Ecological Applications,* **11,** 1027-1045.

Jowett I.G. (1992) River hydraulics and instream habitat modelling for river biota. In: *Waters of New Zealand* (Ed M.P. Mosley), pp. 249-263. New Zealand Hydrological Society, Christchurch, New Zealand.

Jowett I.G. (1997) Environmental effects of extreme flows. In: *Floods and Droughts: the New Zealand Experience* (Eds M.P. Mosley & C.P. Pearson), pp. 104-116. The Caxton Press, Christchurch, New Zealand.

Jowett I.G. (2000) Flow management. In: *New Zealand Stream Invertebrates: Ecology and Implications for Management* (Eds K.J. Collier & M.J. Winterbourn), pp. 289-312. New Zealand Limnological Society, Christchurch, New Zealand.

Kinzie R.A.I., Chong C., Devrell J., Lindstrom D. & Wolff R. (2006) Effects of water removal on a Hawaiian stream ecosystem. *Pacific Science,* **60,** 1-47.

Ladle M. & Bass J.A.B. (1981) The ecology of a small chalk stream and its responses to drying during drought conditions. *Archiv für Hydrobiologie,* **90,** 448-466.

Lenat D.R. (1988) Water quality assessment using a qualitative method for benthic macroinvertebrates. *Journal of the North American Benthological Society,* **7,** 222-233.

McIntosh M.D., Benbow M.E. & Burky A.J. (2002a) Effects of stream diversion on riffle macroinvertebrate communities in a Maui, Hawaii, stream. *River Research and Applications,* **18,** 569-581.

McIntosh A.R., Peckarsky B.L. & Taylor B.W. (2002b) The influence of predatory fish on mayfly drift: extrapolating from experiments to nature. *Freshwater Biology,* **47,** 1497-1513.

Minshall G.W. & Winger P.V. (1968) The effect of reduction in stream flow on invertebrate drift. *Ecology,* **49(3),** 580-582.

Mosley M.P. (1983) Variability of water temperatures in the braided Ashley and Rakaia rivers. *New Zealand Journal of Marine and Freshwater Research,* **17,** 331-342.

Nowell A.R.M. & Jumars P.A. (1984) Flow environments of aquatic benthos. *Annual Review of Ecology and Systematics,* **15,** 303-328.

Petts G.E. & Bickerton M.A. (1994) Influence of water abstraction on the macroinvertebrate community gradient within a glacial stream system: La Borgne d'Arolla, Valais, Switzerland. *Freshwater Biology,* **32,** 375-386.

Poff N.L., Voelz N.J. Ward J.V. & Lee R.E. (1990) Algal colonization under four experimentally-controlled current regimes in a high mountain stream. *Journal of the North American Benthological Society,* **9(4),** 303-318.

Poff N.L. & Ward J.V. (1991) Drift responses of benthic invertebrates to experimental streamflow variation in a hydrologically stable stream. *Canadian Journal of Fisheries and Aquatic Sciences,* **48,** 1926-1936.

Poff N.L., Wellnitz T. & Monroe J.B. (2003) Redundancy among three herbivorous insects across an experimental current velocity gradient. *Oecologia,* **134(2),** 262-269.

Postel S.L. (1997) *Last Oasis.* W.W. Norton & Company, New York, U.S.A.

Rabeni C.F. & Minshall G.W. (1977) Factors affecting microdistribution of stream benthic insects. *Oikos,* **29,** 33-43.

Rader R.B. & Belish T.A. (1999) Influence of mild to severe flow alterations on invertebrates in three mountain streams. *Regulated Rivers: Research and Management,* **15,** 353-363.

Radford D.S. & Hartland-Rowe R. (1971) A preliminary investigation of bottom fauna and invertebrate drift in an unregulated and a regulated stream in Alberta. *Journal of Applied Ecology*, **8,** 883-903.

Richter B.D. (1993) Ecosystem-level conservation at the nature conservancy: growing needs for applied research in conservation biology. *Journal of the North American Benthological Society*, **12,** 197-200.

SAS Institute Inc. (2004) *The SAS System for Windows.* SAS Institute Inc., Cary, North Carolina, U.S.A.

Simpson E.H. (1949) Measurement of diversity. *Nature*, **163,** 688.

Smith B.J. (2003) *Quick Guide to the MCI Invertebrates.* National Institute of Water and Atmospheric Research, Hamilton, New Zealand.

Stark J.D. (1985) *A Macroinvertebrate Community Index of Water Quality for Stony Streams.* National Water and Soil Conservation Authority, Wellington, New Zealand.

Steinman A.D. & Lamberti G.A. (1996) Biomass and pigments of benthic algae. In: *Methods in Stream Ecology* (Eds F.R. Hauer & G.A. Lamberti), pp. 295-313. Academic Press Inc., U.S.A.

Suren A.M., Biggs B.J.F., Duncan M.J. & Bergey L. (2003) Benthic community dynamics during summer low-flows in 2 rivers of contrasting enrichment, 2. Invertebrates. *New Zealand Journal of Marine and Freshwater Research*, **37,** 71-83.

Vinson M.R. & Hawkins C.P. (1996) Effects of sampling area and subsampling procedure on comparisons of taxa richness among streams. *Journal of the North American Benthological Society*, **15,** 392-399.

Winterbourn M.J. (1973) A guide to the freshwater mollusca of New Zealand. *Tuatara*, **20,** 141-159.

Winterbourn M.J., Gregson K.L.D. & Dolphin C.H. (2000) Guide to the aquatic insects of New Zealand. *Bulletin of the Entomological Society of New Zealand*, **13.**

Wood P.J., Agnew M.D. & Petts G.E. (2000) Flow variations and macroinvertebrate community responses in a small groundwater-dominated stream in south-east England. *Hydrological Processes*, **14,** 3133-3147.

Wood P.J. & Armitage P.D. (1999) Sediment deposition in a small lowland stream-management implications. *Regulated Rivers: Research and Management*, **15,** 199-210.

Wood P.J. & Petts G.E. (1994) Low flows and recovery of macroinvertebrates in a small regulated chalk stream. *Regulated Rivers: Research and Management,* **9,** 303-316.

Wright J.F. & Berrie A.D. (1987) Ecological effects of groundwater pumping and a natural drought on the upper reaches of a chalk stream. *Regulated Rivers: Research and Management,* **1,** 145-160.

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

CHAPTER 5

Stream ecosystem functioning under reduced flow conditions

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Dewson Z.S., James A.B.W. & Death R.G. Stream ecosystem functioning under reduced flow conditions.

Abstract

Assessments of flow reduction in streams often focus on changes to biological communities and instream physical characteristics, with little consideration for changes in ecosystem functioning. It is unclear whether functional indicators of ecosystem health may be useful for assessing the impacts of reduced discharge on small streams. Using weirs and diversions to reduce stream discharge, we tested the response of leaf breakdown, coarse particulate organic matter (CPOM) retention, and primary production to water abstraction in before-after, control-impact (BACI) designed experiments. Discharge at impact (downstream) sites decreased by over 85% in each of three small streams compared with controls (upstream). There were also decreases in velocity, depth, and wetted width. Sediment cover increased at impact sites, but there were only small changes to conductivity, pH, and water temperature. We installed mesh bags filled with willow leaves into the stream for one month to measure leaf breakdown. Reduced discharge had little influence on leaf breakdown rate in these streams. Travel distances and retention structures for CPOM were evaluated using releases of paper strips and wooden dowelling over a range of discharges. The distance travelled by released CPOM increased with increasing discharge and the importance of riffles as retention structures increased at lower discharges. We measured the accumulation of chlorophyll *a* after one month on artificial substrates as an estimate of the relative primary production of control and impact sites. The differences in chlorophyll *a* concentrations between control and impact sites were inconsistent among streams. While leaf breakdown and primary production responded inconsistently to water removal in these streams, the strong response of CPOM retention to reduced discharge could complement measures of biological community structure when assessing the influence of reduced discharge. We recommend further investigation in a wide range of streams to assess the utility of these processes as functional indicators of reduced discharge.

Introduction

Escalating global demands for limited fresh water resources are making it increasingly difficult to balance in and out of stream requirements for water. An increased understanding of the impacts of reduced flows on stream ecosystems might assist in finding this balance. Therefore, it is necessary to identify efficient and effective methods of monitoring the impacts of water abstraction from streams. Gessner & Chauvet (2002) stress the importance of including functional measures when undertaking bioassessments, but warn that considerably more attention should focus on identifying useful indicators of functional integrity for specific kinds of anthropogenic stress. We have previously assessed the effects of experimentally reduced discharge on benthic invertebrates (Dewson *et al.* 2007, Chapters 3 and 4), levels of invertebrate drift (A. James, *unpublished data*), and hyporheic usage by invertebrates (A. James, *unpublished data*). To complement these community structural measures, we have investigated the impacts of reduced discharge on three functional attributes of stream ecosystems: leaf breakdown, the retention of coarse particulate organic matter (CPOM) and primary production.

Studies on the importance of leaf litter as an energy source in streams and of the dynamics of leaf breakdown have been conducted over many years (see Webster & Benfield 1986, Royer & Minshall 2003). The promotion of leaf breakdown as a potential functional bioassessment tool (Webster & Benfield 1986, Gessner & Chauvet 2002) may have prompted many recent studies to test this in relation to human induced stressors such as agricultural development, organic pollution and stream acidification (e.g., Young *et al.* 1994, Pascoal *et al.* 2001, Niyogi *et al.* 2001, Dangles *et al.* 2004, Hagen *et al.* 2006).

Factors such as nutrients, water velocity, sedimentation, water temperature and dissolved oxygen can influence breakdown rates (Webster & Benfield 1986, Royer & Minshall 2003). Webster and Benfield (1986) proposed leaf breakdown as a useful measure of impact on freshwater ecosystems, since a combination of physical, chemical, and biological processes control its rate. Results to date suggest that the usefulness of leaf breakdown rates as an indicator of ecosystem impairment may depend on the consequences of the stressor investigated. For example, when a stress alters multiple factors, such as sedimentation, nutrient levels, water temperature and invertebrates, there can simultaneously be positive and negative effects on leaf breakdown rate, and the usage of leaf breakdown as an indicator of ecosystem integrity might be limited (e.g., Pascoal *et al.* 2001, Niyogi *et al.* 2003, Hagen *et al.* 2006, Woodcock & Huryn 2005, Young 2006).

Several of the abiotic and biotic factors that are potentially altered by water abstraction can influence leaf breakdown rates. For example, water abstraction commonly decreases water velocity (e.g., Wright & Berrie 1987, McIntosh *et al.* 2002), alters temperature regimes (e.g., Mosley 1983, Rader & Belish 1999), increases sedimentation (e.g., Wright & Berrie 1987, Castella *et al.* 1995), changes pH (e.g., McIntosh *et al.* 2002, Woodward *et al.* 2002) and decreases invertebrate diversity and abundance (e.g., Cazaubon & Giudicelli 1999, Wood *et al.* 2000). Unfortunately, this diversity of potential changes makes it difficult to predict how leaf breakdown will respond to discharge reduction.

Coarse particulate organic matter (CPOM, > 1 mm) is an allochthonous source of energy for stream ecosystems (Allan 1995, Petersen & Cummins 1974). Allocthonous material that reaches the stream is either broken down, or transported downstream (Webster *et al.* 1999). Consequently, the study of CPOM movement, breakdown and retention in streams has received considerable attention over the years. It has been shown that CPOM generally travels only short distances in streams (e.g., Webster *et al.* 1994, Wallace *et al.* 1995, Snaddon *et al.* 1992). However, a number of studies have described a positive relationship between discharge and CPOM travel distance (e.g., Jones and Smock 1991, Webster *et al.* 1999, Brookshire and Dwire 2003). Webster *et al.* (1994) also showed that retention was greater in shallower stream sites, emphasising the importance of water depth to CPOM retention. The changing prominence of different retention structures with water level probably underlies the importance of water depth.

Discharge – retention relationships suggest that water abstraction will enhance CPOM retention, potentially increasing energy supply or creating anoxic conditions among decomposing leaves. Such a change could have implications for higher trophic levels (such as invertebrates and fish). Reduced CPOM retention can have strong bottom-up effects on stream ecosystems, decreasing the abundance and biomass of all invertebrates over time (Wallace *et al.* 1997). We might expect the reverse to occur with increased CPOM retention.

Primary producers are the first trophic level in the food web (Molles 1999). As such, this autochthonous source of energy for the stream ecosystem might provide another useful measure of the impact of reduced discharge, since any alteration to primary production can also have flow on effects to higher trophic levels. A relationship between water velocity and periphyton accrual might exist, since velocity can affect the colonisation, production and loss of the periphyton community (Biggs & Close 1989, Jowett & Biggs 1997). Examinations of this relationship in a variety of natural and experimental situations have produced both positive and negative relationships (e.g., McIntire 1966, Poff *et al.* 1990, Biggs & Hickey 1994, Jowett & Biggs 1997), but tend to indicate that there is some relationship between velocity and primary production.

Using weirs and diversions to create considerable reductions in discharge, our aim was to investigate the influence of decreased discharge on three functional attributes of stream ecosystems (leaf breakdown, CPOM retention and primary production). These ecosystem processes control the energy supply for stream ecosystems and thus, have important consequences for higher trophic levels. We conducted our experiments during the Austral summer (between November 2004 and March 2005), since this is a time of peak irrigation, as well as naturally low flows. At this time, we expected any water removal would have the greatest impact on the stream ecosystem.

Our hypotheses for each of the ecosystem functions were:

1. That reduced discharges would decrease leaf breakdown, through reduced physical abrasion in coarse mesh bags and by reducing microbial activity in fine mesh bags (with increased sedimentation).
2. That reduced discharge, velocity and depth would increase CPOM retention by increasing the efficiency of riffles as retention structures.
3. That decreased velocities would enhance primary production.

Methods

Study sites

This discharge reduction experiment was conducted on three small streams in the Wairarapa Region of the lower North Island, New Zealand: Booths Creek and unnamed tributaries of Kiriwhakapapa Stream and Reef Creek. The three perennial, runoff fed streams range in discharge from 27 to 250 L/s (mean summer discharge) and represent differing levels of water quality.

The stream with the lowest water quality is Booths Creek (41° 04 40.29'S 175° 31 58.53'E). It is a small (250 L/s), low gradient, meandering stream, with pool-riffle morphology and gravel-cobble substrate. This stream receives some inflow from stock watering channels. Cropping land surrounds Booths Creek at the study site, with patches of willow (*Salix* spp.) in the riparian zone.

The Kiriwhakapapa Stream tributary is a small (110 L/s), moderately modified stream in the foothills of the Tararua Ranges (40° 49 07.10'S 175° 34 21.04'E). This meandering stream also has a pool-riffle morphology and gravel-cobble substrate, with fine sediments contributed by bank erosion. The study site on the Kiriwhakapapa Stream tributary is within an extensive sheep and beef farm where stock has access to the stream and the channel has little shading in the study reaches.

The Reef Creek tributary is a relatively pristine, headwater stream (27 L/s) within a native forest catchment (40° 48 34.46'S 175° 32 21.84'E). The high gradient channel of this stream is characterized by pool, step and riffle sequences and gravel-boulder substrate with outcropping bedrock. The study site on the Reef Creek tributary is in a V shaped valley, with the forest canopy providing almost complete shade to the channel in the study reaches. We will subsequently refer to unnamed tributaries by the names of the streams they feed.

Experimental design

We constructed weirs and diversions on three streams to reduce stream discharge for a distance of approximately 100 m. This distance provided enough area for sampling and was not long enough for flow to be restored by groundwater inflow. Weirs extended across the entire stream, with no overflow during the period of the study. The wooden board weirs were not completely sealed so that a proportion of the flow and invertebrates could move through, under and around these weirs, whilst the majority of the flow was diverted out of the experimental reaches through open diversion channels (Booths Creek and Kiriwhakapapa Stream) or diversion pipes (Reef Creek). By removing a high proportion of the discharge in this way, we have created a barrier to invertebrate drift into downstream reaches. This approach is consistent with the type of water abstraction that occurs from streams of this size. All of our ecosystem function experiments have a before-after, control-impact design (BACI) (Downes *et al.* 2002). Study reaches were identified upstream (control) and downstream (impact) of weirs on each stream and ecosystem function experiments were conducted within these reaches both before (between November 2004 and January 2005) and during discharge reduction (between January and March 2005).

Flow related and physicochemical characteristics

Throughout the experiment, we recorded water height at control and impact sites on each stream at intervals of 20 minutes using TruTrack WT-HR 1000 Water Height Data Loggers with an accuracy of ±1%. We calculated discharge on each sampling occasion by measuring depth and velocity at 0.4 × depth from the bed for at least ten equidistant intervals across the stream using a Marsh McBirney Inc. Model 2000 Portable Flowmeter to an accuracy of 0.01 m/s. The relationship between water height and discharge was described using a power function ($y = cx^b$, where c and b are constants) so that discharge could be calculated from the water height records (Gordon *et al.* 2004). At each site, five further depths and velocities were measured within riffles, to characterise the habitat used for the installation of leaf bags, primary production artificial substrates, and sediment traps, and for the release of CPOM. Average measurements of conductivity, dissolved oxygen and pH were recorded twice before and twice during discharge reduction, at installation and collection of leaf bags, from approximately an hour of logging at intervals of one minute using a YSI Incorporated multi-probe system instrument (YSI 556 MPS). Logging was completed over two consecutive hours at control and impact sites on each stream around midday. Temperature was recorded every 30 minutes throughout the study using Onset Hobo® H8 temperature loggers. We measured the wetted width of the channel at 14 fixed locations at five metre intervals along the study reach.

We installed sediment traps in both control and impact reaches to assess how reduced discharge affected the rate of sediment deposition. Our sediment traps were similar to those described by Bond (2002), although we used small plastic buckets as the collection container (depth = 200 mm, radius = 82.5 mm), providing a settlement area of 0.0213 m^2 (Plate 1). Once installed, traps were flush with the streambed and covered with a layer of coarse substrate material, supported by wire mesh over the trap to minimise the alteration of hydraulic conditions (Bond 2002). Sediment was trapped for 24 hours at control and impact sites on two occasions before and three occasions during discharge reduction. We also collected 300 mL water samples at midstream to measure the quantity of suspended sediment in the water column. We analysed the ash free dry mass (AFDM) of suspended and trapped sediment samples by vacuum filtration, using pre-ashed Whatman glass fibre filters (GF/C) (Plate 2). Sample filtration was followed by drying at 50°C for 24 hours, then filters were weighed, ashed for four hours at 450°C and reweighed.

The coverage of fine sediment on the substrate was visually estimated by one person at 15 randomly selected transects at each study site on three occasions while diversions were operating. At each transect, we estimated the percentage of substrate covered by fine sediment within a 300 mm wide strip across the width of the stream. From these measurements, we calculated an average percentage cover of fine sediment for each site and time.

Leaf breakdown

We used leaf samples contained in mesh bags as a measure of leaf breakdown rates in these streams (Plate 3). Abscised leaves were not available at the time of this experiment. To ensure that the initial condition of leaves did not vary between samples, we collected fresh willow leaves (*Salix* spp.) from a single tree seven days before installation and immediately weighed the leaves into approximately 10 g bundles. We recorded exact weights before sealing leaves into 150 mm × 150 mm mesh bags and air-drying for one week. We also weighed five further 10 g samples of fresh willow leaves to calculate the average percentage of weight lost between the fresh and air dried leaves. We used three mesh sizes to exclude progressively larger invertebrates. We included coarse (5 mm) and fine (1 mm) mesh leaf bags and 100 mm lengths of PVC tube (40 mm diameter) with ends covered in 0.25 mm mesh. Tubes only contained approximately 3 g fresh weight of leaves.

Five replicates of each mesh type were attached to the substrate within riffles at control and impact sites before (35 days, December 2004 - January 2005) and during flow reduction (31 days, February – March 2005) at each of the three study streams.

Upon removal from the stream, leaf bags were transported to the laboratory on ice and stored at - 20°C until analysis. The contents of each bag were rinsed through a 250-µm sieve and invertebrates and detritus were removed by hand. Samples were dried at 50°C for 24 hours, weighed, ashed at 600 °C for two hours and then reweighed.

We calculated both the percentage of mass lost during the experiment and the rate of leaf breakdown. The rate of leaf breakdown was calculated using an exponential decay model as described by Petersen & Cummins (1974). By using degree-days for this calculation, we factored out the effects of temperature differences between the before and after periods as suggested by Minshall *et al.* (1983).

Plate 1. Sediment trap ready for installation to collect deposited sediment at Reef Creek.

Plate 2. Filters used to measure the ash free dry mass of suspended sediment at each site.

Plate 3. Fine and coarse mesh leaf bags attached to the streambed in a riffle at Reef Creek.

Coarse particulate organic matter (CPOM) retention

We used paper strips and wooden dowelling as analogues for natural CPOM (leaves and sticks). Artificial leaves were cut as rectangles (100 mm × 15 mm) from heavy red paper (200 g/m^2), and artificial sticks as 100 mm lengths of 8 mm diameter wooden dowelling following the methods of James & Henderson (2005).

We released 30 of each CPOM type from a marked point within riffle habitat in impact reaches of the three streams before and after flow reduction began in order to cover a wide range of stream discharges (0.5 to 180 $L\ s^{-1}$) (Plate 4). There were a total of 15 CPOM releases over the three streams. We recorded the distance travelled downstream for each item after one hour and the mechanism of retention (riffles/rocks, instream or bank vegetation, eddies, undercut banks and other snags). Items not found within 150 m were identified as missing.

Primary production

We assessed periphyton growth on artificial substrates to provide relative comparisons of primary production between control and impact sites (Plates 5, 6). Arrays of six artificial substrates (unglazed terracotta tiles, 100 mm × 100 mm) were attached to modular floor grating tiles (400 mm × 400 mm) with dowelling pegs (10 mm diameter). The purpose of the dowel pegs was to elevate the tiles slightly and minimise colonisation by invertebrate grazers. Before flow reduction, floor gratings were attached to the streambed with tent pegs so that tiles were between 50 - 100 mm below the water surface, in velocities of between 0.3 and 0.7 m/s. We ensured that depths and velocities were as consistent as possible between control and impact sites on each stream. Tiles remained in the same location after the diversions began, and hence depths and velocities were lower at impact sites.

After one month in the stream, both before and after discharge reduction, we sampled the tiles for chlorophyll *a* by scouring three circular samples (7.06 cm^2 each) from the surface of each tile (Davies & Gee 1993). Samples were transported on ice in the dark and stored at -20°C. We extracted photosynthetic pigments from scourers by submerging them in 50 mL of 90% acetone for 24 hours at 5°C. Absorbance was read at 750, 665, and 664 nm on a Varian Cary 50 Conc. UV-Visible spectrophotometer™ before and after 0.1 M HCl was added. We calculated the amount of chlorophyll *a* ($\mu g/cm^2$) for each sample as described by Steinman & Lamberti (1996).

Plate 4. Released artificial coarse particulate organic matter (CPOM) trapped in a riffle in the reduced flow reach of Kiriwhakapapa Stream.

Data analysis

Our decomposition and primary production experiments had BACI designs, where measurements were made at control and impact sites once before and once after the impact (Downes *et al.* 2002). In this case, the impact was discharge reduction. Therefore, all physicochemical, leaf breakdown and primary production data were analysed with a two-factor analysis of variance (ANOVA) in SAS (2004). Factors were before-after (BA) and control-impact (CI). Streams were treated as blocks in the analysis of physicochemical data, but each stream was analysed separately for leaf breakdown and primary production, since opposite responses were observed among the streams. The term of interest was the interaction between BA and CI. A significant BA*CI interaction would indicate that the relationship between control and impact was different before from after the impact, suggesting that the discharge reduction might have had some effect. We transformed data using $\log_{10}$ or square root when necessary to reduce heteroscedasticity.

To test the differences in sediment cover between control and impact sites, we used a one-way ANOVA to test the H_0: mean % sediment cover at control = mean % sediment cover at impact, since sediment cover was not recorded at control and impact sites before flow reductions began.

Results

Effects of discharge reduction on flow and physicochemical characteristics

Weirs and diversions decreased the discharge at impact sites by an average of 95, 86 and 91% in Booths Creek, Kiriwhakapapa Stream and Reef Creek respectively (Table 1). Maximum discharge reductions were greater than 97% for each of the streams at some time during this period (based on water heights recorded at intervals of 20 minutes). There were significant decreases in wetted width, depth and water velocity at impact sites compared with controls, but conductivity, pH, and dissolved oxygen were unaltered by discharge reduction in these streams (Table 2). Mean daily water temperatures were lower at impact sites after discharge reduction for Booths Creek ($F_{1,127} = 162.3$, $P < 0.01$), Kiriwhakapapa Stream ($F_{1,130} = 107.5$, $P < 0.01$) and Reef Creek ($F_{1,131} = 3.2$, $P = 0.08$). However, the differences in means were on average less than 1°C, with control means of 19°C, 18°C and 13°C for Booths Creek, Kiriwhakapapa Stream, and Reef Creek respectively. Consequently, control and impact leaf bags in each stream were relatively equal in terms of the number of degree-days exposure they received, although there were differences between streams and the before and after periods.

Discharge reduction did not change the quantity of suspended sediments in the water column ($F_{1,24} = 1.03$, $P = 0.32$). Furthermore, even when corrected for discharge, there was no more sediment deposited in sediment traps at impact sites than controls after flow reduction ($F_{1,14} = 0.62$, $P = 0.45$). However, after flow reduction, fine sediments covered a significantly greater percentage of the substrate at impact sites on Booths Creek (control = 9.2%, impact = 46.4%)($F_{1,88} = 74.1$, $P < 0.01$) and Kiriwhakapapa Stream (control = 43.0%, impact = 81.2%) ($F_{1,88} = 66.5$, $P < 0.01$). There was no difference in sediment cover between control and impact sites on Reef Creek ($F_{1,88} = 0.3$, $P = 0.58$) (Fig. 1).

Table 1. Mean (± 1 S.E.) values of flow related variables at control and impact sites after discharge reduction in Booths Creek, Kiriwhakapapa Stream and Reef Creek between January and March 2005. Percentage changes are from control to impact sites during experimental discharge reduction.

Stream	**Booths Creek**	**Kiriwhakapapa Stream**	**Reef Creek**
Discharge control (L/s)	84.4 ± 0.6	28.2 ± 0.2	10.9 ± 0.6
Discharge impact (L/s)	4.2 ± 0.0	3.9 ± 0.0	1.0 ±0.0
% change discharge	**-95.0%**	**-86.2%**	**-90.6%**
Wetted width control (m)	3.6 ± 0.2	2.2 ± 0.1	1.8 ± 0.2
Wetted width impact (m)	2.6 ± 0.1	1.5 ± 0.1	1.2 ± 0.0
% change wetted width	**-27.8%**	**-31.8%**	**-33.3%**
Depth control (cm)	17.2 ± 4.8	10.0 ± 1.8	6.4 ● 1.2
Depth impact (cm)	6.8 ± 0.1	5.7 ± 0.4	6.6 ± 0.5
% change depth	**-60.5%**	**-43.0%**	**+3.1%**
Velocity control (m/s)	0.49 ± 0.06	0.58 ± 0.07	0.18 ± 0.10
Velocity impact (m/s)	0.14 ± 0.04	0.08 ± 0.01	0.03 ± 0.00
% change velocity	**-71.4%**	**-86.2%**	**-83.3%**

Table 2. *F* values for ANOVAs testing for the impacts of flow reduction on physicochemical measures at Booths Creek, Kiriwhakapapa Stream and Reef Creek during installation of leaf bags between December 2004 and March 2005. A significant BA*CI interaction term indicates that discharge reduction affected that factor. Values significant at the 5% level are indicated in bold.

Factor	**d. f.**	**Wetted width**	**Depth**	**Velocity**	**Conductivity**	**pH**	**Dissolved oxygen**
Before-After (BA)	1, 18	**24.47**	**14.13**	**33.78**	**13.44**	0.11	3.74
Control-Impact (CI)	1, 18	3.77	2.35	**11.60**	0.52	1.60	1.68
Stream (blocks)	2, 18	**37.09**	1.85	**10.75**	**817.79**	**4.85**	1.36
BA * CI	1, 18	**14.65**	**4.68**	**9.90**	0.07	1.65	0.26

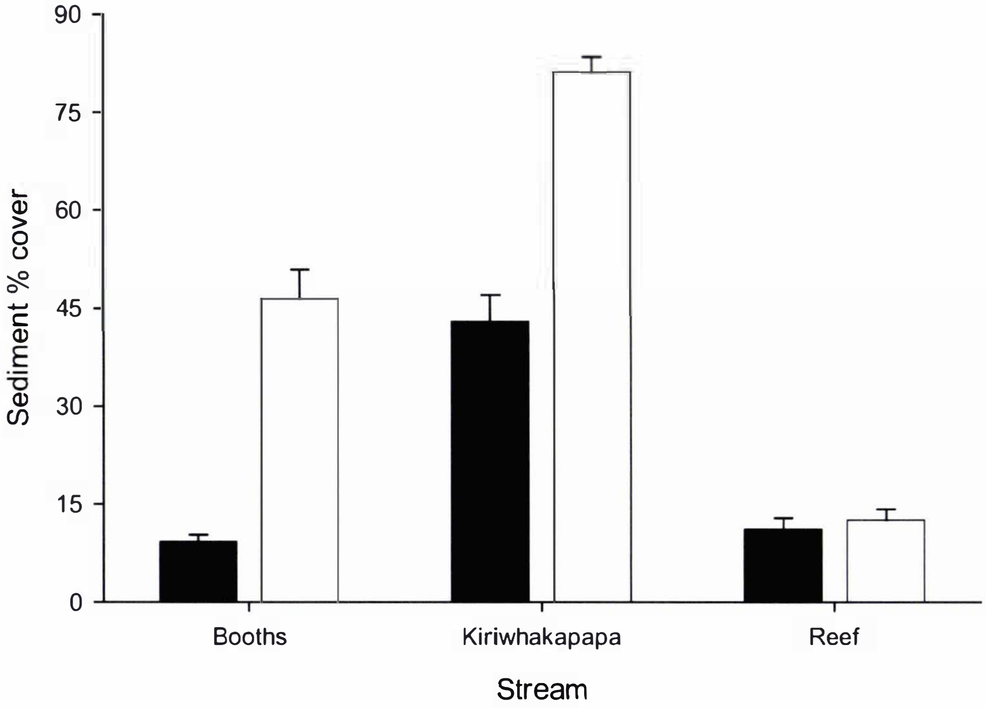

Figure 1. Mean (± 1 S.E.) percentage cover of the substrate by fine sediments for control (black) and impact (open) sites on Booths Creek, Kiriwhakapapa Stream and Reef Creek.

Effects of discharge reduction on leaf breakdown

Leaf breakdown occurred faster at warmer streams in both coarse (linear, $F_{1,10} = 40.65$, $P < 0.01$) and fine mesh bags (2nd order polynomial, $F_{2,9} = 5.34$, $P = 0.03$) at control and impact sites (Figs. 2A, 2B). We allowed for this in all subsequent analyses by using breakdown rate per degree-day. There was no apparent relationship between leaf breakdown and degree days in the leaf tubes (linear, $F_{1,9} = 1.78$, $P = 0.22$).

Breakdown rates were often higher in the before than after period (Fig. 3). Leaf breakdown was also faster in coarse mesh bags than in fine mesh bags and leaf tubes (Fig. 3). In two instances, breakdown at impact sites changed relative to control sites between before and after the discharge reduction. However, in both cases, breakdown rates were more similar at control and impact sites after flow reduction (Fig. 3). In Reef Creek, breakdown in coarse mesh bags decreased at impact sites relative to controls ($F_{1, 16} = 6.67$, $P = 0.02$). Conversely, breakdown at the impact site on Kiriwhakapapa Stream increased relative to the control in fine mesh bags ($F_{1, 16} = 5.7$, $P = 0.03$).

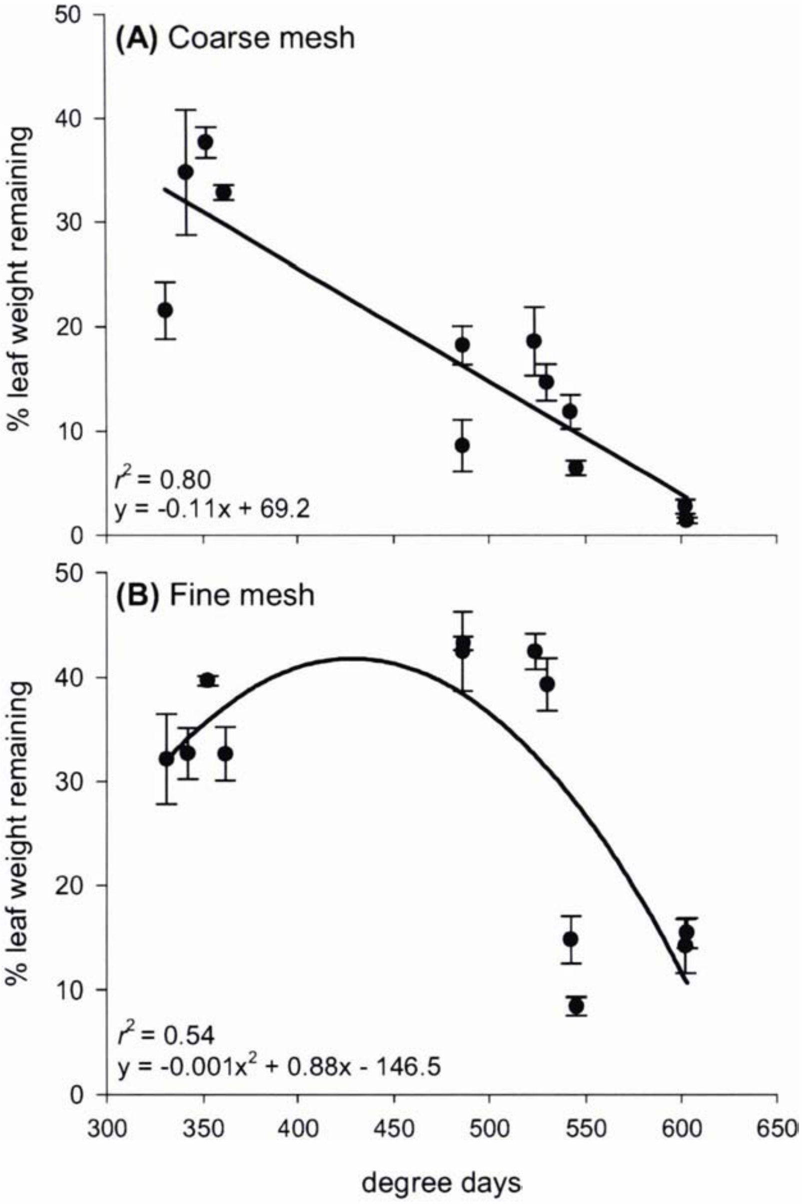

Figure 2. Relationship between mean percentage of leaf weight remaining (± 1 S.E.) and number of degree days exposed in (A) coarse mesh bags and (B) fine mesh bags for all treatments (before control, before impact, after control and after impact) on Booths Creek, Kiriwhakapapa Stream and Reef Creek.

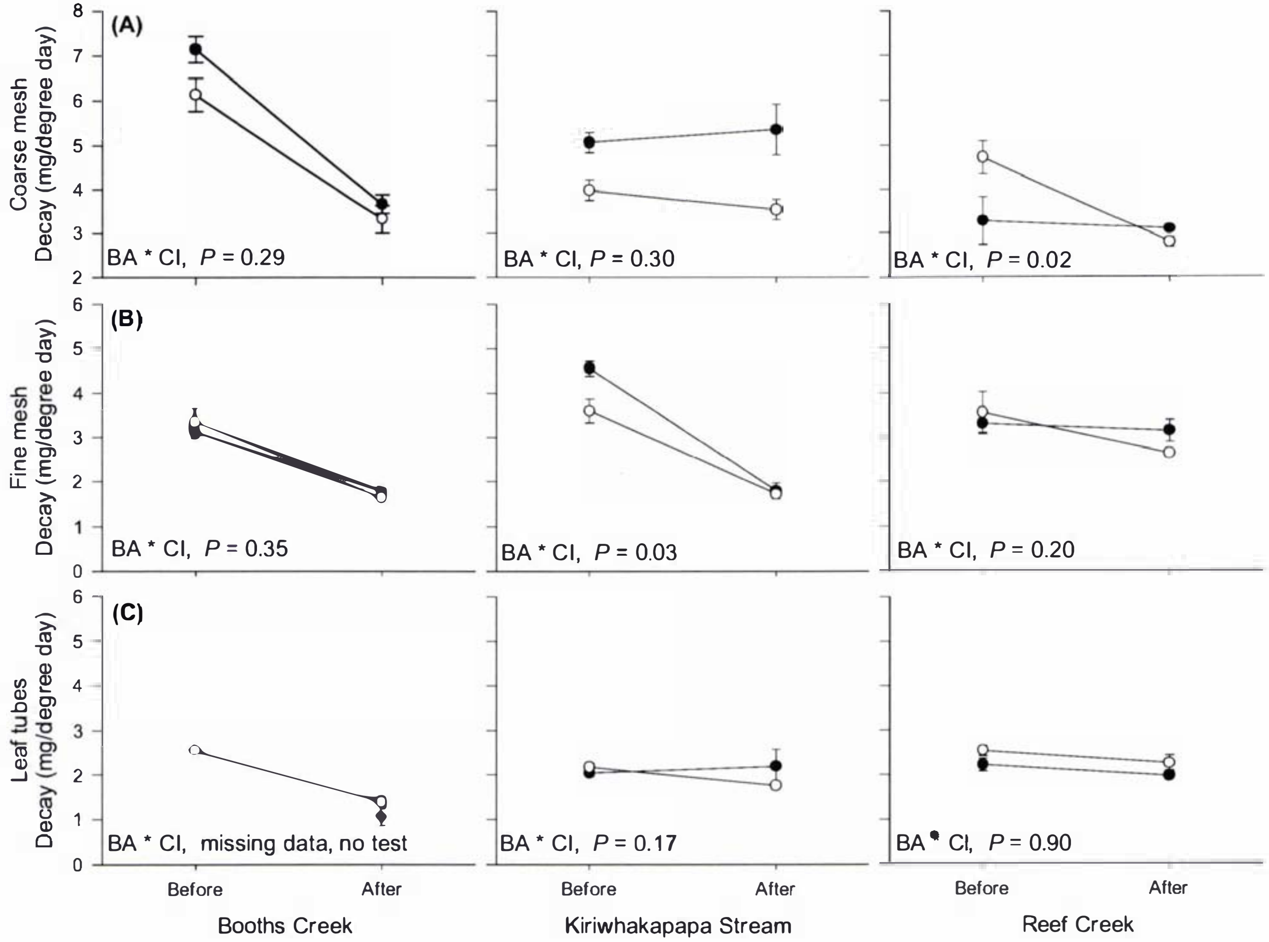

Figure 3. Mean (± 1 S.E.) leaf breakdown rate (mg/degree day) for control (black symbols) and impact (open symbols) treatments in (A) coarse (5 mm) mesh bags, (B) fine (1 mm) mesh bags and (C) leaf tubes (0.25 mm mesh) installed in Booths Creek, Kiriwhakapapa Stream and Reef Creek for one month before and after discharge reduction between December 2004 and March 2005.

Effects of discharge reduction on coarse particulate organic matter (CPOM) retention

There was an increase in the distance travelled by released artificial leaves ($F_{1, 13}$ = 22.06, $P < 0.001$) and wooden dowelling ($F_{1, 13}$ = 13.70, $P = 0.003$) with increasing discharge (Fig. 4). Therefore, the average distance travelled by CPOM until retention was lower after flow reduction. In this study, the average distance travelled for leaves was between 0.5 and 51 m, while for sticks the range was from 0.4 to 37 m. The maximum travel distances observed were 125 m for leaves and 75 m for sticks.

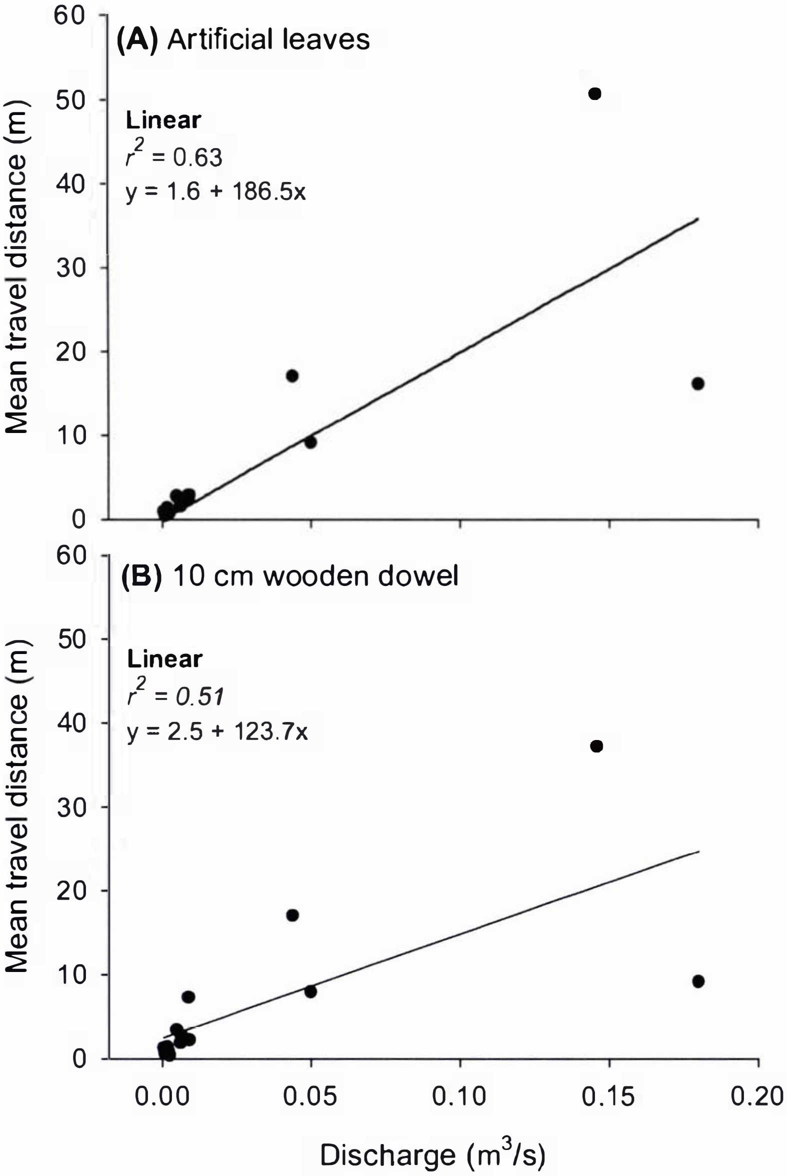

Figure 4. Relationship between mean CPOM travel distance and discharge for (A) artificial leaves and (B) 10 cm wooden dowels in Booths Creek, Kiriwhakapapa Stream and Reef Creek.

Changes in discharge also affected the type of structure that retained CPOM (Fig. 5). At higher discharges, the range of retention structures included riffles, edge and instream vegetation, eddies, snags and undercut banks. After flow reduction, riffles were the dominant retention structure, retaining on average 91% of artificial leaves and 85% of dowels.

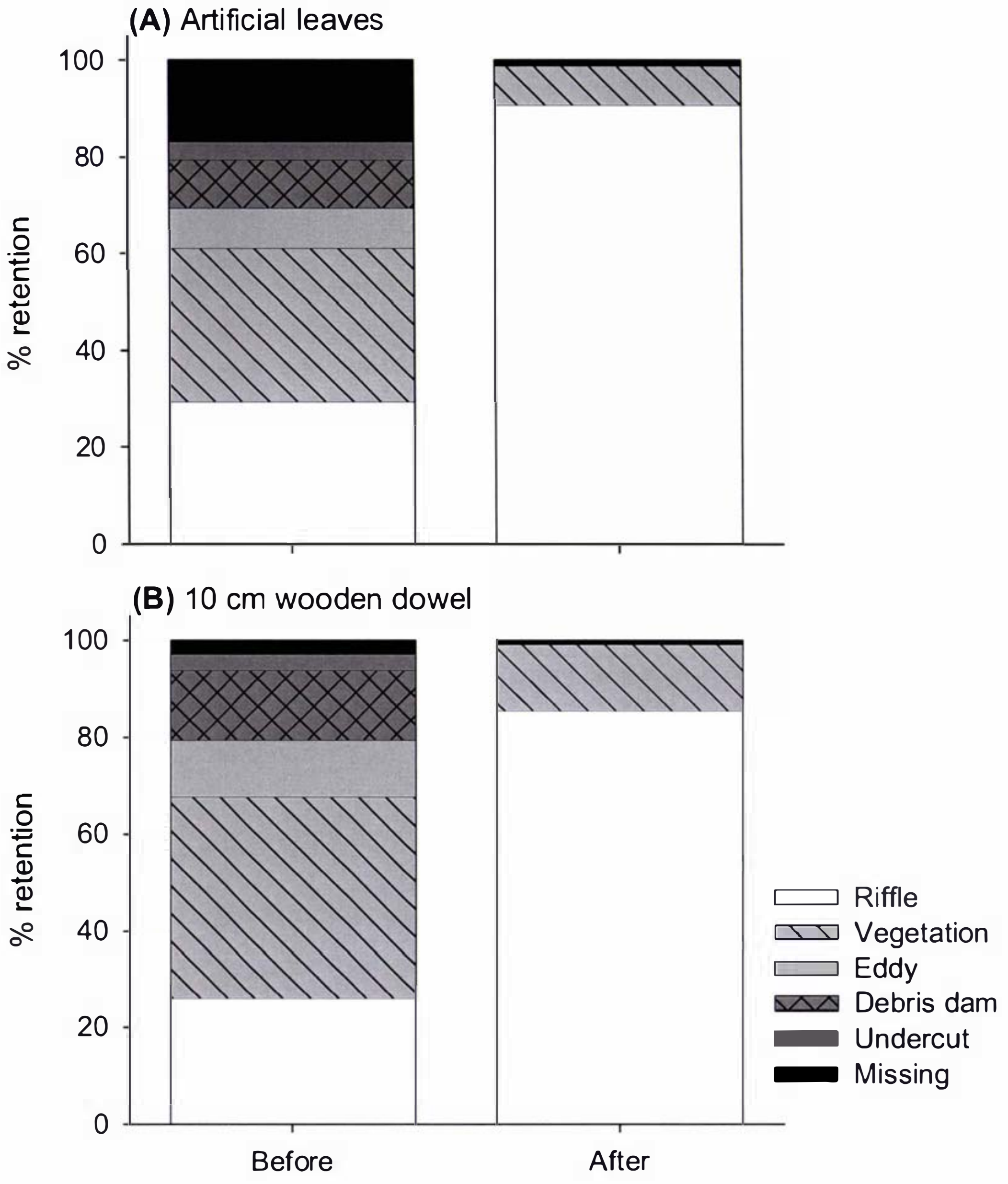

Figure 5. Percentage of (A) artificial leaves and (B) 10 cm wooden dowels captured by each type of retention structure before ($n = 6$) and after ($n = 9$) discharge reduction in impact reaches at Booths Creek, Kiriwhakapapa Stream and Reef Creek.

Effects of discharge reduction on primary production

Higher algal biomass accumulated over one month at the impact site on Booths Creek both before and after discharge reduction, but chlorophyll *a* concentration was relatively unchanged by flow reduction ($F_{1,20} = 0.33$, $P = 0.57$). There was less algal accumulation at the impact site on Kiriwhakapapa Stream after discharge reduction ($F_{1,20} = 27.3$, $P < 0.01$). Algal accumulation increased at the impact site on Reef Creek relative to the control site after reduction ($F_{1,20} = 4.5$, $P = 0.05$), however, after flow reduction, chlorophyll *a* concentrations were very similar at control and impact sites (Fig. 6).

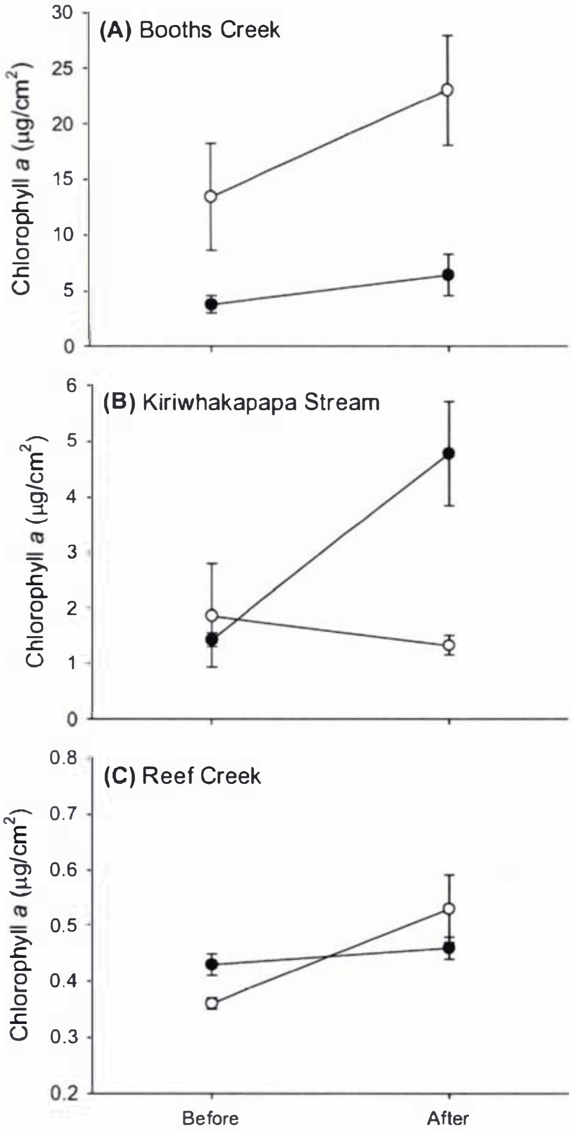

Figure 6. Mean (± 1 S.E.) chlorophyll *a* concentration (µg/cm²) for control (black symbols) and impact (open symbols) treatments installed in (A) Booths Creek, (B) Kiriwhakapapa Stream and (C) Reef Creek for one month before and after discharge reduction between December 2004 and March 2005

Discussion

Effects of discharge reduction on leaf breakdown

Reduced discharge had little influence on leaf breakdown rate in these streams. Leaf breakdown rate was always fastest in the coarse mesh bags and slowest in the leaf tubes. We anticipated this response, since leaves in large mesh bags are more likely to lose particles through physical abrasion than those in finer mesh bags (Webster & Benfield 1986). Leaves in coarse mesh bags had the greatest exposure to physical abrasion, as well as being the most accessible to invertebrate shredders, suggesting that these factors might have an important role in leaf breakdown in these streams.

The only apparent change in leaf breakdown rate following flow reduction was a decrease in breakdown in the coarse mesh bags at Reef Creek. There was decreased breakdown at the impact site relative to the control, but the difference in breakdown between control and impact sites was small. Reduced physical abrasion could explain this pattern, because we would expect more physical abrasion and faster leaf breakdown at the higher velocity control sites. However, despite low velocities in the reduced flow reaches of the other two streams, there were no decreases in leaf breakdown rates, making the physical abrasion explanation less plausible. Comparable findings are reported in the literature. Although physical abrasion controlled leaf breakdown during short-term peaks in flow, reduced flows did not decrease leaf breakdown rates downstream of a headwater dam (Casas *et al.* 2000). Similarly, Rader *et al.* (1994) found no difference in breakdown rates between fast and slow water and concluded that flow related fragmentation was not an important determinant of leaf breakdown.

Macroinvertebrates may also play an important role in leaf breakdown (Wallace & Webster 1996), and faster leaf breakdown rates in larger mesh bags are often attributed to invertebrates (Webster & Benfield 1986). However, specialised leaf shredding taxa are rare in New Zealand streams (Winterbourn 2000). We did not assess leaf pack invertebrate communities in this study, but discharge reduction did decrease invertebrate densities and the proportion of EPT individuals present in the riffle habitat where leaf packs were installed in Reef Creek (Chapter 4). This potentially reduced the density of shredding invertebrates for the impact site and could be responsible for the decrease in leaf breakdown at this site. In contrast, invertebrate densities did not decrease significantly in the other streams in our study (Chapter 4), with correspondingly no change in leaf breakdown rate.

Leaf breakdown was very similar at control and impact sites in the fine mesh bags. Although breakdown rate increased at the impact site on Kiriwhakapapa Stream relative to the control site, control and impact breakdown rates were the same during the flow reduction. Large invertebrates were excluded from these bags, so any changes were thought to be attributable to changes in microbial decomposition. We expected microbial decomposition to decrease at impact sites because of an increase in sedimentation (Rader *et al.* 1994, Niyogi *et al.* 2003), but there was no evidence that sedimentation at impact sites was reducing leaf breakdown rates. Sediment cover of the substrate was greater for impact sites on Booths Creek and Kiriwhakapapa Stream. We expected this, since lower water velocities allow more sediment to settle out of the water column and we found that quantities of suspended sediment were unchanged by the flow reductions. The percentage cover of fine sediments was highest at Kiriwhakapapa Stream (62%), followed by Booths Creek (28%) and Reef Creek (12%). Other studies generally agree that sedimentation increases with reductions in discharge (e.g., Kraft 1972, Castella *et al.* 1995, Wood & Petts 1999, Wood & Armitage 1999). In contrast, there was no difference in sediment cover between control and impact sites on Reef Creek. The low sediment supply from the forested catchment of Reef Creek probably limited the potential for sedimentation to increase in that stream.

It is surprising that leaf breakdown rates did not consistently decrease with flow reduction. Increases in sedimentation could have decreased breakdown, as could decreases in physical abrasion and invertebrate abundance. Perhaps other factors that were not altered by flow reduction had more influence on leaf breakdown in these streams. For example, temperature differences between control and impact sites were small and there were no differences in conductivity, pH, or dissolved oxygen between sites. Leaf breakdown occurred faster in warmer streams, probably as a result of temperature differences and faunal differences. Temperature primarily controls microbial processing (Minshall *et al.* 1983), so in the absence of temperature differences between control and impact sites, perhaps we should not expect differences in leaf breakdown.

Effects of discharge reduction on coarse particulate organic matter (CPOM) retention

Discharge strongly influences the retention of CPOM in streams. In this study, CPOM travelled further before retention at higher discharges and impact reaches accumulated noticeably more organic material (particularly leaf litter) than controls (Plate 7). Many previous studies have related higher discharges to higher CPOM transport distances (Raikow *et al.* 1995, Larned 2000). Snaddon *et al.* (1992) also found that at any discharge, slow flowing reaches generally retained more CPOM than medium or fast flowing reaches. Therefore, over time, reduced discharge would tend to enhance the accumulation of CPOM. The distance travelled by released CPOM increased with discharge over the range of discharges tested in these streams. In the longer term, flow variability might be equally as important as discharge when considering the implications of water abstraction on CPOM retention. The relationship between discharge and CPOM transport depends on the temporal scale of CPOM measurement. Longer-term studies have demonstrated the importance of storms and the size of storm discharges as determinants of CPOM export (Cuffney *et al.* 1990, Cuffney & Wallace 1989, Wallace *et al.* 1995). Similarly, Jones & Smock (1991) found that mean travel distance of leaves was significantly greater at winter base discharges than summer base discharges and higher again during winter spates.

Riffles retained a much higher proportion of released CPOM at low discharges in our study. In shallower water, rocks were closer to, or protruding from the water surface, making riffles more effective retention structures. Similarly, Snaddon *et al.* (1992) reported that the trapping efficiency of riffles decreased with increasing discharge since the proportions of retention features alter with discharge, and Webster *et al.* (1994) found greater retention in shallower stream sites, with rocks, boulders and woody debris as the most important retention structures.

Plate 5. Leaf bags and primary production tiles installed in the control reach of Reef Creek.

Plate 6. Primary production tiles installed in the control reach of Booths Creek.

Plate 7. Leaves accumulating in the reduced flow reach of Booths Creek

Effects of discharge reduction on primary production

Sampling of artificial substrates showed that relatively less algal biomass accumulated at the impact site on Kiriwhakapapa Stream after discharge reduction, whilst there was relatively more accumulation at the impact site on Reef Creek. The impact site on Booths Creek was unchanged relative to the control. These inconsistencies between the study streams are consistent with the varying responses presented in the literature. Studies of water velocity and algae generally report that there are relationships between water velocity and periphyton (e.g., McIntire 1966, Poff *et al.* 1990, Biggs & Hickey 1994). However, relationships between water velocity and algae can vary depending on the growth form of the algae (Biggs *et al.* 1998), levels of light and nutrients, and the influence of velocity on the distribution of grazing invertebrates (Stevenson 1996). Early laboratory investigations showed that biomass and chlorophyll *a* were higher in fast (38 cm/s) than slow (9 cm/s) velocity channels and that slow velocities promoted filamentous growth forms while diatoms were dominant at faster velocities (McIntire 1966). Subsequently, Poff *et al.* (1990) found much lower algal biomass in fast velocity treatments on tiles in instream channels, and Jowett & Biggs (1997) found that less periphyton and sediment accrued on plastic artificial substrates at higher velocities. By reviewing the findings of numerous studies investigating the effects of water velocity on algae, Stevenson (1996) concluded that intermediate current velocities (10-50 cm/s) tend to promote the highest algal biomasses in most habitats. Increased velocities increase algal metabolism up to a point, after which the drag caused by the faster water velocities increases algal export and decreases algal biomass (Stevenson 1996).

Invertebrate grazer densities go some way to explaining the differences between sites in our study. After discharge reduction, there were significant decreases in the abundance of *Deleatidium* sp., the most common mayfly grazer at Reef Creek (Chapter 4). This decrease in density of an important grazer might be responsible for the relative increase in algal biomass at the impact site. In Booths Creek, we observed no change to invertebrate densities (Chapter 4), and periphyton growth was unchanged by the discharge reduction. However, grazer densities cannot explain decreased algal biomass at the impact site on Kiriwhakapapa Stream, although increased sediment cover in this stream could have inhibited periphyton growth. In Kiriwhakapapa Stream, densities of *Potamopyrgus antipodarum,* the dominant grazer, decreased at the impact site following discharge reduction, as did densities of *Deleatidium* sp. (Chapter 4).

The application of stream ecosystem functions to assess the effects of water abstraction

Evaluations of stream ecosystem function can complement structural measures when assessing the effects of water abstraction. Functional measures add another dimension to ecological impact monitoring and can be cost effective and informative. Furthermore, this approach might assist with interpreting the longer-term implications of reduced discharge on stream ecosystems by enhancing our understanding of changes to energy supply and habitat. There can be both positive and negative effects on an ecosystem function from a single anthropogenic stress (Niyogi *et al.* 2003). Therefore, it is important to identify appropriate ecosystem functions for assessing the effects of water abstraction. In addition, it is necessary to identify what level of change to ecosystem functions will be considered as a cause for concern.

In this study, evaluations of stream ecosystem functioning in response to water abstraction generally provided small or inconsistent responses that were not easily explained by changes to physicochemical characteristics and the macroinvertebrate community with reduced discharge. Leaf breakdown was relatively insensitive to marked decreases in discharge over a one month period. The relative importance of factors such as sedimentation, physical abrasion, and invertebrate processing on leaf breakdown were unclear. The responses of periphyton production to severely reduced discharges in these streams were inconsistent. Of the three ecosystem functions investigated in this study, CPOM retention was the most responsive to reduced discharge. The negative relationship between CPOM retention and discharge has been documented in numerous studies (e.g., Jones and Smock 1991, Raikow et al. 1995, Larned 2000) and was evident in the streams we studied. There may be threshold discharges, below which CPOM retention increases greatly (Raikow et al. 1995), but we did not observe this pattern over the range of discharges observed in our streams. Increases in CPOM accumulation were not matched by increases in decomposition, and invertebrate densities were lower at reduced flow reaches. Therefore, increases in CPOM retention could alter food web dynamics, habitat types and flow characteristics, having wider implications for the invertebrate community in the longer term than a change in hydrology alone.

If the responses of leaf decomposition, CPOM retention and primary production to flow reduction were tested over a wider range of streams, predictable responses may emerge (e.g., consistent responses within stream types, land uses, or levels of water abstraction). If so, measures of ecosystem function could enhance assessments of water abstraction impacts, and might help interpret the longer-term implications of reduced discharge on stream ecosystems by enhancing our understanding of changes to energy supply and habitat.

References

Allan J.D. (1995) *Stream Ecology: Structure and Function of Running Waters.* 1st edn. Chapman & Hall, London.

Biggs B.J.F. & Close M.E. (1989) Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients. *Freshwater Biology,* **22,** 209-231.

Biggs B.J.F., Goring D.G. & Nikora V.I. (1998) Subsidy and stress responses of stream periphyton to gradients in water velocity as a function of community growth form. *Journal of Phycology,* **34,** 598-607.

Biggs B.J.F. & Hickey C.W. (1994) Periphyton responses to a hydraulic gradient in a regulated river in New Zealand. *Freshwater Biology,* **32,** 49-59.

Bond N.R. (2002) A simple device for estimating rates of fine sediment transport along the bed of shallow streams. *Hydrobiologia,* **468,** 155-161.

Brookshire E.N.J. & Dwire K.A. (2003) Controls on patterns of coarse organic particle retention in headwater streams. *Journal of the North American Benthological Society,* **22,** 17-34.

Casas J.J., Zamora-Munoz C., Archila F. & Alba-Tercedor J. (2000) The effect of a headwater dam on the use of leaf bags by invertebrate communities. *Regulated Rivers: Research and Management,* **16,** 577-591.

Castella E., Bickerton M., Armitage P.D. & Petts G.E. (1995) The effects of water abstractions on invertebrate communities in U.K. streams. *Hydrobiologia,* **308,** 167-182.

Cazaubon A. & Giudicelli J. (1999) Impact of the residual flow on the physical characteristics and benthic community (algae, invertebrates) of a regulated Mediterranean river: the Durance, France. *Regulated Rivers: Research and Management,* **15,** 441-461.

Cuffney T.F. & Wallace B. (1989) Discharge-export relationships in headwater streams: the influence of invertebrate manipulations and drought. *Journal of the North American Benthological Society,* **8,** 331-341.

Cuffney T.F., Wallace B. & Lugthart G.J. (1990) Experimental evidence quantifying the role of benthic invertebrates in organic matter dynamics of headwater streams. *Freshwater Biology,* **23,** 281-299.

Dangles O., Gessner M.O., Guerold F. & Chauvet E. (2004) Impacts of stream acidification on litter breakdown: implications for assessing ecosystem functioning. *Journal of Applied Ecology,* **41,** 365-378.

Davies A.L. & Gee J.H.R. (1993) A simple periphyton sampler for algal biomass estimates in streams. *Freshwater Biology,* **30,** 47-51.

Downes B.J., Barmuta L.A., Fairweather P.G., Faith D.P., Keough M.J., Lake P.S., Mapstone B.D. & Quinn G.P. (2002) *Monitoring Ecological Impacts: Concepts and Practice in Flowing Waters.* Cambridge University Press, Cambridge.

Gessner, M.O. & Chauvet E. (2002) A case for using litter breakdown to assess functional stream integrity. *Ecological Applications,* **12,** 498-510.

Gordon N.D., McMahon T.A., Finlayson B.L., Gippel C.J. & Nathan R.J. (2004) *Stream Hydrology: An Introduction for Ecologists.* 2nd edn. John Wiley & Sons Ltd., West Sussex, England.

Hagen E.M., Webster J.R. & Benfield E.F. (2006) Are leaf breakdown rates a useful measure of stream integrity along an agricultural landuse gradient? *Journal of the North American Benthological Society,* **25,** 330-343.

James A.B.W. & Henderson I.M. (2005) Comparison of coarse particulate organic matter retention in meandering and straightened sections of a third-order New Zealand stream. *River Research and Applications,* **21,** 641-650.

Jones J.B. & Smock L.A. (1991) Transport and retention of particulate organic-matter in 2 low-gradient headwater streams. *Journal of the North American Benthological Society*, **10,** 115-126.

Jowett I.G. & Biggs B.J.F. (1997) Flood and velocity effects on periphyton and silt accumulation in two New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research,* **31,** 287-300.

Kraft M.E. (1972) Effects of controlled flow reduction on a trout stream. *Journal of the Fisheries Research Board of Canada,* **29,** 1405-1411.

Larned S.T. (2000) Dynamics of coarse riparian detritus in a Hawaiian stream ecosystem: a comparison of drought and post-drought conditions. *Journal of the North American Benthological Society,* **19,** 215-234.

McIntire C.D. (1966) Some effects of current velocity on periphyton communities in laboratory streams. *Hydrobiologia,* **27,** 559-570.

McIntosh M.D., Benbow M.E. & Burky A.J. (2002) Effects of stream diversion on riffle macroinvertebrate communities in a Maui, Hawaii, stream. *River Research and Applications,* **18,** 569-581.

Minshall G.W., Petersen R.C., Cummins K.W., Bott T.L., Sedell J.R., Cushing C.E. & Vannote R.L. (1983) Interbiome comparison of stream ecosystem dynamics. *Ecological Monographs,* **53,** 1-25.

Molles M.C.J. (1999) *Ecology: Concepts and Applications.* 1st edn. WCB/McGraw-Hill, USA.

Mosley M.P. (1983) Variability of water temperatures in the braided Ashley and Rakaia rivers. *New Zealand Journal of Marine and Freshwater Research,* **17,** 331-342.

Niyogi D.K., Lewis W.M. & McKnight D.M. (2001) Litter breakdown in mountain streams affected by mine drainage: biotic mediation of abiotic controls. *Ecological Applications,* **11(2),** 506-516.

Niyogi D.K., Simon K.S. & Townsend C.R. (2003) Breakdown of tussock grass in streams along a gradient of agricultural development in New Zealand. *Freshwater Biology,* **48,** 1698-1708.

Pascoal C., Cassio F. & Gomes P. (2001) Leaf breakdown rates: a measure of water quality. *International Review of Hydrobiology,* **86,** 407-416.

Petersen R.C. & Cummins K.W. (1974) Leaf processing in a woodland stream. *Freshwater Biology,* **4,** 343-368.

Poff N.L., Voelz N.J., Ward J.V. & Lee R.E. (1990) Algal colonization under four experimentally-controlled current regimes in a high mountain stream. *Journal of the North American Benthological Society,* **9,** 303-318.

Rader R.B. & Belish T.A. (1999) Influence of mild to severe flow alterations on invertebrates in three mountain streams. *Regulated Rivers: Research and Management,* **15,** 353-363.

Rader R.B., McArthur J.V. & Aho J.M. (1994) Relative importance of mechanisms determining decomposition in a Southeastern blackwater stream. *American Midland Naturalist,* **132,** 19-31.

Raikow D.F., Grubbs S.A. & Cummins K.W. (1995) Debris dam dynamics and coarse particulate organic matter retention in an Appalachian Mountain stream. *Journal of the North American Benthological Society,* **14,** 535-546.

Royer T.V. & Minshall G.W. (2003) Controls on leaf processing in streams from spatial-scaling and hierarchical perspectives. *Journal of the North American Benthological Society,* **22,** 352-358.

SAS Institute Inc. (2004) *The SAS System for Windows.* SAS Institute Inc., Cary, North Carolina, U.S.A.

Snaddon C.D., Stewart B.A. & Davies B.R. (1992) The effect of discharge on leaf retention in two headwater streams. *Archiv für Hydrobiologie,* **125,** 109-120.

Steinman A.D. & Lamberti G.A. (1996) Biomass and pigments of benthic algae. In: *Methods in Stream Ecology* (Eds F.R. Hauer & G.A. Lamberti), pp. 295-313. Academic Press Inc., USA.

Stevenson R.J. (1996) The stimulation and drag of current. In: *Algal Ecology: Freshwater Benthic Ecosystems* (Eds R.J. Stevenson, M.L. Bothwell & R.L. Lowe), pp. 321-340. Academic Press, San Diego, U.S.A.

Wallace J.B. & Webster J.R. (1996) The role of macroinvertebrates in stream ecosystem function. *Annual Review of Entomology,* **41,** 115-139.

Wallace J.B., Eggert S.L., Meyer J.L. & Webster J.R. (1997) Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science,* **277,** 102-104.

Wallace J.B., Whiles M.R., Eggert S., Cuffney T.F., Lughart G.J. & Chung K. (1995) Long-term dynamics of coarse particulate organic-matter in 3 Appalachian mountain streams. *Journal of the North American Benthological Society,* **14,** 217-232.

Webster J.R. & Benfield E.F. (1986) Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics,* **17,** 567-594.

Webster J.R., Benfield E.F., Ehrman T.P., Schaeffer M.A., Tank J.L., Hutchens J.J. & D'Angelo D.J. (1999) What happens to allochthonous material that falls into streams? A synthesis of new and published information from Coweeta. *Freshwater Biology,* **41,** 687-705.

Webster J.R., Covich A.P., Tank J.L. & Crockett T.V. (1994) Retention of coarse organic particles in streams in the southern Appalachian Mountains. *Journal of the North American Benthological Society,* **13,** 140-150.

Winterbourn M.J. (2000) Feeding ecology. In: *New Zealand Stream Invertebrates: Ecology and Implications for Management* (Eds K.J. Collier & M.J. Winterbourn), pp. 100-124. New Zealand Limnological Society, Christchurch, New Zealand.

Wood P.J., Agnew M.D. & Petts G.E. (2000) Flow variations and macroinvertebrate community responses in a small groundwater-dominated stream in south-east England. *Hydrological Processes,* **14,** 3133-3147.

Wood P.J. & Armitage P.D. (1999) Sediment deposition in a small lowland stream-management implications. *Regulated Rivers: Research and Management,* **15,** 199-210.

Wood P.J. & Petts G.E. (1999) The influence of drought on chalk stream macroinvertebrates. *Hydrological Processes,* **13,** 387-399.

Woodcock T.S. & Huryn A.D. (2005) Leaf litter processing and invertebrate assemblages along a pollution gradient in a Maine (USA) headwater stream. *Environmental Pollution,* **134,** 363-375.

Woodward G., Jones J.I. & Hildrew A.G. (2002) Community persistence in Broadstone Stream (U.K.) over three decades. *Freshwater Biology,* **47,** 1419-1435.

Wright J.F. & Berrie A.D. (1987) Ecological effects of groundwater pumping and a natural drought on the upper reaches of a chalk stream. *Regulated Rivers: Research and Management,* **1,** 145-160.

Young R.G., Huryn A.D. & Townsend C. (1994) Effects of agricultural development on processing of tussock leaf litter in high country New Zealand streams. *Freshwater Biology,* **32,** 413-427.

Young R.G. (2006) *Functional Indicators of River Ecosystem Health – Results from Regional Case Studies of Leaf Decomposition.* Cawthron Report No. 1054, Nelson, New Zealand.

CHAPTER 6

Invertebrate community responses to changes in algae and velocity with reduced discharge

Abstract

Water abstraction decreases stream discharge and can alter invertebrate community composition, abundance, and taxonomic richness. The cause of these changes can be difficult to interpret, since invertebrates can respond to many of the environmental changes that result from flow reduction, including decreased water velocity, lowered habitat diversity and increased finer substrate. The aim of this study was to test whether decreased water velocity or altered algal resources could account for invertebrate community responses to flow reduction in Kiriwhakapapa Stream, a small stream, moderately impacted by extensive farming. To achieve this, I manipulated algal resources and water velocities in separate experiments in instream channels for two days. After a year of experimentally reduced discharge, invertebrate density and taxonomic richness were reduced in Kiriwhakapapa Stream. At the same time, filamentous green algae became widespread throughout the reduced flow reach, but remained sparse and patchy in the control flow reach of this stream. By installing substrate from both control and reduced flow reaches of the stream into channels of equal velocity, I found that the influence of algal resources on invertebrates varied between taxa. Substrate from the control flow reach had higher ash free dry mass (AFDM) of organic matter than substrate from the reduced flow reach. The abundance of browsing invertebrates increased with the AFDM of organic matter on the substrate, but this did not affect filter feeder abundance. In contrast, by manipulating water velocity, I found that the abundance of filter feeders decreased at low velocities but had no effect on the abundance of browsing invertebrates. I concluded that the acquisition of resources (availability of organic matter for browsers, rate of food delivery for filter feeders) provided some explanation for invertebrate responses to reduced flow in this stream.

Introduction

In stream ecosystems, flowing water is a direct physical force on stream organisms, as well as a determinate of substrate composition, and the delivery mechanism for nutrients and food particles (Allan 1995). Water velocity is commonly reduced when stream discharge decreases (e.g., Wright & Berrie 1987, McIntosh *et al.* 2002, Dewson *et al.* 2007). Decreased discharge can alter invertebrate community composition, abundance, and taxonomic richness (e.g., Wood & Petts 1994, Rader & Belish 1999, Suren *et al.* 2003a). However, the proximate cause of these changes can be difficult to interpret. It is unclear whether invertebrates respond directly to decreased water velocity, increased periphyton growth or a reduction in the rate of food particle delivery (Doisy & Rabeni 2001). Instream habitat characteristics are strongly linked to flow, making it difficult to identify the individual effects of changes in water depth, velocity and substrate size on benthic invertebrate distribution (Hart & Finelli 1999, Jowett 2000). It is likely that multiple factors, including both water velocity and algal abundance interact to control invertebrate distribution.

Water velocity can influence invertebrate distribution and abundance (e.g., Quinn & Hickey 1994, Doisy & Rabeni 2001, Brooks *et al.* 2005), as well as the movements of individuals (e.g., Poff & Ward 1992, Malmqvist & Sackmann 1996, Lancaster 1999). By determining the rate of food delivery (Nowell & Jumars 1984, Hart & Finelli 1999), water velocity controls the distribution of filter feeders such as Hydropsychidae (Georgian & Thorp 1992) and Simuliidae (Malmqvist & Sackmann 1996). Water velocity also controls the delivery rate of resources such as dissolved nutrients and dissolved oxygen for invertebrates (Hart & Finelli 1999). In addition, water velocity can affect food resources for grazers, by controlling algal community composition and biomass (Stevenson 1996). Brooks *et al.* (2005) recently suggested that the influence of hydraulic characteristics on periphyton might help to explain patterns of invertebrate abundance. Water velocity can affect accrual, production and sloughing of the periphyton community (Biggs & Close 1989, Jowett & Biggs 1997). Low velocities often result in higher algal biomass (e.g., McIntire 1966, Poff *et al.* 1990) and prolonged low flows tend to promote high biomass green filamentous algae, at the expense of diatoms and cyanobacteria (Biggs *et al.* 2005). High velocities increase the sloughing of filamentous periphyton, whereas denser growth forms can increase with water velocity by increasing nutrient uptake (Biggs *et al.* 1998).

Experimental flow reductions in a small stream with moderate water quality (Kiriwhakapapa Stream) caused changes to the invertebrate community and a visible increase in filamentous algae (Chapter 4). The aim of this study was to use instream channels to test whether either decreased water velocity, or altered algal resources could explain the changes to invertebrate community structure in reduced flow sections of Kiriwhakapapa Stream. I hypothesised that the invertebrate community was responding to changes in algal resources in this stream, rather than the direct effects of velocity, because invertebrate browsers dominate the community in this stream and rely on algae as a food source. Therefore, I expected that in open-ended, artificial channels:

1. under equal velocity conditions, invertebrate communities would be distinct on substrate collected from control and reduced flow reaches of the stream (given that substrate from each site had different algal resources).
2. differences in velocity would not result in different invertebrate communities when algal resources on the substrate were equal.

Methods

Study site

This experiment was conducted in an unnamed tributary of Kiriwhakapapa Stream in the foothills of the Tararua Ranges (40° 49 07.10'S 175° 34 21.04'E), in the lower North Island, New Zealand. The Kiriwhakapapa Stream tributary is a small (110 L/s, mean summer discharge 2005), perennial, runoff fed stream. This meandering stream has a pool-riffle morphology and gravel-cobble substrate, with fine sediments contributed by bank erosion. Flood flows produce a narrow, peaked hydrograph for this stream. The study site is within an extensive sheep and beef farm where stock has access to the stream and the channel has little shading in the study reaches.

At the time of this study, there had been a weir and diversion installed in the stream for 12 months to reduce downstream discharge by around 85% for a channel distance of approximately 100 m (see Chapters 3-5). The weir was constructed of wooden boards, and extended across the entire stream, but was not completely sealed, so that a proportion of the flow and invertebrates could move through, under and around the weir. Streamflow was unaltered upstream of the weir (control reach).

Artificial channels and cobble baskets

Instream channels were used for two separate experiments to assess the effects of algae (February 2006) and velocity (May 2006) on the invertebrate community. Channels were made of PVC pipes that were halved lengthwise (2.5 m length, 0.3 m diameter). For each experiment, two instream channels were positioned side by side at midstream, parallel to the direction of flow in the control flow reach of the stream (Plate 1). Wire mesh baskets (120 mm × 120 mm size, 10 mm square mesh) were used as the sampling units in each experiment and the base of each basket was covered with cobbles (< 60 mm, *a*-axis) collected from the study stream. Nine baskets were installed in each channel for each experiment.

Experiment 1: algae manipulations in instream channels

To assess the effect of algal differences on the invertebrate community, the two channels were positioned so that velocity was similar in each. Nine baskets were filled with cobbles from the reduced flow reach and a further nine baskets with cobbles from the control flow reach (Plate 2). Invertebrates were not intentionally removed from cobbles, to avoid disturbing algal cover, but two further baskets of cobbles were collected from each site and sampled immediately, rather than being installed in a channel to provide an indication of initial invertebrate densities in the baskets. I randomly allocated baskets to the two channels, but ensured that no more than five baskets from a single treatment were in one channel. After 48 hours, baskets of cobbles were collected. Working from the downstream end of each channel, a 250-μm mesh net was placed behind each basket and it was lifted into the net to avoid a loss of invertebrates during sampling. The entire basket was emptied into a 10 L bucket, ¼ filled with stream water, and all surfaces of the cobbles and basket were scrubbed to remove invertebrates and algae. Contents of the bucket were then filtered through the 250-μm net, rinsed into a container and preserved in 10% formalin. Invertebrate samples were rinsed through a 500-μm Endecott sieve and sub-sampled. A sample splitter was used to divide the sample into four parts and sequential sub-samples were sorted until at least 200 individuals were removed. The entirety of each sub-sample was processed. To avoid missing rare taxa, the remainder of the sample was scanned for taxa not present in the sub-sample. Invertebrates were identified to genus or species level where possible using the keys of Winterbourn (1973), Chapman & Lewis (1976), Winterbourn *et al.* (2000) and Smith (2003), except for oligochaetes (class) and chironomids (sub-family).

Once invertebrates were removed, each sample was dried at 50°C for 72 hours, weighed, ashed at 600 °C for two hours and then reweighed to assess the ash free dry mass (AFDM) of organic matter (>250 μm) in each sample.

In addition, I used invertebrate and chlorophyll *a* data collected from control and reduced flow reaches at Kiriwhakapapa Stream (Chapter 4) to characterise the source of control and reduced flow samples in this experiment. This data was collected after 9 and 12 months of flow reduction within riffle habitat at sites upstream and downstream of weirs as described in Chapter 4.

Algal samples were also collected from control and reduced flow reaches of Kiriwhakapapa Stream to assess periphyton community composition at the start of this experiment. From each of ten randomly selected cobbles, periphyton was scraped from an area of 2 cm^2, using a scalpel blade and rinsed into a container. Samples were transported on ice in the dark and frozen at -20°C, before being sent to NIWA, Christchurch, where community composition was assessed using the relative abundance methods of Biggs & Kilroy (2000). This method involves identifying a dominant taxon, then ranking the other main taxa into a maximum of eight categories, depending on their contribution to the biovolume of the sample in relation to the dominant taxon (Biggs & Kilroy 2000).

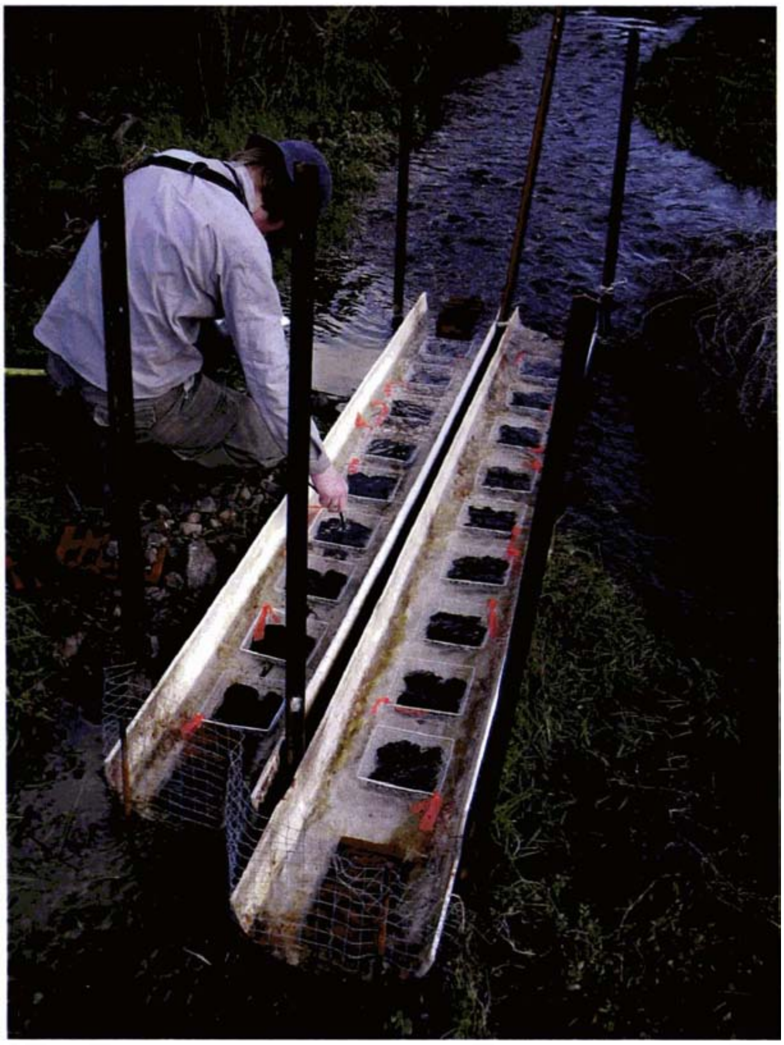

Plate 1. Baskets of cobble substrate installed in instream channels at Kiriwhakapapa Stream.

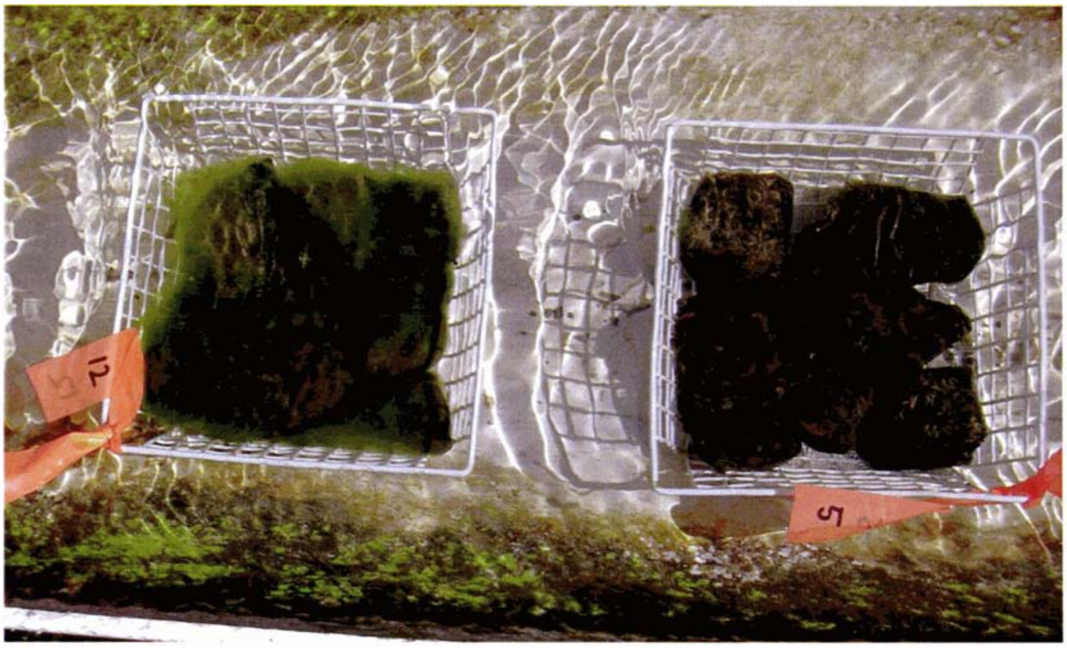

Plate 2. Cobble baskets from control (right) and reduced flow (left) algae treatments installed in an instream channel at Kiriwhakapapa Stream.

Experiment 2: velocity manipulations in artificial channels

To assess the importance of velocity to invertebrates, the two channels were positioned side by side in the control flow reach of the stream, so that one had high velocity and the other low velocity. A brick was placed at the upstream end of the low velocity channel to further slow water velocity without altering depth. Water velocities were between 0.03 and 0.13 m/s in the low velocity channel and between 0.19 and 0.25 m/s in the high velocity channel. These velocities were representative of water velocities in the reduced flow and control reaches of the study stream at the time of the experiment. I filled 23 baskets with cobbles from the control reach, then randomly allocated nine baskets to each channel and immediately preserved five control samples in 10% formalin. Water depth and velocity above each basket was recorded. After 48 hours, invertebrate samples were collected and processed as described above for Experiment 1.

Data analysis

I calculated the total number of individuals, taxonomic richness, rarefied number of taxa, the percentage of Ephemeroptera, Plecoptera, and Trichoptera (EPT) individuals and taxa (Lenat 1988) and Simpson's index (Simpson 1949) to describe the invertebrate communities of each sample. Since *Oxyethira albiceps* is a particularly pollution tolerant taxon compared to other Trichoptera (Boothroyd & Stark 2000), it was excluded from percentage EPT calculations, but included for all other analyses. I used linear regression in STATISTIX 8 (Analytical Software 2006) to examine relationships between invertebrate indices and the AFDM of organic matter in samples from the algae experiment.

Invertebrate abundances were pooled into five taxonomic groupings (Ephemeroptera, Trichoptera, Diptera, Mollusca and Other), to calculate relative abundances for each treatment in the algae and velocity experiments. Functional feeding categories were also assigned to each taxon identified in the channel experiments using Cowie (1980) and Winterbourn (2000).

One-way analysis of variance (ANOVA) in SAS (2004) was used to examine differences in invertebrate indices, the abundances of common taxa, chlorophyll *a* concentrations and water velocities between treatments. There were two treatments for each channel experiment, cobbles from control and reduced flow reaches (algae experiment) and control and low velocities (velocity experiment). All factors were treated as fixed effects, and the channels were included as blocks in the analysis of the algae experiment, since treatments were randomly allocated between the channels. Samples were treated as replicates in all analyses.

Similarities between invertebrate assemblages of experimental channel treatments (after fourth root transformation) were presented in two dimensions using non-metric multi-dimensional scaling (MDS) in PRIMER 6.1.5 (Clarke & Gorley 2006). I then used one-way analysis of similarities (ANOSIM) to test the null hypothesis that there were no differences between the treatments (control and reduced flow algae, or control and low velocity) for each set of data using PRIMER. ANOSIM computes a test statistic that contrasts the differences between sites with those within sites using ranked similarities and then calculates statistical significance by permutation (Clarke & Warwick 2001).

Results

Effects of discharge reduction on periphyton community composition and biomass

Filamentous algae were more prevalent in the reduced flow reach of this stream (personal observation). Differences in relative community abundance between reduced flow and control flow sites reflect this difference. *Synedra ulna,* a diatom was clearly dominant in the control flow reach, whereas *Spirogyra* sp., a filamentous green algae dominated the community in the reduced flow reach. Overall, there were 17 taxa recorded for the control flow site and 15 at the reduced flow site (Table 1). However, there was no difference in chlorophyll *a* concentration between the two reaches in the stream ($F_{1,\,18} = 0.17$, $P = 0.69$).

Table 1. Relative abundances of taxa in the algal community at control and reduced flow sites on Kiriwhakapapa Stream at the start of the algae manipulation experiment, February 2006. Taxa are ranked, relative to the dominant taxa, according to their contribution to the biovolume of the sample using the methods of Biggs & Kilroy (2000).

Major algal group	Taxa	Control flow	Reduced flow
Chlorophyta	*Spirogyra* sp.	6	8
Chlorophyta	*Oedogonium* sp.	4	4
Cyanobacteria	*Oscillatoria* sp.		1
Rhodophyta	*Batrachospermum* sp.		
Diatom	*Cocconeis placentula*	4	
Diatom	*Cymbella aspera*	1	
Diatom	*Cymbella kappii*	4	2
Diatom	*Cymbella tumida*	5	7
Diatom	*Encyonema minutum*	3	
Diatom	*Epithemia* sp.		1
Diatom	*Eunotia* sp.		1
Diatom	*Fragilaria vaucheriae*	2	
Diatom	*Gomphoneis minuta*	1	
Diatom	*Gomphonema parvulum*	3	3
Diatom	*Gomphonema truncatum*	1	3
Diatom	*Melosira varians*	3	
Diatom	*Navicula cryptocephala*	1	
Diatom	*Navicula radiosa*		1
Diatom	*Navicula rhynchocephala*	1	
Diatom	*Navicula* sp.	2	4
Diatom	*Nitzschia* sp.		2
Diatom	*Reimeria sinuate*	1	
Diatom	*Rhoicosphenia abbreviata*		1
Diatom	*Synedra acus*		3
Diatom	*Synedra ulna*	8	5

Experiment 1: effects of algae manipulations on the invertebrate community

Benthic invertebrate communities were different in the flow reduced and control flow reaches of the stream at the start of the channel experiments (ANOSIM global $R = 0.72$, $P < 0.01$) (Fig. 1). Invertebrate densities in the reduced flow reach were around half of those in the control flow reach ($F_{1,18} = 10.87$, $P < 0.01$), and there were fewer taxa present (even when rarefied to allow for density differences) ($F_{1,18} = 6.60$, $P = 0.02$). In the control flow reach, 18% of individuals were Ephemeroptera, Plecoptera, or Trichoptera (EPT), while in the reduced flow reach, only 9% of individuals were EPT ($F_{1,18} = 5.86$, $P = 0.03$). Similarly, the percentage of EPT taxa was considerably higher in the control flow reach (41%) than the reduced flow reach (24%) ($F_{1,18} = 32.35$, $P < 0.01$).

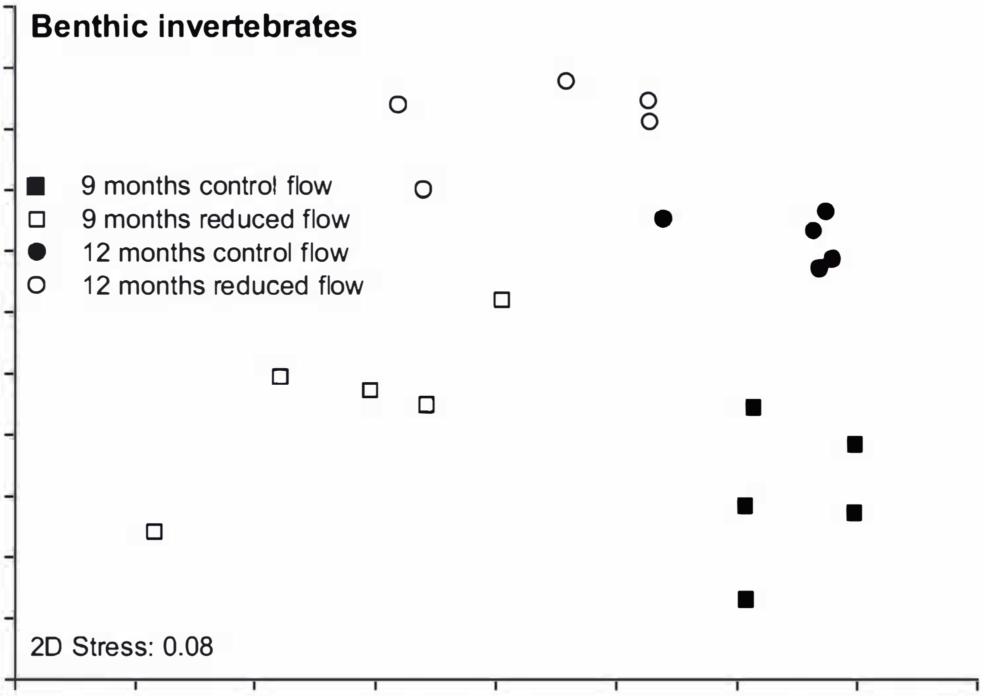

Figure 1. Non-metric multi-dimensional scaling (MDS) ordination of invertebrate assemblages at control and reduced flow reaches of Kiriwhakapapa Stream after 9 and 12 months of experimentally reduced flow.

Invertebrate assemblages on cobbles from control and reduced flow reaches became more similar after two days in the artificial channels at equal velocity, but remained distinctive (ANOSIM global $R = 0.60$, $P < 0.01$) (Fig. 2). Of the baskets of cobbles that were sampled immediately, rather than being installed in the channels, those from the control flow reach of the stream had higher densities of invertebrates (mean = 874.5) than those from the reduced flow reach (mean = 85.5). Invertebrate density remained higher in the control baskets after two days in the channels (Table 2). There was also a higher percentage of EPT individuals, more taxa, and a higher percentage of EPT taxa in control flow samples (Table 2). However, when rarefied to allow for density differences, the number of taxa did not differ between samples collected from the control and reduced flow reaches (Table 2).

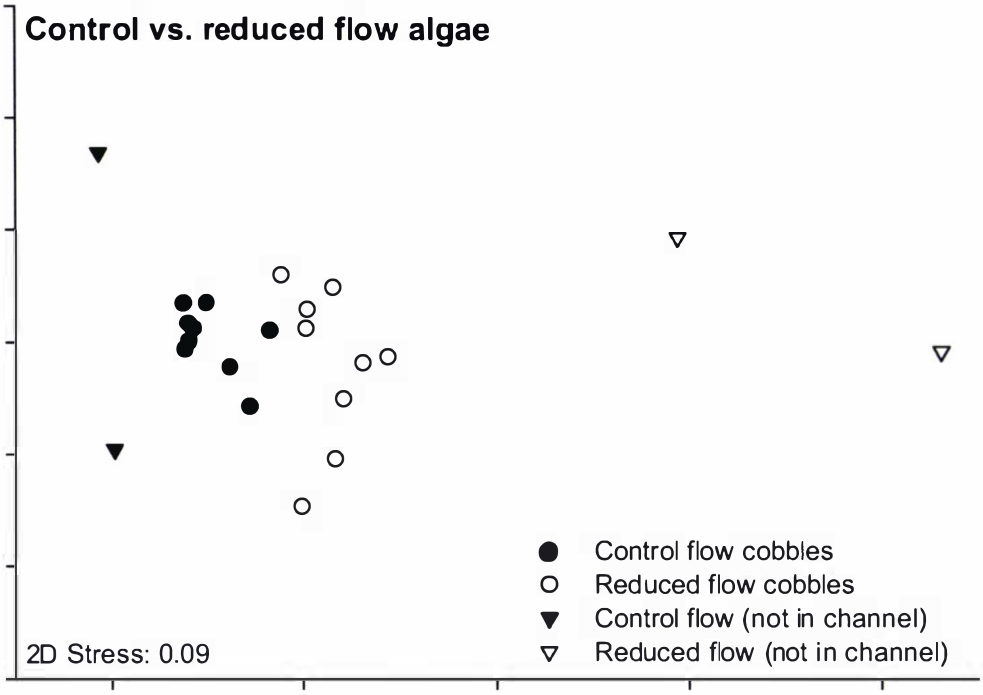

Figure 2. Non-metric multi-dimensional scaling (MDS) ordination of invertebrate assemblages from control and reduced flow reaches after occupying instream channels at equal velocity for two days. Samples collected directly from control and reduced flow reaches of the stream, without installation in channels are included for comparison (triangles).

Table 2. Mean (± 1 S.E.) invertebrate community indices for samples from control and reduced flow reaches of the stream after occupying instream channels at equal velocity for two days. Differences significant at the 5% level are indicated in bold.

	Control flow algae	**Reduced flow algae**	**$F_{1,15}$**
Number of individuals	1428.7 ● 111.6	819.9 ± 72.3	**36.50**
Number of taxa	19.7 ● 0.5	16.2 ± 0.8	**14.47**
Number of taxa (rarefied)	9.7 ± 0.4	9.8 ± 0.4	0.03
% EPT individuals	7.8 ± 1.2	3.3 ± 0.4	**13.23**
% EPT taxa	43.2 ± 1.7	36.5 ● 2.0	**6.09**
Simpson's index	0.74 ● 0.01	0.72 ± 0.02	3.16

Mollusca, Oligochaeta, and Platyhelminthes dominated cobbles from the reduced flow reach before installation in the channels, but relative abundances of these taxa had decreased in favour of Diptera by the end of the experiment (Fig. 3). Therefore, the relative abundances of invertebrate taxa in samples from control and reduced flow reaches were much more similar after two days in instream channels at equal velocities (Fig. 3). In this algal manipulation experiment, 66% of invertebrates were browsers and the six most common taxa in the channels made up 92% of invertebrate abundance. Of these common taxa, the reduced flow algae supported significantly fewer Orthocladiinae, Chironominae and *Pycnocentrodes* sp. than the control treatment (Table 3).

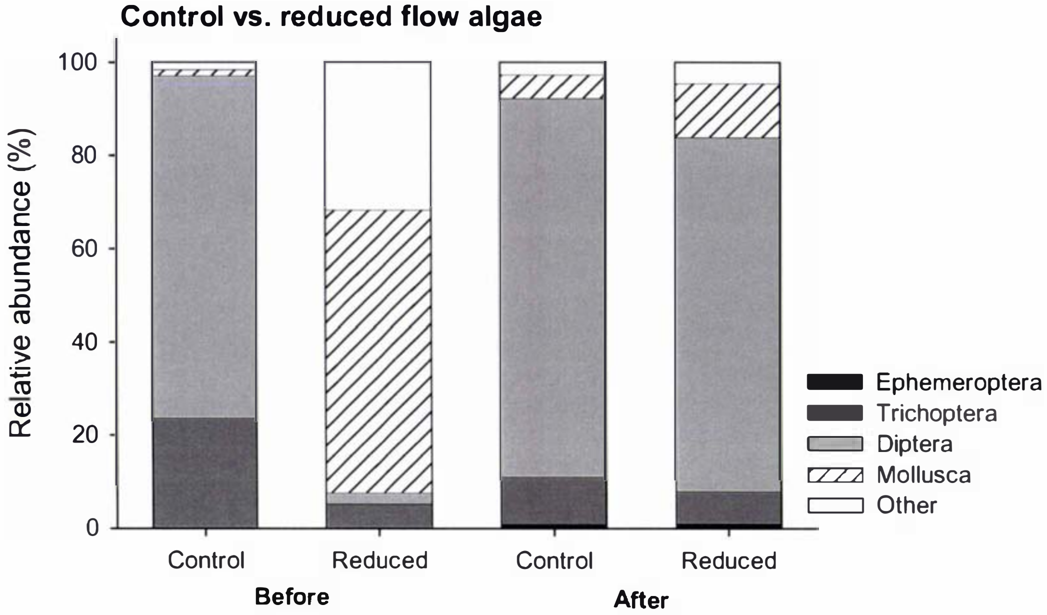

Figure 3. Relative abundances of Ephemeroptera, Trichoptera, Diptera, Mollusca and Other invertebrate groups in samples from control and reduced flow algae treatments before and after occupying instream channels at equal velocity for two days.

Table 3. The six most common taxa in the algae channel experiment in order of decreasing abundance. Percentage difference in abundance is from control to reduced flow algae samples after two days in instream channels at equal velocity. Differences significant at the 5% level are indicated in bold.

Taxa	**Classification**	**Feeding type**	**Difference in abundance**	**$F_{1,15}$**
Orthocladiinae	Diptera	Browser	-50.1%	**66.60**
Austrosimulium sp.	Diptera	Filterer	-12.4%	0.20
Chironominae	Diptera	Browser	-85.4%	**33.06**
Potamopyrgus antipodarum	Gastropoda	Browser	+27.6%	0.95
Oxyethira albiceps	Trichoptera	Browser	-24.8%	0.09
Pycnocentrodes sp.	Trichoptera	Browser	-92.6%	**22.37**

At the completion of the channel experiment, cobbles collected from the control flow reach had higher AFDM of organic matter associated with them (mean = 0.28 g) than cobbles from the reduced flow reach (mean = 0.18 g) ($F_{1,15} = 5.42$, $P = 0.03$). There was a positive relationship between the AFDM of organic matter associated with cobbles in each basket and the number of individuals ($F_{1,16} = 8.67$, $P < 0.01$) (Fig. 4A) and number of browsing individuals ($F_{1,16} = 9.28$, $P < 0.01$) (Fig. 4B) in that basket. However, there was no relationship between AFDM and the number of filter feeders ($F_{1,16} = 0.58$, $P = 0.46$) (Fig. 4C).

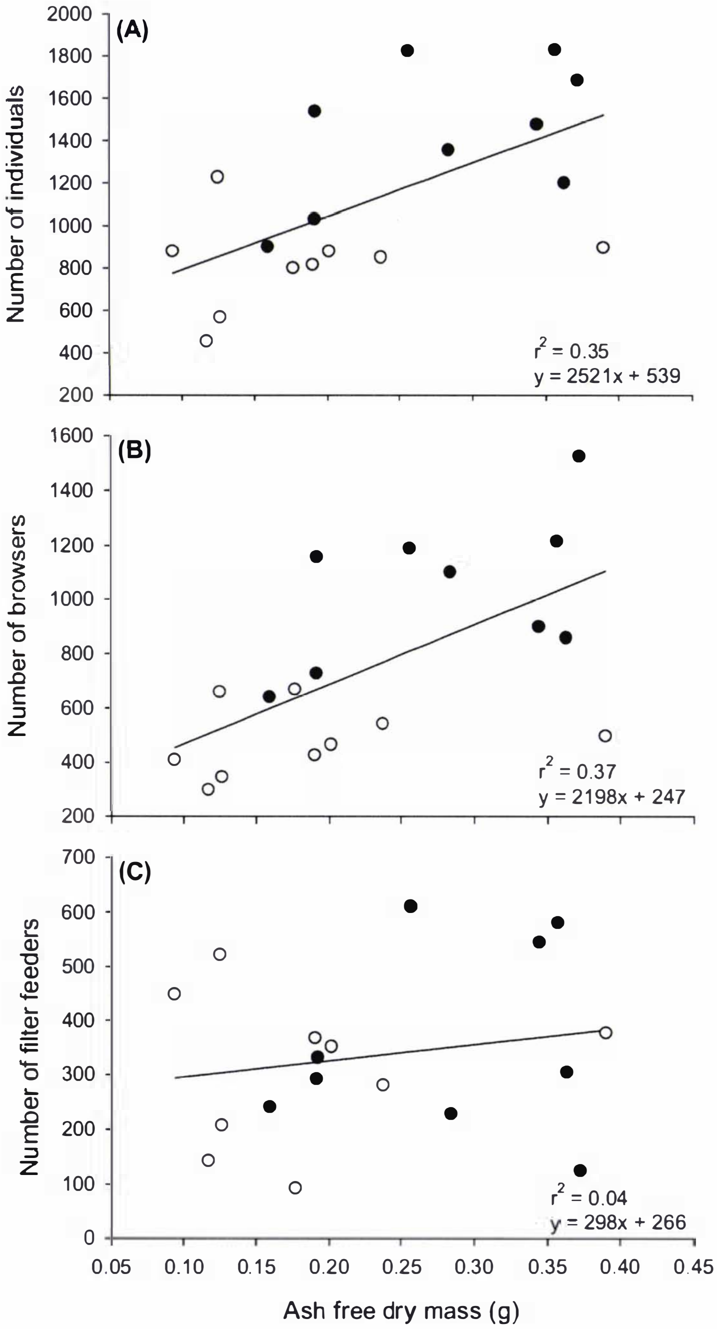

Figure 4. Relationship between (A) number of invertebrate individuals, (B) number of browsers, (C) number of filter feeders, and AFDM of organic matter (> 250 μm) associated with cobbles for control (black symbols) and impact (open symbols) samples after occupying instream channels at equal velocity for two days.

Experiment 2: effects of velocity manipulations on the invertebrate community

I assumed that invertebrate assemblages were comparable before exposure to the two velocity treatments, since substrate for this experiment came from one location. Velocities in the control channel were between 0.19 and 0.25 m/s, compared to between 0.03 and 0.13 m/s in the low velocity channel ($F_{1,16} = 142.4$, $P < 0.01$). After two days at different velocities, the invertebrate community in the low velocity channel did not differ from the control velocity channel (ANOSIM $R = -0.03$, $P = 0.64$) (Fig. 5). Nor were those cobbles sampled immediately from the stream (not installed in channels) any different from those in the channels (ANOSIM $R = 0.10$, $P = 0.08$).

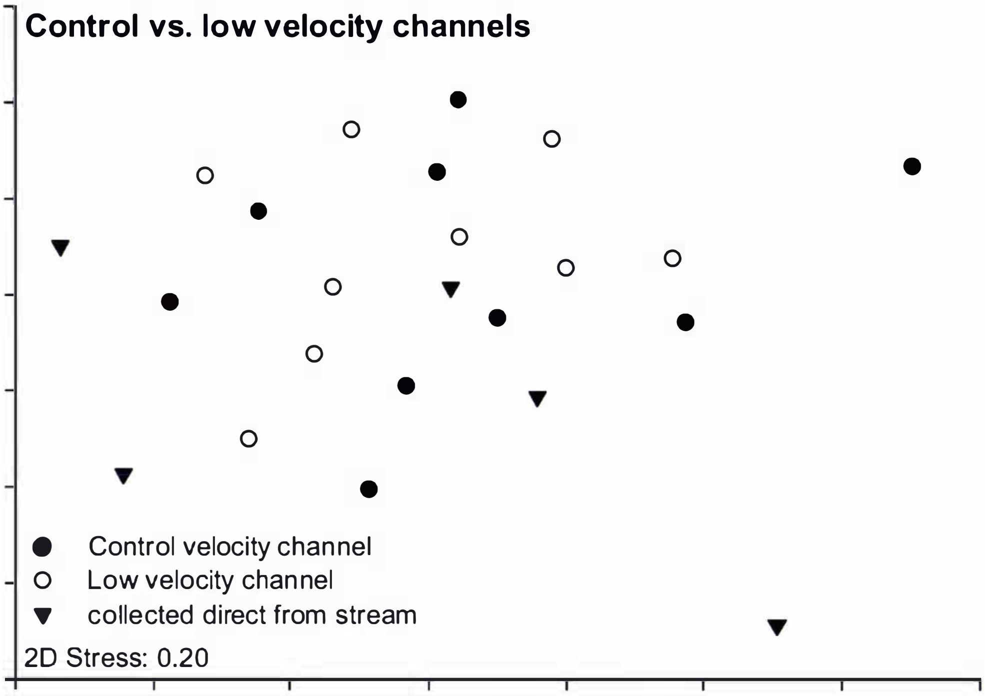

Figure 5. Non-metric multi-dimensional scaling (MDS) ordination of invertebrate assemblages in samples exposed to either control or low velocity in instream channels for two days. Samples collected directly, without installation in channels are included for comparison (triangles).

The baskets of cobbles that were sampled immediately, rather than being installed in the channels, contained fewer invertebrates (mean = 170.6 ± 23.1) than the baskets sampled at the end of the experiment (Table 4). After two days in the instream channels, invertebrate density and taxonomic richness did not differ between the control and low velocity treatments (Table 4). There was also no difference in the percentage of EPT individuals or taxa (Table 4), and the relative abundances of invertebrate groups in the control and low velocity treatments were very similar (Fig. 6). In this velocity manipulation experiment, 91.5% of invertebrates were browsers and the six most common taxa in the channels made up 92% of invertebrate abundance. Of these, the low velocity treatment had significantly fewer of the filter feeder *Austrosimulium* sp. (Table 5).

Table 4. Mean (± 1 S.E.) invertebrate community indices for samples exposed to either control or low velocity treatment in instream channels for two days. Differences significant at the 5% level are indicated in bold.

	Control velocity	**Low velocity**	**$F_{1,16}$**
Number of individuals	248.2 ± 31.2	245.2 ± 28.2	0.01
Number of taxa	13.1 ± 0.8	13.9 ± 0.8	0.44
Number of taxa (rarefied)	9.4 ± 0.5	9.7 ± 0.7	0.12
% EPT individuals	63.4 ± 4.6	63.0 ± 6.6	0.00
% EPT taxa	53.4 ± 3.7	45.9 ● 2.1	2.61
Simpson's index	0.61 ± 0.04	0.58 ± 0.05	0.20

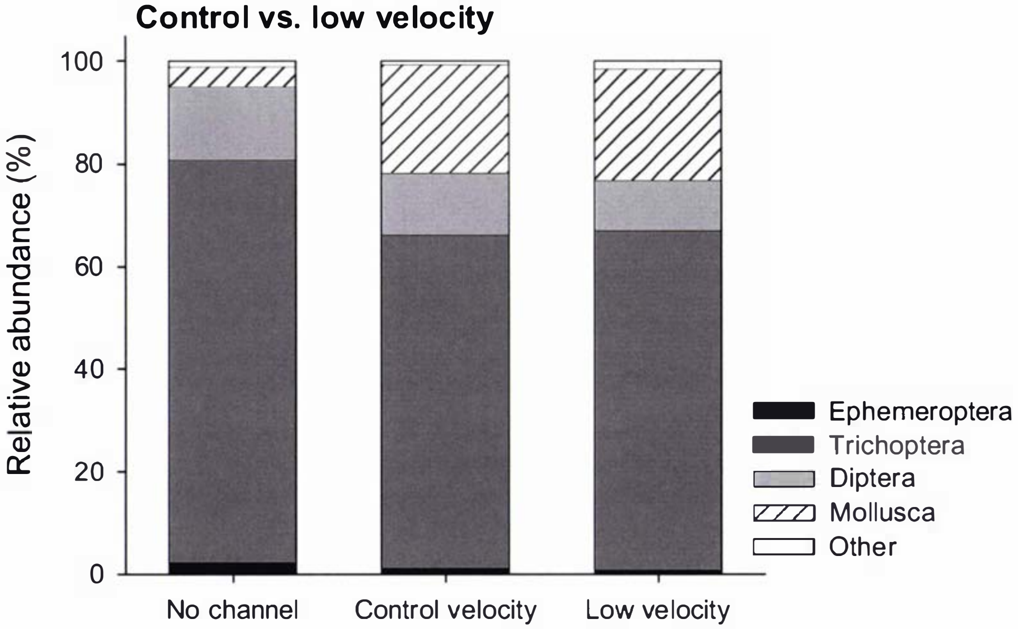

Figure 6. Relative abundances of Ephemeroptera, Trichoptera, Diptera, Mollusca and Other invertebrate groups in samples from control and low velocity treatments at the end of the two day experiment and those collected directly from the stream (no channel).

Table 5. The six most common taxa in the velocity manipulation experiment in order of decreasing abundance. Percentage difference in abundance is from control to low velocity samples after two days in instream channels. Differences significant at the 5% level are indicated in bold.

Taxa	Classification	Feeding type	Abundance difference	$F_{1,16}$
Pycnocentrodes sp.	Trichoptera	Browser	+1.2%	0.01
Potamopyrgus antipodarum	Gastropoda	Browser	-1.8%	0.01
Orthocladiinae	Diptera	Browser	+1.0%	0.18
Austrosimulium sp.	Diptera	Filterer	-65.5%	**4.99**
Chironominae	Diptera	Browser	+5.5%	0.01
Helicopsyche sp.	Trichoptera	Browser	+27.8%	0.45

Discussion

Decreased discharge is known to cause changes to stream biota (e.g., Englund & Malmqvist 1996, Rader & Belish 1999, McIntosh *et al.* 2002). Often, such changes are assumed to result from correlated environmental changes such as decreased habitat area, increased sedimentation or decreased water velocity. However, since there might be numerous environmental changes occurring simultaneously, it is impossible to know whether these assumptions are valid. For example, reduced discharge resulted in lower benthic invertebrate densities and taxonomic richness in Kiriwhakapapa Stream (Chapter 4). Mayflies and caddisflies were also underrepresented at the reduced flow site relative to the control. These invertebrate community differences were accompanied by an increase in the prominence of filamentous algae. Filamentous green algae became widespread throughout the reduced flow reach, but remained sparse and patchy in the control flow reach of this stream. Such proliferations of filamentous algae are a common consequence of low flow (e.g., McIntire 1966, Suren *et al.* 2003b, Biggs *et al.* 2005). Water velocity, depth and wetted width also decreased in the flow reduced reach of this stream, and sediment cover increased (Chapter 4). Previously, Poff & Ward (1992) found that both water velocity and the density and composition of the algal community independently affected the activity and distribution of a grazer (*Agapetus boulderensis* Milne: Trichoptera). To determine whether algal resource levels and water velocities could individually influence invertebrates in response to reduced flow at Kiriwhakapapa Stream, I manipulated these factors in two separate experiments. I hypothesised that the invertebrate community was responding to changes in algal resources in this stream, since invertebrate browsers dominate the community and rely on algae as a food source.

Effects of algae on the invertebrate community

The invertebrate assemblages on cobbles from the control and reduced flow reaches of Kiriwhakapapa Stream differed upon installation in the instream channels and remained distinctive after two days at similar velocity. However, the invertebrate assemblages on cobbles collected from the control and reduced flow reaches of the stream were much more similar at the completion of the experiment, although algal cover remained visibly different for the two treatments. Filamentous algae covered the cobbles from the reduced flow reach, whereas thick layers of diatoms and mucilage covered the control cobbles (Plate 2). The higher AFDM of organic matter collected from control than reduced flow samples at the completion of the experiment reflected this difference in algal cover. Differences between the cobble samples that were installed in the channels, and further samples that were collected without installation in the channels, demonstrated that there was plenty of migration between the stream and the channels during the two-day period of this experiment. Invertebrate densities increased on cobbles from both control and reduced flow reaches while they were installed in the channels. Although this experiment does not explain the role of algal resources in determining overall community composition in this stream, the results do indicate that differences in algal resources alone are not sufficient to maintain the invertebrate community differences observed between reduced and control flow reaches of Kiriwhakapapa Stream.

Although chlorophyll *a* concentrations did not differ between the control and reduced flow reaches of this stream, control cobbles in this channel experiment had higher AFDM of organic matter than cobbles from the reduced flow reach. Biggs & Hickey (1994) showed that AFDM of algae could increase with velocity, with no change in the concentration of chlorophyll *a*, indicating that there was no increase in viable algal cells with velocity. Samples with higher AFDM of organic matter generally supported higher densities of invertebrate individuals, particularly browsers. There was no relationship between the abundance of filter feeders and AFDM. This result suggested that the availability of food resources was influencing the invertebrate community in this experiment and that the greater availability of organic matter in the control reach of the stream might be contributing to the higher densities of invertebrates found there.

The responses of individual taxa to the manipulations undertaken in this experiment suggest that changes to algal community composition and biomass with reduced flow will affect invertebrate taxa differently, depending on their feeding requirements. Previous findings agree that the biomass and composition of the algal community has a strong influence on invertebrate distributions (Dudley *et al.* 1986).

Effects of velocity on the invertebrate community

Invertebrate assemblages on cobbles in control and low velocity channels remained the same after two days at different velocities. Again, the increase in density between the cobble samples that were installed in the channels, and further samples that were collected without installation in the channels, demonstrated that there was plenty of migration between the stream and the channels during the two-day period of the experiment. The invertebrate community in Kiriwhakapapa Stream did not respond to decreased velocity in the short term, suggesting that the influence of velocity on other features of the instream environment, such as algae or sediment might be more important than the direct influence of velocity on invertebrates. The predominance of browsers in this stream might explain the lack of response to decreased velocity in this experiment. The only common filter feeder present in this experiment was *Austrosimulium* sp., and this was the only taxon whose abundance varied between the velocity treatments. A marked decline in the abundance of this taxon in the low velocity channel suggested that the decrease in velocity was a disadvantage to these filter feeding animals. Previous studies have also observed that filter feeding species have particularly strong positive relationships with velocity (Quinn & Hickey 1994, Hart *et al.* 1996). This is a logical response if you consider that current velocity can control feeding efficiency and predator avoidance in Simuliidae (Malmqvist & Sackmann 1996), and they may develop slower, and have lower survival when reared at slower velocities, reflecting a difference in resources (Zhang & Malmqvist 1997).

Synthesis

Algal resources and water velocity both had some influence on the invertebrates in our instream channels. The responses of individual taxa to the changes initiated in each experiment tended to depend on their mode of feeding, and the responses of individual taxa proved more dramatic than overall community responses. The provision of food resources provided an explanation for the responses of both browsers and filter feeders to the changes initiated by reduced flow. The lower AFDM on cobbles from the reduced flow reach supported lower densities of Orthocladiinae, Chironominae and *Pycnocentrodes* sp.. Changes in velocity did not alter the abundances of these taxa when algal resources were equal. These browsing taxa probably distributed themselves primarily with regard to food resources, although another common browser in this stream, *Potamopyrgus antipodarum* did not differ between algae or velocity treatments in these channel experiments. Fuller *et al.* (1986) also found that changes to algal resources were more important to invertebrates whose major energy source was algae, for example, collector-gatherers as opposed to filter feeders. The only common filter feeder present in both channel experiments was *Austrosimulium* sp.. There was no difference in the abundance of *Austrosimulium* sp. between treatments in the algae experiment, and no relationship between AFDM of organic matter and the number of filter feeders. However, there was a marked decrease in *Austrosimulium* sp. abundance in the low velocity channel. The lack of change to the abundances of other taxa in the velocity experiment suggests that a loss of velocity alone is not sufficient to explain invertebrate community differences between reduced and control flow reaches of Kiriwhakapapa Stream. However, further exploration of the indirect influences of reduced flow on invertebrates is necessary to resolve this.

I suggest that resources are an important control over invertebrate responses to flow reduction. Therefore, invertebrate community composition might determine the relative importance of velocity and algae to invertebrates following flow reduction. As browsers dominated the invertebrate community in this stream, changes to algal resources were more likely to be important. However, the responses of algae to changes in flow vary between studies (e.g., McIntire 1966, Poff *et al.* 1990, Biggs & Hickey 1994, Jowett & Biggs 1997), as a consequence of algal growth form (Biggs *et al.* 1998) or the level of enrichment of the river (Suren *et al.* 2003b). In addition, the availability of light or nutrients might limit changes to the algal community. Therefore, differences in algal community responses to reduced flow might subsequently affect invertebrate community responses to flow reduction. Given the potential importance of algal resources to the invertebrate community, I suggest that minimising changes to the algal community is an important aspect of managing water allocation. This might mean that less water can be allocated from streams with a tendency towards algal proliferations.

Conversely, by improving water quality or decreasing enrichment, it might be possible to abstract more water for out-of-stream uses. This important area of research is poorly understood and deserves further attention.

References

Allan J.D. (1995) *Stream Ecology: Structure and Function of Running Waters*, 1st edn. Chapman & Hall, London.

Analytical Software (2006) *Statistix 8*. Analytical Software, Tallahassee, Florida, USA.

Biggs B.J.F. & Close M.E. (1989) Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients. *Freshwater Biology*, **22**, 209-231.

Biggs B.J.F., Goring D.G. & Nikora V.I. (1998) Subsidy and stress responses of stream periphyton to gradients in water velocity as a function of community growth form. *Journal of Phycology*, **34**, 598-607.

Biggs B.J.F. & Hickey C.W. (1994) Periphyton responses to a hydraulic gradient in a regulated river in New Zealand. *Freshwater Biology*, **32**, 49-59.

Biggs B.J.F. & Kilroy C. (2000) *Stream Periphyton Monitoring Manual*. NIWA, Christchurch, New Zealand.

Biggs B.J.F., Nikora V.I. & Snelder T.H. (2005) Linking scales of flow variability to lotic ecosystem structure and function. *River Research and Applications*, **21**, 283-298.

Boothroyd I. & Stark J. (2000) Use of invertebrates in monitoring. In: *New Zealand Stream Invertebrates: Ecology and Implications for Management* (Eds K.J. Collier & M.J. Winterbourn), pp. 344-373. New Zealand Limnological Society, Christchurch, New Zealand.

Brooks A.J., Haeusler T., Reinfelds I. & Williams S. (2005) Hydraulic microhabitats and the distribution of macroinvertebrate assemblages in riffles. *Freshwater Biology*, **50**, 331-344.

Chapman M.A. & Lewis M.H. (1976) *An Introduction to the Freshwater Crustacea of New Zealand*. Collins, Auckland, New Zealand.

Clarke K.R. & Gorley R.N. (2006) *PRIMER v6: User Manual/Tutorial*. PRIMER-E: Plymouth.

Clarke K.R. & Warwick R.M. (2001) *Change to Marine Communities: An Approach to Statistical Analysis and Interpretation*. 2nd edn. PRIMER-E: Plymouth.

Cowie B. (1980) *Community Dynamics of the Benthic Fauna in a West Coast Stream Ecosystem*. Ph.D. thesis, University of Canterbury, Christchurch.

Dewson Z.S., James A.B.W. & Death R.G. (2007) Invertebrate responses to short-term water abstraction in small New Zealand streams. *Freshwater Biology*, **52**, 357-369.

Doisy K.E. & Rabeni C.F. (2001) Flow conditions, benthic food resources, and invertebrate community composition in a low-gradient stream in Missouri. *Journal of the North American Benthological Society*, **20**, 17-32.

Dudley T.L., Cooper S.D. & Hemphill N. (1986) Effects of macroalgae on a stream invertebrate community. *Journal of the North American Benthological Society*, **5**, 93-106.

Englund G. & Malmqvist B. (1996) Effects of flow regulation, habitat area and isolation on the macroinvertebrate fauna of rapids in north Swedish rivers. *Regulated Rivers: Research and Management*, **12**, 433-445.

Fuller R.L., Roelofs J.L. & Fry T.J. (1986) The importance of algae to stream invertebrates. *Journal of the North American Benthological Society*, **5**, 290-296.

Georgian T. & Thorp J.H. (1992) Effects of microhabitat selections on feeding rates of net-spinning caddisfly larvae. *Ecology*, **73**, 229-240.

Hart D.D., Clark B.D. & Jasentuliyana A. (1996) Fine-scale field measurements of benthic flow environments inhabited by stream invertebrates. *Limnology and Oceanography,* **41(2)**, 297-308.

Hart D.D. & Finelli C.M. (1999) Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms. *Annual Review of Ecology and Systematics*, **30**, 363-395.

Jowett I. (2000) Flow management. In: *New Zealand Stream Invertebrates: Ecology and Implications for Management* (Eds K.J. Collier & M.J. Winterbourn), pp. 289-312. New Zealand Limnological Society, Christchurch, New Zealand.

Jowett I.G. & Biggs B.J.F. (1997) Flood and velocity effects on periphyton and silt accumulation in two New Zealand rivers. *New Zealand Journal of Marine and Freshwater Research*, **31**, 287-300.

Lancaster J. (1999) Small-scale movements of lotic macroinvertebrates with variations in flow. *Freshwater Biology*, **41**, 605-619.

Lenat D.R. (1988) Water quality assessment using a qualitative method for benthic macroinvertebrates. *Journal of the North American Benthological Society*, **7**, 222-233.

Malmqvist B. & Sackmann G. (1996) Changing risk of predation for a filter-feeding insect along a current velocity gradient. *Oecologia*, **108**, 450-458.

McIntire C.D. (1966) Some effects of current velocity on periphyton communities in laboratory streams. *Hydrobiologia*, **27**, 559-570.

McIntosh M.D., Benbow M.E. & Burky A.J. (2002) Effects of stream diversion on riffle macroinvertebrate communities in a Maui, Hawaii, stream. *River Research and Applications*, **18**, 569-581.

Nowell A.R.M. & Jumars P.A. (1984) Flow environments of aquatic benthos. *Annual Review of Ecology and Systematics*, **15**, 303-328.

Poff N.L., Voelz N.J., Ward J.V. & Lee R.E. (1990) Algal colonization under four experimentally-controlled current regimes in a high mountain stream. *Journal of the North American Benthological Society*, **9**, 303-318.

Poff N.L. & Ward J.V. (1992) Heterogenous currents and algal resources mediate in situ foraging activity of a mobile stream grazer. *Oikos*, **65**, 465-478.

Quinn J.M. & Hickey C.W. (1994) Hydraulic parameters and benthic invertebrate distributions in two gravel-bed New Zealand rivers. *Freshwater Biology*, **32**, 489-500.

Rader R.B. & Belish T.A. (1999) Influence of mild to severe flow alterations on invertebrates in three mountain streams. *Regulated Rivers: Research and Management*, **15**, 353-363.

SAS Institute Inc. (2004) *The SAS System for Windows.* SAS Institute Inc., Cary, North Carolina, U.S.A.

Simpson E.H. (1949) Measurement of diversity. *Nature*, **163**, 688.

Smith B.J. (2003) *Quick Guide to the MCI Invertebrates.* National Institute of Water and Atmospheric Research, Hamilton, New Zealand.

Stevenson R.J. (1996) The stimulation and drag of current. In: *Algal Ecology: Freshwater Benthic Ecosystems* (Eds R.J. Stevenson, M.L. Bothwell & R.L. Lowe), pp. 321-340. Academic Press, San Diego, U.S.A.

Suren A.M., Biggs B.J.F., Duncan M.J. & Bergey L. (2003a) Benthic community dynamics during summer low-flows in two rivers of contrasting enrichment 2. Invertebrates. *New Zealand Journal of Marine and Freshwater Research*, **37**, 71-83.

Suren A.M., Biggs B.J.F., Kilroy C. & Bergey L. (2003b) Benthic community dynamics during summer low-flows in two rivers of contrasting enrichment 1. Periphyton. *New Zealand Journal of Marine and Freshwater Research*, **37**, 53-70.

Winterbourn M.J. (1973) A guide to the freshwater Mollusca of New Zealand. *Tuatara*, **20**, 141-159.

Winterbourn M.J. (2000) Feeding ecology. In: *New Zealand Stream Invertebrates: Ecology and Implications for Management* (Eds K.J. Collier & M.J. Winterbourn), pp. 100-124. New Zealand Limnological Society, Christchurch, New Zealand.

Winterbourn M.J., Gregson K.L.D. & Dolphin C.H. (2000) Guide to the aquatic insects of New Zealand. *Bulletin of the Entomological Society of New Zealand*, **13**.

Wood P.J. & Petts G.E. (1994) Low flows and recovery of macroinvertebrates in a small regulated chalk stream. *Regulated Rivers: Research and Management*, **9**, 303-316.

Wright J.F. & Berrie A.D. (1987) Ecological effects of groundwater pumping and a natural drought on the upper reaches of a chalk stream. *Regulated Rivers: Research and Management*, **1**, 145-160.

Zhang Y. & Malmqvist B. (1997) Phenotypic plasticity in a suspension-feeding insect, *Simulium lundstromi* (Diptera: Simuliidae), in response to current velocity. *Oikos*, **78**, 503-510.

CHAPTER 7

Why should we worry about water abstractions from small streams?

The intention of the following chapter was to synthesise the findings of our research on the effects of reduced flow on stream ecosystems into an article that clearly communicates the main outcomes to a management audience. Therefore, the chapter includes a summary of results that have been presented in earlier chapters of this thesis, as well as a summary of work on invertebrate drift and refugia usage completed by Alex James. The chapter will be submitted to Frontiers in Ecology and the Environment.

Abstract

Information on the implications of water abstraction for small stream ecosystems is scarce compared to that for large rivers. An improved understanding of the water requirements of small stream ecosystems will be necessary to manage the increasing demands on water resources appropriately. Using experimental flow reductions to investigate the impacts of water abstraction in small streams, we examined invertebrate behavioural responses to flow reduction, benthic community structure and ecosystem functioning. The results of our experimental flow reductions suggest that water abstractions may have less impact on streams that are already degraded by other human modifications. We also found that the duration of water abstraction, the relative sensitivity of invertebrate communities present and the extent to which water removal modifies the instream environment have an influence on ecosystem responses to water removal.

Introduction

There is an increasing awareness by scientists and the general public that stream ecosystems have water requirements (e.g., Baron *et al.* 2002, Richter *et al.* 2003). However, there is a shortage of scientific data describing the quantity and timing of water required to protect small stream ecosystems (Richter 1993). Not only is it necessary to sustain these ecosystems for ecological reasons, but the maintenance of adequate water quality and quantity ensures the ongoing usefulness of water resources for out of stream uses. The increasing size and urbanisation of the human population, along with continually expanding water requirements for agriculture are among several factors leading to an expanding global demand for water resources (Postel 1997, Arnell 1999). Increased demand alone would make it more difficult to balance the needs of human society with the requirements of freshwater ecosystems, but changes to climate are expected to complicate matters further. Recent predictions suggest that as well as lowering summer flows, climate change may extend the duration of low flows (Gibson *et al.* 2005), and increase the competition between in and out of stream uses for water (Meyer *et al.* 1999). To manage increasing demands on water resources, we need to improve our understanding of the water requirements of stream ecosystems and the environmental, social and economic costs of water losses from them.

Water removal schemes on large rivers attract public and media attention, however, the numerous small water removals from streams might also substantially alter these ecosystems. Small streams often have high biodiversity values compared to large rivers, because many large rivers are highly impaired by pollution. Even though small streams are often targets for small-scale water abstraction, there is relatively little research focusing on the effects of abstraction on small stream ecosystems. The responses of large rivers to flow reduction are unlikely to apply to small streams. Water demand is often greatest through the summer season, especially for irrigation and potable water supply. Elevated water temperatures and algal proliferations are more likely at this time, and permitted abstractions can comprise a relatively high percentage of total discharge during these low flow periods.

Flow influences stream invertebrates by controlling characteristics of the physical habitat such as current velocity, depth, wetted width, sedimentation, and water temperature (Hart & Finelli 1999, Bunn & Arthington 2002) (Fig. 1). Changes to these variables can alter habitat availability and suitability for invertebrates, the delivery rate of nutrients and food particles, and might alter the rates of ecosystem processes such as decomposition. Changes to the physical and chemical characteristics of the instream environment with decreasing flow are highly interrelated, making it difficult to ascertain the specific cause of invertebrate responses to reduced flow. Invertebrate taxa differ in their environmental tolerances and requirements and consequently, loss of habitat area, changes in habitat quality or alteration of food supply will affect taxa differently.

Water removal commonly decreases the water velocity, depth and wetted width of streams (Fig. 1). These changes can reduce the available habitat for invertebrates (wetted width), reduce dissolved oxygen, decrease the delivery rate of suspended material for filter feeders (water velocity), and alter invertebrate food resources such as periphyton and coarse particulate organic matter (velocity and depth) (Chapter 1). Increased sedimentation and alterations to the temperature regime and water chemistry often accompany these flow related changes, although there may be considerable variation between streams (Chapter 1). For instance, reduced flows can result in either increased or decreased water temperatures, depending on stream size or the contribution of groundwater. Similarly, reduced flows often result in increased deposition of fine sediments, but this depends on the sediment supply.

Individual invertebrates may drift downstream or seek refuges to escape unfavourable conditions during reduced flows. Increased active drift behaviour is a common response to flow reduction (e.g., Poff & Ward 1991, James *et al.* unpublished data), although responses vary considerably between taxa. Pools and the hyporheic zone are often considered as refuges from reduced flows, but have been studied predominantly in intermittent or temporary streams (e.g., Boulton 1989, Delucchi 1989). Studies of permanent streams suggest that the hyporheic zone is not used as an invertebrate refuge (Delucchi 1989, James *et al.* unpublished data, Chapter 1).

Invertebrate taxonomic richness frequently decreases along with habitat diversity during low flows. This may be attributed to the loss of certain habitats (e.g., shallow fast flowing water), or to changes in habitat condition (e.g., sediment accumulation, proliferation of filamentous algae) (Fig. 1). In contrast, invertebrate density does not respond consistently to flow reduction. Changes to biotic interactions, and decreased habitat availability can explain decreased invertebrate densities at reduced flow sites, whereas increased invertebrate densities might result when invertebrates crowd into a reduced wetted area, or from increased habitat suitability for some taxa. Invertebrate community responses to changing flows probably result from increases in habitat suitability for some species and decreases for others (Gore *et al.*

2001). The invertebrate community response to flow reduction is dependent on the composition of the invertebrate community. Reduced flows can have a greater impact on those taxa with preferences for higher velocity habitats or those with more specific habitat requirements.

The severity (magnitude/duration) of flow reduction can have an influence on both invertebrate abundance and diversity (Chapter 1). This is probably because the magnitude and duration of flow reductions control the level of change to flow characteristics, wetted width, periphyton biomass and sediment accumulation within the stream.

The effects of drying on intermittent streams are reasonably well understood (e.g., Boulton & Lake 1992, Boulton 2003), but information on water loss from small permanent streams is scarce. In our study, experimental flow reductions were used to examine the effects of water abstraction on small stream ecosystems. Experimental manipulations in replicate streams are an ideal mechanism for investigating the effects of water abstractions. By allowing the collection of appropriate before and after data, flow manipulation experiments minimise the confounding effects that limit the usefulness of studies of existing water abstractions.

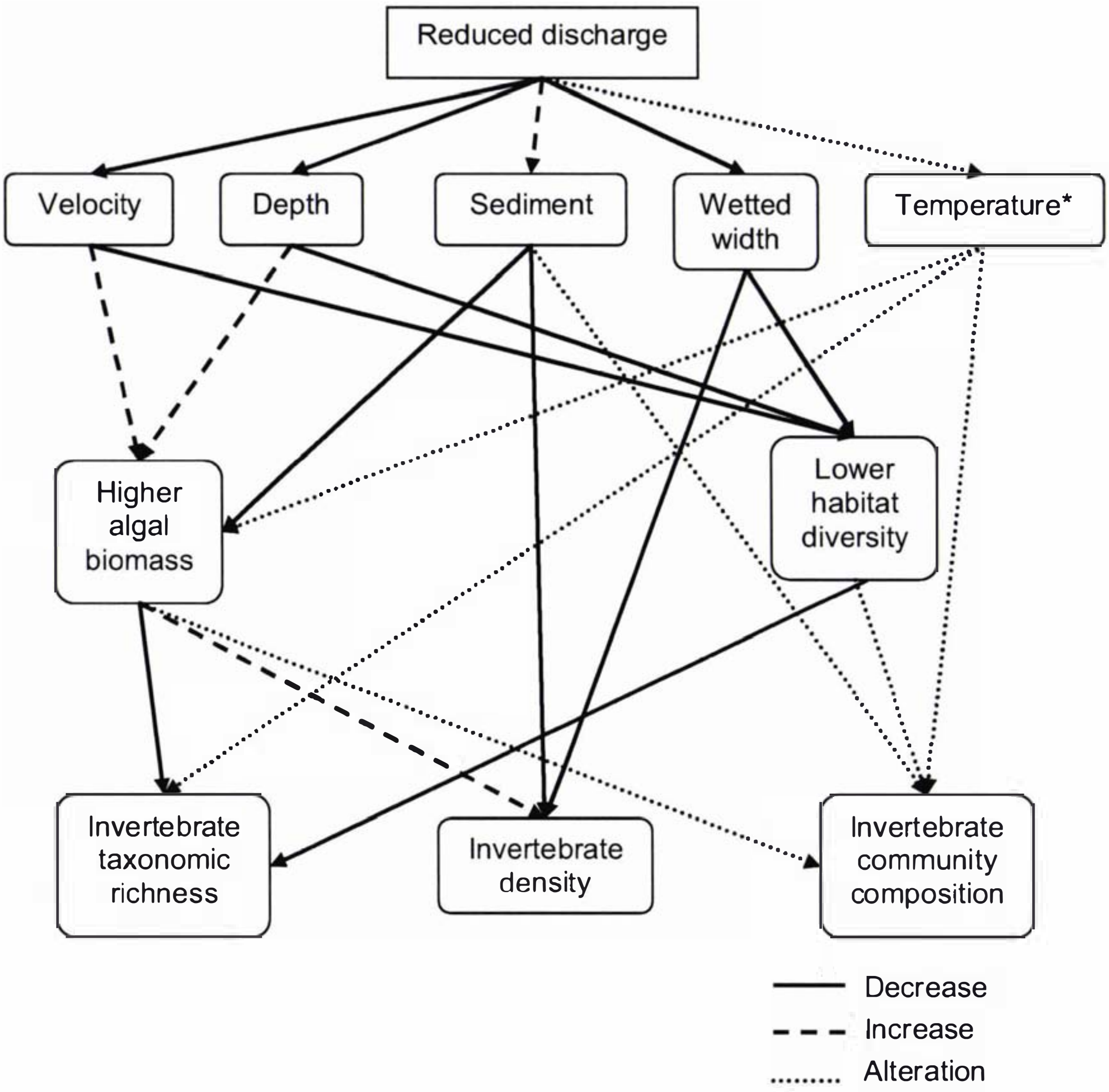

Figure 1. A summary of the effects of reduced stream flow on habitat condition, invertebrate density, richness and community composition. * Note that the response of water temperature to reduced flow varies between studies.

Flow reduction experiments

We used weirs and diversions to decrease stream discharge by at least 85% in three streams of contrasting water quality for one year. Study sites ranged from a pristine forested stream with excellent water quality, to a stream with low water quality, in agricultural land (Fig. 2, Table 1).

Figure 2. Weir and diversion structures used for experimental flow reductions at Booths Creek (left photo, intensive agricultural land use), Kiriwhakapapa Stream tributary (middle photo, low intensity agricultural land use), and Reef Creek tributary (right photo, pristine forested catchment). All streams are located in the lower North Island, New Zealand.

Table 1. Summary of invertebrate community changes in response to experimentally reduced flows in three small streams of different water quality.

Stream	**Water quality**[1]	**Invertebrate density**	**Taxonomic richness**	**% EPT**[2] **individuals**
Reef Creek	Clean water	Decrease	No change	Decrease
Kiriwhakapapa Stream	Mild pollution	No change	Decrease	No change
Booths Creek	Moderate pollution	No change	No change	No change

[1] the New Zealand equivalent of the Hilsenhoff Biotic Index (Hilsenhoff 1987), the Macroinvertebrate Community Index (MCI) (Stark 1985) classifies water quality with regard to organic enrichment in stony streams.

[2] EPT = Ephemeroptera (mayflies), Plecoptera (stoneflies), Trichoptera (caddisflies). These are taxa that are particularly sensitive to water quality impairment.

Water temperatures tended to decrease downstream of diversions in these streams, probably because cool groundwater constituted a higher proportion of surface flow in the reduced flow reaches of these small streams (Mosley 1983). Changes to conductivity, pH, and dissolved oxygen with discharge reduction were negligible, but there were substantial decreases to velocity, depth and wetted width after flow decreased. Lower water velocities allowed more sediment to settle out of the water column, and sediment cover of the substrate increased at reduced flow sites, except for the pristine stream, where sediment supply was low (Fig. 3). Several other studies have also found sedimentation increases with reductions in discharge (e.g., Wood & Armitage 1999).

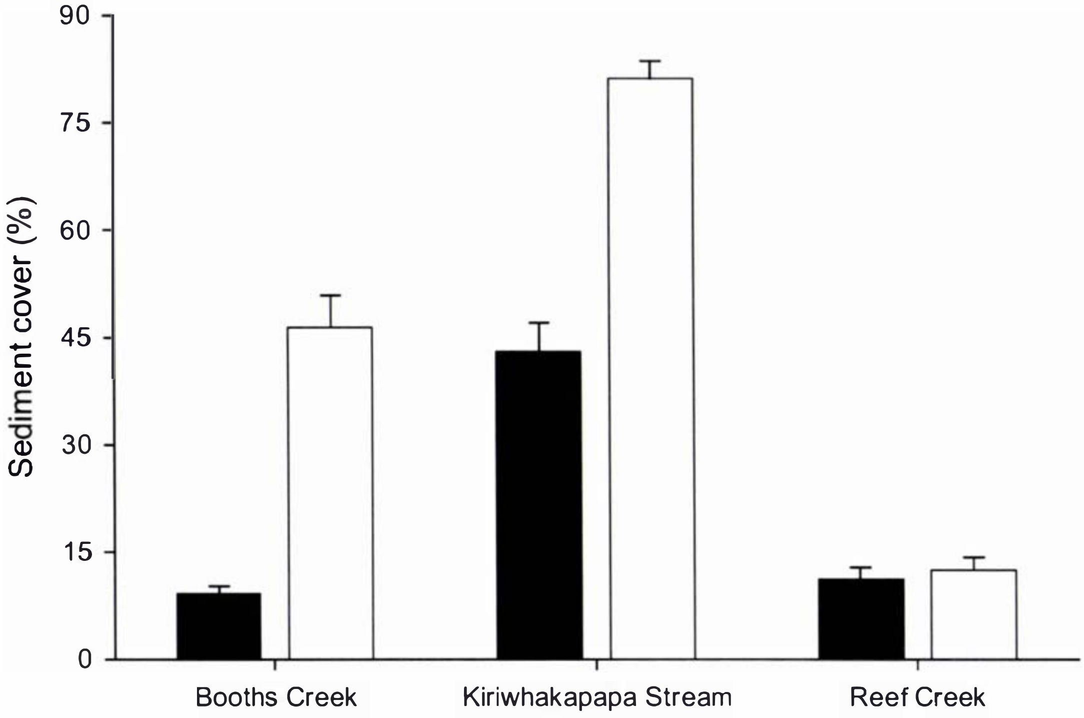

Figure 3. Mean (± 1 S.E.) percentage cover of substrate by fine sediments for control (black) and reduced flow (open) sites on Booths Creek, Kiriwhakapapa Stream tributary and Reef Creek tributary.

Drift behaviour

The start of water abstraction initiated sudden increases in invertebrate drift in these streams, but drift generally returned to pre-abstraction levels within a week (Fig. 4). Previous studies have also observed increases in invertebrate drift after decreases in flow (e.g., Hooper & Ottey 1988). Not all taxa exhibited drift behaviour in response to flow reduction. The main drifters in each stream were filter feeders (e.g., *Coloburiscus humeralis* and *Orthopsyche* sp.). Perhaps drift was necessary for these taxa to find optimal conditions for food collection. In the lowest water quality stream, the amphipod *Paracalliope fluviatilis* dominated the invertebrate community, and flow reduction tended to induce a sustained increase in the drift for this taxon (Hughes 1970).

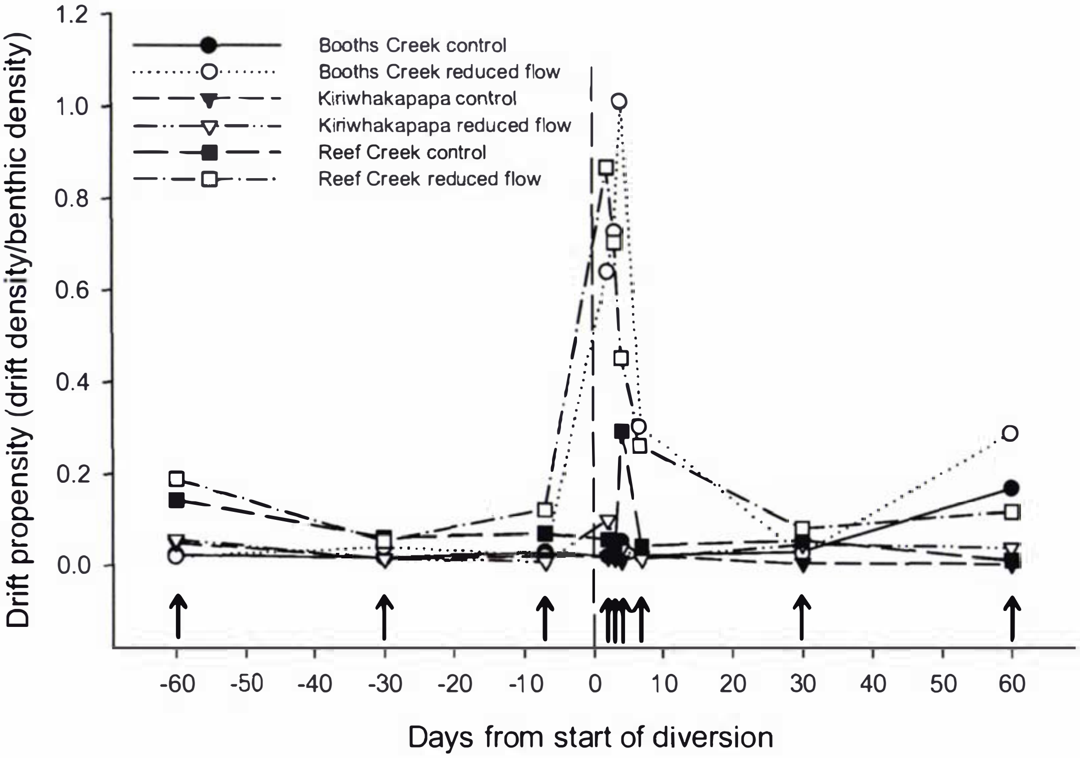

Figure 4. Invertebrate drift propensity over time for control and reduced flow sites at Booths Creek, Kiriwhakapapa Stream tributary and Reef Creek tributary before (November 2004-January 2005) and after (January-March 2005) discharge reduction began. The vertical dashed line indicates the start of diversions and arrows indicate sampling times.

Refugia use

The hyporheic zone and pools did not appear to provide a refuge from low flows in these streams (Fig. 5). We suspect that at this level of flow reduction, conditions at the surface remained more suitable than in the hyporheic zone. For example, water velocities and dissolved oxygen levels were higher at the surface than in the hyporheic zone. Similarly, pools could not provide a refuge from low velocities. However, if pools were the only remaining habitat, we expect their importance as a refuge would increase. Similarly, with complete drying of surface water, utilization of the hyporheic zone might increase.

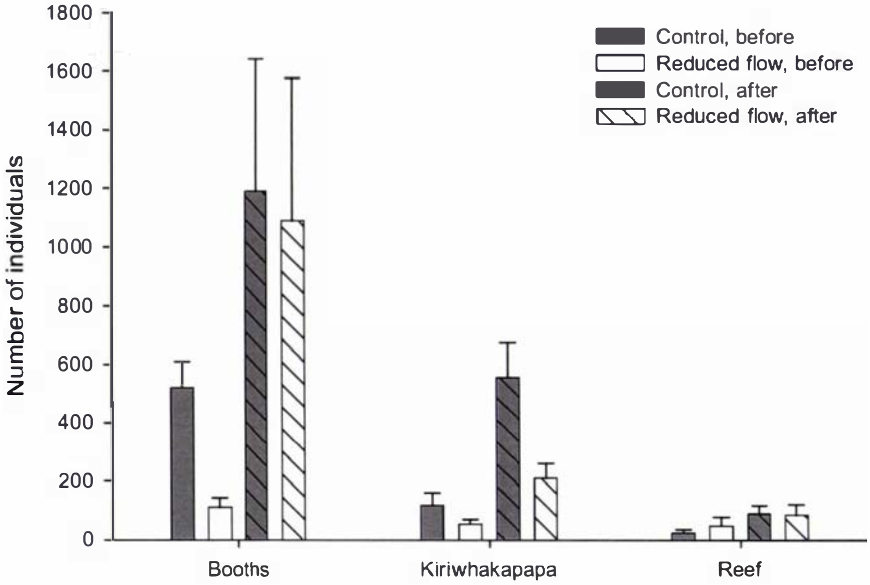

Figure 5. Mean number of invertebrates collected per kick net sample (n=3) in pools at control and reduced flow sites at Booths Creek, Kiriwhakapapa Stream tributary and Reef Creek tributary before (January 2005) and after (March 2005) discharge reduction began.

Benthic invertebrates

Invertebrate community responses to experimental flow reductions over the austral summer differed between the three streams in this study (Table 1). The relative sensitivities of taxa in each community to the habitat changes initiated by flow reduction might explain this, because the invertebrate communities in each stream are distinctive. At the pristine site, overall invertebrate densities decreased (Fig. 6). This was largely a result of decreases in the density of several common taxa (e.g., *Deleatidium* sp., *Zelandobius* sp., *Orthopsyche* sp.), and was probably a response to reduced habitat availability or suitability for these taxa. The relative proportions of mayflies, stoneflies and caddisflies in the community also decreased at this site. Declining proportions of mayflies, stoneflies and caddisflies can be used as an indicator of reduced water quality (Lenat 1988), and in this situation, their decline highlights the potential of certain taxa to be used as indicators of water abstraction impacts. Taxonomic richness decreased after flow reduction at the mildly polluted stream in this study, as we collected fewer rare taxa at the reduced flow site. Although the densities of some common taxa decreased in response to flow reduction in this stream, there was no overall decrease in invertebrate density. The invertebrate community at this stream included relatively fewer sensitive taxa than the pristine stream because of its lower water quality, and this might account for the lack of an overall density response. Reduced discharge had no affect on the invertebrate community at the stream with the lowest water quality. The environmental changes brought about by flow reduction had no further impact on the already tolerant invertebrate assemblage at this site.

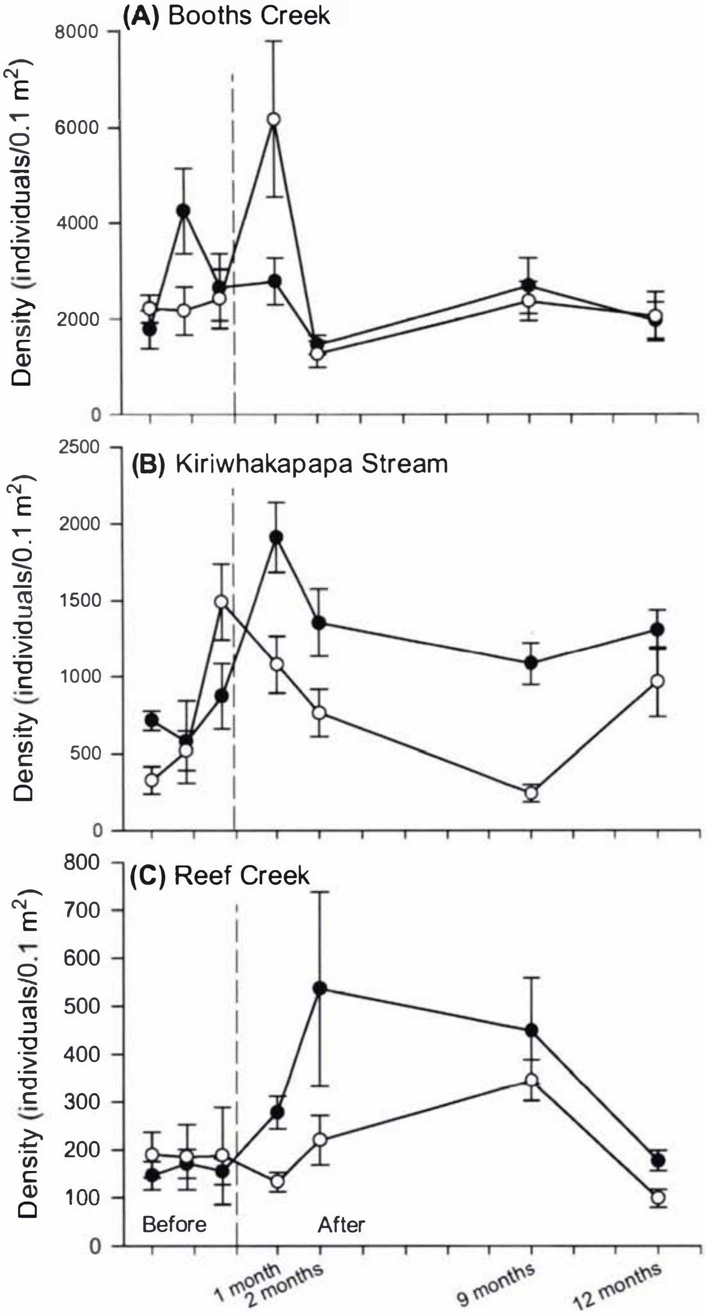

Figure 6. Mean density of individuals per 0.1 m^2 (± 1 S.E.), on three sampling occasions before discharge reduction, and 1 month, 2 months, 9 months and 12 months after discharge reduction began for control (black symbols) and reduced flow (open symbols) sites on (A) Booths Creek, (B) Kiriwhakapapa Stream tributary and (C) Reef Creek tributary between November 2004 and January 2006. The vertical dashed lines indicate the start of diversions.

Ecosystem function consequences

As a measure of the impact of flow reduction on ecosystem functioning, we measured the breakdown rate of willow leaves in mesh bags at control and reduced flow sites in these streams. Our results suggested that reduced discharge had little influence on leaf decomposition. We expected lower velocities at reduced flow sites to reduce physical abrasion and decrease the breakdown rate of leaves, but our results did not support this. The few other studies on this have found similar null effects (Rader *et al.* 1994, Casas *et al*. 2000). Even the differences in invertebrate abundances between control and reduced flow sites in these streams did not translate into altered leaf breakdown rates, although macroinvertebrates are known to play an important role in leaf breakdown (Wallace & Webster 1996). Furthermore, we found no evidence that increased sedimentation was decreasing the microbial decomposition of leaves at reduced flow sites.

The retention of coarse particulate organic matter (CPOM) was another ecosystem function that we anticipated would be altered by flow reduction. Using paper strips and wooden dowelling as analogues for CPOM, we found that CPOM travelled further before retention at higher discharges. Previous studies have also related higher discharges to higher CPOM transport distances (Raikow *et al.* 1995, Larned 2000). Therefore, over time, reduced discharge would tend to enhance the accumulation of CPOM. It was especially noticeable that reduced flow reaches accumulated more organic material (particularly leaf litter) than control reaches in our study streams.

The accumulation of CPOM increased with flow reduction in these streams, but there was no matching increase in decomposition. This change could lead to negative feedback loops in food web dynamics, habitat structure and flow characteristics that might in turn influence the invertebrate community more than the altered hydrology alone.

Management implications

Responses to water abstraction vary between invertebrate taxa. This means that invertebrate community responses to flow reduction are dependent on the invertebrate assemblage present in a stream. Consequently, the outcomes of water abstraction might vary among streams of differing water quality, stream morphology, water source or geographic region. These differences should be an important consideration when managing water allocation (Fig. 7). We suggest that there is potential for responsive taxa to be useful indicators of water abstraction impacts.

Although water abstractions are one of many factors contributing to declining water quality in small streams, our research suggests that water abstraction does not overwhelm land use effects. Therefore, restricting water removal will not necessarily improve water quality in small streams and perhaps degradation from land use change should be addressed first (Fig. 7).

When studying water abstractions of short duration (< 1 month, seasonal), we observed less impact on the invertebrate community (Dewson *et al.* 2007) than that observed in the longer term (1 year) water removal described above (Fig. 7). Clearly, the effects of water removal on stream invertebrates can develop over time, perhaps as environmental characteristics respond to changes in hydrology (e.g., fine sediment accumulates or algal proliferations occur). Multi-year studies are needed to assess the long-term implications of water abstractions for small streams.

Why should we worry about water abstractions from small streams? When large proportions of stream flow are withdrawn, there are likely to be lasting downstream effects on invertebrate communities because of major changes to the availability and suitability of instream habitat and changes to ecosystem functioning. Our results show that we do need to be careful about removing water from small streams, especially those with high water quality.

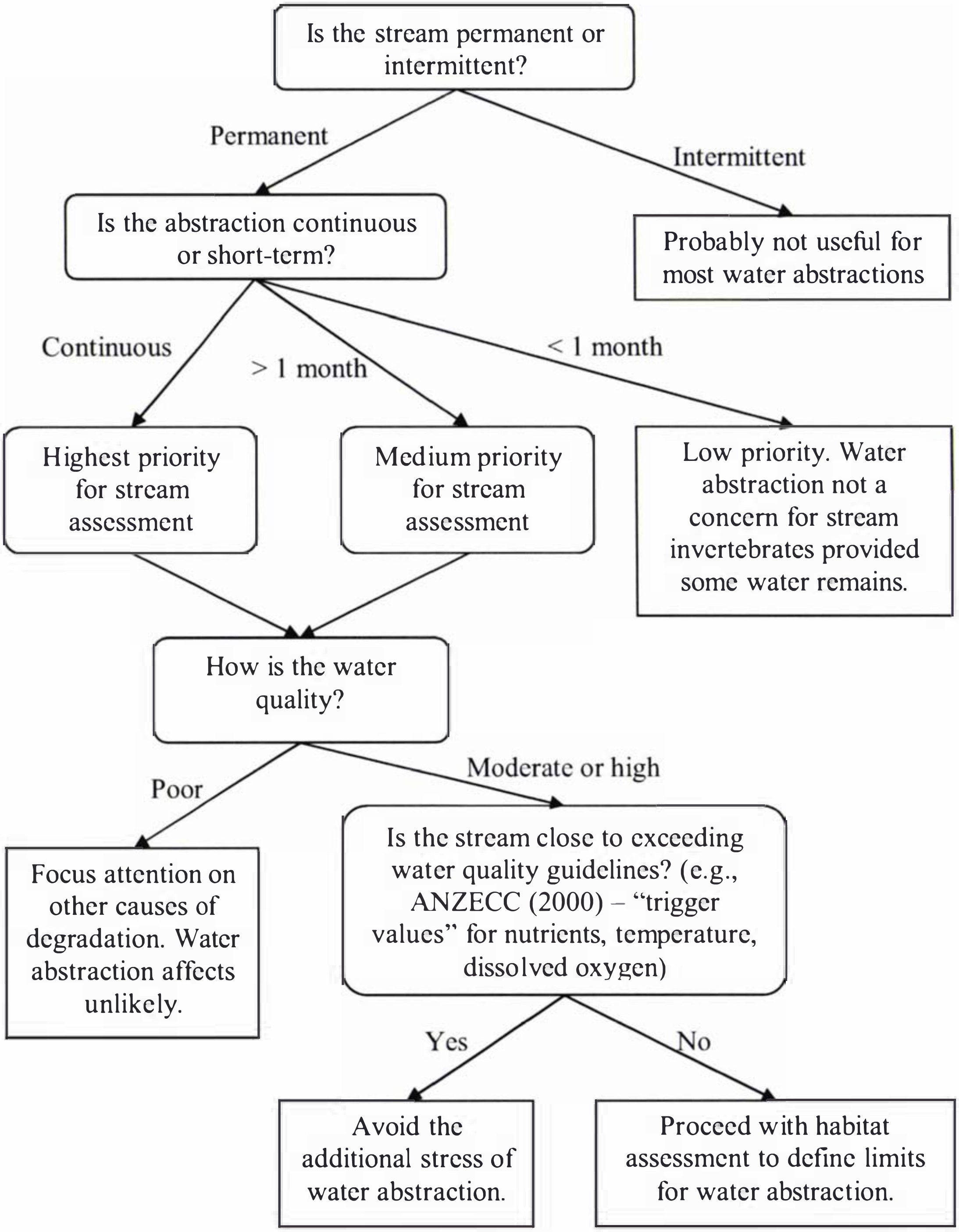

Figure 7. Prioritising small streams for water allocation investigation using invertebrates.

References

ANZECC (2000) *Australia and New Zealand Guidelines for Fresh and Marine Water Quality.* Australian and New Zealand Environment and Conservation Council and Agriculture and Resource Management Council of Australia and New Zealand.

Arnell N.W. (1999) Climate change and global water resources. *Global Environmental Change*, **9**, S31-S49.

Baron J.S., Poff N.L., Angermeier P.L., Dahm C.N., Gleick P.H., Hairston N.G., Jackson R.B., Johnston C.A., Richter B.D. & Steinman A.D. (2002) Meeting ecological and societal needs for freshwater. *Ecological Applications*, **12**, 1247-1260.

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

Boulton A.J. (2003) Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. *Freshwater Biology*, **48**, 1173-1185.

Boulton A.J. & Lake P.S. (1992) The ecology of two intermittent streams in Victoria, Australia. II. Comparisons of faunal composition between habitats, rivers and years. *Freshwater Biology*, **27**, 99-121.

Bunn S.E. & Arthington A.H. (2002) Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, **30**, 492-507.

Casas J.J., Zamora-Munoz C., Archila F. & Alba-Tercedor J. (2000) The effect of a headwater dam on the use of leaf bags by invertebrate communities. *Regulated Rivers: Research and Management*, **16**, 577-591.

Delucchi C.M. (1989) Movement patterns of invertebrates in temporary and permanent streams. *Oecologia*, **78**, 199-207.

Dewson Z.S., James A.B.W. & Death R.G. (2007) Invertebrate responses to short-term water abstraction in small New Zealand streams. *Freshwater Biology,* **52,** 357-369.

Gibson C.A., Meyer J.L., Poff N.L., Hay L.E. & Georgakakos A. (2005) Flow regime alterations under changing climate in two river basins: implications for freshwater ecosystems. *River Research and Applications*, **21**, 849-864.

Gore J.A., Layzer J.B. & Mead J. (2001) Macroinvertebrate instream flow studies after 20 years: a role in stream management and restoration. *Regulated Rivers: Research and Management*, **17**, 527-542.

Hart D.D. & Finelli C.M. (1999) Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms. *Annual Review of Ecology and Systematics*, **30**, 363-395.

Hilsenhoff W.L. (1987) An improved biotic index of organic stream pollution. *Great Lakes Entomologist,* **20,** 31-39.

Hooper F.F. & Ottey D.R. (1988) Responses of macroinvertebrates of two headwater streams to discharge fluctuations. *Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie*, **23**, 1159-1166.

Hughes D.A. (1970) Some factors affecting drift and upstream movements of *Gammarus pulex. Ecology*, **51**, 301-305.

Larned S.T. (2000) Dynamics of coarse riparian detritus in a Hawaiian stream ecosystem: a comparison of drought and post-drought conditions. *Journal of the North American Benthological Society*, **19**, 215-234.

Lenat D.R. (1988) Water quality assessment using a qualitative method for benthic macroinvertebrates. *Journal of the North American Benthological Society*, **7**, 222-233.

Meyer J.L., Sale M.J., Mulholland P.J. & Poff N.L. (1999) Impacts of climate change on aquatic ecosystem functioning and health. *Journal of the American Water Resources Association*, **35**, 1373-1386.

Mosley M.P. (1983) Variability of water temperatures in the braided Ashley and Rakaia rivers. *New Zealand Journal of Marine and Freshwater Research*, **17**, 331-342.

Poff N.L. & Ward J.V. (1991) Drift responses of benthic invertebrates to experimental streamflow variation in a hydrologically stable stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **48**, 1926-1936.

Postel S.L. (1997) *Last Oasis.* 1st edn. W.W. Norton & Company, New York, N.Y., U.S.A.

Rader R.B., McArthur J.V. & Aho J.M. (1994) Relative importance of mechanisms determining decomposition in a Southeastern blackwater stream. *American Midland Naturalist*, **132**, 19-31.

Raikow D.F., Grubbs S.A. & Cummins K.W. (1995) Debris dam dynamics and coarse particulate organic matter retention in an Appalachian Mountain stream. *Journal of the North American Benthological Society*, **14**, 535-546.

Richter B.D. (1993) Ecosystem-level conservation at the nature conservancy: growing needs for applied research in conservation biology. *Journal of the North American Benthological Society*, **12**, 197-200.

Richter B.D., Mathews R., Harrison D.L. & Wigington R. (2003) Ecologically sustainable water management: managing river flows for ecological integrity. *Ecological Applications*, **13**, 206-224.

Stark J.D. (1985). *A Macroinvertebrate Community Index of Water Quality for Stony Streams.* National Water and Soil Conservation Authority, Wellington, New Zealand.

Wallace J.B. & Webster J.R. (1996) The role of macroinvertebrates in stream ecosystem function. *Annual Review of Entomology*, **41**, 115-139.

Wood P.J. & Armitage P.D. (1999) Sediment deposition in a small lowland stream - management implications. *Regulated Rivers: Research and Management*, **15**, 199-210.

CHAPTER 8

Synthesis

The goal of this research was to review and extend current knowledge of the effects of water abstractions on the instream environment, invertebrate communities and ecosystem functioning in small permanent streams. This led me from a simple upstream-downstream approach for assessing the impacts of water abstraction, to a more novel and robust experimental design that involved whole stream manipulations of flow. Although the experimental approach has clear advantages over observational studies, this research represents one of the first attempts to reduce flow at this scale for experimental purposes, while gauging the responses of benthic invertebrate communities.

This study demonstrated that water abstractions that reduce discharge in small streams do alter stream ecosystems. This was evident in a review of previous studies (Chapter 1), by the increased densities of invertebrates and altered community composition at sites downstream of existing water abstractions (Chapter 2), and by the changes to invertebrate density, taxonomic richness, community composition and ecosystem function that were initiated by experimental flow manipulations (Chapters 3, 4 & 5).

Throughout the research, changes to the density of individual invertebrate taxa and the entire invertebrate community were the most common responses to reduced flow. However, the directions of these changes were not always consistent within the study. Consequently, this research has identified several factors that influence the responses of invertebrate communities to water abstraction. These factors might also account for some of the variability observed within and between previous studies of reduced flows. The review of literature (Chapter 1) and survey of existing water abstractions (Chapter 2) indicated that invertebrate community responses to reduced flow tended to increase with the proportion of flow removed. The magnitude of changes to habitat availability and suitability at different levels of water abstraction provide a likely explanation for this. Experimental flow reductions (Chapter 4) indicated that water abstractions could have more impact on streams of higher water quality. The greater sensitivity of invertebrate taxa in these types of streams explains this pattern. In addition, the results of experimental flow reductions of different length (Chapters 3 & 4) suggested that the length and/or timing of water abstractions could influence their affect on invertebrates.

At the beginning of this research, I hypothesised that invertebrate communities would be affected by flow reduction because of changes to the availability or suitability of habitat. I expected that the availability of habitat would decrease with flow reduction, since it would decrease the wetted width of streams. I also expected that habitat suitability would change as flow decreased, and although this would decrease habitat suitability for some taxa, it would increase habitat suitability for other taxa. In this way, I expected invertebrate community composition to alter with flow reduction. Although my hypotheses focused on habitat as the most important factor influencing the invertebrate community, the alteration of food resources as a consequence of reduced flow has emerged as an equally important reason for invertebrate community responses to flow reduction. For example, higher conductivities and periphyton biomasses at sites downstream of existing water abstractions corresponded with higher invertebrate densities at these sites (Chapter 2). In the channel experiments (Chapter 6), invertebrate densities were higher on cobbles with greater ash free dry mass (AFDM) of organic matter, and the density of filter feeders decreased with velocity (and hence food supply). Changes in ecosystem function with reduced discharge (Chapter 5) have long-term implications for invertebrate communities, since there is a close relationship between invertebrates and their food resources. In particular, the increased potential for coarse particulate organic matter (CPOM) to be retained at lower discharges has implications for the entire food web.

In summary, this thesis combines observational and experimental research to investigate the effects of reduced discharge on the instream environment, invertebrate communities and ecosystem functioning in small permanent streams, thereby extending current knowledge on the effects of water abstractions on stream ecosystems.

APPENDICES

Appendix 1. Summary of invertebrate data for survey of existing water abstractions (Chapter 2). Values are the average ($n = 9$) of all samples collected at each site on each sampling occasion. Sample codes include three digits representing stream (1=Mangatarere, 2=Tamaki, 3=Raparapawai), treatment (1=upstream, 2=downstream), and time (1-6). For example, 123 = Mangatarere, downstream, 3rd sampling.

	#		**111**	**121**	**211**	**221**	**311**
Ephemeroptera	**1**	*Acanthophlebia cruentata*	0.7	0.0	0.0	0.0	0.0
	2	*Amelotopsis* sp.	0.0	0.0	0.0	0.0	0.0
	3	*Atalophlebioides cromwelli*	2.1	0.6	0.0	0.0	0.0
	4	*Austroclima sepia*	0.6	0.0	0.0	0.0	0.9
	5	*Coloburiscus humeralis*	5.4	0.6	0.3	2.4	0.1
	6	*Deleatidium* sp.	64.4	125.6	141.6	211.1	179.4
	7	*Mauiulus luma*	2.9	0.0	0.0	0.0	0.0
	8	*Neozephlebia scita*	0.0	0.0	0.0	0.0	0.0
	9	*Nesameletus* sp.	2.8	6.8	2.9	2.8	0.9
	10	*Zephlebia* sp.	0.0	0.0	0.0	0.0	0.0
Plecoptera	**11**	*Austroperla cyrene*	0.0	0.0	0.6	0.2	0.0
	12	*Megaleptoperla diminuta*	0.0	0.0	0.7	1.1	0.0
	13	*Megaleptoperla grandis*	0.0	0.0	0.0	0.0	0.1
	14	*Stenoperla prasina*	0.4	0.3	0.0	0.3	0.3
	15	*Zelandobius* sp.	0.0	0.0	0.0	0.0	0.0
	16	*Zelandoperla* sp.	0.0	0.0	1.0	0.0	0.0
Trichoptera	**17**	*Aoteapsyche* sp.	12.3	22.0	8.0	18.9	36.7
	18	*Beraeoptera roria*	0.0	0.0	0.0	0.0	0.3
	19	*Costachorema callistum*	0.0	0.0	0.0	0.0	0.0
	20	*Costachorema xanthopterum*	6.2	1.0	2.1	0.4	1.0
	21	*Helicopsyche* sp.	1.3	0.0	0.4	0.4	0.0
	22	*Hudsonema amabile*	0.0	0.0	0.0	0.0	0.6
	23	*Hydrobiosis parumbripennis*	0.0	0.9	1.3	1.0	1.3
	24	*Hydrobiosis soror*	0.0	2.2	2.6	3.1	1.4
	25	*Hydrobiosis umbripennis*	4.1	7.2	2.6	1.7	2.9
	26	*Neurochorema confusum*	0.0	0.8	0.0	0.0	0.0
	27	*Neurochorema forsteri*	0.0	0.8	0.0	0.0	0.0
	28	*Olinga feredayi*	9.7	4.0	1.2	7.6	1.2
	29	*Oxyethira albiceps*	0.2	0.2	0.0	0.0	0.0
	30	*Plectrocnemia maclachlani*	0.4	1.2	0.0	1.2	0.0
	31	*Psilochorema* sp.	6.6	13.1	12.1	7.4	11.1
	32	*Pycnocentria evecta*	3.0	5.4	0.8	3.9	1.8
	33	*Pycnocentrodes* sp.	13.4	64.4	12.8	21.9	8.0
	34	*Triplectides* sp.	0.0	0.0	0.0	0.0	0.0

#	321	112	122	212	222	312	322	113	123	213	223
1	0.0	2.6	0.3	0.0	2.9	0.2	0.0	0.3	0.7	0.0	0.0
2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0
3	0.0	2.2	0.0	0.0	2.2	0.0	0.0	0.0	0.0	0.0	0.0
4	8.2	0.4	0.6	0.2	0.7	0.3	7.1	0.3	1.0	0.0	0.0
5	0.3	13.3	2.3	1.0	15.3	2.0	2.1	57.0	1.7	3.4	2.9
6	190.6	127.0	108.2	183.9	132.2	85.0	285.7	134.8	161.0	120.4	72.4
7	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
8	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
9	0.0	3.8	6.0	2.7	4.8	4.8	3.8	11.9	9.6	1.9	0.4
10	0.3	0.4	0.3	0.0	0.8	0.2	0.3	0.0	0.3	0.0	0.2
11	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.0
12	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0
13	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
14	0.0	1.2	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.6	0.0
15	0.0	0.0	0.0	0.2	0.0	0.0	0.6	0.0	0.0	0.0	0.0
16	0.0	2.1	0.0	0.7	2.3	0.0	1.2	1.7	0.0	1.2	0.0
17	37.8	19.8	25.4	15.1	22.6	23.3	37.1	29.3	29.3	8.1	12.7
18	0.0	1.1	0.3	0.8	1.3	0.2	1.1	1.1	0.0	0.0	0.0
19	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.1	0.2	0.0
20	0.0	4.1	1.9	0.8	4.6	1.3	1.7	4.8	4.8	2.8	0.2
21	0.0	19.6	1.0	17.2	9.3	0.7	0.0	17.8	2.8	0.6	0.2
22	0.0	0.8	0.0	0.0	1.0	0.0	5.1	0.3	0.0	0.0	0.2
23	0.1	6.3	4.7	3.7	7.4	3.4	6.8	6.3	8.2	2.2	0.7
24	0.6	3.1	2.7	2.9	4.2	2.1	5.1	5.7	2.4	2.7	2.6
25	0.0	0.9	3.0	6.0	1.7	2.9	10.3	6.0	7.0	3.9	3.9
26	0.0	0.0	0.6	0.0	0.0	0.3	0.0	0.0	1.0	0.0	0.0
27	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
28	2.0	24.7	9.0	12.4	25.4	6.8	26.0	27.7	7.9	7.0	6.9
29	0.0	2.1	1.8	0.3	2.8	1.2	1.2	1.7	1.4	0.0	0.2
30	0.0	0.4	0.9	0.0	0.8	0.4	0.1	0.0	0.7	0.0	0.0
31	12.3	4.6	7.9	8.4	5.3	6.4	13.2	1.4	6.7	9.0	4.4
32	6.1	3.6	10.2	6.1	3.4	7.3	18.1	7.9	5.2	1.0	3.1
33	2.2	40.7	91.3	47.3	42.9	74.4	58.8	70.7	154.6	9.7	14.4
34	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0

#	313	323	114	124	214	224	314	324	115	125	215
1	0.0	0.0	1.0	1.1	0.0	0.0	0.0	0.0	1.2	0.6	0.3
2	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.6	0.6	0.0
3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4	0.2	1.1	0.6	0.0	0.0	0.2	1.9	6.2	0.0	0.0	1.2
5	4.9	0.6	92.1	1.1	4.4	7.9	5.4	2.0	112.6	6.3	16.9
6	72.0	108.7	131.7	287.9	162.0	114.8	254.7	138.4	97.7	236.8	200.7
7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.6
9	0.9	0.0	7.1	5.7	2.0	0.4	0.4	0.0	5.7	4.8	3.7
10	0.0	0.7	0.2	0.3	0.0	0.8	0.8	1.7	0.6	0.3	0.0
11	0.0	0.0	1.2	0.0	0.9	0.4	0.0	0.0	0.0	0.0	1.0
12	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
13	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
14	0.0	0.1	0.0	0.3	0.0	0.3	0.0	0.0	0.0	0.0	0.3
15	0.0	0.0	0.0	0.0	0.2	0.4	0.0	0.0	0.0	0.0	0.0
16	0.0	0.0	2.1	0.6	0.8	0.2	0.3	0.0	3.3	0.0	0.4
17	18.7	28.6	40.0	31.9	5.1	13.3	45.9	41.2	46.3	47.3	22.7
18	0.0	0.0	3.6	1.4	0.2	0.3	0.3	0.0	12.8	1.1	2.1
19	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0
20	0.0	0.7	13.3	2.2	0.4	0.0	0.6	3.7	18.3	14.6	3.0
21	0.0	0.0	6.9	15.4	0.4	0.4	0.0	0.0	25.6	11.8	2.0
22	0.9	1.3	0.0	0.0	0.4	0.0	0.6	0.7	0.0	0.1	0.6
23	0.2	3.2	3.4	3.0	1.9	0.9	1.7	1.1	1.4	4.4	1.1
24	1.2	0.6	2.4	3.4	3.0	2.8	1.9	1.2	3.7	3.2	2.6
25	2.9	3.7	0.3	3.2	2.4	0.6	2.1	2.4	0.6	7.2	2.2
26	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.1	1.4	0.0
27	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.0
28	0.8	0.6	20.8	15.7	11.8	11.9	2.6	2.3	27.9	11.8	15.7
29	0.2	0.2	2.7	0.6	0.2	0.0	0.0	0.3	1.9	0.7	0.0
30	0.2	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0
31	5.0	4.7	2.2	6.1	8.0	3.2	9.3	8.0	3.2	7.7	5.7
32	1.3	4.9	6.1	6.7	2.1	4.1	5.6	8.8	8.7	8.1	3.2
33	9.7	10.2	77.1	288.6	9.7	23.1	9.9	6.7	204.8	606.8	61.0
34	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.6	0.0	0.0

#	225	315	325	116	126	216	226	316	326
1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0
3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4	0.2	0.0	2.0	0.1	0.0	0.7	0.0	0.0	0.2
5	15.8	1.8	2.0	34.4	4.3	11.2	5.1	0.9	0.1
6	185.4	221.4	186.8	49.7	80.9	142.6	89.2	78.4	108.6
7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
8	0.0	0.0	0.0	0.4	0.0	0.0	0.3	0.0	0.0
9	1.1	1.6	0.0	0.7	1.7	3.3	0.1	0.1	0.0
10	0.3	0.0	1.4	0.2	0.0	0.6	0.3	0.1	0.3
11	0.0	0.0	0.0	0.0	0.1	0.7	0.0	0.0	0.0
12	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
13	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
14	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
15	1.1	0.3	0.0	2.2	0.8	10.2	2.4	2.6	1.2
16	0.1	0.0	0.0	4.9	0.4	2.8	0.1	0.1	0.0
17	16.9	30.4	47.8	7.0	4.4	17.4	5.0	2.2	0.4
18	0.3	0.0	0.0	3.1	0.6	0.4	0.2	0.0	0.0
19	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
20	4.4	3.1	0.6	1.0	0.3	1.0	0.4	0.1	0.0
21	0.2	0.0	0.0	6.0	1.2	1.9	0.1	0.0	0.0
22	0.0	0.3	1.1	0.0	0.0	0.1	0.0	0.0	0.0
23	0.9	1.2	0.8	0.4	0.2	0.3	0.9	0.1	0.1
24	4.7	3.1	1.3	0.9	1.1	0.7	2.2	0.4	1.1
25	1.2	1.7	0.3	0.1	0.0	0.1	1.9	0.0	0.2
26	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0
27	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
28	24.2	1.0	2.2	6.6	1.9	2.0	2.4	0.2	0.2
29	0.3	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
30	0.0	0.0	0.0	0.0	0.0	0.2	0.1	0.0	0.1
31	4.3	4.0	4.8	1.1	1.3	9.9	4.2	2.1	1.3
32	8.6	0.1	8.4	0.3	0.4	0.3	0.9	0.0	0.2
33	31.2	6.1	16.2	56.9	36.3	17.0	25.3	4.1	10.9
34	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

	#		111	121	211	221	311
Diptera	**35**	*Aphrophila neozelandica*	7.9	7.8	1.6	1.3	0.3
	36	*Austrosimulium* sp.	64.0	21.8	8.7	5.0	1.7
	37	Chironominae	3.2	5.7	2.6	1.3	1.0
	38	Diamesinae	1.7	3.1	5.9	1.9	0.0
	39	Empididae	0.0	0.0	0.0	0.0	0.0
	40	Ephydridae	0.0	0.0	0.0	0.0	0.0
	41	Eriopterini	0.2	0.7	8.1	4.7	10.3
	42	Hexatomini	0.0	0.0	0.0	0.0	0.0
	43	*Limonia nigrescens*	0.0	0.0	0.0	0.0	0.0
	44	*Mischoderus* sp.	0.0	0.0	0.0	0.0	0.0
	45	*Molophilus* sp.	0.0	0.0	0.2	0.0	0.0
	46	Muscidae	0.0	0.0	0.0	0.0	0.2
	47	*Neoscatella* sp.	0.0	0.0	0.0	0.0	0.0
	48	Orthocladiinae	25.9	71.4	36.2	5.0	2.3
	49	*Paradixa* sp.	0.0	0.0	0.0	0.0	0.0
	50	*Paralimnophila skusei*	0.0	0.0	0.0	0.0	0.0
	51	Stratiomyidae	0.0	0.0	0.0	0.0	0.0
	52	Tabanidae	0.0	0.0	0.0	0.0	0.0
	53	Tanyderidae	0.0	0.0	0.0	0.0	0.0
	54	Tanypodinae	0.0	0.1	0.0	0.0	0.2
Coleoptera	**55**	*Berosus* sp.	0.0	0.0	0.0	0.0	0.0
	56	Elmidae	31.8	126.8	48.2	132.4	108.3
	57	Hydraenidae	0.0	0.0	0.3	0.4	0.0
	58	Staphylinidae	0.0	0.0	0.0	0.3	0.0
Crustacea	**59**	Amphipoda	0.0	0.0	0.0	0.3	1.2
	60	Collembola	0.0	0.3	0.0	1.0	0.0
	61	Ostracoda	0.0	0.0	0.0	0.0	0.0
Mollusca	**62**	*Gyraulus* sp.	0.0	0.0	0.0	0.0	0.0
	63	*Latia neritoides*	0.0	0.0	0.0	0.0	0.0
	64	*Physa* sp.	0.0	0.0	0.0	0.0	0.0
	65	*Potamopyrgus* sp.	0.0	0.9	0.0	0.0	0.5
Oligochaeta	**66**	Small Oligochaete	0.3	0.6	0.6	0.2	0.5
	67	Medium Oligochaete	0.0	0.0	0.2	1.1	0.3
	68	Large Oligochaete	0.0	0.0	0.2	0.6	0.0
Hemiptera	**69**	*Sigara* sp.	0.0	0.0	0.0	0.0	0.0
Other	**70**	Acari	0.0	0.0	0.0	0.0	0.0
	71	*Archichauliodes diversus*	5.1	2.8	0.0	1.7	1.9
	72	Nematode	0.1	0.0	0.0	0.0	0.0
	73	Nemertea	0.0	0.0	0.0	0.0	0.0
	74	Platyhelminthes	0.2	1.1	0.3	0.6	0.0
	75	Polychaete	0.0	0.0	0.0	0.0	0.0

#	321	112	122	212	222	312	322	113	123	213	223
35	0.0	9.6	17.0	3.1	11.0	11.4	2.7	15.3	12.8	0.9	0.4
36	7.0	17.4	7.4	7.8	18.8	5.7	4.3	72.3	16.7	1.8	2.8
37	4.6	13.6	62.3	3.2	19.6	43.1	5.2	34.2	11.9	0.0	0.0
38	0.0	3.0	3.1	1.6	3.9	2.4	2.7	16.7	1.8	0.0	0.2
39	0.0	0.3	0.0	0.0	0.3	0.0	0.0	0.6	0.0	0.0	0.0
40	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
41	12.7	1.0	2.0	17.4	1.4	2.4	9.4	2.1	2.0	2.3	2.7
42	0.0	0.0	0.0	0.0	0.1	0.0	0.2	0.0	0.0	0.0	0.0
43	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
44	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0
45	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
46	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
47	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
48	10.2	79.7	221.6	59.7	117.7	142.8	111.7	116.7	23.1	3.3	1.7
49	0.0	0.3	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
50	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
51	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
52	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
53	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
54	0.0	1.4	0.7	0.0	1.7	0.6	0.0	1.4	0.6	0.0	0.0
55	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
56	279.6	46.4	100.8	225.6	60.3	67.1	243.4	53.6	109.9	20.2	67.2
57	0.0	0.8	0.0	0.4	0.9	0.0	0.9	2.2	0.0	1.7	0.6
58	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4
59	2.7	0.0	0.0	1.1	0.0	0.0	7.2	0.0	0.0	0.2	0.8
60	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.2	0.3	0.2	0.2
61	0.0	0.3	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
62	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
63	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0
64	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
65	8.3	0.9	1.8	0.8	1.4	0.8	32.0	4.6	3.1	0.2	0.2
66	6.2	1.1	1.6	3.8	1.3	1.0	3.6	8.0	2.9	0.6	0.0
67	3.3	0.0	0.3	0.6	0.1	0.3	3.4	0.3	0.3	0.0	0.7
68	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
69	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2
70	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0
71	4.9	17.0	0.8	0.2	15.1	0.3	2.9	26.7	1.7	0.7	0.9
72	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
73	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
74	0.3	0.4	1.1	0.0	0.3	0.8	0.3	3.6	0.9	0.0	0.0
75	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

#	313	323	114	124	214	224	314	324	115	125	215
35	0.7	0.0	7.9	3.2	0.6	0.4	0.0	0.6	10.4	4.1	1.2
36	2.4	7.3	12.4	5.2	4.3	4.1	8.0	12.8	14.3	14.7	6.2
37	0.8	0.4	37.3	10.1	0.8	0.8	31.3	8.8	49.7	34.3	7.0
38	0.0	0.0	11.3	2.1	0.2	0.0	0.2	0.0	58.1	7.0	0.8
39	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
40	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
41	6.1	13.3	1.6	3.6	2.1	2.4	15.1	8.2	3.7	3.0	3.6
42	0.0	0.0	0.0	0.0	0.0	0.3	0.6	0.0	0.0	0.1	0.0
43	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
44	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
45	0.0	0.2	0.0	0.0	0.0	0.0	0.6	0.0	0.0	0.0	0.0
46	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.2
47	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
48	0.7	3.4	130.6	42.6	10.4	4.0	165.4	8.4	118.1	123.0	93.9
49	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
50	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3
51	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
52	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
53	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
54	0.0	0.2	0.6	0.0	0.0	0.0	0.0	0.2	2.4	0.0	0.0
55	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
56	151.6	262.8	46.2	168.2	37.2	137.2	371.7	283.0	47.2	120.8	51.3
57	0.0	0.0	1.9	0.0	0.6	0.4	0.0	0.0	1.4	0.6	0.4
58	0.0	0.1	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.9	0.0
59	0.8	0.6	0.0	0.0	0.2	1.2	0.3	1.7	0.0	0.0	0.0
60	0.2	0.3	0.0	1.2	0.8	0.2	0.6	0.7	3.1	0.6	0.0
61	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
62	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
63	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.6	0.0
64	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
65	0.8	31.8	1.6	2.7	0.8	0.8	2.6	19.7	5.2	5.0	4.0
66	0.2	11.6	1.7	5.9	0.3	1.8	9.3	16.7	0.9	5.2	0.2
67	0.0	3.1	0.0	0.0	0.0	0.0	1.0	0.1	0.0	0.0	0.3
68	0.0	0.0	0.0	0.3	0.0	0.0	0.1	0.0	0.0	0.0	0.0
69	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
70	0.0	0.3	0.0	0.0	0.9	0.0	0.0	0.3	0.0	0.0	0.0
71	0.4	19.6	27.6	7.8	0.4	1.6	1.6	12.6	38.1	6.1	0.8
72	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
73	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.3	0.0	0.0
74	0.0	2.4	1.2	6.6	0.0	0.2	0.8	2.7	2.3	2.0	0.0
75	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

#	225	315	325	116	126	216	226	316	326
35	0.0	0.2	0.0	1.4	0.6	1.7	0.0	0.0	0.0
36	7.2	1.3	0.6	3.6	1.6	1.1	0.8	0.3	0.4
37	10.1	1.6	3.4	0.0	0.1	0.0	0.1	0.0	0.0
38	0.3	0.0	0.0	0.1	0.3	0.1	0.1	0.0	0.0
39	0.0	0.0	0.0	0.1	0.0	0.1	0.0	0.1	0.0
40	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
41	1.6	8.4	13.4	1.4	0.3	0.9	1.3	2.6	2.8
42	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0
43	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
44	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
45	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
46	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
47	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
48	36.8	3.0	21.8	10.6	9.9	2.1	2.2	6.1	3.6
49	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
50	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
51	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
52	0.0	0.1	1.2	0.0	0.0	0.0	0.0	0.0	0.1
53	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
54	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
55	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
56	117.8	205.8	350.4	6.6	2.8	3.3	4.0	3.8	35.9
57	0.7	0.0	0.0	0.0	0.1	0.1	0.0	0.0	0.0
58	0.3	0.0	0.9	0.0	0.0	0.0	0.1	0.0	0.0
59	2.7	0.6	1.1	0.0	0.0	0.9	1.2	0.0	0.6
60	0.2	0.8	0.0	0.0	0.1	0.8	0.2	0.1	0.2
61	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
62	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
63	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
64	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0
65	1.2	1.1	39.1	0.7	0.1	0.8	0.3	0.7	4.9
66	0.8	0.4	18.3	1.2	0.4	1.0	1.1	0.8	6.4
67	0.3	0.0	2.4	0.0	0.0	0.0	1.6	0.1	4.6
68	0.1	0.0	0.3	0.0	0.0	0.0	0.1	0.0	0.2
69	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
70	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
71	1.4	0.6	15.2	1.7	0.4	0.2	0.4	0.0	0.7
72	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
73	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.1	0.0
74	1.2	0.2	2.8	0.1	0.6	0.0	0.0	0.3	0.7
75	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Appendix 2. Summary of invertebrate data for short-term flow reduction experiment (Chapter 3). Values are the average (n = 5) of all samples collected at each site on each sampling occasion. Sample codes include three digits representing stream (1=Booths, 2=Kiriwhakapapa, 3=Reef), treatment (0=control, 1=impact), and time (1-7). For example, 103 = Booths, control, 3rd sampling.

	#		101	111	201	211	301
Ephemeroptera	1	*Acanthophlebia cruentata*	0	0	0	0	9.4
	2	*Amelotopsis* sp.	0	0	0	0	0.4
	3	*Austroclima sepia*	75.2	25.6	1.4	0.6	0.6
	4	*Coloburiscus humeralis*	0	0	0.4	0.2	27.6
	5	*Deleatidium* sp.	2.4	0.8	21.6	4.8	96.4
	6	*Ichthybotis* sp.	0	0	0	0	0.6
	7	*Neozephlebia scita*	0	0	0.2	0	1.8
	8	*Nesameletus* sp.	0	0	0	0	1.2
	9	*Zephlebia dentata*	0	0.8	2	0.2	22.2
Plecoptera	10	*Austroperla cyrene*	0	0	0	0	4.2
	11	*Spaniocerca* sp.	0	0	1	0.2	0
	12	*Stenoperla prasina*	0	0	0	0	8.2
	13	*Zelandobius* sp.	0	0	0	0	52
	14	*Zelandoperla denticulata*	0	0	0	0	0.6
Trichoptera	15	*Aoteapsyche* sp.	4.8	2	10.6	19	0
	16	*Costachorema callistum*	0	0	0	0	0
	17	*Costachorema xanthopterum*	0.2	1.6	0.6	0.8	0
	18	*Diplectrona zelandensis*	0	0	0	0	2.4
	19	*Helicopsyche* sp.	0	0	1.6	0.6	0.8
	20	*Hudsonema amabile*	0	0	3.2	2.2	0
	21	*Hydrobiosella mixta*	0	0	0	0	1.4
	22	*Hydrobiosis gollanis*	0	0	0	0	0
	23	*Hydrobiosis parumbripennis*	22.6	15.5	2.7	7.7	0.5
	24	*Hydrobiosis soror*	0	0	0	0	0
	25	*Hydrobiosis umbripennis*	15.2	10.3	7.7	10.9	0.5
	26	*Hydrochorema tenvicaudatum*	0	0	0	0	0.6
	27	*Neurochorema confusum*	0	0	0.4	0	0.6
	28	*Neurochorema forsteri*	0	0	0	0	0
	29	*Oeconesus* sp.	0	0	0	0	0.2
	30	*Olinga feredayi*	0	0	5.4	8.6	0.2
	31	*Orthopsyche thomasi*	0	0	0	0	12.2
	32	*Oxyethira albiceps*	0	0	7.4	11	0
	33	*Plectrocnemia maclachlani*	0	0	0	0	0.2
	34	*Psilochorema* sp.	0.2	1.6	5.2	15.6	0.8
	35	*Pycnocentrella eruensis*	0	0	0	0	3.6
	36	*Pycnocentria evecta*	0.4	0	0	0.4	0
	37	*Pycnocentria funera*	0	0	0	0	0
	38	*Pycnocentrodes* sp.	0	0	11	4	0
	39	*Triplectides* sp.	0	0	0.2	0.2	0.2

#	311	102	112	202	212	302	312	103	113	203	213
1	4.2	0	0	0	0	7.6	11	0	0	0	0
2	0	0	0	0	0	0.6	1.2	0	0	0	0
3	0.4	16	19.2	2	6.8	0.6	3.2	1.6	1	0.6	0.8
4	9.8	0	0	0	0.8	5.2	23.8	0	0	0	0
5	62.6	1.6	0.8	117.2	82.2	22.4	48	0	0	51.8	43
6	0.4	0	0	0	0	0.2	0.2	0	0	0	0
7	0.6	0	0	0.2	0	1.2	1.4	0	0	0.6	0
8	0.6	0	0	0	0	1.8	0.8	0	0	0	0
9	1.8	0.8	0	0	0	9.8	6.2	0	0	0	0
10	0.2	0	0	0	0	1.4	1	0	0	0	0
11	0	0	0	0	0.2	0.4	0.6	0	0	0	0
12	2.8	0	0	0	0	3.4	6.2	0	0	0	0
13	9.6	0	0	0	0	22.4	30.6	0	0	0.2	0
14	0.4	0	0	0.4	1.2	0.2	0.6	0	0	0	0.2
15	0	0.8	0.8	9.6	58.8	0	0	0	0	4.4	7.6
16	0	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0.2
18	0	0	0	0	0	0.4	2	0	0	0	0
19	1.4	0	0	12.4	64.8	2.8	5	0	0	6.2	9
20	0	0	0	26.8	77	0	0.4	0	0	10.8	6.6
21	0.8	0	0	0	0	2.8	3.2	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0
23	0	1.6	0.4	9.3	12.4	0	0.8	1.7	0	2.8	5.6
24	0	0	0	0	0	0	0	0	0	0	0
25	0	0.8	1.2	8.1	14.8	0	0.8	1.7	0.4	2.2	5
26	0	0	0	0	0	0	1	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	1.6	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0.8	6	42.6	0.4	0.6	0	0	2.8	1.8
31	6.8	0	0	0	0	4.6	19	0	0	0	0.2
32	0	5.6	2.4	11	34.4	0	0	0.4	1.4	0.6	0
33	0	0	0	0	0	0	0	0	0	0	0
34	0.4	0	0	6	2.2	0.8	3	0	0	5.2	2.2
35	0.4	0	0	0	0	1	2	0	0	0.2	0
36	0	0	0.8	14.8	0	0	0	0	0	2	4.2
37	0	0	0	0	34.4	0	0	0	0	0	0
38	0	0	0	15.8	74.2	0	0	0	0	9.6	18.8
39	0	0	0	0	0	0	0.2	0	0	0.2	0.2

#	303	313	104	114	204	214	304	314	105	115	205
1	0.2	0	0	0	0	0	0	0.8	0	0	0
2	0.4	0	0	0	0	0	0	0	0	0	0
3	0	0.4	8.4	72.8	0.2	8.2	0.4	0.2	6.4	68	0.4
4	2	3.8	0	0	0.8	2.6	5	16.2	0	0	2
5	26	23.2	0.8	0.8	62.2	116.2	36.8	39.2	0.8	2.4	38.8
6	0	0	0	0	0	0	0	0	0	0	0
7	0.4	0.2	0	0	3.6	18	0.4	0.8	0	0	4
8	0	0.8	0	0	0	0	0.2	0.8	0	0	0
9	4.8	2.8	0	0	0	0	8.4	14.4	0.8	0	0
10	0	0	0	0	0	0	0.2	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0
12	0.4	0.6	0	0	0	0	0.4	1	0	0	0
13	7.2	8	0	0	0	0	10.4	6.8	0	0	0
14	0	0.2	0	0	0.2	0.4	0.2	1	0	0	1.4
15	0	0	3.6	26.4	5.2	22.6	0	0	5.6	6.4	3.4
16	0	0	0	0	0	0	0	0	0	0	0.2
17	0	0	0	0	0.2	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0
19	0	1	0	0	14.2	33.6	0.4	1	0	0	4.4
20	0	0	0	0	11.2	15.4	0	0	0	0	6
21	0	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	0	0	0	0	0	0	0
23	0	0.1	7.6	11.6	3	5.2	0	0.2	9.6	10.4	2.6
24	0	0	0.4	4.8	0.4	1.6	0	0	0	0.8	0.2
25	0	0.1	9.6	18.8	4.6	15.4	0	0.2	10.4	14.4	3
26	0	0	0	0	0	0	0	0.2	0	0	0
27	0	0	0	0	0	0.8	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0	0	0
30	0	0	0	0	19.4	22.4	0	0	0	0	9
31	4.4	5.4	0	0	0	0	4.8	4.8	0	0	0
32	0	0	0.8	0	0	0	0	0	0	1.6	0
33	0	0	0	0	0	0	0	0	0	0	0
34	0.2	0	0.4	6.4	4.4	11.4	1	0.6	0	1.6	7.6
35	0	0.2	0	0	0	0	0.2	0.2	0	0	0
36	0	0	0	0.8	4	17.8	0	0	0	0	6.6
37	0	0	0	0	0	0	0	0	0	0	0
38	0	0	0	0	30.4	41.6	0	0	0	0.8	17.2
39	0	0	0	0	0.2	0	0	0	0	0	0.4

#	215	305	315	206	216	306	316	207	217	307	317
1	0	0	1.2	0	0	0.8	1.2	0	0	0.8	2
2	0	0	0	0	0	0.2	0.4	0	0	0	0.2
3	1.8	1.6	0.2	3.2	0.6	0.4	0.2	1.8	1.6	0	0.2
4	1	14	9.6	9.2	2.6	2.2	7.8	7.6	2.4	10	21.6
5	103	41.6	52	96.2	177.8	26	32.6	116	203.6	64.6	90
6	0	0.2	0.6	0	0	0	0.4	0	0	0	0.2
7	7.4	0	1.2	28.8	52.4	0.4	0.4	13.4	40	0.6	2.4
8	0	0	0	0	0	0.2	1.4	0	0	0.4	1.6
9	0	12	9	2.4	0	3.6	8.2	0	0.8	5	9.8
10	0	0.8	0.6	0	0	0.2	0.6	0	0	0.4	0.6
11	0	0.4	0.2	0	0	0.4	0	0	0	0	0
12	0	0.8	1.2	0	0	0.6	0.2	0	0	1.2	2.8
13	0	20.2	17.4	0	0	4	11.6	0	0	11	16.6
14	0.6	0.6	1	2	0	0.6	0	2.4	0	1	0
15	9.8	0	0	8	9.4	0	0	4.8	6.4	0	0
16	0	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0.2	0	0	0	0	0	0	0
18	0	0.6	1.2	0	0	0.6	0	0	0	0	0.2
19	6	0.2	0.2	7.8	5	0.6	0.6	9	19.2	0.2	0.8
20	14.8	0	0	22.4	9.6	0	0	16.6	25.6	0	0
21	0	1	0	0	0	0	1	0	0	0	0
22	0	1	0.2	0	0	0	0	0	0	0	0
23	3.4	0	0	0.8	1.6	0.2	0	0	1.6	0.6	0
24	0.2	0	0	0	0.2	0	0	0	0	0	0
25	2.6	0	0	2.4	0.2	0.2	0	3.6	4.8	0.4	0.4
26	0	0.2	0	0	0	0.2	0	0	0	0	0
27	0	0	0	0.8	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0
29	0	0	0	0	0	0	0	0	0.8	0	0
30	25	0	0	28.8	18.4	0	0.2	43.4	29.2	0	0
31	0	5.8	7.8	0	0	1.2	3.8	0	0	7	6.4
32	0	0	0	0	0.4	0	0	0	2.8	0	0.2
33	0	0	0	0	0	0	0	0	0	0.2	0.8
34	14.2	0.4	1.4	9.6	9.8	0.4	1.4	6	12.8	1.4	1.4
35	0	0.8	0.4	0	0	0	0.2	0	0	0.4	0
36	23.2	0	0	13.2	9.8	0	0	10.4	26.4	0	0
37	0	0	0	0	0	0	0	0	0	0	0
38	29.8	0	0	46.6	32	0	0	41.2	88.4	0	0
39	0.8	0	0	0	0.4	0	0	0	0	0	0

	#		101	111	201	211	301
Diptera	**40**	*Aphrophila* sp.	0	0	0.6	0.8	0
	41	*Austrosimulium* sp.	9	6.8	91.6	157	0.4
	42	Ceratopogoninae	0	0	0.2	0	0
	43	Chironominae	5.6	4	12.2	18.8	10.4
	44	Diamesinae	0	0	24.6	50.2	0
	45	Empididae	0.8	0	0.6	1	0.4
	46	Eriopterini	0	0	0	0	1.6
	47	Hexatomini	0	0.2	0	0	0.8
	48	*Molophilus* sp.	0	0	0	0	0.2
	49	*Nothodixa* sp.	0	0	0	0	0.2
	50	Orthocladiinae	89.8	18.4	168.8	213.6	34.8
	51	Psychodidae	0	0	0	0	0
	52	Stratiomyidae	0	0	0	0	0
	53	Tanypodinae	0	1	0.8	1	1
Coleoptera	**54**	Dytiscidae	2	0	0	0	0
	55	Elmidae	123	95	28.6	18.8	6.4
	56	Hydraenidae	0	0	0	0	1.8
	57	Hydrophilidae	0	0	0.2	0	0
	58	Ptilodactylidae	0	0	0	0	2.8
	59	Staphylinidae	0.2	0	0	0	0
Crustacea	**60**	Amphipoda	1876.2	1852	0.8	2.4	1.2
	61	Cladoceran	0	0	0.2	0	0
	62	Copepod	0	0	0.8	0	0
	63	Ostracoda	1	0	0	0	0
Mollusca	**64**	*Ferrissia* sp.	0	0	62	7.2	0
	65	*Physa* sp.	3.2	1.2	4.6	1.6	0
	66	*Potamopyrgus* sp.	285	180	355	64.6	0
Oligochaeta	**67**	Small Oligochaete	187.8	131.2	120.8	53.2	40.4
	68	Medium Oligochaete	30	2.4	97.6	0.2	0
	69	Large Oligochaete	0.8	0.2	3	1.4	0
Hemiptera	**70**	*Sigara* sp.	0.8	0	0	0	0
Other	**71**	Acari	0	0	0	0	0.2
	72	*Archichauliodes diversus*	0	0	2.4	2.2	0
	73	Collembola	0	0	1.4	0	0
	74	Hirudinea	0.2	0	0	0	0
	75	*Hydra* sp.	8.6	0.6	9.2	0.2	0
	76	*Hygraula nitens*	0	0	0	0	0
	77	Nematode	0	0.2	0	0	0
	78	Nemertea	1.6	0	0	0.2	0
	79	*Pisidium* sp.	0	0	1.4	0	0
	80	Platyhelminthes	2.4	0.8	12	1	1.4
	81	*Xanthocnemis zealandica*	0	0	0	0	0

#	311	102	112	202	212	302	312	103	113	203	213
40	0	0	0	0.4	49	0	0	0	0	0	3.4
41	0	7.2	9.6	21.2	56.6	0	0	3.4	6	11	8.4
42	0	0	0	0	0	0	0	0	0	0	0
43	1.2	0	0.8	41.8	530.8	4.8	11	0.6	0.2	0.4	5.8
44	0	0	0	3.2	16	0	0	0	0	0	3.4
45	0	0.8	0	2	20.2	0	0.2	0	0	0	0
46	0.6	0	0	0	0	0.4	1.4	0	0	0	0
47	0.2	0	0	0	0	0.4	0.4	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0
50	6.8	94.4	44	31.8	281.2	5.2	10.2	27.2	5	3.8	25.4
51	0	0	0	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0	0.4	0	0
53	0.4	0	0.8	1	0.4	0.2	0.6	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0
55	7.2	124	200	38.4	28.8	9.2	24.4	97.4	87	12.6	10.6
56	0.4	0	0	0	1.6	0	1.4	0	0	0	0
57	0	0	0	0	0	0	0	0	0	0	0
58	1.6	0	0	0	0	0.6	4.4	0	0	0	0
59	0	0	0	0	0	0	0	0	0	0	0
60	0	908	365.6	0.8	0.2	0.6	0	122.2	83.2	0	0
61	0	0	0	0	0	0	0	0.2	0	0	0
62	0	0	0	0	0	0	0	0	0	0	0
63	0	24.8	15.2	0.8	1.8	0	0	16.6	11.2	0	0
64	0	0	0	6.4	86.6	0	0	0	0	0	0.2
65	0	21.6	10.4	0.8	2.8	0	0	1.2	0.4	0.2	0.6
66	0.4	210.4	472	227.8	215.6	0.2	2.4	59	68.2	72	63.8
67	7.4	162.4	213.6	151.6	44.4	7.8	10.8	37	31.8	31.2	17.2
68	0	0	47.2	1.6	26.2	0	0.6	0	0.6	0.6	0.2
69	0	3.2	0.8	1.6	3.2	0	0.2	0.8	1.2	0	0
70	0	0	0.8	0	0	0	0	0.6	0	0	0
71	0	0	0	0	0	0	0	0	0	0	0
72	0	0	0.8	2.6	3.8	0	0.2	0	0	1.6	2.6
73	0	0	0	0	0.8	0	0	0	0	0	0
74	0	4	3.2	0.4	0	0	0	1.8	1.4	0	0
75	0	0.8	1.6	0	5	0	0	0	0	0	0
76	0	0	1.6	0	0	0	0	0	0	0	0
77	0	0.8	0	0	0	0	0	0.6	0	0	0
78	0	3.2	18.4	0.4	6	0	0	0.8	1.4	0	0.8
79	0	0	0	0.6	1.4	0	0	0	0	0	0
80	2.4	12.8	24.8	8.2	9.2	1	1.6	3	1	7.4	3.6
81	0	0	1.6	0	0	0	0	0	1	0	0

#	303	313	104	114	204	214	304	314	105	115	205
40	0	0	0	0	1	13.4	0	0	0	0	0
41	0	0	32.8	48.8	18.8	25	0	0	20.8	7.2	18.6
42	0	0	0	0	0	0	0	0	0	0	0
43	0.4	0	0.8	0	3.6	65.8	0.4	1	0.8	0	2.6
44	0	0	0	0	3	22.2	0	0	0	0	0.8
45	0	0	0	0	0	0	0	0	0	0	0
46	0.2	0.4	0	0	0	0	0	0.4	0	0	0
47	0	0.2	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0
50	0.2	0.4	66.4	8.8	8.2	82.4	0.4	0	13.6	13.6	7.2
51	0	0	0	0	0	0	0	0	0	0.8	0
52	0	0	0	0	0	0	0	0	0	0	0
53	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0
55	3.2	1	56.4	323.2	35	47.2	0.8	2	79.2	138.4	23
56	0.2	0.4	0	0	0	0	0.6	1	0	0	0.2
57	0	0	0	0	0	0	0	0	0	0	0
58	0.2	0	0	0	0	0	0	0	0	0	0
59	0	0	0	0	0	0	0	0	0	0	0
60	0	0.6	904	1424	0	0	0	0	1147.2	749.6	0
61	0	0	0	0	0	0	0	0	0	0	0
62	0	0	0	0	0	0	0	0	0	0	0
63	0	0	8	1.6	0	0	0	0	3.2	0	0
64	0	0	0	0	4	8.8	0	0	0	0	2
65	0	0	1.6	0.8	0.4	0.4	0	0	1.6	2.4	0
66	0	0.4	73.2	192.8	234.4	120.8	0	0	81.6	116	128.8
67	2.4	1.6	142.4	362.4	31	69.8	0.4	0	112.8	246.4	29.6
68	0	0	2.4	5.6	0	0	0	0	0.8	1.6	0.4
69	0	0	0.4	1.6	0.4	1.6	0	0	2.4	0.8	0.2
70	0	0	0	0	0	0	0	0	0.8	0	0
71	0	0	0	0	0	0	0	0	0	0	0
72	0.2	0	0	0	7.4	11.2	0	0	0	0	1.8
73	0	0	0	0	0	0	0	0	0	0	0
74	0	0	2.4	5.6	0	0	0	0	6.4	8	0
75	0	0	0	0	0	0	0	0	0	0.8	0
76	0	0	0	0	0	0	0	0	0	0	0
77	0	0	0	0.8	0	0	0	0	0	0	0
78	0	0	7.2	0.8	0	3.2	0	0	3.2	2.4	0
79	0	0	0	0	0.8	0	0	0	0	0	0.2
80	0.2	1.4	12	10.4	12.8	6	0.6	0.8	10.4	8	9.2
81	0	0	0	0	0	0	0	0	0	0	0

#	215	305	315	206	216	306	316	207	217	307	317
40	2	0	0	1.2	1	0	0	0	0	0	0
41	6.8	0	0	16.8	5.4	0	0	24.4	114	0	0
42	0	0	0	0	0	0	0	0	0	0	0
43	12.8	1.4	1.8	3.4	20.4	1	0.8	0.4	21.2	6.6	3.2
44	4	0	0	1.8	0	0	0	3	3.6	0	0
45	0	0.2	0.2	0	0	0	0	0	0	0	0.2
46	0	0	0.2	0	0	0	0.6	0	0	0	0
47	0	0	0	0	0	0	0	0	0	0	0.4
48	0	0	0.2	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0	0	0	0
50	17.6	1.4	3.4	13.2	9.4	2.8	1.8	49.4	200.4	3.4	3.6
51	0	0	0	0	0	0	0	0	0	0	0.2
52	0	0	0	0.8	0	0	0	0	0	0	0
53	0	0	0	0	0	0	0	0	0	0	0
54	0	0	0	0	0	0	0	0	0	0	0
55	47.2	1	1.4	38.2	26.4	0	0.6	59.2	53.2	1.8	4
56	0	0.2	0.8	0.4	0	1	0	0.2	0	0.6	0.2
57	0	0	0	0	0	0	0	0	0	0	0
58	0	0.2	0.4	0	0	0	0.8	0	0	0.6	1.6
59	0	0	0	0	0	0	0	0	0	0	0
60	0	0	0.2	0	0	0	0	0	0	0.2	0
61	0	0	0	0	0	0	0	0	0	0	0
62	0	0	0	0	0	0	0	0	0	0	0
63	0	0	0	0	0	0	0	0	0	0	0
64	0	0	0	6.4	4.4	0	0	3.2	4	0	0
65	0.2	0	0	3.8	0.2	0	0	0.8	0	0	0
66	81.6	0	0	257.6	212.2	0	0	263.8	563.6	0	0.2
67	78.4	1.2	0	19.4	19	4.8	2	44.2	162.4	3.8	1.8
68	0	0	0	0	0	0	0	0	0	0	0
69	0	0	0	1.4	0	0	0	4	0	0	0
70	0	0	0	0	0	0	0	0	0	0	0
71	0	0	0	0	0	0	0	0	0	0	0
72	7.6	0	0	8.2	6.8	0.2	0	5.2	6.4	0	0.2
73	0	0.2	0	0	0	0	0	0	0	0	0
74	0	0	0	0	0	0	0	0	0	0	0
75	0	0	0	0	0	0	0	0	0	0	0
76	0	0	0	0	0	0	0	0	0	0	0
77	0	0	0	0	0	0	0	0	0	0	0
78	2.6	0	0	0	1	0	0	0	2.4	0	0
79	0	0	0	0	0.2	0	0	0	0	0	0
80	20.2	0.2	2	18.2	19	1	1.8	5	22	1.4	10.6
81	0	0	0	0	0	0	0	0	0	0	0

Appendix 3. Summary of invertebrate data for long-term flow reduction experiment (Chapter 4). Values are the average (n = 5) of all samples collected at each site on each sampling occasion. Sample codes include three digits representing stream (1=Booths, 2=Kiriwhakapapa, 3=Reef), treatment (0=control, 1=impact), and time (1-8). For example, 103 = Booths, control, 3rd sampling.

	#		**101**	**111**	**201**	**211**	**301**
Ephemeroptera	**1**	*Acanthophlebia cruentata*	0	0	0	0	2.8
	2	*Amelotopsis* sp.	0	0	0	0	0
	3	*Austroclima sepia*	20.8	13.6	4	1.2	0
	4	*Coloburiscus humeralis*	0	0	1.8	0.4	5.8
	5	*Deleatidium* sp.	4.8	4	24	12.4	68
	6	*Ichthybotis* sp.	0	0	0	0	0.6
	7	*Neozephlebia scita*	0	0	2.8	0.4	1.4
	8	*Nesameletus* sp.	0	0	0	0	0.2
	9	*Oniscigaster distans*	0	0	0	0	0
	10	*Zephlebia dentata*	0	0	0	0	2.2
	11	*Zephlebia versicolor*	0	0	0	0	0
Plecoptera	**12**	*Austroperla cyrene*	0	0	0	0	2
	13	*Spaniocerca* sp.	0	0	0.8	0.2	0
	14	*Stenoperla prasina*	0	0	0	0	1.4
	15	*Zelandobius* sp.	0	0	0	0	5.4
	16	*Zelandoperla denticulata*	0	0	0	0	0.2
Trichoptera	**17**	*Aoteapsyche* sp.	25.6	12.8	1.8	0	0
	18	*Costachorema xanthopterum*	0	0	2.6	0.6	0
	19	*Diplectrona zelandensis*	0	0	0	0	0
	20	*Helicopsyche* sp.	0	0	0.8	0.2	0.6
	21	*Hudsonema amabile*	0	0	1.2	3.2	0
	22	*Hydrobiosella mixta*	0	0	0	0	0.8
	23	*Hydrobiosis parumbripennis*	19.4	19.2	2.6	1	0.4
	24	*Hydrobiosis soror*	0	0	0	0	0
	25	*Hydrobiosis umbripennis*	16.8	4.2	4.2	1	0.8
	26	*Hydrochorema tenvicaudatum*	0	0	0	0	0
	27	*Oeconesus* sp.	0	0	0	0	0
	28	*Olinga feredayi*	0	0	10	6.8	0
	29	*Orthopsyche thomasi*	0	0	0	0	2.4
	30	*Oxyethira albiceps*	0	0	0	0.6	0
	31	*Paroxythira* sp.	0	0	0	0	0
	32	*Plectrocnemia maclachlani*	0	0	0	0	0
	33	*Polyplectropus* sp.	0	0	0	0	0
	34	*Psilochorema* sp.	0	0.8	2.4	1.4	3
	35	*Pycnocentrella eruensis*	0	0	0	0	1.4
	36	*Pycnocentria evecta*	0	0	0	0	0
	37	*Pycnocentrodes* sp.	0	0	1.2	0.6	0
	38	*Triplectides* sp.	0	0	0	0	0

#	311	102	112	202	212	302	312	103	113	203	213
1	2.6	0	0	0	0	2.8	2.6	0	0	0	0
2	0.2	0	0	0	0	0	0.4	0	0	0	0
3	0.8	74.4	30.4	1	1.2	0	0.2	59.2	100	6	2
4	7	0	0	0	0.6	2.8	11.8	0	0	0	0.4
5	101	5.6	2	10.4	5.6	81.8	59.4	0.4	1	22	27.6
6	0.2	0	0	0	0	0	0.8	0	0	0	0
7	1.4	0	0	1.2	0.2	3.4	3.8	0	0	0	0
8	1.2	0	0	0	0	1.2	0.2	0	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0
10	4	0	0	0	0	3	8.8	0	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0
12	1.8	0	0	0	0	1	7.6	0	0	0	0
13	0	0	0	0	0	0	0.2	0	0	0	0
14	1.8	0	0	0	0	1.8	3	0	0	0	0
15	9.8	0	0	0	0	7.4	12.4	0	0	0	0.8
16	0	0	0	0	0	0	0.2	0	0	0	0
17	0	57.6	52.8	0.6	1.4	0	0	21.8	27.2	7.6	14
18	0	0	5.6	3.8	6.6	0.2	0.4	0	0	3.4	4.8
19	0.6	0	0	0	0	0	0	0	0	0	0
20	1.6	0	0	0	0.4	0	1	0	0	0	0
21	0	0	0	4.8	2.8	0	0	0.8	0	5.6	8.4
22	1.8	0	0	0	0	0.2	0.6	0	0	0	0
23	0	33.6	32.8	1	1.6	0.2	0.4	11.2	14.4	7.2	4.8
24	0	0	0	0	0	0	0.2	0	0	0	0
25	0.2	28.8	28	1.6	0	0.2	0.2	6.6	14.4	6.4	10.6
26	0	0	0	0	0	1	1	0	0	0	0
27	0	0	0	0	0	0	0	0	0	0	0
28	0	0	1.6	11.4	4.2	0	0	1.6	0.8	7.2	9.6
29	3	0	0	0	0	3.4	2.6	0	0	0	0
30	0	0	0	1	2.8	0	0	1.6	1.6	6	14.4
31	0	0	0	0	0	0	0	0	0	0	0
32	0.2	0	0	0	0	0	0	0	0	0	0
33	0	0	0	0	0	0	0.2	0	0	0	0
34	1.8	8	4	3.4	8.8	2	3.6	5	1	4.8	25.2
35	0.2	0	0	0	0	0	1	0	0	0	0
36	0	0	0	0.4	0	0	0	14.4	10.4	0.8	0
37	0	20	4.2	0	0	0	0	69.6	26.6	0.8	3.6
38	0	0	0	0	0	0	0	0	0	0	0

#	303	313	104	114	204	214	304	314	105	115	205
1	0.4	4.2	0	0	0	0	0.8	3.2	0	0	0
2	0.4	1	0	0	0	0	0.4	1.6	0	0	0
3	0	0	44	516.8	4	3.2	0	0.4	20.8	6.4	1.6
4	2.2	2	0	0	2.4	0	1.6	3.8	0	0	2.4
5	75.4	65.4	1.6	2.4	99.2	85.6	120	84.4	0.8	0	179.2
6	0.2	0.4	0	0	0	0	0.4	1	0	0	0
7	0.4	0.8	0	0	0	0	0.4	0.8	0	0	0.8
8	0.2	0.8	0	0	0	0	1.4	1.4	0	0	0
9	0	0	0	0	0	0	0	0	0	0	0
10	8.2	3.4	0	0	0.8	0	3.6	26.4	0	0	0
11	0	0	0	0	0	0	0	0	0	0	0
12	1	12.6	0	0	0	0	3	16.6	0	0	0
13	0	0	0	0	0	0	0.2	0.4	0	0	0
14	2.2	4.4	0	0	0	0	1.2	2.4	0	0	0
15	8.8	16.2	0	0	0	0	28.6	36	0	0	0
16	0	1.6	0	0	3.2	0	0.2	0	0	0	0
17	0	0	12.8	86.4	24.8	7.4	0	0	16	16	15.2
18	0	0.4	0	1.6	11.4	2.4	0.8	0.2	0	0	0
19	0.2	0	0	0	0	0	0.6	0	0	0	0
20	0.2	2.2	0	0	1.6	5.8	1.2	4	0	0	5.6
21	0	0	0	0	24.8	52.8	0	0.2	0	0	56
22	0.6	0	0	0	0	0	0.2	0	0	0	0
23	0	0.8	10.4	20	8.2	8.8	2	2	0	0	15.2
24	0.2	0.4	0	0	0	0.8	0.4	0.8	0	0	0
25	0.6	0.4	0	10.4	4	8	1.4	0.8	0	0.8	11.2
26	0.4	0.4	0	0	0	0	0	0.8	0	0	0
27	0	0.2	0	0	0	0	0	0	0	0	0
28	0.6	0	0	0	23.2	19.4	0.2	0	0	0	11.2
29	2.8	1.4	0	0	0	0	30	22.6	0	0	0
30	0	0	20	48	8	26.4	0	0	37.6	61.6	28.8
31	0	0	1.6	4.8	0	0	0	0	0.8	8	0
32	0	0	0	0	0	0	0.2	0.8	0	0	0
33	0	0	0	0	0	0	0	0	0	0	0
34	2.4	2.2	2.4	6.4	30.4	71.2	8.6	10.4	0	3.2	12
35	0.6	0.2	0	0	0	0	0.6	0.4	0	0	0
36	0	0	5.6	28.8	11.2	4.8	0	0	1	7.2	17.6
37	0	0	26.6	51.2	8.8	3.2	0	0	7.4	2.6	9.8
38	0	0.4	0	0	0	2.4	0	1	0	0	0.8

#	215	305	316	106	116	206	216	306	107	117	207
1	0	0.2	5.8	0	0	0	0	1.8	0	0	0
2	0	0	2.1	0	0	0	0	0.4	0	0	0
3	0	0	0	12.8	8.4	4.8	0.4	15.4	149.6	82.4	4
4	0	3.8	6.9	0	0	0	0	111.4	0	0	0
5	43.4	127	31.3	0	0.8	137.6	4.8	153.2	25.8	12	64
6	0	0	1.7	0	0	0	0	0.8	0	0	0
7	0	0.2	0.9	0	0	5.6	0	2	0	0	2
8	0	0.8	1.1	0	0	0	0	0.4	0	0	0
9	0	0	0.1	0	0	0	0	0	0	0	0
10	0	7	10.6	0	0	0	0	5.4	0	0	0
11	0	0	1.2	0	0	0	0	0	0	0	0
12	0	2.8	9.2	0	0	0	0	4.8	0	0	0
13	0	0	0.1	0	0	0	0	0	0	0	0
14	0	1.6	2.2	0	0	0	0	3.8	0	0	0
15	0	28	10	0	0	0	0	20.8	0	0	0
16	0	0.2	0	0	0	0	0	0.2	0	0	0
17	5.6	0	0	0	1.8	25.6	0	0	5.6	1.8	1.8
18	0	0	0	0	0	0	0	0	0	0	1
19	0	0	0.3	0	0	0	0	0	0	0	0
20	2.8	1.8	2	0	0	1.6	3.2	0.4	0	0	0.8
21	202	0	0	0	0.4	108.8	140.8	0.2	0	0	4
22	0	0	0	0	0	0	0	0	0	0	0
23	0	0	0	4.8	0	12	0.4	0.2	12.8	4	11.2
24	0	0.2	0	0	0	2.4	0	2	3.2	0	0
25	0.8	0	0	8	0	12.8	2.2	0	8.8	4.8	9.6
26	0	0.8	0.9	0	0	0	0	4.6	0	0	0
27	0	0	0.6	0	0	0	0	0	0	0	0
28	17	1.2	0	0	0	34.4	2.4	5.2	0	0	10.8
29	0	24.4	8.6	0	0	0	0	81.2	0	0	0
30	147.2	0	0	240.8	52.8	15.2	32	0	0	0	0
31	0	0	0	4.8	0.8	0	0	0	0	0	0
32	0	0.6	0.1	0	0	0	0	0	0	0	0
33	0	0	0.5	0	0.2	0	0	0	0	0	0
34	13	6.6	2.4	0	0.2	10.6	2	5	0	0.8	5.4
35	0	0.4	0.7	0	0	0	0	1	0	0	0
36	10.6	0	0	0.8	0	16.8	1.8	0	0	0	1
37	6.4	0	0	15.2	2	10.4	2.4	0	0	0	1
38	0	0	4.2	0	0	0	2.4	1	0	0	1.2

#	217	307	317	108	118	208	218	308	318
1	0	3.6	5.4	0	0	0	0	0.6	1.4
2	0	0.2	1.4	0	0	0	0	0	1.4
3	0	0.8	0	25	65.6	11.2	0	0.4	0.2
4	0	24.4	20.6	0	0	1.6	0	11	1.6
5	0.6	231.4	141.2	0.8	0.8	170.4	53.2	88.6	40.8
6	0	1.4	1.6	0	0	0	0	0.4	1.2
7	0	6	6.4	0	0	0	0	1.8	1
8	0	0.8	0.4	0	0	0	0	0.2	0.4
9	0	0	0	0	0	0	0	0	0
10	0	2.8	16	0	0	1.6	0	7.6	7
11	0	0	0	0	0	0	0	0	0
12	0	0.4	5	0	0	0	0.8	4.4	2.8
13	0	0	0	0	0	0	0	0	0
14	0	3.6	4.4	0	0	0	0	3.6	1.4
15	0	12.6	18.6	0	0	0	0	10.8	3
16	0	0	0	0	0	1.6	0	0	0
17	0	0	0	10.4	4.2	34.4	8	0	0
18	0	0	0	0	0	0	0	0	0.4
19	0	2.6	1.2	0	0	0	0	0.2	0
20	1.2	3.8	2	0	0	2.4	0	1.4	1.6
21	11.4	0	0	0.8	0	7.2	24.8	0	0
22	0	0.2	0	0	0	0	0	0.2	0
23	0	0	0	6.4	16	23.2	0	0	0
24	0	0	0	0	0	0.4	0	0	0
25	0	0	0	3.2	7.2	4.8	0.2	0.6	0
26	0	0.8	0.8	0	0	0	0	1	0
27	0	0	0.2	0	0	0	0	0	0.4
28	4	0.4	0	0	0	6	1.4	0.2	0
29	0	14.8	4	0	0	0	0	10.4	0.8
30	0	0	0	182.4	40.8	30.4	21.2	0	0
31	0	0	0	9.6	1.6	0	0	0	0
32	0	0	0.4	0	0	0	0	0	0
33	0	0	0.2	0	0	0	0	0	0
34	0.2	3.6	3	0	0	28	4.8	2	0.6
35	0	6.8	2	0	0	0	0	1	0.8
36	0.2	0	0	2.4	2.4	18.4	9.2	0	0
37	0.4	0	0	4	8	31.2	10.6	0	0.2
38	0.2	0.6	0.4	0	0	0	3.2	0	0

	#		101	111	201	211	301
Diptera	**39**	*Aphrophila* sp.	0	0.8	2.6	0.8	0
	40	*Austrosimulium* sp.	5.6	4	160	31.2	0
	41	Chironominae	14.4	5.6	10.4	1.2	7.2
	42	*Culex* sp.	0	0	0	0	0
	43	Diamesinae	0	0	11.2	2	0
	44	Empididae	0	0	2	0.2	0
	45	Eriopterini	0	0	0	0	0
	46	Hexatomini	0	0	0	0	0
	47	Muscidae	0	0	0	0	0
	48	Orthocladiinae	305.6	155.2	357.6	156.4	16.8
	49	*Paradixa* sp.	0	0	0	0	0
	50	*Paralimnophila* sp.	0.2	0	0	0	0
	51	Tanypodinae	0	0	0.8	1.4	0
	52	*Zelandotipula* sp.	0	0	0	0	0
Coleoptera	**53**	Elmidae	55.2	110.4	22	25	6.2
	54	Hydraenidae	0	0	0	0	0.2
	55	Hydrophilidae	0	0	0	0	0
	56	Ptilodactylidae	0	0	0	0	0.4
	57	Scirtidae	0	0	0	0	0
Crustacea	**58**	Amphipoda	1138	1641	1.6	0.4	0
	59	Ostracoda	0.8	0	0	0	0
Mollusca	**60**	*Ferrissia* sp.	0	0	0	0	0
	61	*Gyraulus* sp.	0	0	0	0	0
	62	*Physa* sp.	0	1.6	0	0	0
	63	*Pisidium* sp.	0	0	0	0.2	0
	64	*Potamopyrgus antipodarum*	17.6	15.2	13	18.8	0
Other	**65**	Small Oligochaete	145.6	213.6	64.8	52.2	14
	66	Medium Oligochaete	0	3.2	0.2	0.2	0
	67	Large Oligochaete	0.8	3.6	0.4	0.4	0
	68	*Archichauliodes diversus*	0	0	3.2	3	0
	69	Collembola	0	0	0	0	0
	70	Hirudinea	0.8	0	0	0	0
	71	*Hydra* sp.	0	0	0	0	0
	72	*Hygraula nitens*	0	0	0	0	0
	73	Nematode	0	0	0	0	0
	74	Nemertea	0	0	0	0	0
	75	Platyhelminthes	2.4	7.2	3.2	2.4	2.2
	76	*Sigara* sp.	0.8	0	0	0	0
	77	*Xanthocnemis zealandica*	0	0	0	0	0

#	311	102	112	202	212	302	312	103	113	203	213
39	0	0	0	0	2.8	0	0	0	0	4.6	13.2
40	0	11.2	2.4	14	24.2	0	0	16	12	72	46.8
41	3.8	0.8	3.2	12.8	37.2	15	16	1.6	2.4	110.4	260.8
42	0	0	0	0.2	0	0	0	0	0	0	0
43	0	0	0	5.2	84.6	0	0	0	0	37.6	74.8
44	0	0	0	3.6	3.4	0.2	0.2	0	0	6.8	34.8
45	1	0	0	0.2	0.2	0	0.8	0	0	0	0
46	0	0	0	0	0	0.2	0	0	0	0	0
47	0	0	0	0	0	0	0	0	0	0	0
48	9.8	78.4	140	60	131.6	10.8	11.2	36.8	71.2	120.8	457.2
49	0	0	0	0	0	0	0	0	0	0	0
50	0	2.4	0	0	0	0	0	0	0	0	0
51	0.6	0	0	0.4	0.2	0.8	2.4	0	1.6	0.4	0.4
52	0	0	0	0.2	0	0	0	0	0	0	0
53	8.6	124	138.4	20.4	28.6	7.2	6	104.8	132.8	16.4	30.4
54	0.2	0	0	0	0	0	0	0	0	0	0.8
55	0	0	0	0.4	0	0	0	0	0	0	0
56	0.6	0	0	0	0	0.4	1.2	0	0	0	0
57	0	0	0	0	0	0	0	0	0	0	0
58	0	3094	1394	0	0.4	0.2	0.6	2014	1682	0.4	0
59	0	0.8	1.6	0.2	0	0	0.2	6.4	8.8	0	0.4
60	0	0	0	0	2.8	0	0	0	0	10.4	5.6
61	0	0	0	0	0	0.2	0	0	0	0	0
62	0	0.8	2.4	0.2	0	0	0	3.2	4	0	0.8
63	0	0	0	0	0	0	0	0	0	0	0
64	0	47.2	68	51.4	71.2	0.4	0.4	41.6	66.4	310.4	278.8
65	18.2	632.8	246.4	350.4	84.8	18.8	21.6	224.8	232.8	89.2	145.2
66	0	2.4	1.6	0.4	0	0	0	0	0.8	0	0.6
67	0	5.2	0.6	0.8	0.8	0	0	1.6	4	0	0.2
68	0	0	0.2	0.8	2.2	0.2	0.2	0	0	1.4	1
69	0	0	0	0.6	3.2	0.2	0.6	0	0	0.4	1.2
70	0	0	0	0	0	0	0	1.6	0	0.8	0
71	0	6.4	4.8	1.4	1.6	0	0	0	1.6	5.2	1.2
72	0	0	0	0	0	0	0	0	0	0	0
73	0	5.6	0.8	0	0.4	0	0	4.8	0.8	0	0
74	0	0	0.8	0	0	0	0	0	0	0	0
75	5.4	12	6.4	9.6	0.6	3.8	1	6.4	2.4	5.2	9.6
76	0	0	0.2	0	0	0	0	0	0	0	0
77	0	0	0	0	0	0	0	0	0	0	0

#	303	313	104	114	204	214	304	314	105	115	205
39	0	0	0	0	13.6	7.2	0.2	0	0	0	3.4
40	0	0	8	3.2	35.2	2.4	0	0	5.6	2.4	55.2
41	11.2	12.8	0.8	0	423.2	345.6	25.2	24.2	0	18.6	801.6
42	0	0	0	0	0	0	0	0	0	0	0
43	0	0	0	0	22.4	1.6	0	0	0	0	20.8
44	0	0	0	0	12.8	18.4	0	0.4	0	0	16
45	0	0.2	0	0	0	0	0.4	0.6	0	0	0
46	0	0	0	0	0	0	0	0	0	0	0
47	0	0	0	0	0	0.8	0	0	0	0	0
48	14	17.2	9.6	28.8	467.2	479.2	14.6	18.4	17.6	52	194.4
49	0	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0	0	0	0	0
51	1.2	3.8	5.6	3.2	1.6	4	0.6	2.8	1.6	12.8	5.6
52	0	0	0	0	0	0	0	0	0	0	0
53	5.8	9.4	122.4	266.4	26.4	96	9.8	12	179.2	444	45.6
54	0.8	1	0	0	0	0	0.8	2	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0
56	1.8	3.4	0	0	0	0	0.6	3.8	0	0	0
57	0	0	0	0	0	0	0	0	0	0	0
58	0	2.4	2415	2487	1.6	0	0.2	0	1682	4814	0.8
59	0	0.6	91.4	52.8	0.8	0	0	0	176.8	158.4	0
60	0	0	0	0	42.4	7.2	0	0	0	0	5.6
61	0	0	0	0	0	0	0	0	0	0	0
62	0	0	5	4	1	0	0	0	11.2	1.8	0
63	0	0	0	0	0	0	0	0	0	0	0
64	0	0.4	24.8	75.2	332	315.2	0.4	0	48	96	264
65	10.4	14	179.2	97.6	9.8	2.4	11.2	6.2	559.2	388.8	74.4
66	0.2	0	0.8	0.2	0.4	0.2	0	0	0.8	0	1.6
67	0	0	0.8	3.4	1.6	0.2	0	0	3.2	6.4	0.2
68	0	0	0	0.2	19.2	17.8	0	0	0	0	20.8
69	0	0	0	0	0	0	0	0	0	0	0
70	0	0	1	0	0	0	0	0	0	0.8	0
71	0	0	4	0	1.6	0	0	0	0	11.2	16
72	0	0	0	0.8	0	0	0	0	0.2	0.8	0
73	0.2	0	1.6	0	0	0	0	0	3.2	0.8	0
74	0	0	0	0	0	0	0	0	0	0	0
75	1	0.4	0.8	5.6	0.8	0	2.4	3	4.8	54.4	16.8
76	0	0	3.2	0	0	0	0	0	0	0	0
77	0	0	0	0	0	0	0	0	0	0	0

#	215	305	316	106	116	206	216	306	107	117	207
39	2.6	0	0	0	0	0	0	0	0	0	1
40	3.4	0	0	55.2	37.2	4.8	0.8	0	16.8	173.6	194
41	155.4	32	16.9	3.2	0.8	204	50.8	48.6	3.2	0	88
42	0	0	0	0	0	0	0	0	0	0	0
43	0	0	0	0	0	1.8	0	0	0	0	90
44	5.2	0.2	0.1	0	0	2.4	2.6	0	0	0	0.4
45	0	0.4	0.3	0	0	1	0	0.8	0	0	0
46	0	0	0	0	0	0	0	0.2	0	0	0
47	19	0	0.1	0	0	0	0.8	0	0	0	0
48	226	12.4	35.2	44	12.4	28	18.6	25.2	44	60.8	177.2
49	0	0	0	0.8	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0	0.8	0	0	0
51	17.2	0.2	0.2	0.8	0	0	1.4	0	0	0	6
52	0	0	0	0	0	0	0	0	0	0	0
53	41.8	11.2	10.6	159.2	248.4	118.4	57.6	9.2	21.6	41.6	91.2
54	0	3.6	0.1	0	0	0	0	0.4	0	0	0
55	0	0	0	0	0	0	0	0	0	0	0
56	0	1	0.8	0	0	0	0	1.2	0	0	0
57	0.2	0	0.7	0	0	0	0.4	0	0	0	0
58	0	0.2	0	470.4	422.8	0	8	0	1778	1620	1.6
59	4.8	0	0	84	24.4	0.8	25.6	0	253.6	7.2	0
60	0	0	0	0	0	36	2.8	0	0	0	7.2
61	0	0	0	0	0	0	0	0	0	0	0
62	0	0	0	15.2	6.4	0.8	0	0	7.2	18.4	0.4
63	0	0	0	0	0	4	0	0	0	0	0.8
64	54.4	0.2	0.2	100.8	107.6	350.4	26.4	1.6	17.6	45.6	80
65	81.2	5.8	3.9	133.6	178.8	132.8	322.2	18.4	324.8	269.6	200
66	0	0	0	1.6	0.2	2.4	13.2	0	1	0	0.4
67	0.2	0	0	3.2	5.2	1	0.2	0	0	8.8	0.2
68	12.4	0	0	0.2	0	40.8	2.4	0.6	0.2	0	14
69	0	0	0	0	0	0	0	0	0	0	0
70	0	0	0	1.6	0.8	0	0	0	0	0	0
71	4	0	0	1.6	48.8	1.6	1.4	0	0	1.6	4.8
72	0	0	0	8	0	0	0	0	0	0	0
73	0	0	0	0.8	0	0	0	0.2	2.4	2.4	0.4
74	0	0	0	0	1.2	8	0	0	0	0	0
75	1.6	2.6	3.7	84.8	101.6	16	29.8	7.8	8.8	12	8.6
76	0	0	0	0.8	0	0.8	1.6	0	1.6	0.8	0
77	0	0	0	0.8	0	0	0	0	0	1.8	0

#	217	307	317	108	118	208	218	308	318
39	0	0	0	0	0	5.6	0	0	0
40	0.6	0	0	247.2	162.4	78.4	12.6	0	0
41	4.8	34.8	20.8	3.2	1.6	81.6	12.6	3	2.6
42	0	0	0	0	0	0	0	0	0
43	0.4	0	0	0	0	13.6	0	0	0
44	0.6	0.8	0.2	0	0	6.4	1	0	0.2
45	0	2.4	1.2	0	0	0	0	3.6	3.4
46	0	0.2	0.4	0	0	0	0	0	0.2
47	0	0	0	0	0	0	0.2	0.2	0
48	20.8	41.2	24.2	62.4	15.2	146	14.4	2.8	2.8
49	0	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	0	0	0
51	5.6	6.2	25.2	3.2	0.8	2.8	5	0.8	2
52	0	0	0	0	0	0	0	0	0
53	14.8	23.6	22	4.8	41.6	40.8	9.8	6.2	8.4
54	0	3.2	1.6	0	0	0	0	0.4	0.6
55	0	0	0	0	403.2	0	0	0	0
56	0	0.8	0.4	0	0	0	0	1.2	1.6
57	0	0	0	0	0	0	0	0	0
58	0	0.4	0	1034.4	853.6	0	0	0.2	0
59	6.6	0	0	73.6	50.4	2.4	38.2	0	0
60	0.6	0	0	0	0	31.6	1.6	0	0
61	0	0	0	0	0	0	0	0	0.2
62	2.2	0	0	25.6	52	2.8	98.2	0	0
63	0.6	0	0	0	0	6.4	7.8	0	0
64	28.2	0.6	0.2	32	121.6	333.2	317.8	0.2	0.2
65	109.8	9.4	4	179.2	116	148	232.6	10	6.2
66	0	0	0	0.2	0	0	0	0	0.2
67	0.2	0	1.4	0.2	2.4	1	0.8	0	0
68	1.6	0	0	0	0	8.8	5.2	0	0
69	0	0	0	0	0	0	0	0.2	0
70	0	0	0	0	0	0	0	0	0
71	1.6	0	0	1.6	1.6	3.2	6.4	0	0
72	0	0	0	7.4	13.6	0	0	0	0
73	0.2	0.4	0.2	2.4	0	0	0	0	0
74	0	0	0	0	0.8	0	0	0	0
75	21.4	2.8	8.2	38.4	68.8	23.6	61	0.8	2.8
76	0.2	0	0	4.8	0	0	2.2	0	0
77	0	0	0	2.4	0.2	0	0.8	0	0

Appendix 4. Reprint of paper relating to Chapter 2.

Dewson Z.S., Death R.G. & James A.B.W. (2003) The effects of water abstractions on invertebrate communities in four small North Island streams. *New Zealand Natural Sciences,* **28,** 51-65.

The effect of water abstractions on invertebrate communities in four small North Island streams

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Abstract

The effect of water abstraction on invertebrate communities was investigated in four small streams (<1000 l/sec mean annual low flow (MALF)) in the lower North Island, New Zealand. Tukipo River (Hawkes Bay), Mangatarere Stream (Wairarapa), Tamaki River and Raparapawai Stream (Tararua) were sampled at sites upstream and downstream of water abstraction points during February 2003. Nine benthic invertebrate samples and cobbles for periphyton biomass analysis were collected from each site and three flow gaugings were measured at the time of sampling. The results from this study must be interpreted with caution as they only represent a single sampling occasion from a very limited set of North Island small streams. However, of the eight community metrics examined, none showed a uniform response to abstraction in the four rivers studied. There was an overall increase in number of individuals found below abstractions, the percentage of EPT individuals was slightly higher above abstractions and there was a small increase in species evenness (Simpson's index) above abstractions for the four streams combined. All other community measures showed no significant change upstream and downstream of abstractions. Invertebrate communities from above and below abstraction sites were separated in ordination space along an axis correlated with discharge, average flow velocity and conductivity.

Keywords: macroinvertebrate communities - water abstraction - low flow - New Zealand.

Introduction

Flowing water is one of the dominant forces structuring stream ecosystems and creates the physical environment in which lotic faunas survive. Abstractions of water from stream ecosystems modify the instream environment and the availability of habitat for lotic organisms. There are an ever increasing number of competing uses for water resources, many of which require the removal of water from streams. With increasing demand for water, small streams are increasingly being targeted, although the impacts of water abstraction on small stream ecosystems are not well documented. When water is taken from small streams it constitutes a greater proportion of the mean annual low flow (MALF) than a similar take from a larger stream.

The response of invertebrates to water abstraction may vary with river type and size, geographic location, season, the influence of groundwater recharge and the type of invertebrates present. Few studies in New Zealand have looked at the downstream effects of flow reduction on stream invertebrates (Jowett 2000). Castella *et al.* (1995) investigated the impacts of water abstraction on invertebrate communities in the U.K. and found a lack of consistent response, highlighting the variability of faunal responses to flow reduction in different river types. Even the changes to invertebrate community composition that occur as flow is naturally reduced over the summer period are not well known, nor is it clear whether the response of invertebrate communities to decreasing flow is consistent among river types (Suren *et al.* 2003a).

Reductions in invertebrate abundance have been observed during low flow conditions in several drought studies (Cowx *et al.* 1984; Wood & Petts 1999). Caruso (2002) studied the effects of drought on invertebrates in New Zealand, however, the Macroinvertebrate Community Index (MCI) was the only biotic measure used and failed to indicate any changes in the invertebrate communities. The MCI is designed to detect the impacts of organic pollution (Stark 1985) and hence may not be suitable for the detection of flow reduction impacts. Studies of drought mediated low flows are much more common than studies of flow reduction via water abstraction and it is unclear whether macroinvertebrate responses to these conditions will be similar.

Our study aimed to quantify differences in invertebrate communities upstream and downstream of water abstractions in four lower North Island, New Zealand streams. We wanted to test the hypothesis that downstream sites would appear more impacted in terms of macroinvertebrate diversity and community composition than upstream sites on these streams. A site impacted by reduced flow may be characterized by species commonly associated with lower flow conditions such as oligochaetes, chironomids, and snails (Jowett 1997) and it may have lower species richness or evenness than a non-impacted site.

Study sites

Local regional councils in the lower North Island identified four streams as having significant consented water abstractions where usage is either continuous throughout the year for potable water supply and water race supply or concentrated over the summer period for irrigation (Table 1). They were Tukipo River (Hawkes Bay), Mangatarere Stream (Wairarapa), Tamaki River (Tararua) and Raparapawai Stream (Tararua); all small lowland streams with mean annual low flow (MALF) <1000 l/sec. They are located on the east of the lower North Island of New Zealand and run through predominantly agricultural and horticultural land where they are

Table 1. Features of sampling sites and water abstractions from the Tukipo River, Mangatarere Stream, Tamaki River and Raparapawai Stream.

Stream	Distance between sites (km)	Abstraction to downstream site (km)	Consented abstraction between sites (l/sec)	Mean annual low flow(MALF) (l/sec)	Abstraction as % of MALF	Purpose
Tukipo River	5	0.1	47	167	28%	Crop and pasture irrigation
Mangatarere Stream	3.5	0.5	113	168	67%	Carrington water race system
Tamaki River	4.25	2	100	235	43%	Dannevirke town water supply
Raparapawai Stream	6.75	3.25	54	55	98%	Dairy farm irrigation

largely unshaded at the sampling sites. Two sites on each stream were sampled, one above and one below water abstracting points where between 47 and 113 l/sec may be taken (Table 1). The wetted width, mean depth and velocity of individual transects across each stream ranged from 2.4 to 12.3 m, 3 to 18 cm and 0.03 to 0.40 m s $^{-1}$, respectively. Conductivity ranged from 70 to 167 µS/cm and pH was between 8.2 and 9.7 (Table 2).

Methods

Physicochemical measures

Measurements of temperature and conductivity were made at each site with an Orion 122 conductivity meter and pH was measured with a pHTestr 2. At each site, three riffles approximately 20 metres long were identified, and flow was gauged within each riffle by measuring depth and velocity at 0.4 x depth from the bed. Riffles were used since they were the dominant or only available habitat at the four study sites. Measurements were made at approximately 20 equidistant intervals across the stream using a Marsh McBirney velocity meter. At each interval estimates were also made of substratum size and percent cover of filamentous algae and diatoms within a circle of 30 cm diameter. The presence of macrophytes, type and percentage of riparian vegetation, amount of riparian shade, and dominant riparian land use were also noted.

Invertebrate and periphyton sampling protocol

Samples were collected in early February 2003. Within the three riffles at each site, three Surber samples (250 µm mesh, area = 0.1 m^2) were taken at random. A stone (<6 cm length) was selected adjacent to each Surber sample for periphyton biomass analysis. Invertebrate samples were preserved in 10% formalin and periphyton stone samples were transported on ice in the dark and stored at -20°C. Invertebrate samples were rinsed through a 500 µm

Table 2. Characteristics of above and below abstraction sites on four North Island streams in February 2003. Values are means of three riffles at each site ± standard error.

Site	**Map coordinates**	**Width (m)**	**Depth (cm)**	**Flow velocity (ms^{-1})**	**Discharge (m^{3}s^{-1})**	**Conductivity (μS /cm)**	**pH**	**Chlorophyll *a* (μg cm^{-2})**
Tukipo above	39° 57.15′S 176° 19′ E	4.30 ±1.06	8.3 ±1.2	0.110 ±0.010	0.044 ±0.003	147	8.6	1.91 ±0.16
Tukipo below	39° 58.30′S 176° 20.10′ E	8.25 ±2.75	10.7 ±2.7	0.229 ±0.044	0.205 ±0.013	167	9.4	1.80 ±0.58
Mangatarere above	40° 56.46′S 175° 31.04′ E	7.17 ±1.17	11.2 ±0.1	0.267 ±0.074	0.260 ±0.010	72	8.6	0.59 ±0.12
Mangatarere below	40° 57.44′S 175° 32′ E	6.50 ±0.50	12.0 ±2.2	0.199 ±0.020	0.204 ±0.023	85	8.2	1.10 ±0.17
Tamaki above	40° 08.55′S 176° 04.09′ E	6.00 ±0.29	15.9 ±1.0	0.324 ±0.034	0.400 ±0.022	70	8.6	1.68 ±0.19
Tamaki below	40° 10.57′S 176° 03.25′ E	7.00 ±0.52	12.5 ±1.6	0.257 ±0.014	0.286 ±0.028	74	8.2	0.84 ±0.09
Raparapawai above	40° 16.55′S 175° 59.50′ E	4.27 ±0.27	8.4 ±0.40	0.221 ±0.002	0.107 ±0.008	88	8.3	2.36 ±0.25
Raparapawai below	40° 19.24′S 175° 59.32′ E	4.00 ±0.82	5.1 ±1.0	0.058 ±0.018	0.020 ±0.008	133	9.7	3.11 ±0.62

Endecott sieve and sub-sampled. A sample splitter was used to divide the sample into four parts and the entire 25% of the sample was sorted or further subsamples were sorted until at least 200 individuals were counted (each successive 25% was fully counted). The remainder of the 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), Winterbourn *et al.* (2000) and Smith (2003). Chironomids were identified to sub-family level.

Chlorophyll *a* and phaeophytin were extracted from cobbles by submerging them in 90% acetone for 24 hours at 5°C. Absorbancy was read at 750, 665 and 664 nm on a Varian Cary 50 Conc. UV-Visible spectrophotometer™ before and after 0.1M HCl was added. The amount of chlorophyll *a* ($\mu g\ cm^{-2}$) was calculated for 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).

Data analysis

Invertebrate communities were described using total number of individuals, total number of taxa, Berger-Parker dominance index (Berger & Parker 1970), Simpson's index (Simpson 1949), and the percentage of Ephemeroptera, Plecoptera and Trichoptera (EPT) individuals and taxa (Lenat 1988) in each sample. *Oxyethira albiceps* was excluded from EPT calculations since its pollution tolerance may skew the results. Although not designed to detect the effects of flow reductions, the Macroinvertebrate Community Index (MCI) (Stark 1985) and Quantitative MCI (QMCI) were calculated for each sample to assess whether they may be useful for this purpose.

Ordination of the mean invertebrate community for each riffle (mean of three samples) was conducted with Non-metric Multidimensional Scaling (NMS) in the PCORD statistical package (McCune & Mefford 1995). Environmental measures were correlated with each axis using Pearson's correlation coefficient.

Analysis of Variance (ANOVA) was used to investigate differences in invertebrate communities above and below water abstraction sites (SAS 2003). The ANOVA design included the categorical variables stream, above/below abstraction, and riffle section (nested within sampling site) and was used to test differences for all invertebrate community measures calculated. Data were log transformed where required to meet normality assumptions.

Analysis of similarity (ANOSIM) of above and below abstraction sites was conducted using the Bray-Curtis similarity measure in the PRIMER 5 multivariate statistical package (Clark & Warwick 1994). The contributions of individual species to the difference between upstream and downstream communities were examined with the similarity percentages (SIMPER) routine in Primer.

Results

Physicochemical characteristics

The percentage decrease in discharge (m^3s^{-1}) between above and below abstraction sites was greatest for

Raparapawai Stream (-81%). Tamaki River (-28%) and Mangatarere Stream (-22%) showed smaller decreases and Tukipo River had a substantial increase in discharge (+363%) downstream. This increase for the Tukipo River was in part a result of the non-operation of water abstractions for irrigation at the time of sampling and also inputs from small tributaries and numerous groundwater seepages. Stream width, mean cross sectional depth and flow velocity did not always decrease at the below abstraction sites for Mangatarere Stream, Tamaki River and Raparapawai Stream but they were all higher at the below abstraction site on the Tukipo River (Table 2).

Spot measurements of conductivity were greater at downstream sites on all streams, with the greatest downstream increase in the Raparapawai Stream (45.7 μS/cm) and the smallest in the Tamaki River (4.1 μS/cm). There was no consistent change in pH between upstream and downstream sites with increases in Raparapawai Stream (+1.4) and Tukipo River (+0.8) and decreases in Mangatarere Stream (-0.4) and Tamaki River (-0.4) (Table 2).

Community metrics

There were greater densities of invertebrates below (mean = 535) than above (mean = 397) water abstractions ($F_{1,23}$= 7.38, P = 0.01) (Table 3), and more in the Tukipo River than in the other streams ($F_{3,23}$= 4.62, P = 0.01) (Table 4). The number of individuals increased below abstractions in all streams except Tukipo River (Fig. 1A).

There was no difference in the number of taxa above and below abstraction sites overall ($F_{1,23}$= 0.30, P = 0.59) (Table 3, Fig. 1B). However, there were differences in the number of taxa between streams with Tukipo River (mean = 17) and Mangatarere Stream (mean = 16) having more than Tamaki River (mean = 14) and Raparapawai Stream (mean = 13) (Table 4). No taxa that were common (present in > 5 samples) at above abstraction sites were absent from below abstraction sites. Three rare taxa were only found in below abstraction samples (Tabanidae,

Table 3. Results of ANOVAs testing for differences in community metrics from nine 0.1 m² Surber samples above and below abstraction sites in the Tukipo River, Mangatarere Stream, Tamaki River and Raparapawai Stream in February 2003.

	Number of individuals	Number of taxa	% EPT individuals	% EPT taxa	Berger Parker index	Simpson's index	MCI	QMCI
Above abstraction mean	397.34	14.81	56.64	58.76	0.419	0.268	116.1	5.90
Below abstraction mean	535.53	15.17	50.80	56.30	0.438	0.296	112.5	6.02
F	7.38	0.30	4.50	2.04	0.94	4.62	3.29	0.68
d.f.	1, 23	1, 23	1, 23	1, 23	1, 23	1, 23	1, 23	1, 23
probability	0.01	0.59	0.04	0.16	0.34	0.04	0.08	0.42

Stratiomyidae, Collembola) and 11 rare taxa were found only in above abstraction samples (*Neozephlebia scita*, *Mauiulus luma*, *Acanthophlebia cruentata*, *Zelandoperla denticulata*, *Austroperla cyrene*, Tanypodinae, *Beraeoptera roria*, *Helicopsyche* sp., *Molophilus* sp., Muscidae, and Ephydridae). Each of these 11 taxa were found at either 1 or 2 of the above abstraction sites and were not collected at any of the downstream sites.

Percentage EPT individuals was higher above (mean = 57%) than below (mean = 51%) abstraction sites ($F_{1,23}$= 4.50, P = 0.04) (Table 3). There were also significant differences in the percentage of EPT individuals between the four streams ($F_{3,23}$= 11.31, P = <0.001) (Table 4) (Fig. 1G). No differences were found in the percentage of EPT taxa between streams ($F_{3,23}$= 0.74, P = 0.54), or above and below abstraction sites ($F_{1,23}$= 2.04, P = 0.16) (Fig. 1H).

MCI and QMCI did not differ significantly above and below the abstraction points (Table 3), although small increases or decreases occurred on each stream (Fig. 1C, D).

The Berger-Parker index showed variable increases in dominance below abstraction sites on the Tukipo River, Tamaki River and Raparapawai Stream, and a small decrease in dominance on the Mangatarere Stream (Fig. 1E). There was no significant difference in the Berger-Parker dominance index above and below abstractions ($F_{1,23}$= 0.94, P = 0.34) (Table 3) but there were differences in dominance between streams ($F_{3,23}$= 22.95, P < 0.001) (Table 4). Species dominance was greater for Tamaki River (mean = 0.51) and Raparapawai Stream (mean = 0.51) than for Tukipo River (mean = 0.37) and Mangatarere Stream (mean = 0.33).

Percentage change in Simpson's index showed decreases in species evenness below abstraction sites on the Tukipo River, Mangatarere Stream and Tamaki River and a small increase in evenness for Raparapawai Stream (Fig. 1F). Evenness was higher at the above abstraction sites ($F_{1,23}$= 4.62, P = 0.04) (Table 3) and differed between streams ($F_{3,23}$= 37.26, P = <0.001) (Table 4). The Tukipo River (mean = 0.23) and Mangatarere Stream (mean = 0.20) had higher

Table 4. Results of ANOVAs testing for differences in community metrics using 18 0.1 m^2 Surber samples from each of Tukipo River, Mangatarere Stream, Tamaki River and Raparapawai Stream in February 2003.

Stream	Number of individuals	Number of taxa	% EPT individuals	% EPT taxa	Berger Parker index	Simpson's index	MCI	QMCI
Tukipo	650.89	16.72	42.90	59.51	0.369	0.227	112.9	5.02
Mangatarere	372.39	16.22	50.03	57.68	0.331	0.201	114.4	5.44
Tamaki	356.67	14.17	64.19	56.87	0.506	0.341	116.7	6.69
Raparapawai	485.80	12.83	57.76	56.06	0.508	0.359	113.3	6.67
F	4.62	7.49	11.31	0.74	22.95	37.26	0.74	27.25
d.f.	3, 23	3, 23	3, 23	3, 23	3, 23	3, 23	3, 23	3, 23
Probability	0.01	<0.001	<0.001	0.54	<0.001	<0.001	0.53	<0.001

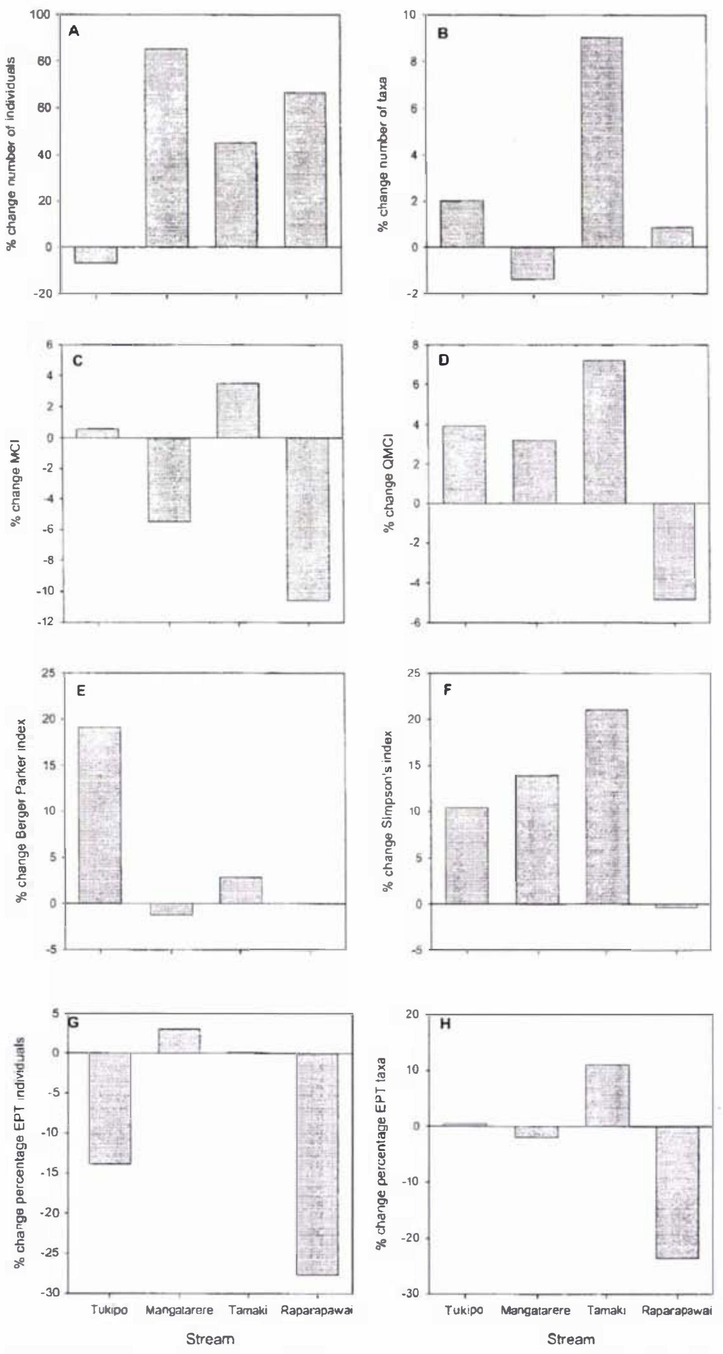

Figure 1. Percentage change in invertebrate community measures between above and below abstraction sites on the Tukipo River, Mangatarere Stream, Tamaki River and Raparapawai Stream in February 2003. **(A)** Number of individuals per sample; **(B)** number of taxa per sample; **(C)** MCI; **(D)** QMCI; **(E)** Berger Parker index; **(F)** Simpson's index; **(G)** % EPT individuals; **(H)** % EPT taxa.

species evenness than the Tamaki River (mean = 0.34) and Raparapawai Stream (mean = 0.36).

Community composition

Axis 1 of the ordination (Fig. 2) explained 33% of the variation in the invertebrate data, and axis 2 explained a further 55% of the variation. The final stress of the ordination was 9.3 which indicates that it is "a good ordination with no real risk of drawing false inferences" (McCune & Grace 2002). Samples from the three riffles at each site were grouped closely in ordination space. Axis 2 roughly divided the above abstraction samples from the below abstraction samples except in the Tukipo River where the communities from above and below abstraction riffles were grouped together. Axis 2 was negatively correlated with discharge (r = -0.56) and average flow velocity (r = -0.57), and positively correlated with conductivity (r = 0.76), pH (r = 0.43) and chlorophyll *a* (r = 0.44).

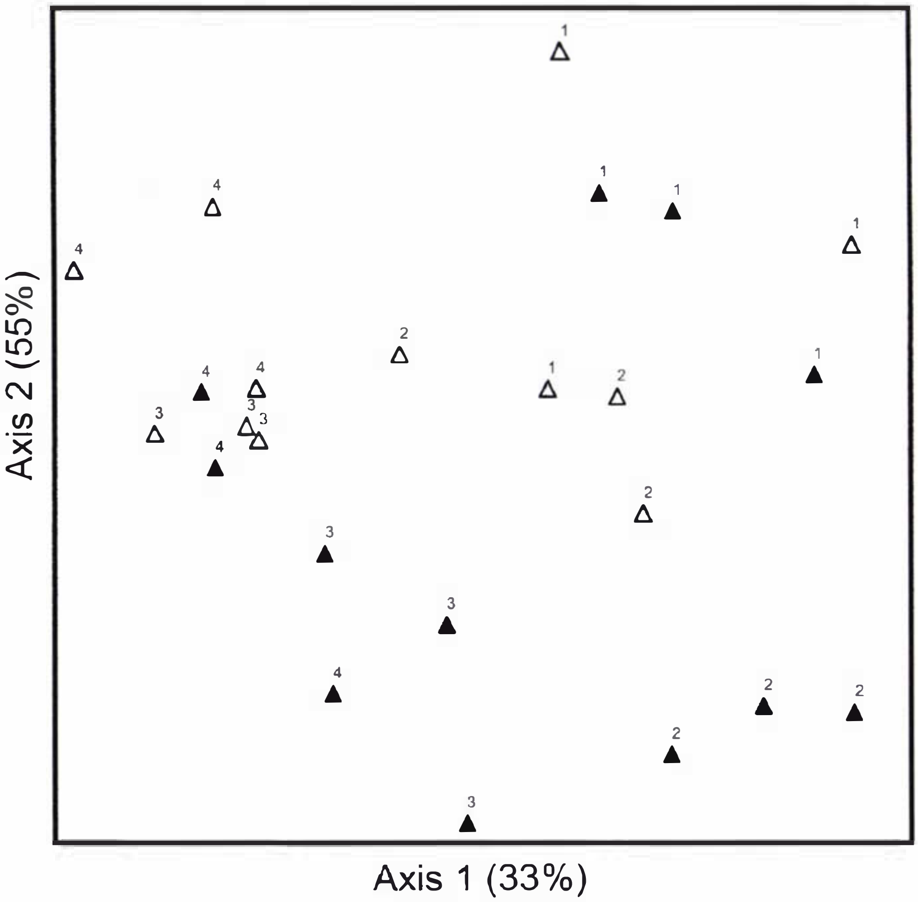

Figure 2. NMS ordination of invertebrate communities (mean values of three 0.1 m^2 Surber samples from each of three riffles at each site). Above abstraction (black triangles) and below abstraction (open triangles) sites on (1) Tukipo River; (2) Mangatarere Stream; (3) Tamaki River; (4) Raparapawai Stream.

A number of taxa were also significantly correlated with each of the ordination axes (Table 5).

Above and below abstraction sites were significantly different in invertebrate community structure (R = 0.141, P = 0.04). This difference was greater with the exclusion of the Tukipo River (R = 0.297, P = 0.01). Elmidae, *Deleatidium* sp., Orthocladiinae, *Pycnocentrodes* sp., *Austrosimulium* sp., *Aoteapsyche* sp., Hydrobiosidae, Eriopterini, *Olinga feredayi*, *Aphrophila* sp., and *Pycnocentria evecta* made the largest contributions to the dissimilarity of communities between above and below abstraction sites (Table 6). There were also differences in invertebrate communities between the four streams (R = 0.541, P = 0.001).

Periphyton

Chlorophyll *a* concentration did not differ significantly above and below water abstractions ($F_{1, 23}$ = 0.00, P = 0.99), although small increases or decreases occurred on each stream (Fig. 3). The amount of chlorophyll *a* was highest at Raparapawai Stream (mean = 2.74 µg cm^{-2}) but there was no significant difference in chlorophyll *a* between the Tukipo River (mean = 1.86 µg cm^{-2}) and Tamaki River (mean = 1.26 µg cm^{-2}) or between the Tamaki River and the Mangatarere Stream (mean = 0.85 µg cm^{-2}).

Discussion

The aim of this study was to investigate the effect of water abstraction on the invertebrate fauna in small streams. At sites above water abstractions we found lower densities of animals, a higher percentage of Ephemeroptera, Plecoptera and Trichoptera and higher species evenness (Simpson's index). These results do not coincide with the results of several drought studies. In U.K chalk streams, low densities of macroinvertebrates were associated with severe low flows during drought conditions, and invertebrate abundance recovered steadily with increases in flow that increased habitat availability

Table 5. Taxa correlated (α = 0.05) with NMS ordination axes shown in Figure 2, using Pearson's correlation coefficient (r).

Axis 1		Axis 2	
Taxa	***r***	**Taxa**	***r***
Orthocladiinae	0.52	Orthocladiinae	0.57
Austrosimulium sp.	0.53	Chironominae	0.60
Aphrophila sp.	0.66	*Olinga feredayi*	0.42
Deleatidium sp.	-0.88	*Pycnocentria evecta*	0.56
Eriopterini	-0.70	*Pycnocentrodes* sp.	0.51
Amphipoda	-0.56	*Hudsonema amabile*	0.44
		Neurochorema confusum	0.62
		Psilochorema sp.	0.66
		Aoteapsyche sp.	0.70
		Oxyethira albiceps	0.49
		Elmidae	0.81
		Austrosimulium sp.	-0.44

Table 6. Taxa that contributed to differences in invertebrate communities above and belo abstraction points on the Mangatarere Stream, Tamaki River and Raparapawai Stream in Februa 2003. Taxa are listed in order of their contribution to community dissimilarity. Sample statist global *R* = 0.297, *P* = 0.009.

Taxa	**Average abundance** (number of individuals) above abstraction	**Average abundance** (number of individuals) below abstraction
Elmidae	61.78	185.67
Deleatidium sp.	127.48	174.74
Orthocladiinae	20.59	27.33
Pycnocentrodes sp.	10.49	28.93
Austrosimulium sp.	24.07	10.19
Aoteapsyche sp.	18.15	25.59
Hydrobiosidae	10.04	7.63
Eriopterini	5.52	5.48
Olinga feredayi	3.41	3.63
Aphrophila sp.	2.75	2.33
Pycnocentria evecta	1.41	4.11

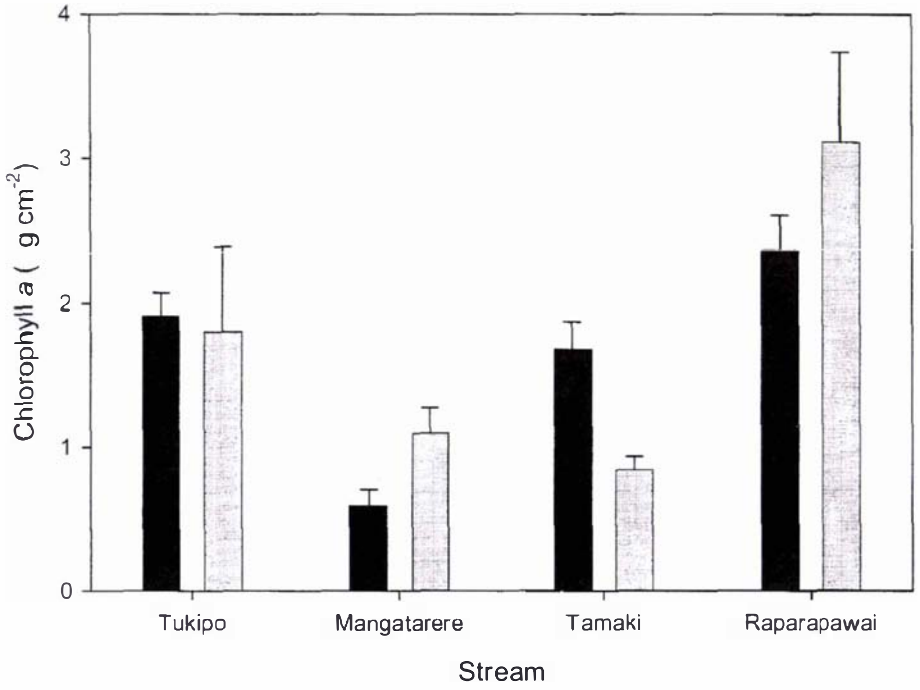

Figure 3. Chlorophyll *a* concentration (mean ± 1 SE, *n*=9) on cobbles from sites above (black bars) and below (grey bars) water abstractions, February 2003.

and channel width (Wood & Petts 1999). Wood & Petts (1999) indicated that channel habitat diversity was maintained throughout the drought in their study stream and this enabled rapid recovery from refugia once normal flow returned. Cowx *et al.* (1984) also found decreases in the abundance of invertebrates during a drought and attributed the change to decreases in potential habitats at lower flow. In the present study, densities of individuals increased below water abstractions but this was not the result of a decrease in wetted area. Similarly, increased quantities of periphyton downstream could provide a greater food supply for increased densities of some invertebrates but this did not occur at our sites. The observed increase may simply be a result of an increase in the abundance of species that prefer reduced flow conditions.

During a drought the entire length of a stream will be affected and its width may decrease throughout its length. Any change to the wetted area of a stream below a water abstraction point will depend on the initial depth of the water and the shape of the channel. In our study, a reduction in river width (and hence wetted area) did not usually occur downstream of water abstraction sites because of the flat U-shaped nature of the channel. This may have contributed to the lack of invertebrate community response to the scale of water abstraction permitted in the study streams by preventing the streams from reaching a threshold level of change that would cause an impact on their invertebrate communities.

There was no decrease in the percentage of EPT taxa, or the overall number of taxa below sites of water abstraction. No common taxa were eliminated, although a number of the rarer taxa were not found below water abstraction sites. Wood & Petts (1999) also found that very few taxa were eliminated during drought. They suggested that this was because of recolonization from refugia, since a considerable variety of hydraulic habitats remained within the river even when mean flow velocity was severely reduced. In the case of water abstractions, the ability of taxa to rapidly recolonize from upstream sources (above the abstraction) may explain the absence of significant differences in the number of taxa above and below abstraction sites.

In a study of rivers in the Otago region, Caruso (2002) used MCI to measure changes in invertebrate communities. The results of his study showed that although MCI appeared to decrease as flow decreased, the changes were not significant and the values of MCI recorded during the drought were not significantly lower than in years prior to the drought. Decreased flow as a result of abstraction has not produced significant changes to the MCI in our study. However, any difference may have been more obvious if pristine streams with higher initial MCI scores had been studied. The water quality indices MCI and QMCI did not differ at sites above and below abstractions indicating that lower discharge was not impacting overall stream health below abstractions.

ANOVA results indicated a number of interactions between site (above or below abstraction) and stream (the four streams used). This interaction is also apparent in Figure 1 where for some community measures, one stream reacts in one direction and another shows the opposite response. Invertebrate communities may not respond consistently to water abstractions in all rivers because of the large variety of environmental features and invertebrate communities that characterize different streams, even when they are in a pristine state. Castella *et al.* (1995) also found that invertebrate community responses to water abstractions varied over 22 U.K. streams of several types. Whereas flow is one of many factors implicated in shaping the composition of invertebrate communities, other factors influence the response of invertebrates to flow. For example, nutrient enrichment has been implicated by Suren *et al.* (2003a; b) as affecting the responses of invertebrate and periphyton communities to low flow. Although differences in conductivity between our four rivers were considerably smaller than those investigated by Suren *et al.* (2003a; b) they may also help explain the considerable between stream variations in community composition observed.

The results from this study must be interpreted with some caution as they only represent a single sampling occasion from a very limited set of North Island small streams. However, of the eight invertebrate community metrics examined, none showed a uniform response to abstraction in the four rivers studied. Nevertheless, significant overall changes were found for number of individuals (overall increase in abundance below abstractions), percentage of EPT individuals (higher overall above abstractions) and Simpson's index of species evenness (higher species evenness above abstractions). In contrast, number of taxa, percentage of EPT taxa, Berger-Parker dominance index, MCI and QMCI did not change significantly between above and below abstraction site, and there was no loss or gain of common taxa below abstraction sites. Invertebrate communities from above and below abstraction sites were usually separated in ordination space along an axis correlated with discharge, average flow velocity and conductivity. The results of the study demonstrate that removal of water from a stream can affect invertebrate communities, but that the response can vary considerably depending on the physicochemical characteristics of the stream and the nature of its community.

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References

Berger, W.H. & Parker, F.L. (1970). Diversity of planktonic Foraminifera in deep sea sediments. *Science* 168: 1345-1347.

Caruso, B. S. (2002). Temporal and spatial patterns of extreme low flows and effects on stream ecosystems in Otago, New Zealand. *Journal of*

Hydrology 257: 115-133.

Castella, E., Bickerton, M., Armitage, P.D. & Petts, G.E. (1995). The effects of water abstractions on invertebrate communities in U.K. streams. *Hydrobiologia* 308: 167-182.

Clarke, K.R. & Warwick, R.M. (1994). *Change in marine communities: an approach to statistical analysis and interpretation.* Plymouth Marine Laboratory, Plymouth.

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

Graham, A.A., McCaughan, D.J. & McKee, F.S. (1988). Measurement of surface area of stones. *Hydrobiologia* 157: 85-87.

Jowett, I. G. (1997). Environmental effects of extreme flows. In *Floods and Droughts: the New Zealand experience* (eds. M.P. Mosley & C.P. Pearson), pp. 104-116. The Caxton Press, Christchurch, New Zealand.

Jowett, I. (2000). Flow management. In *New Zealand stream invertebrates: ecology and implications for management* (eds. K.J. Collier & M.J. Winterbourn), pp. 289-312. New Zealand Limnological Society, Christchurch, New Zealand.

Lenat, D.R. (1988). Water quality assessment using a qualitative method for benthic macroinvertebrates. *Journal of the North American Benthological Society* 7: 222-233.

McCune, B. & Grace, J.B. (2002). *Analysis of ecological communities.* MjM Software Design, Gleneden Beach, Oregon, USA.

McCune, B. & Mefford, M.J. (1995). *PC-ORD. Multivariate Analysis of Ecological Data, Version 4.0.* MjM Software Design, Gleneden Beach, Oregon, USA.

SAS (2001). Version 8.02. SAS Institute Inc., Cary, North Carolina.

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

Smith, B.J. (2003). *Quick guide to the MCI invertebrates.* National Institute of Water and Atmospheric Research, Hamilton, New Zealand.

Stark, J.D. (1985). *A macroinvertebrate community index of water quality for stony streams.* Water & soil miscellaneous publication 87. National Water and Soil Conservation Authority, Wellington, New Zealand.

Steinman, A.D. & Lamberti, G.A. (1996). Biomass and pigments of benthic algae. In *Methods in stream ecology* (eds. F.R. Hauer & G.A. Lamberti), pp. 295-313. Academic Press, Inc., U.S.A.

Suren, A. M., Biggs, B.J.F., Duncan, M.J. & Bergey, L. (2003a). Benthic community dynamics during summer low-flows in two rivers of contrasting enrichment 2. Invertebrates. *New Zealand Journal of Marine and Freshwater Research* 37: 71-83.

Suren, A. M., Biggs, B.J.F., Kilroy, C., & Bergey, L. (2003b). Benthic community dynamics during summer low-flows in two rivers of contrasting enrichment 1. Periphyton. *New Zealand Journal of Marine and Freshwater Research* 37: 53-70.

Winterbourn, M.J. (1973). A guide to the freshwater Mollusca of New Zealand. *Tuatara* 20: 141-159.

Winterbourn, M.J., Gregson, K.L.D. &

Dolphin, C.H. (2000). *Guide to the aquatic insects of New Zealand.* Bulletin of the Entomological Society of New Zealand 13.

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