The Relationships Between Headwater Stream Macroinvertebrate Communities

and Summer Low-flow Events in a Temperate Rainforest

by

AYA MURAKAMI

BSc. Malaspina University-College, 2007

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES

(Forest Sciences)

THE UNIVERSITY OF BRITISH COLUMBIA
(Vancouver)

JULY 2009

ABSTRACT

Using a forested headwater stream system as a model, the effects of inter-annual variation in summer discharge regimes on aquatic insect communities were investigated. More specifically, the benthic invertebrate community response to the intensity, minimum discharges, frequency, duration and abruptness of summer low-flow events were examined. We hypothesized that intensification of summer low-flow events, both in duration and magnitude, have some negative impacts on benthic macroinvertebrate communities in riffles. Examples of negative impacts include reduction in their abundance and/or biodiversity.

First, the abundance and functional trait data of the benthic macroinvertebrates in the three streams in the Malcolm Knapp Research Forest, British Columbia, Canada, were analyzed with respect to the low-flow events. Second, population models were built to simulate the potential responses of lotic aquatic insect communities to future climate change scenarios that differ in the rate of intensifications in extreme flow events: a low-flow event scenario within the current range versus 10% increase in intensity.

The summer low-flow events were found to have a significant relationship with benthic macroinvertebrate communities through three-table ordinations of the empirical data. The community structure was correlated with a major ocean-atmosphere regime shift (Pacific Decadal Oscillation). The intensity and duration of low-flow events explained the observed shift in community structure favouring r-selected traits (e.g. short life cycle, high reproduction rate).

The two low-flow severity scenarios showed the significant differential impacts on the aquatic insect community structures when individual populations were modeled according to their traits. Aquatic insects could be separated into three groups according to their sensitivities, measured by extinction rates, toward the two scenarios.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

CO-AUTHORSHIP STATEMENT

The ideas for Chapters 2 and 3 were both discussed and conceptualized with the help of John

S. Richardson, along with the interpretation of the outcomes and the preparation of this thesis.

I am solely responsible for all data analyses and programming codes used for modelling.

Chapter 1 Disturbances and their effects in streams

Physical disturbances are one of the main factors that affect a biological community, its species and the interactions among them (e.g. Sousa 1984). Freshwater communities are no exception (e.g. Resh et al. 1988; Lytle and Poff 2004). A disturbance can be defined as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or physical environment" (Pickett and White 1985). Physical disturbances such as fires and storms can affect the structure of a biological community directly or indirectly by having tremendous impacts on their physical environment (Fisher et al. 1982; Minshall 2003). Forest fires can affect the structure of a biological community directly by burning, or indirectly by impacting resource availabilities, and/or changing physicochemical characteristics of the region (e.g. Minshall 2003). Flow-generated disturbances (flood and drought) are a fundamental part of flowing waters (lotic ecosystems), influencing population dynamics (Holomuzki and Biggs 2000), community structures (Fisher et al. 1982; Townsend et al. 1997) and ecosystem functions (Grimm and Fisher 1986). High-flow events can physically remove individuals – e.g. algae, macrophytes, and benthic invertebrates – from substrates affecting their survival as well as reproductive rates, the latter depending on the timing of such an event. They also move sediments, benthic organic matter and structural components, such as wood, by force (e.g. Fisher et al. 1982; Lytle 2000), creating a mosaic of substratum patches (Matthaei et al. 2004) and changing channel morphology (Gordon et al. 2004). Rapid colonization usually follows a flood, resulting in a different community composition from the one before the high-flow event. The resulting composition of the new community depends on the timing and magnitude of the flood as well as the availabilities of refugia, such as wood and leaf jams (Lancaster and Hildrew 1993) that act as sources for colonizers (Lytle and Smith 2004).

Other examples of disturbances in streams include events such as drought, ice scour, contamination, irrigation and dam construction.

Benthic macroinvertebrates

The benthic macroinvertebrates play central ecological roles in lotic systems (Hynes 1970; Wallace and Webster 1996; Malmqvist 2002). They occupy a large part of the in-stream and riparian food webs, and are important contributors to stream ecosystem functions for the following reasons. Some regulate biofilms and algae through consumption, while some provide food for others including many vertebrates. Others process organic matter and transport energy from detritus back into the food web. For example, benthic macroinvertebrates mediate leaf litter breakdown, especially in forested headwater streams. Some 'shred' leaves into pieces, increasing surface area for microbial and fungal colonization (Cummins and Klug 1979). By reducing the size of other coarse particulate organic matter, they supply nutrients, carbon and energy to the stream (e.g. Cummins and Klug 1979). Leaf litter breakdown rates have been experimentally shown to be sensitive to the species identity (i.e. which combination of benthic invertebrate species is present) (e.g. Jonsson and Malmqvist 2003), indicating the importance of community structures to ecosystem functioning. Also, benthic macroinvertebrates can alter water quality and flow patterns through their activities across multiple scales (e.g. O'Connor and Lake 1994; Cardinale et al. 2002; Wiens 2002). High density of filterers such as black fly larvae in a stream can convert suspended organic matter (seston) into fecal pellets, altering the location and size of organic matter (Wotton et al. 1998) affecting the water quality around them. Some caddisfly larvae create their cases or their retreats using silk, altering flow patterns around them (Nowell and Jumars 1984), provide food for others by trapping fine organic matter (O'Conner 1993), and/or increase substrate stabilities (Takao et al. 2006).

The benthic macroinvertebrates are an effective indicator group to study impacts of many environmental changes for multiple reasons (Bonada et al. 2006). They are a ubiquitous group with high species richness, providing a spectrum of biological responses to any changes in environment. They depend on freshwater for a part or all of their life cycles, leading to their sensitivities that are ideal for assessing impacts of abiotic changes. Also, their generation times integrate the recent history of the environment.

Future predicted changes in freshwater ecosystems

The rapid changes in global climate are apparent, with increases in the frequency and magnitude of extreme events (e.g. Poff et al. 2002; Allan et al. 2004; Jentsch et al. 2007). For example, seasonal variations within annual precipitation regimes are expected to become more pronounced, increasing winter precipitation and decreasing summer precipitation in many mid to high latitude areas (Hulme 2004). Changes up to ± 20% in global annual precipitation causing ± 50% changes in runoff are predicted under some scenarios, the predicted degrees depending on the geographic location and topography (e.g. Schneider et al. 1990). The amount of runoff would also be affected by the predicted increase in evapotranspiration due to warming, especially during the growing seasons, resulting for example in lowered summer stream flows (Stockton and Boggess 1979; IPCC 1996; Mulholland et al. 1997).

The impacts of these changes on ecosystems are predicted to increase in severity under most global climate change models (Jackson et al. 2001; Walther et al. 2002; Hulme 2004). For instance, a 50% reduction in runoff can easily be too extreme for rheostenic (confined to streams; Jaag and Ambühl 1964) species to cope with (e.g. Castella et al. 1995; James et al. 2008). They require flow for their survival such as respiration and feeding (Hynes 1970). For example, filter-feeding hydropsychid caddisfly larvae have external gills that rely on currents to provide enough

dissolved oxygen to respire, while larval black flies (Simuliidae) 'filter' food that are carried to them by the flow (Hynes 1970). Thus, a reduction in flows could result in loss of the rheostenic group (Lytle and Poff 2004; Boulton and Lake 2008) that include some important contributors to ecosystem functions as discussed above.

If such predicted extreme conditions affect certain ecological groups that are fundamental to the system's function, the effect can be tremendous. For example, a functional feeding group of stream invertebrates, called shredders, are primarily composed of caddisflies, some mayflies and stoneflies. Shredders provide food for scrapers by increasing surface area for microbial colonization, as well as collectors and filterers by 'shredding' discussed above (Cummins 1974). Shredders also increase the patchiness of fine particulate organic matter availability and quality (Short and Maslin 1977; Ward and Cummins 1979; Short et al. 1980). Therefore, shredders are an important group for ecosystem productivity, especially in forested streams (e.g. Lugthart and Wallace 1992; Dietrich et al. 1997). Many shredder families are intolerant to extreme droughts. Erman and Erman (1995) found that fluctuations in discharges accounted for 50% of the variations in caddisfly abundances of Sierra Nevada cold spring sources during a six-year drought event. Hence, a supraseasonal (extreme) drought event can cause a local extinction of shredders, reducing the leaf-litter breakdown rates considerably. This would, in turn, affect collectors and filterers and potentially higher trophic levels (e.g. Kirby et al. 1983; Acuña et al. 2004), transmitting the impacts of such extreme conditions.

The impacts of droughts or reduced flows have been less documented than those of flood events, even though they are equally important to the lotic ecosystems (Lytle 2000; Boulton 2003; Lake 2003; 2008; Boulton and Lake 2008). Predicting drought events tends to be difficult, and observations often miss a clear starting point in time (Lake 2003; 2008). Also, unlike flood events that are considered pulse disturbances, low-flow events are ramp disturbances that steadily

increase in intensity with time without a clear endpoint (Lake 2000). Biological communities experience low-flow events differently depending on the history of such events and their magnitudes, as well as river types and morphologies, making their effects difficult to generalize (Boulton 2003; Lake 2003).

The importance of investigating the impacts of such events is increasing due to recent and predicted changes despite the difficulties described above. In addition to the predicted intensification of droughts (e.g. Dracup and Kendall 1990), the anthropogenic uses of freshwater as resources are expected to increase for agriculture, industries, residential use, and generation of electricity (Waggoner and Schefter 1990; Gleick 1998). The anthropogenic rate of water withdrawal and the area in irrigation in the past 100 years have increased exponentially (Gleick 1998; Jackson et al. 2001). To maintain healthy freshwater ecosystems and their services, preservation or restoration of natural flow regimes is necessary (Poff et al. 1997; Bunn and Arthington 2002). Given the importance of biological communities to lotic ecosystems, it is necessary to gain better understanding of how biological communities respond to current climatic variations and use that knowledge to predict how they will respond in the future.

Traits vs. abiotic factors

Species' traits include organisms' body structures (morphology), life histories such as longevity and timing of reproduction, and behaviours. As outlined by the habitat templet concept (Southwood 1977; 1988), abiotic factors such as major shifts in climate (e.g. El Niño Southern Oscillation; Bêche and Resh 2007; Gilbert et al. 2008) and extreme events are thought to act as environmental 'filters' (Poff 1996; 1997; Statzner et al. 2001; Lytle and Poff 2004). Only the traits that allow organisms to cope with the particular abiotic factors survive that filter, thus selecting these traits over others. The habitat templet concept has been tested in lotic systems (e.g.

Scarsbrook and Townsend 1993; Resh et al. 1994; Statzner et al. 1997; Townsend et al. 1997; Gjerløv et al. 2003) showing the importance of hydrological patterns to the biological communities in streams. For example, Statzner et al. (1997) found a significant relationship between reproductive traits and habitat use. Assessments of community compositions with respect to such environmental filters would allow one to infer potential effects of filters on biodiversity and perhaps ecosystem functions but not the underlying mechanisms. The mechanisms of how the filters shape biological communities can be examined by studying the changes in trait compositions with respect to the filters (e.g. Townsend and Hildrew 1994). Therefore, examining both the species composition of a community and the suite of biological traits is crucial to understand the impacts that changes in climate variables have on biological communities. Moreover, analyzing traits avoids geographic and system specificity of species, increasing the potential for a wider application of the results from such analysis.

A decrease in discharges is an example of environmental filters for lotic systems. Decreased discharges have both direct and indirect effects on biological communities within streams. For example, decreased discharge has a direct effect on benthic macroinvertebrates by decreasing the volume, and possibly the area, of the habitat depending on the intensity of flow reduction (Stanley et al. 1994; Millar and Golladay 1996; Stanley et al. 1997; Dewson et al. 2007; Miller et al. 2007). According to the habitat "compression" hypothesis (MacArthur 1972; Harvey et al. 2005), the decrease in habitat size will, in turn, increase the intensity of biotic interactions between individuals within streams, as well as between streams and the adjacent terrestrial area or the riparian zone. Two major biotic interactions are anticipated to be predation on benthic macroinvertebrates especially by birds or terrestrial insects (Boulton 2003; Lake 2003; but see Canton et al. 1984 for increased benthic macroinvertebrate predator density) and intensified competition between benthic macroinvertebrates for space and resources, such as food and

dissolved oxygen for respiration (Feminella and Resh 1990; Covich et al. 2003; Dewson et al. 2007). Indirect effects of decreased discharge include more temporal and spatial variability in stream temperatures and overall decrease in dissolved oxygen levels (Riggs 1980; Everard 1996; Gunduz 2006; Daufresne et al. 2007; Dewson et al. 2007), potentially intensifying the competition mentioned above. These indirect effects are caused by the following two factors. First, decreased water volume allows higher exogenous impacts from environmental factors such as solar energy (Riggs 1980; Everard 1996). Second, the patchily distributed groundwater input, which feeds cooler (about 8°C in coastal BC), less oxygenated water, may affect water quality more when the flow is low (Gunduz 2006; Dewson et al. 2007). Decrease in dissolved oxygen could also result from increased water temperature. The oxygen saturation levels decreases with increase in water temperature. Also, the metabolic activities increase in warmer water causing the biological oxygen demand to increase, decreasing the dissolved oxygen especially at night when photosynthesis by algae ceases (e.g. Acuña et al. 2005; Daufresne et al. 2007). Thus, in the case of decreased precipitation, some traits would be more vulnerable than others. For example, larger species would be affected more negatively than smaller species as larger species require higher total respiration and larger habitat for resources and to escape predation (as discussed by Boulton and Lake 2008, for example). Likewise, species that disperse more actively or have high vagility will have higher survival rates than passive dispersers or species with low vagility. High vagility will allow faster response to shifts in discharge regime as well as an increased probability of finding the next suitable habitat. Different modes of respiration may also lead to bias between species due to differences in oxygen uptake efficiency. Decrease in species diversity through such processes may then decrease ecosystem functioning (Cardinale et al. 2002).

Small streams and the potential impacts of climate change

Headwater streams are ideal model systems to test the impacts of climate change on biological communities for three reasons. First, headwater streams are important to downstream ecosystems as they act as critical conduits for the delivery of water and nutrients (Wipfli and Gregovich 2002; Compton et al. 2003; Wipfli et al. 2007). The biodiversity of headwater streams (an alpha diversity) contributes to that of a river system and adjacent riparian network (beta diversity) (Meyer et al. 2007; Clark et al. 2008). Second, changes in discharge regimes due to shifts in precipitation patterns can have a tremendous effect on the biological community structure and function of streams (Williams 2006; Nelson and Palmer 2007). Small streams, such as in the case of headwater streams, are especially vulnerable to these disturbances because of their limited hydrological buffering capacity due to their small catchment sizes (Bêche et al. 2007; Miller et al. 2007). Thus, the effects should be more directly observable than those in downstream rivers. Third, because of their relatively small sizes, experimental manipulation and data collection are easier on headwater streams than on larger rivers. In addition, forested headwater streams receive relatively low levels of light due to thick canopy cover (e.g. Brosofske et al. 1997; Pollock 1998). The combination of the low lighting and the stream's proximity to the riparian zone due to its small size increases the importance of allochthonous inputs (reviews in Anderson and Sedell 1979; Cummins et al. 1983) and the detritus food web that relies on this input.

Thesis objectives and approaches

In this thesis, the effects of natural flow regimes on ecosystems were studied using the benthic macroinvertebrate communities in a headwater stream system. Forested, headwater stream ecosystems of south-western British Columbia, Canada, are an ideal system in which to study how individual benthic macroinvertebrate populations respond to shifts in precipitation patterns.

The effects of changes in precipitation patterns on headwater streams can be measured by shifts in summer (May - early October) discharge levels. The summer discharge levels were chosen because the biological communities in small streams experience relatively higher levels of stress in summer. Lowered flow can effectively condense habitat into smaller area increasing the level of competition and/or the risk of predation (e.g. Stanley et al. 1997; Humphries and Baldwin, 2003). In addition, detritus availabilities in early summer are relatively low (Richardson 1991) and increased microbial activities due to higher temperatures often leads to deprivation of oxygen at night or in heavily shaded streams (e.g. Dahm et al. 2003; Williams 2006). Examining the resistance and resilience of a biological community to abiotic changes during periods of elevated environmental stress would be particularly informative as the response of the system to stressors should be more pronounced. Ecosystem responses to changes in discharge regimes will be measured as the change in benthic macroinvertebrate community structure composed mainly of aquatic insects. Insects are the most abundant and species-rich macroinvertebrate taxon in many stream systems and they drive the nutrient processing and cycling (Merritt et al. 1984; Malmqvist 2002; Allan et al. 2004).

In this thesis, changes in summer discharge regime, both in duration and magnitude of low-flow events, were hypothesized to have some negative impacts on aquatic insect community structure: reduction in their abundance, biodiversity and/or ecosystem functions. The overall biodiversity and ecosystem functions may decline through differential impacts on the insect populations, divided either taxonomically or into functional or trait groups, thus affecting the ecosystem function of the community.

To examine the effect of summer discharge regime, summer low-flow events, as well as the measures of such events, have to be defined first. The threshold discharge was calculated by subtracting one standard deviation from the average discharge to define a low-flow event. The

choice of one standard deviation was made to distinguish the low-flow events considered here from extreme low-flow events. Resh et al. (1988) defined extreme high-flow events as flows higher than average discharge plus two standard deviations. Applying this approach to low-flow events, extreme low-flow events were defined as flows lower than average discharge minus two standard deviations, with zero being the minimum. Thus, a summer low-flow event was defined as any period in a particular summer that had discharges lower than the threshold. Common terms used to describe flow variability include frequency, duration, magnitude, timing and predictability (Poff and Ward 1989; Poff et al. 1997; Naiman et al. 2008). Frequency and duration of low-flow events are known to be important in the biological reactions to disturbances (i.e. perturbations) (review in Boulton and Lake 2008). For example, higher frequency of disturbance reduced benthic macroinvertebrate species abundance and richness in summer at the individual substrate scale (Robinson and Minshall 1986). Here, frequency, duration, intensity and abruptness were chosen as the descriptors of low-flow events (Figure 1-1). Frequency was calculated as the total number of low-flow events in a summer. In the case of summer low-flow events, frequency increases as the result of occasional short rainfall events that disrupts otherwise one low-flow event. Therefore, unlike in the case of other disturbances, high frequency may benefit resistant taxa more than low frequency. The maximum number of continuous days that had discharges below the threshold was considered as duration. Intensity included two different ways of measuring magnitude of a low-flow event – minimum discharge and a difference between minimum and average discharge. Throughout this thesis the latter is referred to as intensity while the former is termed as is (minimum discharge). Abruptness was calculated through dividing a difference between the previous peak flow discharge and minimum discharge by the number of days it took to reach the minimum discharge from the peak flow (Jentsch et al. 2007). Total duration, counting the number of days that had discharges below threshold, is often

used when examining temperatures. However, this term is not discussed in this thesis. A preliminary principal component analysis of low-flow variables (Figure 1-1) showed that the maximum and total durations are strongly correlated and the maximum duration had more than six times higher explanatory values (28.9% variance) than that of total duration (4.6%).

To test the hypothesis that the summer low-flow events play a role in shaping the community structure through different effects they have on different macroinvertebrate groups, the following questions were addressed:

1) How do macroinvertebrate communities respond to the inter-annual variations in frequency, duration, intensity and abruptness of summer flow regimes in small headwater streams?

2) How will community structure in headwater streams change as a result of the different responses by macroinvertebrate groups towards shifts in the frequency, duration, intensity and abruptness of low discharge regimes in summer?

Chapter 2 attempts to answer the first question by analyzing the effects of low summer discharge patterns on a small stream benthic macroinvertebrate community. Chapter 3 focuses on the second question by developing a series of population growth models based on the past data analyses to predict the biotic responses to potential changes in discharge regime. Overall discussions and conclusions can be found in Chapter 4.
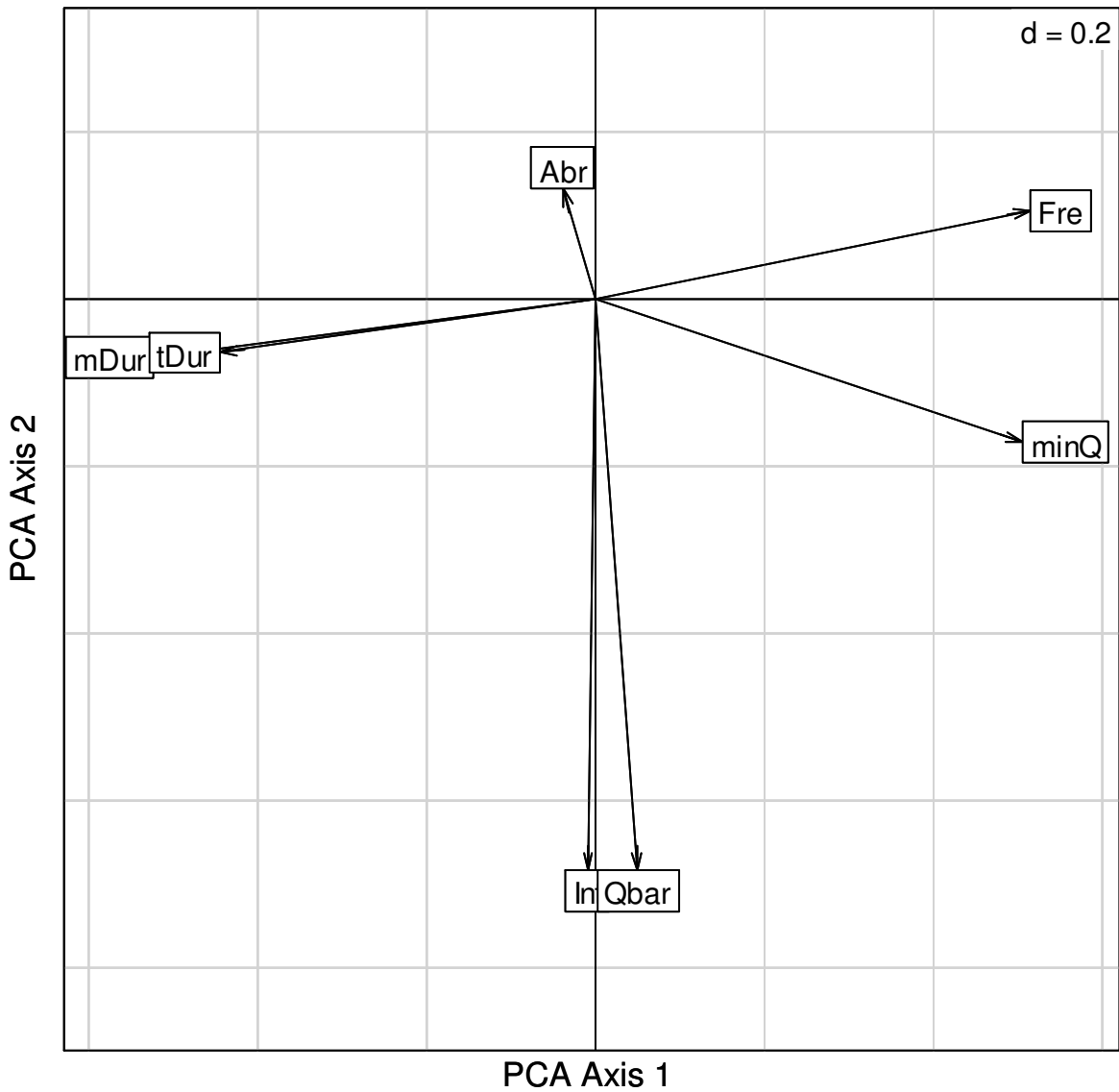
Figure 1-1. The biplot of a preliminary principal component analysis (PCA) on the low-flow parameters of the MKRF data on East, Mike and South Creeks. The preliminary PCA was carried out to minimize the number of low-flow parameters included in the further analyses. Total duration (tDur) and maximum duration (mDur) scored almost identical, and intensity (Int) and average discharge (Qbar) grouped closely. Therefore, frequency (Fre), duration (mDur), intensity (minQ and Int) and abruptness are included in this thesis. Solid lines indicate the 0, 0 lines of x and y axes. The distance scale (d = 0.2 PCA score) indicates the length of a side of grey squares.

Literature Cited

Acuña, V., A. Giorgi, I. Muñoz, U. Uehlinger and S. Sabater. 2004. Flow extremes and benthic organic matter shape the metabolism of a headwater Mediterranean stream. *Freshwater Biology*, 49:960-971

Acuña, V., I. Muñoz, M. Omella, F. Sabater, A. Giorgi and S. Sabater. 2005. Drought and postdrought recovery cycles in an intermittent Mediterranean stream: structural and functional aspects. *Journal of the North American Benthological Society*, 24:919-933

Allan, J.D., M.A. Palmer and N.L. Poff. 2004. Freshwater ecology. *In* Climate Change and Biodiversity. T.E. Lovejoy & L. Hannah (eds). Yale University Press, Grand Rapids, Michigan. pp. 274-290

Anderson, N.H. and J.R. Sedell. 1979. Detritus processing by macroinvertebrates in stream ecosystems. *Annual Review of Entomology*, 24:351-377

Bêche, L.A. and V.H. Resh. 2007. Short-term climatic trends affect the temporal variability of macroinvertebrates in California 'Mediterranean' streams. *Freshwater Biology*, 52:2317–2339

Bonada, N., N. Prat, V.H. Resh and B. Statzner. 2006. Developments in aquatic insect biomonitoring: a comparative analysis of recent approaches. Freshwater Biology, 52:459-523

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

Boulton, A.J. and P.S. Lake. 2008. Effects of drought on stream insects and its ecological consequences. *In* Aquatic Insects: Challenges to Populations: Proceedings of the Royal Entomological Society's 24th Symposium. J. Lancaster and R.A. Briers (eds). CABI Publishing, Cambridge, MA, pp. 81-102

Brosofske, K.D., J. Chen, R.J. Naiman and J.F. Franklin. 1997 Harvesting effects on microclimatic gradients from small streams to uplands in western Washington. *Ecological Applications*, 7:1188–1200

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

Canton, S.P., L.D. Cline, R.A. Short and J.V. Ward. 1984. The macroinvertebrates and fish of a Colorado stream during a period of fluctuating discharge. *Freshwater Biology*, 14:311-316

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

Cardinale, D.E., M.A. Palmer and S.L. Collins. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature*, 415:426-429

Clarke, A., R. MacNally, N. Bond and P.S. Lake. 2008. Macroinvertebrate diversity in headwater streams: a review. *Freshwater Biology*, 53:1707-1721

Compton, J.E., M.R. Church, S.T. Larned and W.E. Hogsett. 2003. Nitrogen export from forested watersheds in the Oregon coast range: the role of N_2-fixing red alder. *Ecosystems*, 6:773-785

Covich, A., T. Crowl and F. Scatena. 2003. Effects of extreme low-flows on freshwater shrimps in a perennial tropical stream. *Freshwater Biology*, 48:1199-1206

Cummins, K.W. and M.J. Klug. 1979. Feeding ecology of stream invertebrates. *Annual Review of Ecology and Systematics*, 10:147-172

Cummins, K.W. 1984. Invertebrate food resource relationships. *North American Benthological Society Bulletin*, 1:44-45

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

Daufresne, M., P. Bady and J. Fruget. 2007. Impacts of global changes and extreme hydroclimatic events on macroinvertebrate community structures in the French Rhône River. *Oecologia*, 151:544-559

Dewson, Z.S., A.B.W. James and R.G. Death. 2007. A review of the consequences of decreased flow for instream habitat and macroinvertebrates. *Journal of North American Benthological Society*. 26:401–415

Dieterich, M., N.H. Anderson and T.M.Anderson. 1997. Shredder-collector interactions in temporary streams of western Oregon. *Freshwater Biology*, 38:387-393

Dracup J.A. and D.R. Kendall. 1990. Floods and droughts. *In* Climate Change and U.S. Water Resources. P.E. Waggoner (eds). Wiley-Interscience, Toronto, 243-267

Erman, N.A. and D.C. Erman. 1995. Spring permanence, Trichoptera species richness, and the role of drought. *Journal of the Kansas Entomological Society*, 68:50-64

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

Feminella, J.W. and V.H. Resh. 1990. Hydrologic influences, disturbance, and intraspecific competition in a stream caddisfly population. *Ecology*, 71:2083-2094

Fisher, S.G., L.J. Gray, N.B. Grimm and D.E. Busch. 1982. Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monographs*, 52:93-110

Gilbert B, P.J. Dillon, K.M. Somers, R.A. Reid and L. Scott. 2008. Response of benthic macroinvertebrate communities to El Niño related drought events in six upland streams in south-central Ontario. *Canadian Journal of Fisheries and Aquatic Sciences*, 65:890-905

Gjerlov, C., A.G. Hildrew and J.I. Jones. 2003. Mobility of stream invertebrates in relation to disturbance and refugia: a test of habitat templet theory. *Journal of the North American Benthological Society*, 22:207-223

Gleick, P.H. 1998. The World's Water 1998-1999. Island Press, Washington D.C., 319p.

Gordon, N.D., B.L. Finlayson, T.A. McMahon and C.J. Gippel. 2004. Stream Hydrology: An Introduction for Ecologists. 2nd ed. John Wiley and Sons, Hoboken, N.J., 429p

Grimm, N.B. and S.G. Fisher. 1986. Nitrogen limitation in a Sonoran Desert stream. *Journal of the North American Benthological Society*, 5:2-15

Gunduz, O. 2006. Surface/subsurface interactions: coupling mechanisms and numerical solution procedures. *In* Groundwater Ecosystems. A. Baba and K.W.F. Howard (eds). NATO Science Series IV. Earth and Environmental Sciences Vol. 70. Springer, Netherlands, pp. 59-69

Harvey, B.C., J.L. White and R.J. Nakamoto. 2005. Habitat-specific biomass, survival, and growth of rainbow trout (*Oncorhynchus mykiss*) during summer in a small coastal stream. *Canadian Journal of Fisheries and Aquatic Sciences*, 62:650-658

Holomuzki, J.R. and B.J.F. Biggs. 2000. Taxon-specific responses to high-flow disturbance in streams:implications for population persistence. *Journal of the North American Benthological Society*, 19:670-679

Hulme, M. 2004. Recent climate trends. *In* Climate Change and Biodiversity. T.E. Lovejoy & L. Hannah (eds). Yale University Press, Grand Rapids, Michigan. pp.31-40

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

Hynes, H.B.N. 1970. Ecology of Running Waters. University of Toronto Press, Toronto. 555p.

Intergovernmental Panel on Climate Change. 1996. Climate Change 1995: Impacts, Adaptations, and Mitigation of Climate Change. Contribution of Working Group II to the Second

Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Jaag, O. and H. Ambühl. 1964. The effect of the current on the composition of biocoenoses in flowing water streams. *In* Advances in Water Pollution Research; Proceedings of the Second International Conference. Pergamon Press, Oxford, pp. 31-49

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

James, A.B.W., Z.S. Dewson and R.G. Death. 2008. The effect of experimental flow reductions on macroinvertebrate drift in natural and streamside channels. *River Research and Applications*, 24:22-35

Jentsch, A., J. Kreyling and C. Beierkuhnlein. 2007. A new generation of climate-change experiments: events, not trends. *Frontiers in Ecology and the Environment* 5: 365–374

Jonnson, M. and B. Malqvist. 2003. Importance of species identity and number for process rates within different stream invertebrate functional feeding groups. *Journal of Animal Ecology*. 72:453-459

Kirby, J.M., J.R. Webster and E.F. Benfield. 1983. Role of shredders in detrital dynamics of permanent and temporary streams. *In* Dynamics of Lotic Systems. T.D. Fontaine & S.M. Bartell (eds). Ann Arbor Science, Ann Arbor MI., pp. 425-435

Lake, P. S. 2000. Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society*, 19:573-592

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

Lake, P.S. 2008. Drought, the 'Creeping Disastor': Effects on Aquatic Ecosystems. Land & Water Australia, Canberra, 47p.

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

Lugthart, G.J. and J.B. Wallace. 1992. Effects of disturbance on benthic functional structure and production in mountain streams. *Journal of the North American Benthological Society*, 11:138-164

Lytle, D.A. 2000. Biotic and abiotic effects of flash flooding in a montane desert stream. *Archiv für Hydrobiologie*, 150:85-100

Lytle, D.A. and N.L. Poff. 2004. Adaptation to natural flow regimes. *Trends in Ecology & Evolution*, 19:94-100

Lytle, D.A. and R.L. Smith. 2004. Exaptation and flash flood escape in the giant waterbugs. *Journal of Insect Behaviour*, 17:169-178

MacArthur, R.W. 1972. Geographical Ecology. Harper and Row, New York. 269p.

Malmqvist, B. 2002. Aquatic invertebrates in riverine landscapes. *Freshwater Biology*. 47:679–694

Matthaei, C.D., C.R. Townsend, C.J. Arbuckle, K.A. Peacock, C. Guggelburger, C.E. Küster and H. Huber. 2004. Disturbance, assembly rules, and benthic communities in running water: a review and some implications for restoration projects. *In* Assembly Rules and Restoration Ecology: Bridging the Gap Between Theory and Practice. V. Temperton, R. Hobbs, T. Nuttle, & S. Halle (eds). Island Press, Washington, USA, pp. 367-388

Merritt, RW., K.W. Cummins and T.M. Burton. 1984. The role of aquatic insects in the processing and cycling of nutrients. *In* The Ecology of Aquatic Insects. V.H. Resh & D.M. Rosenberg (eds). Praeger Publishers, New York, pp.134–163.

Meyer, J.L., D.L. Strayer, J.B. Wallace, S.L. Eggert, G.S. Helfman and N.E. Leonard. 2007. The contribution of headwater streams to biodiversity in river networks. *Journal of the American Water Resources Association*, 43:86-103

Miller, A.M. and S.W. Golladay. 1996. Effects of spates and drying on macroinvertebrate assemblages of an intermittent and a perennial prairie stream. *Journal of the North American Benthological Society*, 15:670-689

Miller, S.W., D. Wooster and J. Li. 2007. Resistance and resilience of macroinvertebrates to irrigation water withdrawals. *Freshwater Biology*. Applied issues: 1-17

Minshall, G.W. 2003. Responses of stream benthic macroinvertebrates to fire. *Forest Ecology and Management*, 178:155-161

Mulholland, P.J., G.R. Best, C.C. Coutant, G.M. Hornberger, J.L. Meyer, P.J. Robinson, J.R. Stenberg, R.E. Turner, F. Vera-Herrera and R.G. Wetzel. 1997. Effects of climate change on freshwater ecosystems of the south-eastern United States and the Gulf Coast of Mexico. *Hydrological Processes*, 11:949-970

Naiman, R.J., J.J. Latterell, N.E. Pettit and J.D. Olden. 2008. Flow variability and the biophysical vitality of river systems. *Comptes Rendus Geosciences*, 340:629-643

Nelson, K.C. and M.A. Palmer. 2007. Stream temperature surges under urbanization and climate change: data, models, and response. *Journal of American Water Resources Association*. 43: 440-452

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

O'Connor, N.A. 1993. Resource enhancement of grazing mayfly nymphs by retreat-building caddisfly larvae in a sandbed stream. *Australian Journal of Marine and Freshwater Research*, 44:353-362

O'Connor N.A. and P.S. Lake. 1994. Long-term and seasonal large-scale disturbances of a small lowland stream. *Australian Journal of Marine and Freshwater Research*, 45:243-255

Pickett, S.T.A. and P.S.White (eds). 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York. 472p.

Poff, N.L. 1996. A hydrogeography of unregulated streams in the United States and an examination of scale-dependence in some hydrological descriptors. *Freshwater Biology*, 36:71-91

Poff, N.L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society*, 16:391-409

Poff, N.L. and J.V. Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, 46:1805-1818

Poff, N.L., J.D. Allan, M.B. Bain, J.R. Karr, K.L. Prestegaard, B.D. Richter, R.E. Sparks and J.C. Stromberg. 1997. The natural flow regime. *BioScience*, 47:769-784

Poff, N.L., M.M. Brinson and J.W. Day. 2002. Aquatic Ecosystems and Global Climate Change: Potential Impacts on Inland Freshwater and Coastal Wetland Ecosystems in the United States. Pew Center on Global Climate Change, Arlington

Pollock, M.M. 1998. Biodiversity. *In* River Ecology and Management. R.J. Naiman & R.E. Bilby (eds), Springer-Verlag, New York, pp. 423–454

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

Resh, V.H., A.G. Hildrew, B. Statzner and C.R. Townsend. 1994. Theoretical habitat templets, species traits, and species richness: a synthesis of long-term ecological research on the Upper Rhône River in the context of concurrently developed ecological theory. *Freshwater Biology*, 31:539-554

Richardson, J.S. 1991. Seasonal food limitation of detritivores in a montane stream: an experimental test. *Ecology*, 72:873- 887

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

Robinson, C.T. and G.W. Minshall. 1986. Effects of disturbance frequency on stream benthic community structure in relation to canopy cover and season. *Journal of the North American Benthological Society*, 5:237-248

Scarsbrook, M.R. and C.R. Townsend. 1993. Stream community structure in relation to spatial and temporal variation: a habitat templet study of two contrasting New Zealand streams. *Freshwater Biology*, 29:395-410

Schneider S.H., P.H. Gleick and L.O. Mearns. 1990. Prospects for climate change. *In* Climate Change and U.S. Water Resources. P.E. Waggoner (eds). Wiley-Interscience, Toronto, pp. 41-74

Short, R.A. and P.E. Maslin. 1977. Processing of leaf litter by a stream detritivore: effect on nutrient availability to collectors. *Ecology*, 58:935-938

Short, R.A., S.P.Canton and J.V. Ward. 1980. Detrital processing and associated macroinvertebrates in a Colorado mountain stream. *Ecology*, 61:728-732

Sousa, W.P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics*, 15:353-391

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? *The Journal of Animal Ecology*, 46:337-365

Southwood, T.R.E. 1988. Tactics, strategies and templets. *Oikos*, 52:3-18

Stanley E.H., D.L. Buschmann, A.J. Boulton, N.B. Grimm and S.G. Fisher. 1994. Invertebrate resistance and resilience to intermittency in a desert stream. *American Midland Naturalist*, 131:288-300

Stanley, E.H., S.G. Fisher and N.B. Grimm. 1997. Ecosystem expansion and contraction in streams. *Bioscience*, 47:427-435

Statzner, B., K. Hoppenhaus, M. Arens, and P. Richoux. 1997. Reproductive traits, habitat use and templet theory: a synthesis of world-wide data on aquatic insects. *Freshwater Biology*, 38:109-135

Statzner, B., A.G. Hildrew and V.H. Resh. 2001. Species traits and environmental constraints: entomological research and the history of ecological theory. *Annual Review of Entomology*, 46:291-316

Stockton, C.W. and W.R. Boggess. 1979. Geohydrological Implications of Climate Change on Water Resource Development. U.S. Army Coastal Engineering Research Center, Ft. Belvoir, V.A.

Takao, A., J.N. Negishi, M. Nunokawa, T. Gomi and O. Nakahara. 2006. Potential Influences of a Net-Spinning Caddisfly (Trichoptera:*Stenopsyche marmorata*) on Stream Substratum Stability in Heterogeneous Field Environments. *Journal of the North American Benthological Society*, 25:545-555

Townsend, C.R. A.G. Hildrew. 1994. Species traits in relation to a habitat templet for river systems. *Freshwater Biology*, 31:265-275

Townsend, C.R., S. Dolédec and M.R. Scarsbrook. 1997. Species traits in relation to temporal and spatial heterogeneity in streams: a test of habitat templet theory. *Freshwater Biology*, 37:367-387

Waggoner, P.E. and J. Schefter. 1990. Future water use in the present climate. *In* Climate Change and U.S. Water Resources. P.E. Waggoner (eds). Wiley-Interscience, Toronto, pp. 19-39

Wallace, J.B. and J.R. Webster. 1996. The role of macroinvertebrates in stream ecosystem function. *Annual Review of Entomology*, 41:115-39

Walther, G-R., E. Post, P. Convey, A. Menzel, C. Parmesank, T.J.C. Beebee, J-M. Fromentin, O. Hoegh-Guldberg I and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature*. 416: 389-395

Ward, G.M. and K.W. Cummins. 1979. Effects of food quality on growth of a stream detritivore, *Paratendipes albimanus* (Meigen) (Diptera: Chironomidae). *Ecology*, 60:57-64

Wiens, J.A. 2002. Riverine landscapes: taking landscape ecology into the water. *Freshwater Biology*, 47:501-515

Williams, D.D. 2006. The Biology of Temporary Waters. Oxford University Press, New York. 337p.

Wipfli, M.S. and D.P. Gregovich. 2002. Export of invertebrates and detritus from fishless
   headwater streams in southeastern Alaska: implications for downstream salmonid production.
   Freshwater Biology, 47:957–969

Wipfli. M.S., J.S. Richardson and R.J. Naiman. 2007. Ecological linkages between headwaters
   and downstream ecosystems: Transport of organic matter, invertebrates and wood down
   headwater channels. *Journal of the American Water Resources Association*. 43:72-85

Wotton, R.S., B. Malmqvist, T. Muotka and K. Larsson. 1998. Fecal pellets from a dense

aggregation of suspension-feeders in a stream: an example of ecosystem engineering. *Limnology*

and Oceanography, 43:719-725

Chapter 2 The relationships between summer low-flow events and the benthic macroinvertebrate community in forested headwater streams.

2.1 Introduction

Communities, the species and interactions among them, in rivers and streams (lotic systems) are largely affected by physical disturbances (e.g. Resh et al. 1988; Power et al. 1988; Poff 1992; Palmer et al. 1995; Lake 2000; Lytle and Poff 2004; see Chapter 1). In lotic systems, hydrological regimes can provide two extreme disturbances, flood and drought events, and their effects have been intensively studied (e.g. Giller et al. 1991; Boulton et al. 1992; Angradi 1997; Williams 2006; Miller et al. 2007). However, the effects of non-extreme hydrological regimes on biological traits, and thus community structures, have not been studied as much (but see e.g. Poff et al. 1997; Rempel et al. 2000; Bêche et al. 2006; Dewson et al. 2007), despite the predicted intensification of the future alterations to the natural flow regimes by human needs or by climatic changes affecting snow accumulations and/or precipitation regimes (Schindler 1997; Hulme 2004). For example, declines in summer runoffs have already been reported in the Rocky Mountains (Rood et al. 2008), Northern Canada (Déry and Wood 2005), and at larger scales (Zhang et al. 2001; Milly et al. 2005; Rood et al. 2005). Given the importance of macroinvertebrate communities to lotic ecosystems (Chapter 1), it is necessary to gain better understanding of how biological communities respond to current climatic variations. Small, forested streams were chosen as a model due to their connectivity to systems downstream (Wipfli and Gregovich 2002; Compton et al. 2003; Wipfli et al. 2007) and sensitivity even to small changes in discharges (Williams 2006; Nelson and Palmer 2007). The summer low-flow events were targeted because macroinvertebrates are already under stress from low availabilities of detritus and

warmer temperatures in summer (Richardson 1991), thus they should respond closely to any additional stress (Williams 2006; Durance and Ormerod 2007; Nelson and Palmer 2007). The macroinvertebrate communities of riffles within small streams were used rather than those of pools because riffles experience the impacts of low-flow events the most (Stanley et al. 1997; Boulton 2003).

We hypothesized that seasonal fluctuations in hydrological regimes play a role in the shaping of community structures in lotic systems. For example, flow regimes are known to be affected by ocean-atmosphere phenomena such as North Atlantic Oscillation (Hurrel 1995), El Niño Southern Oscillation (Molles and Dahm 1990), Pacific Decadal Oscillation (PDO; Mantua et al. 1997) and Interdecadal Pacific Oscillation (Folland et al. 2002; McKerchar and Henderson 2003). For instance, the positive ('warm') PDO phase is correlated with relatively higher temperatures from January through August (Fleming et al. 2007) and less winter precipitations in the Pacific Northwest (Mantua et al. 1997) while the negative ('cold') PDO phase is correlated with increased flows, especially in April and May (Fleming et al. 2007). If community structures are affected by the changes in flow regimes, then patterns of such oscillations should be detectable when analyzing the community with respect to flow parameters.

The objectives of this study were to: 1) test for evidence of summer low-flow events playing a role in shaping the benthic macroinvertebrate communities of riffles in forested, headwater streams, and 2) identify which low-flow parameter explains the community structure the most. If the summer low-flow events affect the community structure, then the low-flow variables must be associated with the patterns of relative abundances and biological traits. A three-table ordination called RLQ analysis (Dolédec et al. 1996) was used to test if there was any underlying structure between summer low-flow parameters (R), species abundances (L) and their biological traits (Q) that explains the particular community

structures observed. The use of RLQ analysis to study the relationships between environment and the occupants' abundance and traits in a particular habitat has been increasing in the past decade (e.g. Dolédec et al. 1996; Thuiller et al. 2006; Barbaro and Halder 2008).

2.2 Methods

2.2.1 Site description

The University of British Columbia's Malcolm Knapp Research Forest (MKRF) is located near Maple Ridge, British Columbia (122°34'W, 49°16'N). MKRF is in the Coastal Western Hemlock biogeoclimatic zone (CWHdm; Pojar et al. 1991) with three dominant tree species: Douglas-fir (*Pseudotsuga menziesii*), western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*). The maritime climate is characterized by dry, warm summers and wet, cool winters. Shallow soils are developed from glacial till and some glacio-marine deposits (Feller and Kimmins 1979). The benthic macroinvertebrate samples were collected from MKRF as a part of the MKRF Riparian project (see Kiffney et al. 2000; Richardson et al. 2002; Kiffney et al. 2003 for the details of the project). The benthic macroinvertebrate abundance data from three headwater streams were used for this study: East Creek, South Creek and Mike Creek (Figure 2-1). These streams experienced minimal anthropogenic disturbances since the forest fire in 1931 as they are either the control (East and Mike Creeks) or 30-m buffer (South Creek) sites (Kiffney et al. 2003). The streams were classified as riffle-pool or step-pool (Montgomery and Buffington 1998) with southerly aspects. The ranges of discharges in all three streams include zero (Table 2-1). The lowest flows occur from July to September, often resulting in discontinuous surface flow.

2.2.2   Data collection

The 9-year record of benthic macroinvertebrate samples from the MKRF riparian project for the three streams (East, Mike and South Creeks) based on Surber samples taken in early autumn were used in this study as abundance data to test for the effect of summer low-flow events on macroinvertebrate communities (Table 2-2). All the data were arranged into three tables to match the requirement of RLQ analysis: low-flow variables (R), abundance (L) and biological traits (Q).

The abundance (L) table consisted of the macroinvertebrate relative abundance data (61 taxonomic units) collected by the MKRF riparian project. The relative abundance (count/Surber sampler; 0.09 m^2) for each taxonomic unit was converted into proportions (per Surber sampler) by each sampling replicate (e.g. the relative abundance of Chironomidae in Fall 2000 sample 1 for Mike Creek was 115/619 while sample 2 had 284/498). An average relative abundance for each sampling event was calculated from the replicates for each taxonomic group (TG). The taxonomic resolutions in this study were based mainly on Merritt and Cummins (1996) and varied from genus to order depending on their identification certainty and rarity of sighting (see Appendix D for the entire list of taxa used in this study). Taxonomic groups that occurred fewer than three times over the 10 years, and/or were unique to one site, were omitted from analyses after the relative abundance calculation to avoid potential misclassifications. The relative abundance data were log(x+1) transformed to correct for the influences of extremely abundant or rare taxonomic group on the ordinations.

Low-flow parameters (R) were obtained based on discharge data (Feller M.C., University of British Columbia, Unpublished data) from weirs at East Creek and South Creek. For Mike Creek, the discharge data were calibrated by taking multiple point discharges using salt dilution gauging (Moore 2005). The result of the calibration showed that Mike Creek discharge is about 0.65 times that of East Creek. A low-flow event was defined as any period

in a particular summer that had discharges lower than the average discharge minus one standard deviation (Figure 2-2). The average discharge was calculated over the 9-year period for each site. The use of one standard deviation was derived from a definition of extreme low-flow events as flows lower than average discharge minus two standard deviations (Resh et al. 1988). Five summer low-flow measures were used as summer low-flow variables: frequency, duration, intensity, abruptness and minimum discharge (see Table 2-3 for description of each parameter). For example, in the case of Figure 2-2, frequency is 2, duration is the number of days in "a", minimum discharge is 0, intensity is about 12, and abruptness is the difference between discharge of the first peak and the minimum discharge divided by number of days it took. Each low-flow parameter was scaled from 0 to 1 to allow comparisons between the parameters. Due to the nature of the definition (Table 3), note that minimum discharge is the lowest at 0 unlike other parameters (1 indicates the strongest). All low-flow parameters were also $\log(x+1)$ transformed.

Biological species traits (Q) were fuzzy-coded (Chevene et al. 1994; Beche et al. 2006; see Table 2-4 for the list of species traits) for the 61 taxonomic units, containing 11 traits with 2-5 modalities that were adapted from Leah A. Bêche (Claude Bernard Université de Lyon; Unpublished data). Each trait of a taxon was given a score (between 0 and 3 for traits with 5 or fewer categories, or 0 and 5 for traits with greater than 5 categories), corresponding to its affinity to the modality (Chevene et al. 1994). Each trait was then standardized so that all modalities in a trait sum to one. For example, the trait Body Size has two modalities, small (a1) and large (a2), that add to one (e.g. a perlid stonefly genus *Calineuria* has a1=0.25 and a2=0.75 since the original scores were 1 and 3, respectively). The number of modalities in each trait category was reduced as much as possible. See Appendix A for the list of taxonomic units and B for their fuzzy-coded biological traits.

26

2.2.3   Data analyses

Each data table was analyzed separately using various ordination techniques that attempt to maximize the variance explained within the data. In other words, the explanatory strength of an ordination is higher with larger total variance. The total variance explained by the ordination axes and the percent variance explained by each axis were calculated from the eigenvalues obtained from each analysis. For L, scaled and centered correspondence analysis (CA; e.g. Jongman et al. 1995) was used to create a simultaneous ordination of species and sampling events. R was analyzed using the loadings of low-flow parameters obtained from a principal component analysis (PCA; e.g. Jongman et al. 1995). Q was investigated by fuzzy correspondence analysis (FCA). FCA is an eigen-based ordination method that is an application of multiple correspondence analysis to fuzzy-coded data designed to analyze data that are in multiple categories with subcategories (Chevene et al. 1994). The correlation ratios were compared to select traits that best explained the variance on a given axis.

RLQ analysis (Dolédec et al. 1996; Dray and Dufour 2007) was then carried out. RLQ analysis is a type of constrained ordination, and was used to measure how much of the total macroinvertebrate community structure is associated with low-flow parameters and biological traits. For mathematical explanation of RLQ analysis, see Dolédec et al. 1996. A Monte-Carlo permutation test with 1000 random permutations of the rows of Q and R tables was used to investigate the significance of the relationship between the species traits and low-flow parameters (Dolédec et al. 1996). The test was repeated 10,000 times to evaluate the total co-inertia value obtained (Kazi-Aoual et al. 1995). RLQ analysis expresses the co-structure between low-flow parameters and species traits (R-Q co-structure) by optimizing the correlation between species-by-site (L) scores with those of constrained environment-by-site (R) and trait-by-species (Q). The factor loadings on the main RLQ analysis indicate the relative contribution of each environmental variable to the constrained ordination, while

relative position of biological traits along the first RLQ axis show the main traits responsible

for the observed variability. The strength of relationships between R, L and Q was assessed

by comparing the constrained ordination with the unconstrained separate analysis of the three

tables. All analyses were carried out using the package ade4 (Dray and Dufour 2007) in R

2.7.0 (R Development Core Team 2009).

2.3   Results

2.3.1   Separate analyses of the three tables

Even though the three sites differ in their characteristics (Table 1), no separation between

sites was seen in either the CA of L or PCA of R, confirming the use of the three MKRF sites

together as samples rather than separating them and treating each site individually or

comparing between sites.

Low-flow variables (R): The first two principal component axes explained 70.8% of the

total variance from the PCA on R (Table 2-5). The frequency, minimum discharge and

duration were correlated strongly with the first PCA axis while intensity and abruptness

correlated with the second PCA axis (Figure 2-3). Only the frequency and minimum

discharge showed a strong positive correlation with each other. On the first PCA axis, the

sample scores could be distinguished by years until or after 2003 (i.e. 1998-2003 and 2004-

2007, respectively). Duration showed positive correlation with post-2003 data while 1998-

2003 data were best explained by higher frequency and lower minimum discharge (Figure 2-

4). No obvious patterns between the three sites were observed by the PCA of low-flow

variables.

Species abundances (L): For the species abundance data (L), 42.9% of the total variance of

the spread between taxonomic groups explained by CA axes could be explained by the first

four axes (Table 2-5). Rare taxa correlated positively with the first CA axis (Figure 2-5). The second axis showed a correlation with the preferred habitats that macroinvertebrates occupy: pools (positive) or riffles (negative). The taxonomic orders of macroinvertebrates did not show clear distances from each other to be separated from others on the first CA axis, except for Megaloptera (Figure 2-6). On the second axis, separations between taxonomic orders were small, and nematodes and oligochaetes correlated negatively. Similarly, functional feeding groups (FFGs; Anderson and Sedell 1979) did not show clear separations between each other and the spread was along with the first CA axis more.

Biological traits (Q): The first four FCA axes explained 52.3% of the total variance (Table 2-5). The first FCA axis was correlated negatively with body size, and life cycle traits showed the largest spread along the first axis (Figure 2-7). The first axis of FCA analysis on biological traits (Q) showed positive correlations between having diapause stages as larvae or pupae, and small body size with multiple generations per year, while large body size correlated positively with desiccation resistance. The modes of respiration and locomotion, as well as body shape and emergence synchrony spread along the second FCA axis more than other traits. The second FCA axis showed a positive correlation between the close emergence synchronization and having no resistance against desiccation, while the least synchronized emergence correlated positively with having adult diapause stages. Trait categories such as aquatic stage, dispersal modes and reproduction period did not show strong correlations with either of the first two FCA axes. Also, desiccation resistance (e1) showed a negative correlation with the first FCA axis (Figure 2-8). Traits separated Ephemeroptera from others, primarily due to their close emergence synchrony (k1) and dorso-ventrally flattened body shape (j1).

2.3.2   RLQ analysis

The RLQ analysis on the MKRF data showed that the summer low-flow parameters (R) and biological traits (Q) were significantly associated with the benthic macroinvertebrate community (repeated Monte Carlo, $p < 0.05$ for 99.91% of the time). Together, the first two RLQ axes explained 94% of the total R-Q co-structure (Table 6). The correlation coefficient with L was 0.195 along the first RLQ axis, accounting for 34% of the first CA axis of L. The first RLQ axis accounted for 55% of the R's inertia and 81% of the Q's inertia.

The intensity of low-flow events contributed to the observed separation of traits by the RLQ analysis the most followed by the duration (Figure 2-9). The duration and intensity had the strongest correlations with the first RLQ axis while the minimum discharge showed the least (Figure 2-9). The RLQ analysis separated mites (taxacode: acarin) and oligochaetes (taxacode: oligoc) from the rest of the taxonomic groups. No clear separation was seen between sampling sites (Figure 2-9).

To visualize any patterns hiding within the summary biplots of R and Q, bar plots were created for the first two RLQ axes choosing traits that showed relatively strong correlations with the axes (Figures 2-10, 2-11 and 2-12). Similarly to the analysis of R by PCA, the first RLQ axis showed separations between years pre-2004 and post-2003 (Figure 2-10). All low-flow variables except for the frequency showed positive correlations with post-2003 years. Duration and intensity had the strongest correlations with the first RLQ axis while minimum discharge showed the least correlation. The positive correlation between minimum discharge and pre-2004 years seen by PCA of R was not observed in RLQ. The first RLQ axis showed a positive relationship between the frequency and large-bodied epibenthic macroinvertebrates that disperse by water (Figure 2-11). The second RLQ axis related the abruptness of the lowest flow event and duration with lack of emergence synchrony and small body size

30

whereas desiccation resistance and large body size showed a positive correlation with the minimum discharge, intensity and frequency (Figure 2-12).

2.4   Discussion

2.4.1   Summer low-flow regime

As stated in the natural flow regime paradigm (Richter et al. 1996; Poff et al. 1997), the forested headwater stream community structure seemed to be affected by the seasonal fluctuations in low-flow regimes. The clear separation between years 1998-2003 and 2004-2007 is likely related to the patterns of decadal oscillation in the North Pacific (PDO; Mantua et al. 1997). Kiffney et al. (2002) have previously identified the relationships between PDO and discharges at MKRF for a 28-year period (1972-2000). According to the PDO Index, 1998-2002 was dominated by the negative ('cool') phase while the positive ('warm') phase dominated 2003-2007 (Mantua 2009; Figure 2-13). Similar relations have been observed with the stream macroinvertebrates in UK responding to the North Atlantic Oscillation (NAO; e.g. Bradley and Ormerod 2001; Durance and Ormerod 2007), and in North America with El Niño Southern Oscillation (ENSO; e.g. Bêche and Resh 2007; Gilbert et al. 2008) both of which affect the precipitation patterns, and therefore the flow levels. The tendencies of the community stability (persistence of species) to be less stable after wet winters (i.e. lower summer flows) that were observed with respect to climate regimes (NAO – Bradley and Ormerod 2001; ENSO – Bêsh and Resh 2007) were not clearly observed in this study, though the composition seemed different. Durance and Ormerod (2007) attributed the correlations between the unstable persistence of macroinvertebrate community and positive NAO years (wet winter, dry summer) to the increased water temperatures. On the other hand, Bêche and Resh (2007) concluded that the precipitation regimes explained the decreased stability of macroinvertebrates in El Niño years (wet winter). In this study, since the water temperatures

31

do not increase with lowered flow as much due to canopy cover and groundwater inputs, the differences in precipitation patterns between warm and cold PDO phases are the most likely explanation for the observed patterns. The frequency, minimum discharge and duration showed relatively strong correlations with this separation between the two time periods (1998-2002 and 2003-2007). Frequency and minimum discharge correlated positively with 1998-2002, which was dominated by the cool phase of PDO, while duration positively correlated with the warm phase (2003-2007). The positive correlation between duration and warm PDO phase was as expected by the reduced winter precipitation. These correlations suggest that warm phases of PDO bring drier summers with longer low-flow durations but not necessarily lower minimum discharge levels. On the other hand, cool phase PDO seems to experience occasional rainfall events during a summer that results in disruption of low-flow events, increasing the frequency and lowering the duration. Unlike in the PCA of low-flow parameters (R), RLQ analysis, i.e. when R was analyzed using taxa abundance (L) and trait (Q) information, identified the potential PDO shift between wet years (1998-2002) and dry years (2003-2007) with one year time lag (1998-2003 vs. 2004-2007). Only the frequency of low-flow events showed the positive correlation with the cool phase PDO (1998-2002) by RLQ analysis. This difference perhaps indicates that the positive correlation between the minimum discharges and cool phase PDO seen in the PCA of R was not a strong one. Overall, the warm phase PDO seems to favour benthic macroinvertebrates with r-selected traits (e.g. small body size, shorter life cycle and mobile; MacArthur and Wilson 1967; Krebs 2001) such as *Dolophilodes* spp. (Trichoptera: Philopotamidae), *Ironodes* spp. (Ephemeroptera: Heptageniidae) and *Yoraperla* spp. (Plecoptera: Peltoperlidae). The selection, which favours r-selected traits, perhaps suggests that in riffles, habitat compression (MacArthur 1972; Harvey et al. 2005; Chapter1) increases the density of benthic invertebrates. Hence, the interactions are perhaps not as important in pools and ponds as suggested.

2.4.2   Summer low-flow parameters

The abruptness of the lowest flow in a summer contributed the least in this study, despite the potential importance of the initiation phase (i.e. abruptness) in acting as a cue for triggering behavioural adaptations against low-flow events (e.g. Hynes 1976; Brock et al. 2003). This finding could be attributed to the way abruptness was calculated, dividing the difference between the last peak and the minimum discharge by the number of days it took to reach the lowest flow may not have represented how macroinvertebrates sense the decrease in discharge. Perhaps this way of calculating abruptness measuring the rate of decreasing flow over days is not sufficient to the exact cues used by macroinvertebrates to detect onset of low-flow events. The time scale (in days) may have been too large a scale for macroinvertebrates. Also the potential diurnal fluctuation in flow levels due to evapotranspiration and groundwater input (e.g. Lundquist and Cayan 2002), which macroinvertebrates encounter, cannot be detected or inferred by this measure.

Since both the intensity and minimum discharge indicate the most stressful point during the summer, it was rather surprising to see that they differed in their relationships with the benthic community. Perhaps the intensity, calculated here as the difference between average and minimum discharge of a summer, explains how benthic macroinvertebrates react to flow conditions more than just the minimum discharge of the year. Moreover, given the importance of the duration in explaining the relationships between traits and low-flow variables, the intensity that could potentially incorporate the overall conditions of the summer through the inclusion of average discharges explained the variations better. The differences between the strengths of intensity and frequency with respect to their correlations with the first RLQ axis would have suggested differences in the importance of resistance (intensity and duration) and resilience (frequency) in structuring the macroinvertebrate communities in these small forested streams (White and Jentsch 2001; Fritz and Dodds 2004). However, unlike high-flow

events, higher frequencies of low-flow events indicate that there were rain fall events disrupting an otherwise long low-flow period. Thus, in the case of low-flow events, frequency not only facilitates resilience (by possible establishment of connectivity between affected areas and refugia), but may also be related to rain events that support resistance by macroinvertebrates.

2.4.2 Macroinvertebrate abundance and traits

The trait-based approach was used in this study to analyse the trait variations among the benthic macroinvertebrates along summer low-flow parameters. This approach is more advantageous than a species-based approach as it is not constrained by taxonomy, allowing for the generalization across geographic ranges (Statzner et al. 2007).

The correspondence analysis of relative taxa abundance (L) should show patterns of community structure relative to the habitats if habitats were different. The separation of species by their relative abundance (high vs. low) was expected since there was no clear difference in community compositions between sites, which would have given the greatest distances between macroinvertebrates in the ordination. The differences in the relative abundance could have resulted from habitat preferences of macroinvertebrates. Riffles and pools are known to be occupied by different groups of macroinvertebrates, while transients in either habitat occur during individual movements from or to their preferred habitats (e.g. Logan and Brooker 1983; Brown and Brussock 1991). Since all the samples came from riffles, riffle species should dominate over pool species, resulting in the separation in abundance seen here.

The main traits that explained the observed variability in this study were the substrate relations, dispersal modes, life cycle types and body size. This explained the separation of mites, nematodes and oligochaetes from the rest of the taxonomic groups (Resh et al. 1994).

This is largely due to their large differences from aquatic insect taxa in these traits, especially the life history trait that mites and oligochaetes do not leave streams, unlike most insect taxa included in the study. Also, these three macroinvertebrate groups are known to be more interstitial and are sometimes separated from benthic macroinvertebrates (mainly insects) due to their substrate relations and small body size (e.g. Fenchel 1978).

The positive correlation between large body size and possession of desiccation resistance suggests that perhaps, in the past, macroinvertebrates with larger body size were more susceptible to decreased flow as previously suggested (e.g. Huryn and Wallace 2000). Thus, they either have acquired desiccation resistance as a necessary adaptation in streams that experience summer low-flow events, or only desiccation-resistant forms survived. In addition, the positive correlation between large-bodied epibenthic macroinvertebrates that disperse mainly by water and the frequency of low-flow events suggests a behavioural adaptation against low-flow events by larger organisms. It is advantageous for macroinvertebrates to swiftly respond to the unpredictable changes in discharge levels (e.g. against high-flow events; Negishi and Richardson 2006), and avoiding low-flow events by the ability to move out of the affected area, for example via active drift (Brittain and Eikeland 1988; Jentsch et al. 2007; James et al. 2008a) when occasional precipitation re-establishes the longitudinal connectivity.

Synchronized emergence facilitates mate finding (Downes 1969) and dilutes the per capita chance of predation on aerial adult stages (Corbet 1957). The close emergence synchronization is thought to be an avoidance strategy towards relatively predictable disturbances such as annual or seasonal events (e.g. Gray 1981; Lytle 2002). So this correlation can be seen as evidence that emergence synchronization is a type of adaptation against desiccation as proposed by some researchers (Williams 2006). However, unlike in the case of pulse disturbances such as flash floods, the correlation between low-flow events and

emergence synchronization is hard to elucidate. This is due to the close associations between temperatures and insect development (e.g. Pittendrigh 1954; Jenkins et al. 2001), potentially causing a closer timing of synchronized emergence upon low-flow events (Merritt and Cummins 1996). For example, many mayflies are known to use temperature as cues to synchronize their lifecycle (Newbold et al. 1994), not necessarily as an adaptation for low-flow events.

2.5   Conclusion

The RLQ analysis of the MKRF data related the summer low-flow events to the species abundance and biological traits, showing a significant underlying structure between them, and following the views of previous studies on the relationships between disturbance parameters and traits' resistance and resilience. Intensity and duration of the low-flow events had the highest explanatory values on the observed community structures. Moreover, the headwater stream community analyzed here showed correlations with Pacific Decadal Oscillation as predicted by the hypothesis that summer low-flow events play a role in the structuring of the community.

The limitation of this study lies in the small spatial scale and relatively short extent of the data analyzed. A synthetic approach such as meta-analysis incorporating other long-term studies on the relationships between the flow variability and biotic community within streams and rivers would be crucial to further our understanding of the relationships. In addition, corroboration with an experimental approach (e.g. flow diversion; Wills et al. 2006; James et al. 2008b) could allow us to build predictions for upon the future scenarios of climate change and provide frameworks for conservation.

Table 2-1. The characteristics of the three experimental sites in Malcolm Knapp Research Forest, Maple Ridge, British Columbia, used in this study (Kiffney et al. 2003). Buffer refers to the riparian treatment type applied for the project. Maximum daily temperatures reported here were measured in July-August 1998-2002 (Karlson et al. 2005; Gomi et al. 2006)

	Buffer	Watershed area (ha)	Summer base-flow discharge $(L\ s^{-1})$	Max. daily temperature (°C)	Elevation range (m)	Stream gradient (%)	Bankfull width (m)
East	Control	44	0-2	16.1	295-555	7	1-3
Mike	Control	25	0-6	16.7	240-310	6	2-4
South	30 m	19	0-3	18.8	175-320	9	1-4

Table 2-2. Available macroinvertebrate abundance data for the three MKRF sites used in this study are indicated by the diagonal lines. Spring samplings were carried out in mid-May to June while Fall samplings were done in mid-September to October.

	1998		2000		2001		2002		2003		2004		2005		2006		2007	
	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall
East																		
Mike																		
South																		

Table 2-3. Descriptions of summer low-flow parameters in the environment-by-site table (R). A summer low-flow event was defined as any days with recorded discharges that were lower than the average discharge minus one standard deviation in a particular summer. One event to the next was distinguished by the presence of discharge above the threshold.

Parameters	Description
Frequency (Fre)	Total number of low-flow events
Duration (Dur)	Total number of days in the max low-flow event (days)
Intensity (Int)	Difference between the average and minimum discharge (Ls^{-1})
Abruptness (Abr)	Difference between the last peak and the min discharge divided by the number of days in between ($Ls^{-1}days^{-1}$)
Minimum discharge (minQ)	Minimum discharge recorded (Ls^{-1})

Table 2-4. The biological trait categories used to create the fuzzy-coded Q table. The traits were adapted from Bêche L.A. (Claude Bernard Université de Lyon; Unpublished data). Note that under Life Cycle, gen is short for generation.

Trait	Categories	Code	Modality
Body size	<20 mm	a1	
	>20 mm	a2	2
Life Cycle	<= 1 yr; 1 gen/yr	b1	
	<= 1 yr; >1 gen/yr	b2	
	> 1 yr; <1 gen/yr	b3	3
Aquatic stage	egg	c1	
	larvae	c2	
	adult	c3	3
Dispersal mode	aquatic	d1	
	aerial	d2	2
Resistance mode	desiccation resistant	e1	
	diapause (egg)	e2	
	diapause (larvae/pupae)	e3	
	diapause (adult)	e4	
	none	e5	5
Respiration	water dependant	f1	
	water independent	f2	2
Substrate relation	mobile	g1	
	epibenthic	g2	
	endobenthic	g3	
	attached	g4	4
Food eaten	POM	h1	
	biofilm	h2	
	animal	h3	3
Reproduction period	November-April	i1	
	May-October	i2	2
Body shape	flattened	j1	
	cylindrical	j2	
	spherical	j3	3
Adult emergence synchronization	hours	k1	
	days	k2	
	weeks	k3	3

Table 2-5. Results for the first four axis components of individual ordination analyses (PCA, CA and FCA) on the three tables: R, L and Q. The total variances (sum of eigenvalues) for the ordinations were 5, 1.94 and 0.819, respectively.

Principal component analysis of environment-by-site (R)				
Eigenvalues (1-4)	2.344	1.194	0.913	0.35
% variance	46.9	23.9	18.3	7
Correspondence analysis of species-by-site (L)				
Eigenvalues (1-4)	0.328	0.228	0.146	0.132
% variance	16.9	11.7	7.5	6.8
Fuzzy correspondence analysis of trait-by-species (Q)				
Eigenvalues (1-4)	0.141	0.114	0.093	0.08
% variance	17.2	13.9	11.4	9.8

Table 2-6. RLQ Analysis results were summarized by first four axes. Eigenvalues with percentage of co-inertia accounted for by first four RLQ axes are shown in the first row, followed by the covariance and correlation between abundance scores (L) constrained by flow variables (R) and traits (Q), projected inertia of matrices R and Q projected onto the RLQ axes. The percentages of the potential inertia that each represents are shown in brackets.

	Axis 1 (%)	Axis 2 (%)	Axis 3 (%)	Axis 4 (%)
RLQ axes eigenvalues	0.26 (73)	0.075 (21)	0.016 (5)	0.0052 (2)
Covariance	0.51	0.27	0.13	0.072
Correlation	0.20 (34)	0.13 (27)	0.074 (19)	0.060 (17)
Projected inertia R	1.28 (55)	3.32 (94)	4.11 (92)	4.68 (98)
Projected inertia Q	5.32 (81)	7.60 (66)	11.3 (71)	13.9 (73)

Figure 2-1. The map of stream sites in Malcolm Knapp Research Forest, Maple Ridge, B.C., Canada. The figure has been removed due to copyright restrictions. The information removed is Figure 1 of Kiffney et al. 2003. The streams from which the data used in this study originated are highlighted by thick circles (East, Mike and South Creeks).
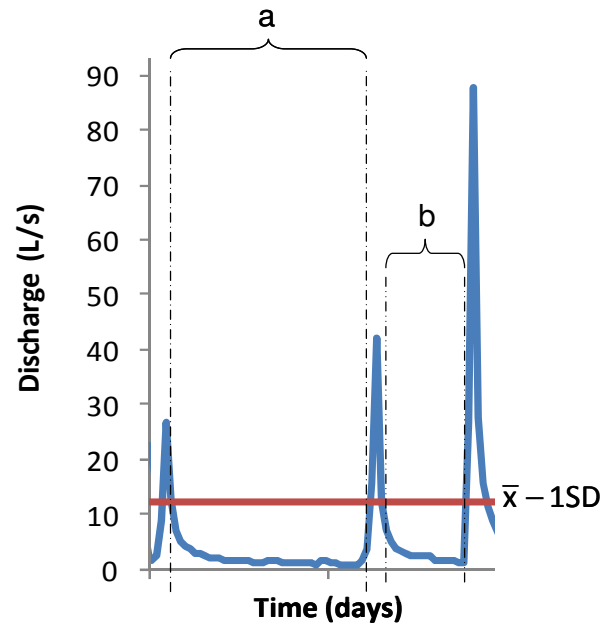
Figure 2-2. A hydrograph depicting the definition of a summer low-flow event used in this study. The horizontal line indicates the threshold of an average discharge minus one standard deviation. Here, "a" indicates the lowest flow event while "b" is another low-flow event in the season.
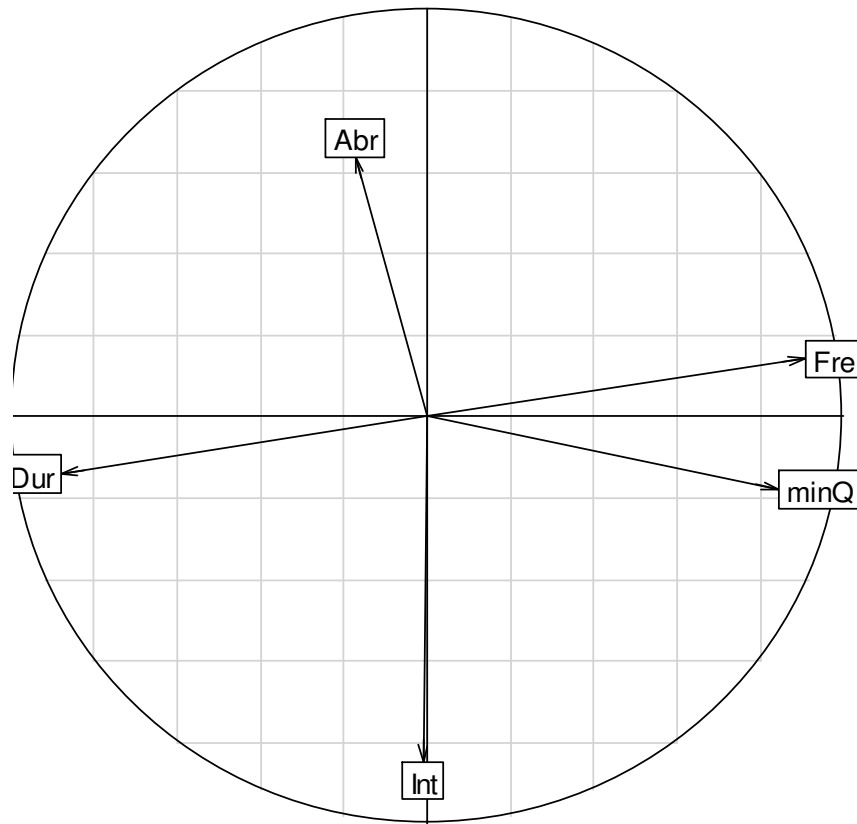
Figure 2-3. Correlation circle of the five low-flow parameters from the environment-by-site (R) analyzed by principal component analysis (PCA). The five parameters are abruptness (Abr), duration (Dur), frequency (Fre), intensity (Int) and minimum discharge (minQ). For definitions of each parameter, see Table 2-3. The radius of the circle is one. Here, frequency and minimum discharges are positively correlated with each other while both of them are negatively correlated with discharge.
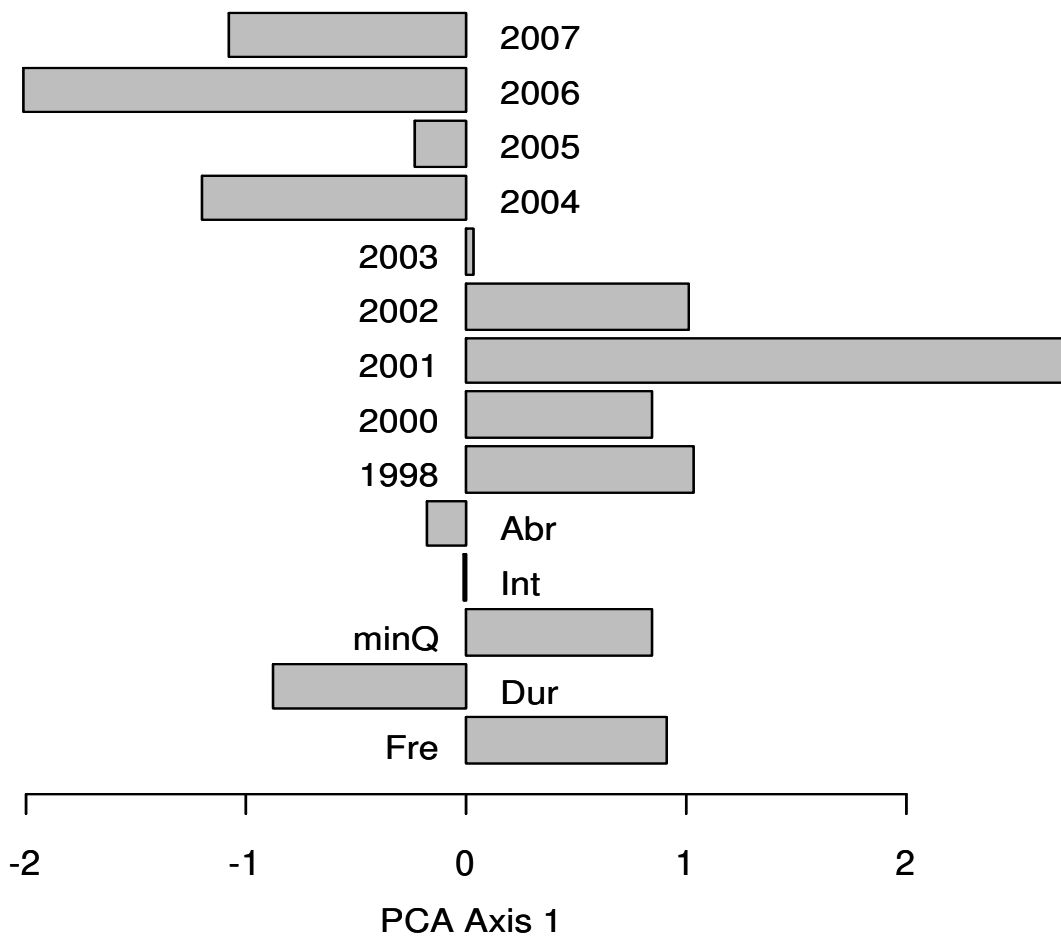
Figure 2-4. The plot of first PCA axis analyzing the low-flow variables (R) showing a clear correlation between the low-flow events and years except for intensity. The five parameters are abruptness (Abr), duration (Dur), frequency (Fre), intensity (Int) and minimum discharge (minQ). For definitions of each parameters, see Table 3. Frequency and minimum discharge best explained 1998-2002 while duration explained 2004-2007. 2003 showed a weak association with the separation of PCA axis 1 that could be attributed to wet versus dry years. The axis accounted for 46.9% of the total variance (Table 5).
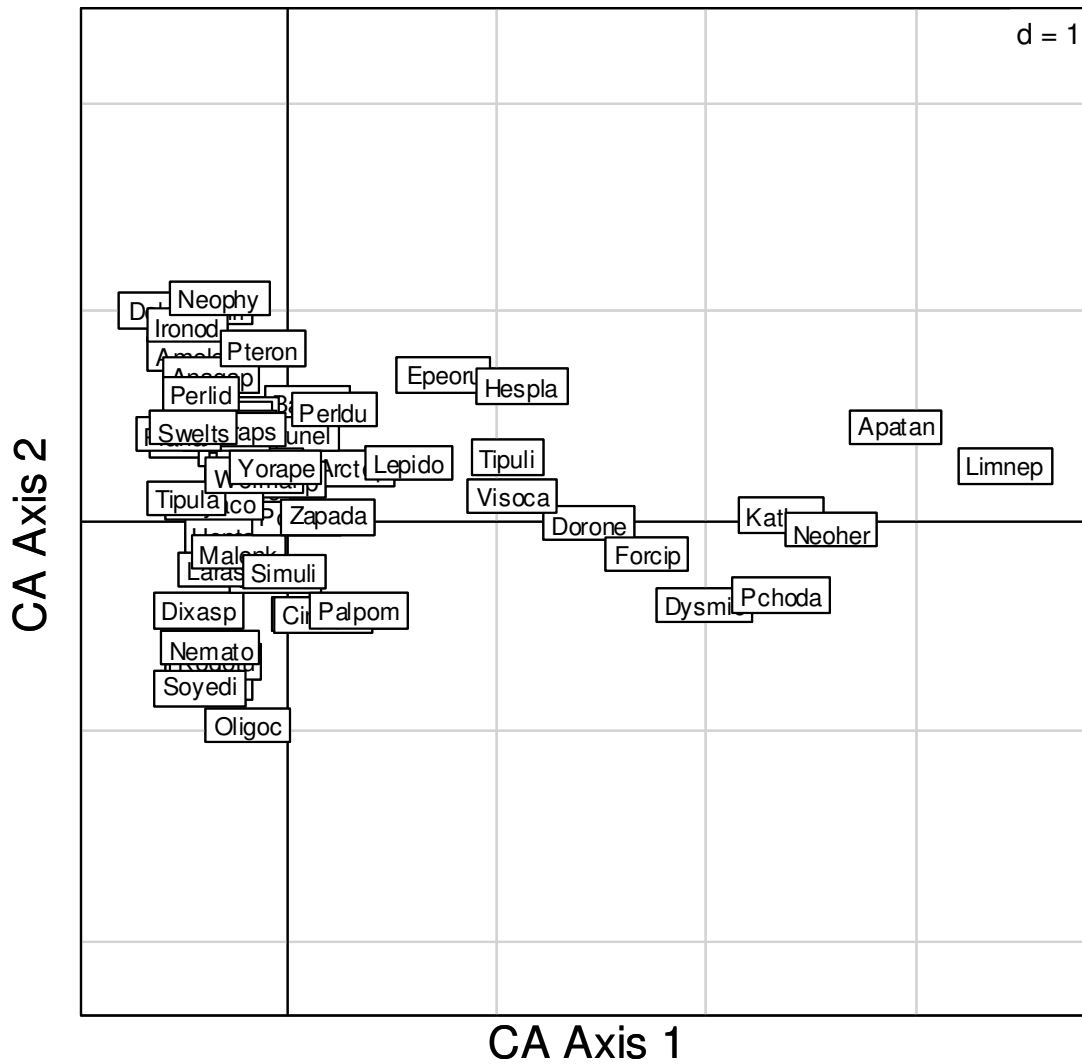
Figure 2-5. The biplot of the first two axes from the correspondence analysis (CA) of relative species abundance (L) explained 28.4% of the total variance. Solid lines indicate the 0, 0 lines of x and y axes. The distance scale (d) is shown above indicating the distance each side of grey squares indicate (d = 1 CA score). For the list of taxonomic codes, see Appendix A. The separation along the first axis is due to the relative abundance of each taxonomic group (positive scores indicate rarer group) while that along the second axis is related to habitat preferences between pools (negative) and riffles (positive).
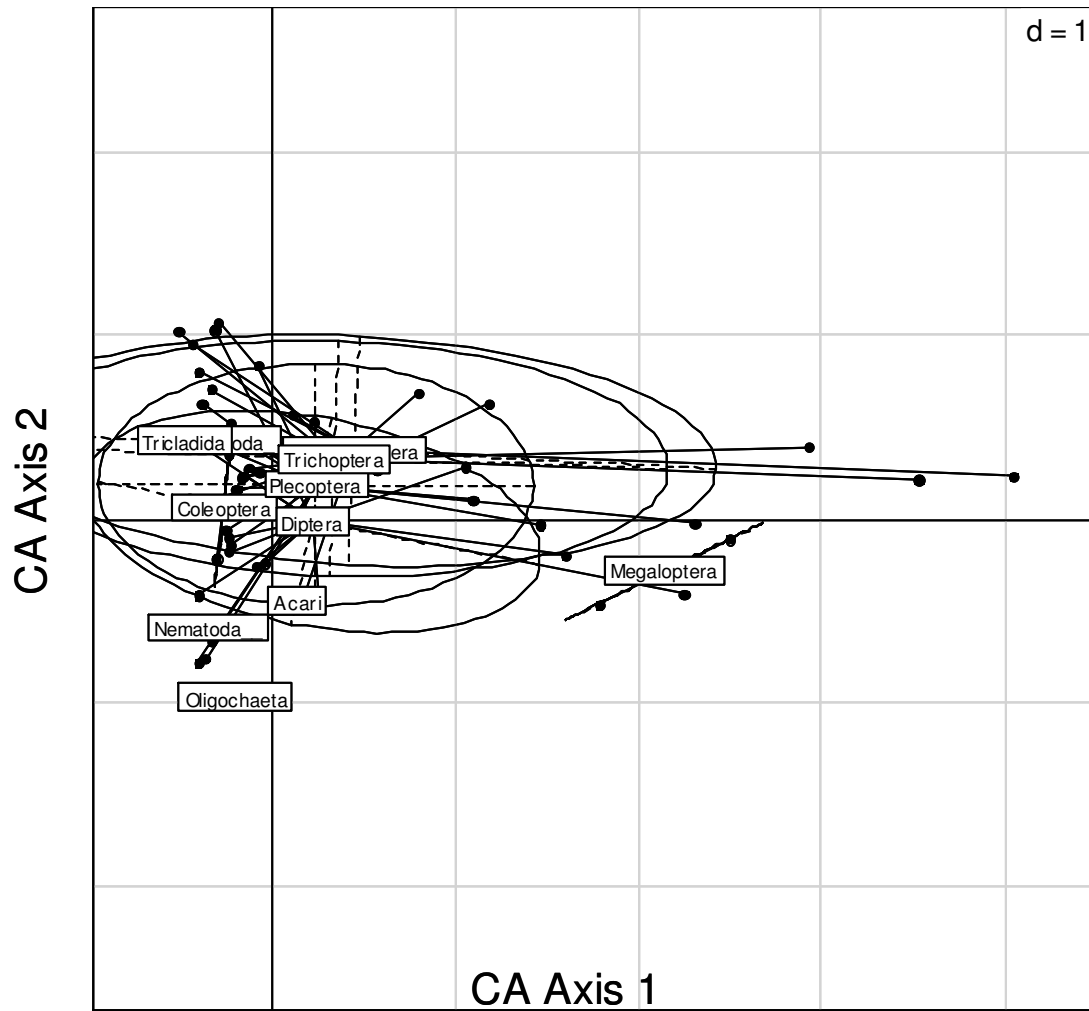
Figure 2-6. The biplot of the first two axes from the correspondence analysis (CA) of relative species abundance table (L) clustered by order or higher levels of taxonomy. Solid lines indicate the 0, 0 lines of x and y axes. Ordination plot scale (the distance of a side of grey square) is d = 1 CA scale, as indicated. Labels indicate the average scores, closed circles indicate taxonomic group scores outside of 95% confidence intervals (circles) No taxonomic group separated distinctively from others except for Oligochaeta.
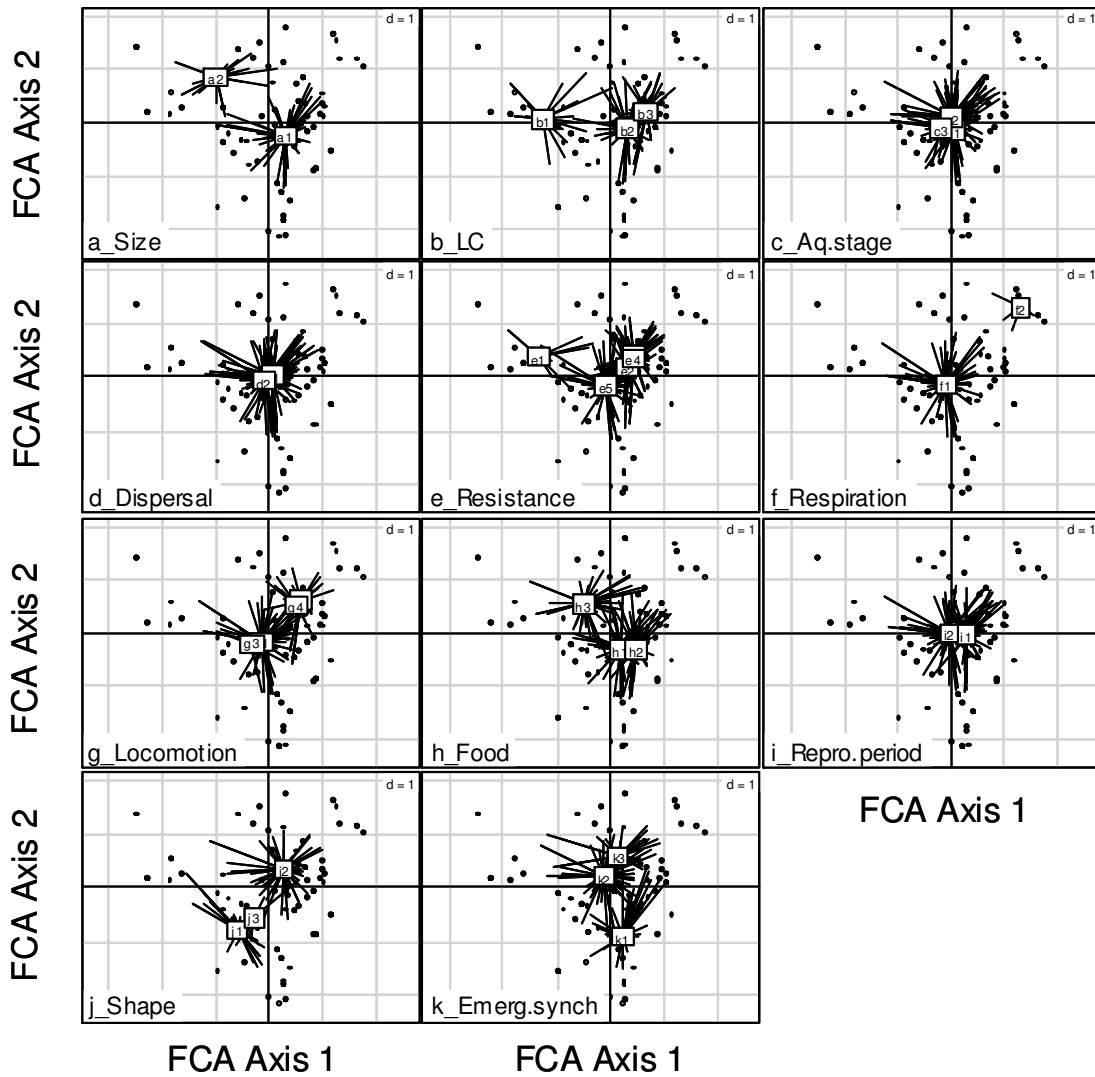
Figure 2-7. Fuzzy-coded correspondence analysis (FCA) of biological traits (Q) plotted by traits. Solid lines indicate the 0, 0 lines of x and y axes. The distance scale (d=1 FCA scale) is shown indicating the length of a side of grey squares. Labels indicate the average scores of the trait modalities, closed circles show scores outside of 95% confidence intervals (lines). Total eigenvalues was 0.819 with the first two axes explaining 31.1% of the variance (Table 5). For the descriptions of each trait and category, see Table 2-4.
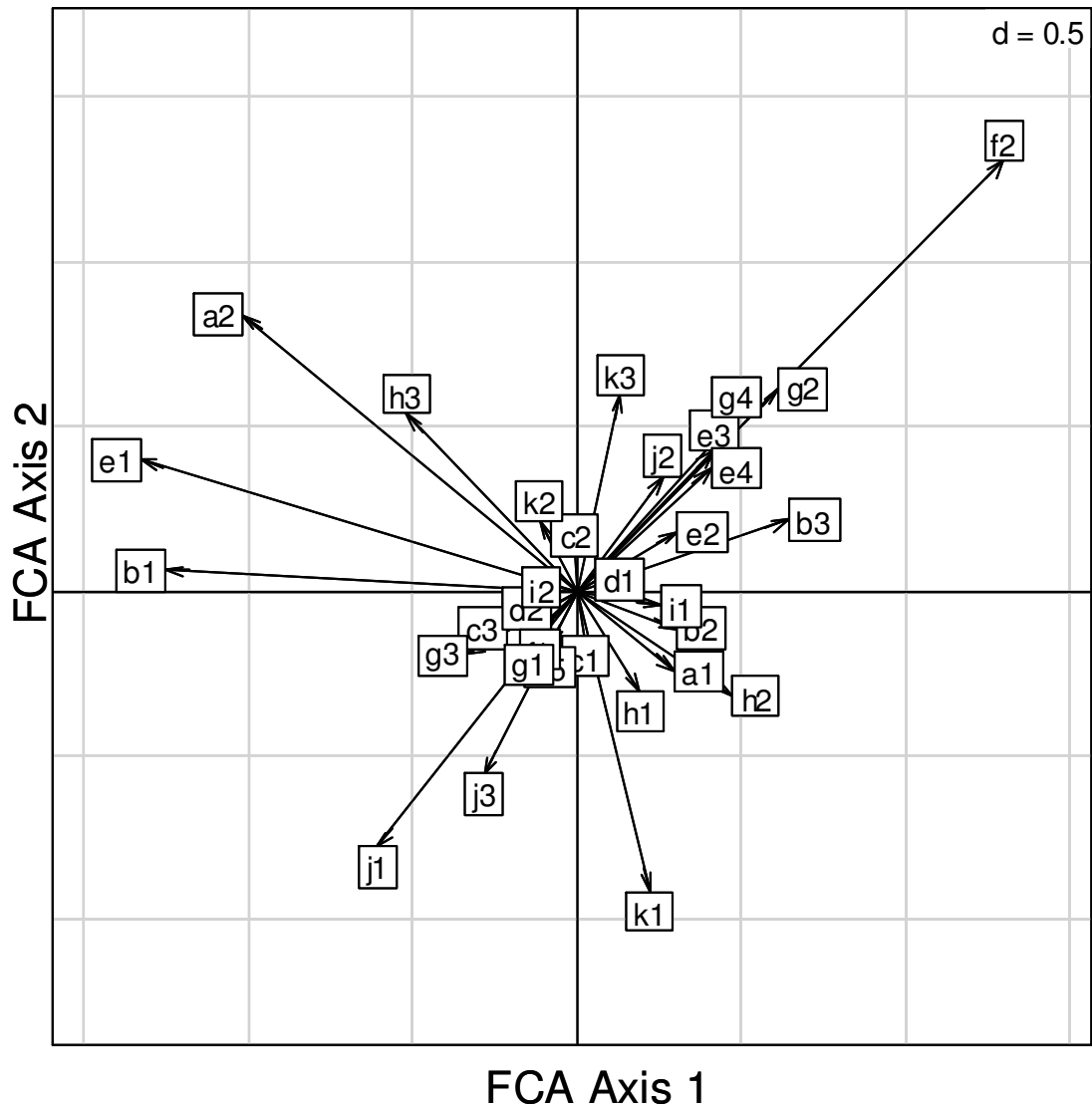
Figure 2-8. The ordination plot from fuzzy correspondence analysis (FCA) of species-trait table (Q) shows the dispersion of traits. Solid lines indicate the 0, 0 lines of x and y axes. The distance scale (the length of a side of grey squares) is d=0.5 FCA scale as shown. Arrows indicate the direction sand magnitudes of the FCA scores for the trait modalities. For the list of trait categories, see Table 2-4. Total variance was 0.819 with the first four axes explaining 52.3% of the total variance (Table 2-5).
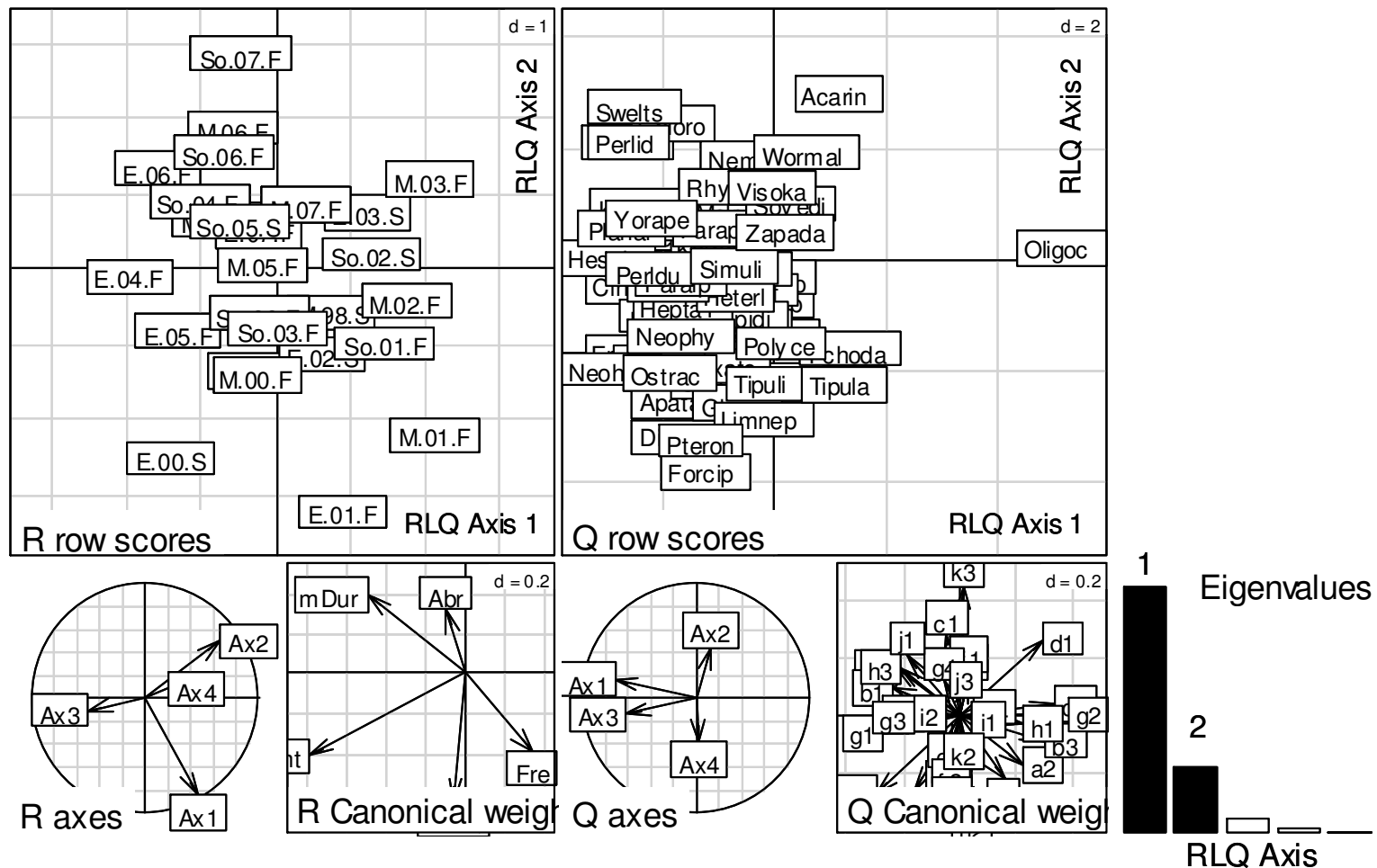
Figure 2-9. Summary of RLQ analysis showing ordination biplots (top), correlations between axes (bottom left) and canonical weights of factors explaining the first biplots (bottom right) for low-flow variables (R) and biological traits (Q). A screeplot shows eigenvalues of first five axes.
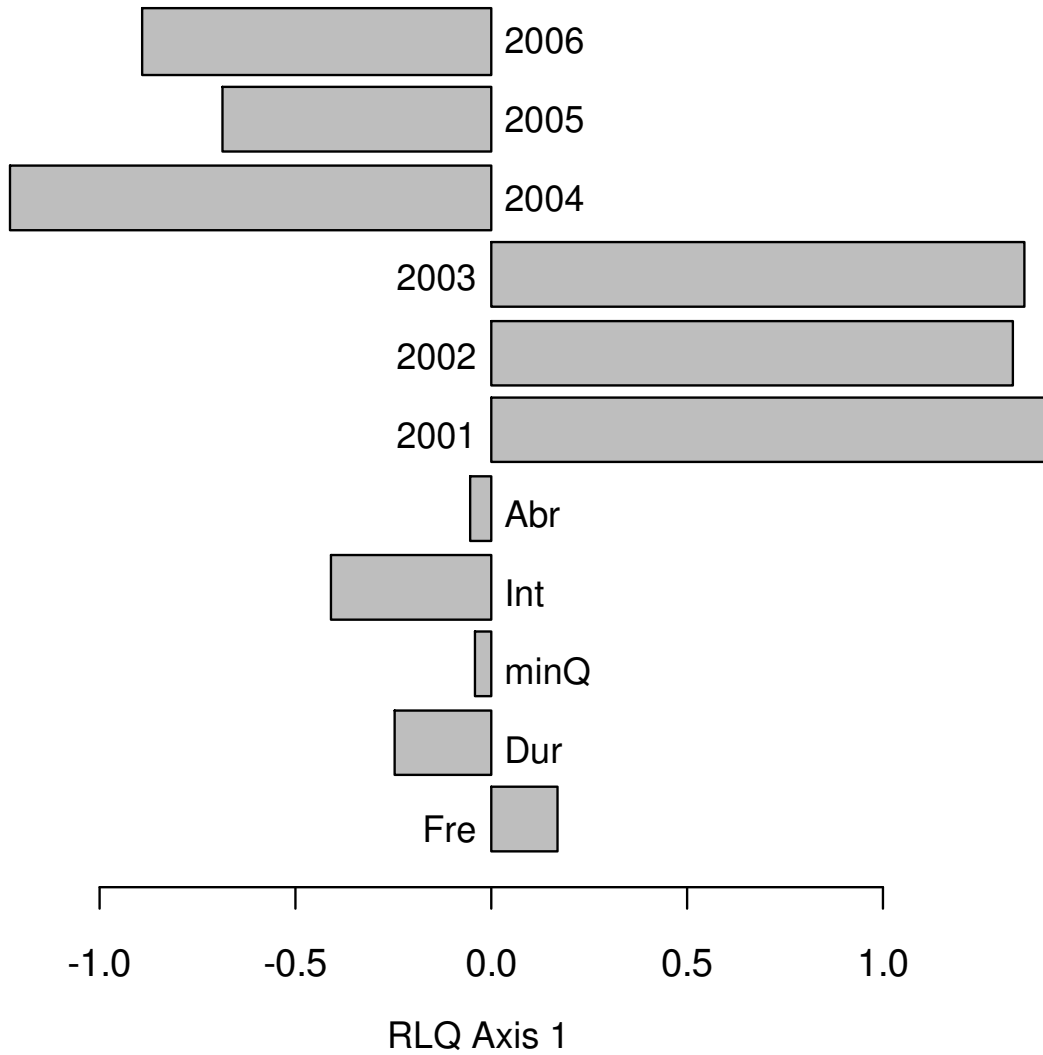
Figure 2-10. The plot of sampling events averaged by year and low-flow variables along the first RLQ axis showing a clear separation of years till and after 2003. Frequency correlated positively with 2001-2003 period while all other low-flow variables did so with post-2003, indicating that the separation is due to wet (positive) versus dry (negative) years. The axis accounted for 72.8% of the total variance.
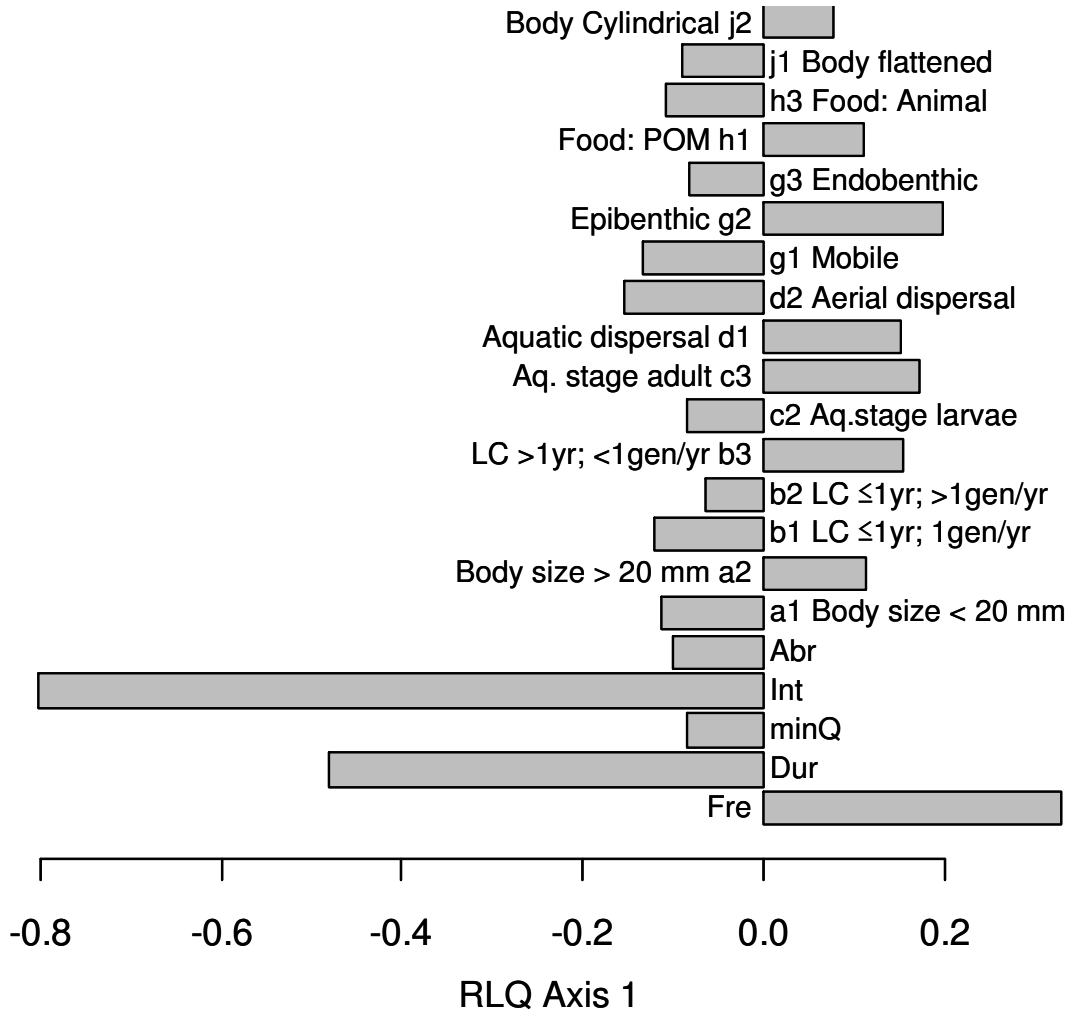
Figure 2-11. The plot of first RLQ axis showing the relationships between the low-flow variables (R) and biological traits (Q). Traits with less than absolute scores (i.e. distance along RLQ axis 1) of 0.06 were omitted. The separation of traits is due to wet (positive) versus dry (negative) years. The axis accounted for 55% of the R's inertia and 81% of the Q's inertia.
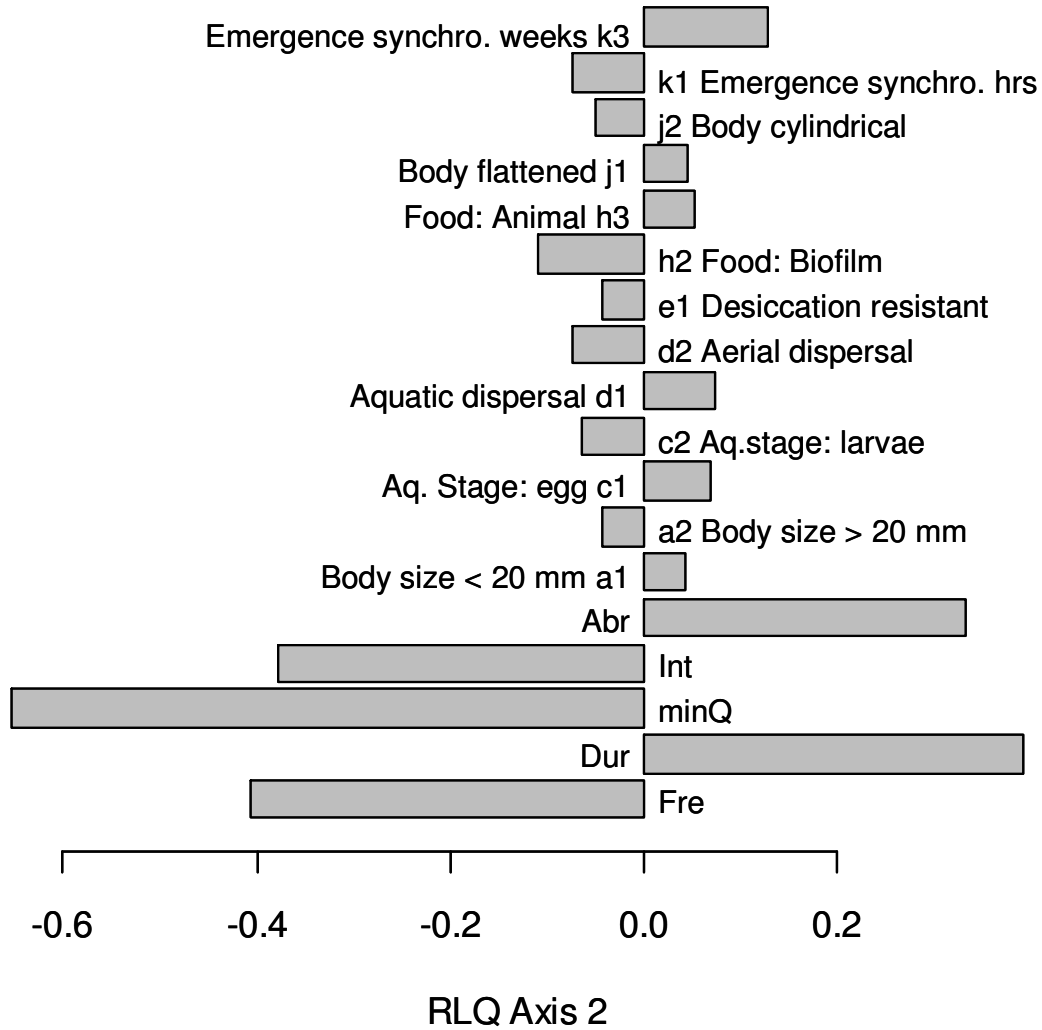
Figure 2-12. The plot of second RLQ axis relating the low-flow variables (R) and biological traits (Q). Traits with less than absolute scores (i.e. distance along RLQ axis 2) of 0.04 were omitted. The axis accounted for 40% of the R's inertia and 65% of the Q's inertia.
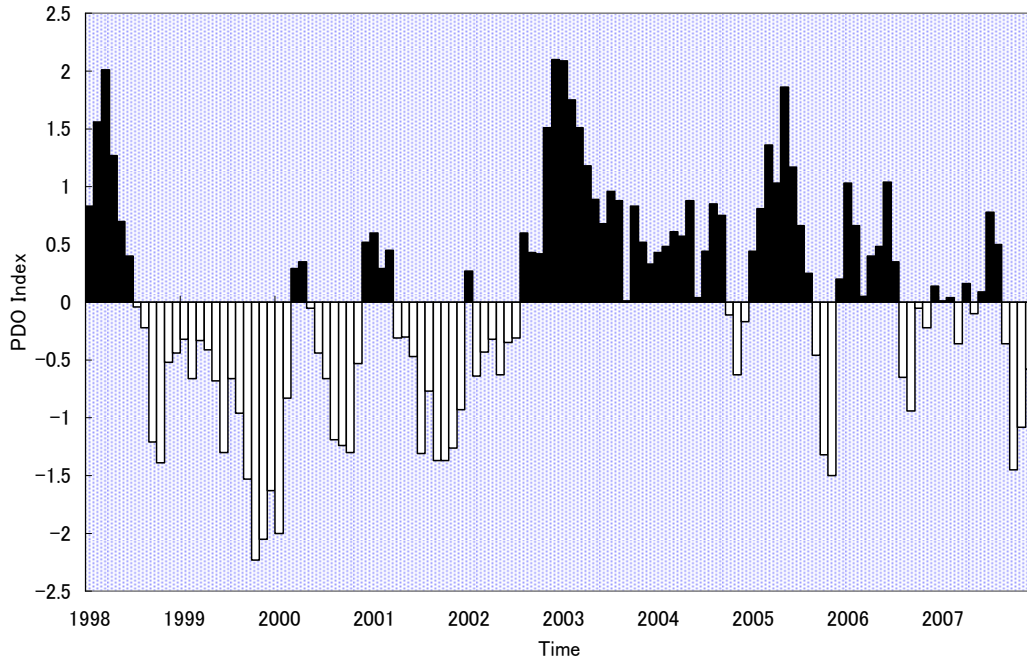
Figure 2-13. The pattern of Pacific Decadal Oscillation (PDO) from 1998 to 2007 is shown by the monthly PDO index. Positive PDO index (solid bar) correlates with warm-phase ENSO-like conditions while negative PDO index (white bar) with cold-phase ENSO-like conditions (Mantua et al. 1997). Data obtained from Dr. N. Mantua, Joint Institute for the Study of the Atmosphere and Oceans, University of Washington through http://jisao.washington.edu/pdo/PDO.latest, last accessed on April 2nd 2009.

2.6   Literature Cited

Anderson, N.H. and J.R. Sedell. 1979. Detritus processing by macroinvertebrates in stream ecosystems. *Annual Review of Entomology*, 24:351-377

Angradi, T.R. 1997. Hydrologic context and macroinvertebrate community response to floods in an Appalachian headwater stream. *American Midland Naturalist*, 138:371-386

Barbaro, L. and I.V. Halder. 2008. Linking bird, carabid beetle and butterfly life-history traits to habitat fragmentation in mosaic landscapes. *Ecography*, Early View. doi: 10.1111/j.1600-0587.2008.05546.x.

Bêche, L.A., E.P. Mcelravy and V.H. Resh. 2006. Long-term seasonal variation in the biological traits of benthic-macroinvertebrates in two Mediterranean-climate streams in California, U.S.A.. *Freshwater Biology,* 51:56-75

Bêche, L.A. and V.H. Resh. 2007. Short-term climatic trends affect the temporal variability of macroinvertebrates in California 'Mediterranean' streams. *Freshwater Biology*, 52:2317-2339

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

Boulton, A. J., C.G. Peterson, N.B. Grimm and S.G. Fisher. 1992. Stability of an aquatic macroinvertebrate community in a multiyear hydrologic disturbance regime. *Ecology*, 73: 2192-2207

Boyero, L. 2003. Multiscale patterns of spatial variation in stream macroinvertebrate communities. *Ecological Research*, 18:365-379

Bradley, D.C. and S.J. Ormerod. 2001. Community persistence among stream invertebrates tracks the North Atlantic Oscillation. *Journal of Animal Ecology*, 70:987-996

Brock, M.A., D.L. Nielsen, R.J. Shiel, J.D. Green and J.D. Langley. 2003. Drought and aquatic community resilience: the role of eggs and seeds in sediments of temporary wetlands. *Freshwater Biology*, 48:1207-1218

Brown A.V. and P.P. Brussock. 1991. Comparisons of benthic invertebrates between riffles and pools. *Hydrobiologia*, 220:99-108

Brittain, J.E. and T.J. Eikeland. 1988. Invertebrate drift - a review. *Hydrobiologia*, 166:77-93

Chevene, F., S. Dolédec and D. Chessel. 1994. A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology*, 31:295-309

Chessman, B.C. 2008. Climatic changes and 13-year trends in stream macroinvertebrate assemblages in New South Wales, Australia. *Global Change Biology*, Published Online. doi: 10.1111/j.1365-2486.2008.01840.x.

Compton, J.E., M.R. Church, S.T. Larned and W.E. Hogsett. 2003. Nitrogen export from forested watersheds in the Oregon coast range: the role of N_2-fixing Red Alder. *Ecosystems* 6:773-785

Corbet, P.S. 1957. The life-history of the emperor dragonfly *Anax imperator* Leach (Odonata: Aeshnidae). *Journal of Animal Ecology*, 26:1-69

Déry, S.J. and E.F. Wood. 2005. Decreasing river discharge in northern Canada. *Geophysical Research Letters*, 32:1-4

Dewson, Z.S., A.B.W. James and R.G. Death. 2007. A review of the consequences of decreased flow for instream habitat and macroinvertebrates. *Journal of North American Benthological Society*. 26:401–415

Dolédec, S., D. Chessel, C.J.F.ter Braak and S. Champely. 1996. Matching species traits to environmental variables: a new three-table ordination method. *Environmental and Ecological Statistics*, 3:143-166

Downes, J.A. 1969. The swarming and mating flight of Diptera. *Annual Review of Entomology*, 14:271-298

Dray, S. and A.B. Dufour. 2007. The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software*, 22:1-20

Durance, I. and S.J. Ormerod. 2007. Climate change effects on upland stream macroinvertebrates over a 25-year period. *Global Change Biology*, 13:942–957

Feller, M.C. and J.P. Kimmins. 1979. Chemical characteristics of small streams near haney in Southwestern British Columbia. *Water Resources Research*. 15:247-258

Fenchel, T.M. 1978. The ecology of micro-and meiobenthos. *Annual Review of Ecology and Systematics*, 9:99-121

Fisher, S.G., L.J. Gray, N.B. Grimm and D.E. Busch. 1982. Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monographs*, 52:93-110

Fleming, S.W., P.H. Whitfield, R.D. Moore and E.J. Quilty 2007. Regime-dependent streamflow sensitivities to Pacific climate modes cross the Georgia–Puget transboundary ecoregion. *Hydrological Processes*, 21:3264–3287

Folland, C.K., J.A. Renwick, M.J. Salinger and A.B. Mullan. 2002. Relative influences of the Interdecadal Pacific Oscillation and ENSO on the South Pacific Convergence Zone. *Geophysical Research Letters*, 29:1643-1647

Fritz, K. and W. Dodds. 2004. Resistance and resilience of macroinvertebrate assemblages to drying and flood in a tallgrass prairie stream system. *Hydrobiologia*, 527:99-112

Gilbert B, P.J. Dillon, K.M. Somers, R.A. Reid and L. Scott. 2008. Response of benthic macroinvertebrate communities to El Niño related drought events in six upland streams in south-central Ontario. *Canadian Journal of Fisheries and Aquatic Sciences*, 65:890-905

Giller, P.S., N. Sangpradub and H. Twomey. 1991. Catastrophic flooding and macroinvertebrate community structure. *Internationale Vereinigung fuer Theoretische und Angewandte Limnologie*. 24:1724-1729

Gomi, T., R.D. Moore & A.S. Dhakal. 2006. Headwater stream temperature response to clear-cut harvesting with different riparian treatments, coastal British Columbia, Canada. *Water Resources Research*, 42, W08437. doi: 10.1029/2005WR004162

Gray, L.J. 1981. Species composition and life histories of aquatic insects in a lowland Sonoran desert stream. *American Midland Naturalist*, 106:229-242

Harvey, B.C., J.L. White and R.J. Nakamoto. 2005. Habitat-specific biomass, survival, and growth of rainbow trout (*Oncorhynchus mykiss*) during summer in a small coastal stream. *Canadian Journal of Fisheries and Aquatic Sciences*, 62:650-658

Hildrew A.G. 1996. Whole river ecology: spatial scale and heterogeneity in the ecology of running waters. *Archiv für Hydrobiologie*, Supplement 113:25–43

Hughes, S.J., T. Ferreira and R.V. Cortes. 2008. Hierarchical spatial patterns and drivers of change in benthic macroinvertebrate communities in an intermittent Mediterranean river. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 18:742-760

Hulme, M. 2004. Recent climate trends. *In* Climate Change and Biodiversity. T.E. Lovejoy & L. Hannah (eds). Yale University Press, Grand Rapids, Michigan. pp.31-40

Hurrell, J.W. 1995. Decadal trends in the North Atlantic Oscillation: regional temperatures and precipitation. *Science*, 269:676-679

Huryn, A.D. and J.B. Wallace. 2000. Life history and production of stream insects. *Annual Review of Entomology*, 45:83-110

Hynes, H.B.N. 1976. Biology of Plecoptera. *Annual Review of Entomology*, 21:135-153

Jackson, J. K. and L. Füreder. 2006. Long-term studies of freshwater macroinvertebrates: a review of the frequency, duration and ecological significance. *Freshwater Biology*, 51:591-603

James, A.B.W., Z.S. Dewson and R.G. Death. 2008a. The effect of experimental flow reductions on macroinvertebrate drift in natural and streamside channels. *River Research and Applications*, 24:22-35

James, A.B.W., Z.S. Dewson and R.G. Death. 2008b. Do stream macroinvertebrates use instream refugia in response to severe short-term flow reduction in New Zealand streams? *Freshwater Biology*, 53:1316-1334

Jenkins, J., J. Powell, J. Logan and B. Bentz. 2001. Low seasonal temperatures promote life cycle synchronization. *Bulletin of Mathematical Biology*, 63:573-595

Jentsch, A., J. Kreyling, and C. Beierkuhnlein. 2007. A new generation of climate-change experiments: events, not trends. *Frontiers in Ecology and the Environment*, 5:365-374

Jongman, R.H.G., C.J.F. ter Braak and O.F.R. van Tongeren, Eds. 1995. Data Analysis in Community and Landscape Ecology. New Ed. Cambridge University Press, New York, 290p.

Karlsson, O.M., J.S. Richardson and P.M. Kiffney. 2005. Modelling organic matter dynamics in headwater streams of south-western British Columbia, Canada. *Ecological Modelling*, 183:463-476

Kazi-Aoual, F., S. Hitier, R. Sabatier and J. Lebreton. 1995. Refined approximations to permutation tests for multivariate inference. *Computational Statistics & Data Analysis*, 20:643-656

Kiffney, P.M., J.S. Richardson, M.S. Feller. 2000. Fluvial and epilithic organic matter dynamics in headwater streams of southwestern British Columbia, Canada. *Archiv für Hydrobiologie*, 149:109-129

Kiffney, P.M., J.P. Bull and M.C. Feller. 2002. Climatic and hydrologic variablity in a coastal watershed of Southwestern British Columbia. *Journal of the American Water Resources Association*, 38:1437-1451

Kiffney, P.M., J.S. Richardson and J.P. Bull. 2003. Responses of periphyton and insects to experimental manipulation of riparian buffer width along forest streams. *Journal of Applied Ecology* 40:1060–1076

Krebs, C.J. 2001. Ecology: the Experimental Analysis of Distribution and Abundance. 5th Ed. Benjamin Cummings,Toronto, 695p.

Lake, P.S. 2000. Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society*, 19:573-592

Logan, P. and M.P. Brooker. 1983. Macroinvertebrate faunas of riffles and pools. *Water Research*, 17:263-270

Lundquist, J.D. and D.R. Cayan. 2002. Seasonal and spatial patterns in diurnal cycles in streamflow in the western United States. *Journal of Hydrometeorology*, 3:591-603

Lytle, D.A. 2002. Flash floods and aquatic insect life-history evolution: evaluation of multiple models. *Ecology*, 83:370-385

Lytle, D.A. and N.L. Poff. 2004. Adaptation to natural flow regimes. *Trends in Ecology and Evolution*, 19:94-100

MacArthur, R.W. 1972. Geographical Ecology. Harper and Row, New York. 269p.

MacArthur, R.W. and E.O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, New Jersey. 203p.

Mantua, N.J. 2009. The Pacific Decadal Oscillation. http://tao.atmos.washington.edu/pdo/. [last accessed 30 April 2009].

Mantua, N.J., S.R. Hare, Y. Zhang, J.M. Wallace and R.C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society*, 78:1069-1079

McKerchar, A.I. and R.D. Henderson. 2003. Shifts in flood and low-flow regimes in New Zealand due to interdecadal climate variations. *Hydrological Sciences Journal*, 48:637-654

Merritt R.W. and K.W. Cummins. 1996. An Introduction to the Aquatic Insects of North America. 3rd ed. Kendall Hunt Publishing, Iowa, 862p.

Miller, S.W., D. Wooster and J. Li. 2007. Resistance and resilience of macroinvertebrates to irrigation water withdrawals. *Freshwater Biology*. Applied issues: 1-17

Milly, P.C.D., K.A. Dunne and A.V. Vecchia. 2005. Global pattern of trends in streamflow and water availability in a changing climate. *Nature*, 438:347-350

Minshall, G.W. 2003. Responses of stream benthic macroinvertebrates to fire. *Forest Ecology and Management*, 178:155-161

Molles, M.C. and C.N. Dahm. 1990. A perspective on El Niño and La Niña: global implications for stream ecology. *Journal of the North American Benthological Society*, 9:68-76

Moore, R.D. 2005. Introduction to salt dilution gauging for streamflow measurement part III: Slug injection using salt in solution. *Streamline*, 8:1-6

Negishi, J.N. and J.S. Richardson. 2006. An experimental test of the effects of food resources and hydraulic refuge on patch colonization by stream macroinvertebrates during spates. *Journal of Animal Ecology*, 75:118-129

Nelson, K.C. and M.A. Palmer. 2007. Stream temperature surges under urbanization and climate change: data, models, and response. *Journal of American Water Resources Association*. 43:440-452

Newbold, J. D., B.W. Sweeney and R.L. Vannote. 1994. A model for seasonal synchrony in stream mayflies. *Journal of the North American Benthological Society*, 13:3-18

Paine, R.T., M.J. Tegner and E.A. Johnson. 1998. Compounded perturbations yield ecological surprises. *Ecosystems*, 1:535-545

Palmer, M.A., P.A. Rensburger, P.S. Botts, C.C. Hakenkamp and J.W. Reid. 1995. Disturbance and the community structure of stream invertebrates: patch-specific effects and the role of refugia. *Freshwater Biology*, 34:343-356

Pickett, S.T.A. and P.S.White (eds). 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York. 472p.

Pittendrigh, C.S. 1954. On temperature independence in the clock system controlling emergence time in Drosophila. *Proceedings of the National Academy of Sciences of the United States of America*, 40:1018-1029

Poff, N.L. 1992. Why disturbances can be predictable: a perspective on the definition of disturbance in streams. *Journal of the North American Benthological Society*, 11:86-92

Poff, N.L. 1996. A hydrogeography of unregulated streams in the United States and an examination of scale-dependence in some hydrological descriptors. *Freshwater Biology*, 36:71-79

Poff, N.L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society*, 16:391-409

Pojar, J., K. Klinka and D.A. Demarchi. 1991. Coastal western hemlock zone. *In* Ecosystems of British Columbia. D.V. Meidinger and J. Pojar (eds). Special Report Series 6. Research Branch, British Columbia Ministry of Forests, Victoria, B.C., pp.95-111

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

R Development Core Team 2007-2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Rempel, L.L., J.S. Richardson and M.C. Healey. 2000. Macroinvertebrate community structure along gradients of hydraulic and sedimentary conditions in a large gravel-bed river. *Freshwater Biology*, 45:57-73

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

Resh, V.H., A.G. Hildrew, B. Statzner and C.R. Townsend. 1994. Theoretical habitat templets, species traits, and species richness: a synthesis of long-term ecological research on the Upper Rhône River in the context of concurrently developed ecological theory. *Freshwater Biology*, 31:539-554

Richardson, J.S. 1991. Seasonal food limitation of detritivores in a montane stream: an experimental test. *Ecology*, 72:873- 887

Richardson, J.S., P.M. Kiffney, K.A. Maxcy and K. Cockle. 2002. An experimental study of the effects of riparian management on communities of headwater streams and riparian areas in coastal BC: how much protection is sufficient? *In* Proceedings from Sustainable Forest Management Network Conference "Advances in Forest Management: From Knowledge to Practice," Edmonton, Alberta, pp.180-186

Rood, S.B., G.M. Samuelson, J.K. Weber and K.A. Wywrot. 2005. Twentieth-century decline in streamflows from the hydrographic apex of North America. *Journal of Hydrology*, 306:215-233

Rood, S.B., J. Pan, K.M. Gill, C.G. Franks, G.M. Samuelson and A. Shepherd. 2008. Declining summer flows of Rocky Mountain rivers: changing seasonal hydrology and probable impacts on floodplain forests. *Journal of Hydrology*, 349:397-410

Schindler, D.W. 1997. Widespread effects of climatic warming on freshwater ecosystems in North America. *Hydrological Processes*, 11:1043-1067

Snyder, C.D. and Z.B. Johnson. 2006. Macroinvertebrate assemblage recovery following a catastrophic flood and debris flows in an Appalachian Mountain stream. *Journal of the North American Benthological Society*, 25:825-840

Sousa, W.P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics*, 15:353-391

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? *The Journal of Animal Ecology*, 46:337-365

Southwood, T.R.E. 1988. Tactics, strategies and templets. *Oikos*, 52:3-18

Stanley, E.H., S.G. Fisher and N.B. Grimm. 1997. Ecosystem expansion and contraction in streams. *Bioscience*, 47:427-435

Statzner, B., B. Bis, S. Dolédec and P. Usseglio-Polatera. 2001. Perspectives for biomonitoring at large spatial scales: a unified measure for the functional composition of invertebrate communities in European running waters. *Basic and Applied Ecology*, 2:73-85

Statzner,B., N. Bonada and S. Dolédec. 2007. Conservation of taxonomic and biological trait diversity of European stream macroinvertebrate communities: a case for a collective public database. *Biodiversity and Conservation*, 16:3609-3632

Thomson, J.R., D.D. Hart, D.F. Charles, T.L. Nightengale and D.M. Winter. 2005. Effects of removal of a small dam on downstream macroinvertebrate and algal assemblages in a Pennsylvania stream. *Journal of the North American Benthological Society*, 24:192-207

Thuiller W., D.M. Richardson, M., Rouget, S. Prochesx and J.R.U. Wilson. 2006. Interactions between environment, species traits, and human uses describe patterns of plant invasions. *Ecology*, 87, 1755–1769.

Townsend, C.R. and A.G. Hildrew. 1994. Species traits in relation to a habitat templet for river systems. *Freshwater Biology*, 31:265-275

Townsend, C.R., M.R. Scarsbrook and S. Doledec. 1997. Quantifying disturbance in streams: alternative measures of disturbance in relation to macroinvertebrate species traits and species richness. *Journal of the North American Benthological Society*, 16:531-544

Williams, D.D. 2006. The Biology of Temporary Waters. Oxford University Press, New York. 337p.

Wills, T.C., E.A. Baker, A.J. Nuhfer and T.G. Zorn. 2006. Response of the benthic macroinvertebrate community in a northern Michigan stream to reduced summer streamflows. *River Research and Applications*, 22:819-836

Wipfli, M.S. and D.P. Gregovich. 2002. Export of invertebrates and detritus from fishless headwater streams in southeastern Alaska: implications for downstream salmonid production. *Freshwater Biology* 47:957–969

Wipfli. M.S., J.S. Richardson and R.J. Naiman. 2007. Ecological linkages between headwaters and downstream ecosystems: Transport of organic matter, invertebrates and wood down headwater channels. *Journal of the American Water Resources Association.* 43:72-85

White, P.S., and A. Jentsch. 2001. The search for generality on studies of disturbance and ecosystem dynamics. *Progress in Botany* 62:399–450

Zhang, X., K.D. Harvey, W.D. Hogg and T.R. Yuzyk. 2001. Trends in Canadian streamflow. *Water Resources Research*, 37:987-998

Chapter 3 Modelling the relationships between headwater stream aquatic insect community and summer low-flow events in the future scenarios.

3.1   Introduction

There is increased theoretical and empirical interest in the relationships between ecosystem functions and community structures, involving the functional trait types within the community in the past 15 or so years, including freshwater ecosystems and adjacent riparian areas (e.g. Resh et al. 1994; Townsend and Hildrew 1994; Townsend et al. 1997; Lambeets et al. 2009). The reason for this can be attributed to the increased understanding of the importance of the roles biotic communities play in ecosystem functions (e.g. Loreau et al. 2001) and the concerns about the conservation of natural systems (Bunn and Archington 2002). Trait-based approaches to understanding the community structures and the community's roles in ecosystem functioning have gained much attention in the past decades (e.g. Cummins 1973; Calow 1987; Dolédec et al. 1999; Petchey and Gaston 2002; McGill et al. 2006). Trait-based approaches attempt to elucidate the relationships between biodiversity and ecosystem functioning through analyses of the trait variations among the organisms along environmental gradients (e.g. Townsend and Hildrew 1994; Statzner et al. 1997; Díaz et al. 2008). The main advantage of this approach, as opposed to a species-based approach, is the ease of generalization across different ecosystems, especially over geography, due to lack of taxonomic constraints (Statzner et al. 2007). However, concerns with possible declines in ecosystem stability associated with species loss (Hooper et al. 2005) suggest that an integrative approach utilizing both species and trait compositions would be better.

Various future climate scenarios suggest that the potential impacts on freshwater ecosystems would likely be substantial (e.g. IPCC 1996; Hulme 2004; Chapter 1). The

impacts would be seen more clearly in small streams and lakes where the buffering capacity against changes in precipitation patterns is low. These impacts will further be complicated by the increasing use of freshwater by humans (Waggoner and Schefter 1990; Gleick 1998; Palmer et al. 2008).

Assessments of community composition with respect to environmental filters (Southwood 1977, 1988; Poff 1996, 1997; Matthews 1998) would allow one to infer potential effects of filters on biodiversity and perhaps ecosystem functions but not the underlying mechanisms. The underlying mechanisms can be examined by studying the changes in trait composition of a community with respect to the filters (e.g. Townsend and Hildrew 1994). Therefore, examining both the species composition of a community and the suite of biological traits is crucial to understand the impacts that changes in climate variables have on biological communities.

To further our understanding of the potential climatic impacts on biological communities in the future, the relationships between the community and low-flow events were investigated through modelling populations within the community. The modelling procedure focused on the differences in life histories and functional traits of the populations included in the community. Here, a community was treated as a collection of populations that exist together in space and time, but without any interaction terms between populations. The community was based on the aquatic insect community of the forested, headwater streams in Malcolm Knapp Research Forest, B.C. Canada. The suitability of headwater streams and aquatic insects to study the potential impacts of future climatic changes has already been introduced in Chapter 1).

The purpose of this study was to analyze the potential impacts of future discharge scenarios on lotic insect communities by developing a set of population models based on observed patterns from existing empirical data (the 9-yr MKRF data; see Chapter 2 for the

descriptions of the data). The biological traits of the taxonomic groups (Q; see Table 2-4) were incorporated as a measure of each taxonomic group's resistance against low-flow events.

In this chapter, two questions were examined specifically. 1) How would a 10-year scenario with random low-flow events that are within the existing non-extreme range (scenario 1; sc1) affect the community structure, given the differences in the population viabilities against summer low-flow events? 2) How would the result of sc1 compare with the one from a 10-year scenario with increasing severity of summer low-flow events (sc2)? To simplify the model to answer the above questions, preliminary analyses utilizing two-table ordinations (see Appendix F for details) were used to determine which of the following low-flow variables best explains the observed community composition provided that summer low-flow events affect population dynamics: minimum discharge, frequency, duration, intensity or abruptness, (see Chapter 2). A community model was then developed as a set of models for populations that differ in their life cycle, starting densities and responses against low-flow events.

3.2   Methods

3.2.1   Model structure

Four simple time-step population models (see Table 3-1 for descriptions) were created matching the four most common life cycle types seen in the MKRF communities. These four life cycle types were based on discrete differences in generations per year (1, <1, >1) and timing of the reproductive period (summer, not summer). Two low-flow event parameters chosen by the preliminary analyses were duration and minimum discharge (Appendix F). A total of 55 taxonomic groups (TGs) were included in this study (See Appendix G for the full list). Each TG was given a model code (LCcode; from A to D), a resistance code that was calculated according to its fuzzy-coded biological traits (rescode; Appendix D), and an initial

population density per m^2 (N.zero.m2). LCcode was used to assign the appropriate model structure to each taxonomic group. The resistance codes were created to incorporate the biological traits into the models. For simplicity, scalars for resistance were set by categorizing each trait into either beneficial (0.5), neutral (1) or disadvantageous (2) against summer low-flow events (Table 3-2). The resistance code of each TG was then calculated by taking the product of the resistance value and the proportion for that TG from fuzzy-coding. Note that when a TG had desiccation resistance (i.e. fuzzy-code for e1>0), the resistance code of 0.5 replaced the sum (i.e. the desiccation resistance was assumed to override any disadvantageous traits). N.zero.m2 was calculated as the average relative density of each taxonomic group in the MKRF benthic invertebrate count data (see Appendix C for the relative abundance data).

Summer mortality (m_s) was assumed to be additive (Figure 3-1; Equation 1): mortality due to duration (m_{Dur}) and one due to minimum discharge (m_{minQ}).

$$m_s = m_{Dur} + m_{\min Q}$$ Equation 1

To set mortality curves, the ranges of Dur and minQ were first standardized from 0-169 days (the maximum number of days in a summer) and 0-1.5 Ls^{-1} to 0-1. For simplicity, m_{Dur} was assumed to follow a sigmoidal curve with 50% mortality rate reached at the duration of the 9-yr average duration + 2 standard deviations (Equation 2; Figure 3-2). In other words, the coefficient of 17.35 was calculated arbitrarily.

$$m_{Dur} = \frac{0.01e^{17.35Dur}}{0.01e^{17.35Dur} + 1 - 0.01}$$ Equation 2

The curve of m_{minQ} was assumed to be sigmoidal with increased rate of change below the average minimum discharge until it reached a mortality rate of 0.7 at the lowest minimum discharge of zero (Equation 3; Figure 3-3). The highest mortality rate of 0.7 was chosen instead of 1 due to the observation that occurrence of 0 Ls^{-1} discharge is relatively common

(within 1 standard deviation) and multiple TGs seem to survive such events (the MKRF data, Chapter 2).

$$m_{\min Q} = \frac{0.7e^{-25\min Q}}{0.7e^{-25\min Q} + 1 - 0.7}$$ Equation 3

Similarly, summer reproduction rate (r_s) was set as Equation 4 where r is the non-summer reproduction rate (r).

$$r_s = r \times e^{Dur \times -\min Q}$$ Equation 4

Other parameters were arbitrarily set to the following in the simulations. Non-summer reproduction rate (r) was set to 2, while winter mortality (ms) to 0.2 and number of generations per year (g) to 2 when the number of generation per year was more than 1. Note that reproduction rates took into account the adult emergence rate, fecundity, egg survival and hatching rates.

The four population models were then used to simulate community structures over a 10-year time period with two different scenarios with respect to low-flow events. Scenario 1 (sc1) treated low-flow events to be normally distributed around the 9-year average from the MKRF data, with each year of simulation taking a sample randomly from this distribution. Scenario 2 (sc2) assumed that the severity of low-flow events would increase each year reaching compound increase of 10% over the 10-year simulation time. Each population was simulated 1,000 times resulting in 1,000 community structures per scenario. All simulations were run using Program R (ver. 2.6-2.9.0; R Development Core Team 2008; 2009).

3.2.2   Data analysis

For each simulation result, three diversity indices were calculated: richness, Simpson's and Shannon. All three widely used indices were included for potential comparisons with other studies since there is no standardization on which index to use. To compare the diversity

indices between the two scenarios (sc1 and sc2), each index was tested for normality using Shapiro-Wilk's test. If the distribution was not normal (α=0.05), then the Wilcoxon Rank Sum test was used instead of a two-sample t-test to compare the means between sc1 and sc2. The proportions of each functional feeding group (FFG; Anderson and Sedell 1979) were calculated at time 10 of all simulations to be compared between the two scenarios. The FFG was assigned according to the fuzzy-coded traits (Appendix F). The proportions of shredders were tested for any significant difference between sc1 and sc2 as an example using either a two-sample t-test or a Wilcoxon (one or two sample/s) or Kruskal-Wallis (multiple samples) Rank Sum test depending on the results from the normality test (Shapiro-Wilk).

Each taxonomic group's local extinction rate over the 1,000 trials and an average time to extinction was calculated for each simulation result. A TG was considered "extinct" when the population density equalled 0. The pattern of extinction rate distribution over the 55 TGs was categorized into three extinction rate groups: High (extinction rate >0.8), Mid (0.06 to 0.8), and Low (<0.06) according to those obtained for sc1. To compare the differences in TGs' responses towards the two scenarios, differences in extinction rates (sc_d) were calculated (sc2-sc1) for all TGs. Analysis of variance for fitted linear model was used to investigate if Order, Family, LCcode, N.zero.m2, rescode or extinction rate categories would explain the patterns seen in sc_d. In addition, to see if sc_d was related to any habitat preferences (e.g. riffle vs. pool) by TGs, information was gathered on habitat preferences using a USGS database (Vieira et al. 2006), field observations and other sources (e.g. E-fauna BC 2009). Gathered information was then fuzzy coded (Chevene et al. 1994) as proportions, e.g., a total of 27 records were found for perlod (Perlodidae; Plecoptera), of which 20 stated riffle as the preferred habitat resulting in a fuzzy code of perlod for riffle of 0.74. To simplify the comparisons between riffle and pool preferences, fuzzy codes > 0.5 for riffle were categorized as riffle group and the rest as pool group. The relationships between sc_d and riffle vs. pool

groups were analyzed using Wilcoxon Rank Sum test. ANOVA was used to test the relationships between the arbitrarily assigned extinction rate categories (High, Mid and Low) and riffle vs. pool groups. When ANOVA involving multiple samples resulted in rejecting the null hypothesis that there is no difference between the groups, Tukey's Honest Significant Differences test (HSD) was used to find the category that differed from others. All analyses were run using Program R 2.9.0 (R Development Core Team 2009).

3.3   Results

3.3.1   Simulation

The relative density of all taxa was simulated for the 2 scenarios (sc1 and sc2) 1,000 times using the 4 population models. For example, the simulations of five trials on three taxonomic groups (TGs) illustrate the differences in responses to low-flow events by different TGs (panels A vs. B vs. C in Figure 3-4) as well as differences between the scenarios (Figure 3-4). TGs can differ in their extinction rates or timings. For instance, the net-spinning caddisfly *Dolophilodes* (Doloph) had the highest extinction rates (Figure 3-4.A), while *Ameletus* spp. (Amelet) was amongst the least affected of TGs with extinction rate of zero (Figure 3-4.B). Doloph's time to local extinction clearly shortened under sc2 compared to one under sc1.

3.3.2   Time to extinction (sc1 vs. sc2)

Time to extinction of TGs did not differ significantly between the two scenarios (Kruskal-Wallis Rank Sum test; $\chi^2 = 0.21$, p = 0.64) with average extinction timings of 8.87 (sc1) and 8.84 year (sc2), and average standard deviations of 0.84 (sc1 and sc2). Most TGs had the same average extinction timings for the two scenarios.

3.3.3   Extinction rates (sc1 vs. sc2)

The model simulations showed that taxonomic groups differ in their response to the two future scenarios of low-flow event severity given here. Some showed significant differences between the two scenarios (*Baetis* spp., *Palpomyia* spp., *Parapsyche* spp., *Tipula* spp.), all of which were categorized as having medium local extinction rates (Figure 3-5). ANOVA of Order, Family, LCcode, N.zero.m2 and rescode with respect to sc_d showed no significant differences (ANOVA; e.g. $F_{3,51} < 0.9$, $p > 0.4$ for LCcode). When TGs were categorized into the three extinction rate groups (High, Mid and Low), Mid differed significantly from the other two groups (ANOVA; $F_{2,52} = 73.7$, $p < 0.001$; Figure 3-6). Furthermore, the arbitrarily chosen extinction rate categories could be explained by the habitat preferences of taxonomic groups (riffle vs. pool; ANOVA $F_{1,53} = 6.62$, $p = 0.013$). Within Mid, insect families explained the variations in sc_d significantly (ANOVA $F_{15,5} = 6.67$, $p = 0.023$). Tukey HSD showed that Rhyacophilidae significantly differed from Hydropsychidae (adjusted $p = 0.028$), Nemouridae (adjusted $p = 0.036$), Baetidae (adjusted $p = 0.038$) and Tipulidae (adjusted $p = 0.038$) in their response to the two low-flow scenarios (sc_d).

3.3.4   Community responses (sc1 vs. sc2)

The differences in community response against the two low-flow scenarios can be seen by comparing the diversity indices. The calculated diversity indices for the two scenarios are summarized in Table 3-3. For both scenarios (sc1 and sc2), the distributions of richness and Shannon's index were not normal ($W < 0.995$, $p < 0.003$). By Wilcoxon Rank Sum test, sc1 and sc2 differed significantly for both Richness and Shannon's index (Wilcoxon > 63383, $p = 0$). Similarly, Simpson's Index was found to differ significantly between the two scenarios ($t = 6.74$, $p < 0.001$). For all the above cases, sc2 showed lower values that sc1. Scrapers, Filterers and Deposit-feeders showed lower total proportions in sc2 then sc1 while Shredders

and Predators showed the opposite. For example, the proportions of Shredders at time 10 for sc2 was significantly higher than that of sc1 (Wilcoxon = 579645, p < 0.001; sc_d = 0.002).

3.4 Discussion

A set of population models applied to the benthic aquatic insects in riffles of forested, headwater streams revealed that traits can be used to predict insects' responses to summer low-flow events. The benthic insect community could be categorized by their differential responses to the two scenarios into three groups that differ in their levels of preference for habitats, i.e. riffles or pools. This indicates that their traits are largely correlated with their habitat preferences. This observation is in agreement with the previous studies suggesting that the riffle and pool communities are different from each other (e.g. Logan and Brooker 1983; Brown and Brussock 1991).

The results of simulations largely agreed with the observations from previous studies and predictions even though the models often did not incorporate the mechanisms. For example, a well-known rheostenic ('confined to streams'; Jaag and Ambühl 1964) taxon, Simuliidae (Diptera), showed relatively high average extinction rates even though their dependence on current for respiration and feeding (Hynes 1970) was not incorporated into the models. Similarly, net-spinning caddisflies (Trichoptera), which also rely on current for feeding (Hynes 1970), appeared most vulnerable to summer low-flow events (Philopotamidae, Polycentropodidae and Hydropsychidae). Another caseless caddisfly family, Rhyacophilidae, also showed differential responses to the two low-flow event scenarios even though the difference was fairly small and their extinction rates were much lower than the other three. This difference could be attributed to the smaller body size of Rhyacophilidae or perhaps their multivoltine lifecycle (Leah A. Bêche, Claude Bernard Université de Lyon; Unpublished data) that was incorporated in the simulations. *Rhyacophila* spp. have been reported to be

reduced in abundance or extirpated by drought events (e.g. Delucchi 1988). Similarly, multiple taxonomic groups that showed mid to high extinction rates in this study have been reported vulnerable to drying events: e.g. *Baetis* spp., *Ephemerella* spp., Capniidae, *Glossosoma* spp., *Hydropsyche* spp. and *Dolophilodes* spp. (Delucchi 1988).

Large-bodied taxa were assumed to be more susceptible to low-flow events than smaller taxa (Huryn and Wallace 2000). The assumption held for Perlidae (Plecoptera; 89-96% extinction rates) but not for Pteronarcyidae (Plecoptera), even though the elimination of both families due to drying has been reported (e.g. Chadwick and Huryn 2005). The only Pteronarcyidae included in this study was *Pteronarcys californica* and this particular species has been reported to survive in temperate, intermittent streams (Muchow and Richardson 2000). The discrepancy probably arose from the differences in the dry conditions between the two studies. The large size of Pteronarcyidae seems to be vulnerable under the climate of south eastern U.S. (Chadwick and Huryn 2005), in which the temperature is much higher than that of streams in the North Pacific temperate rain forests (Muchow and Richardson 2000). Another large-bodied species in these streams with two or more year life cycle is the dragonfly *Cordulegaster dorsalis* (Marczak et al. 2006), which was not included in this study due to their low abundance. *C. dorsalis* in this area has been found to survive late summer drying event by seeking refuge in shrinking pools.

Although having a longer life cycle (two years in this case) seems disadvantageous to seasonal low-flow events (Huryn and Wallace 2000) as they experience the effects twice as often as others when even once seems bad to survive a potentially extreme event, the densities of these taxonomic groups did not differ significantly from others. For example, *Despaxia augusta* (Plecoptera: Leuctridae) showed an extinction rate of zero under both scenarios. Moreover, this result is in agreement with the previous observations of *Despaxia augusta* occupying a large proportion of benthic communities in temperate, intermittent streams

(Richardson 2001; Banks et al. 2007). This was rather surprising as unlike the suggestion by Banks et al. (2007), resistance codes incorporated here had no information on physical refugia or behavioural adaptations to escape low-flow events.

Despite their records of surviving in small, forested streams with intermittent flow (Muchow and Richardson 2000), *Soyedina producta* and *Zapada cinctipes* (Plecoptera: Nemouridae) showed moderate susceptibility to low-flow events according to their traits, unlike in the cases of *Pteronarcys californica* (Plecoptera: Pteronarcyidae) and *Malenka* spp. (Plecoptera: Nemouridae). This implies that tactics of *S. producta* and *Z. cinctipes* on surviving dryness are behavioural rather than physiological ones, since the traits incorporated in this study lacked behavioural avoidance of low-flow events (reviews in Lytle 2008). Upon drying of streams and rivers, a Plecopteran's behaviour of seeking refugia by burrowing into the hyporheic zone has been documented, especially for Capniidae and Taeniopterygidae, along with some Diptera (e.g. Harper and Hynes 1970; Gray and Fisher 1981; Boulton et al. 1992).

The significant differences between the community responses to the two low-flow scenarios indicate the importance of future climate scenarios on the persistence of aquatic insects, which in turn is a structural measure of ecosystem integrity (Death et al. 2009). The decrease in the relative abundance of shredders with low-flow events have been reported around the world due to increased water temperature (Oregon, U.S. – Dietrich et al. 1997; Arizona, U.S. – Bogan and Lytle 2007; U.K. – Durance and Ormerod 2009; Malaysia - Yule et al. 2009), eutrophication (Montana, U.S. – Ward and Stanford 1984; Spain – Camargo and de Jalón 1990; Portugal – Cortes et al. 1998, 2002) or possibly due to the reduced velocity (Italy – Fenoglio et al. 2007), habitat (Czech Republic – Řezníčková et al. 2007) or lateral connectivity (Georgia, U.S. - Griswold 2008). In this study, half of the shredders showed medium extinction rates (e.g. Elmidae: *Lara* sp.) similar to the expectation from their

sensitivity to various abiotic factors mentioned above. However, the rest showed fairly low extinction rates suggesting perhaps that their sensitivity to increased water temperatures is stronger than the one for reduced physical factors such as reduced discharges and habitat volume. Moreover, the relative abundance of shredders was, on average, higher for the scenario with increasing severity of low-flow events due to declines in the abundance of filter feeders and scrapers. This discrepancy from the existing literature could be due to the disconnection between low-flow events and stream temperatures in this study or the types of traits chosen to build the population models with (e.g. adult longevity, emergence timing and fecundity). Under low-flow or drought conditions, stream temperatures are often found to have larger impacts on aquatic insect assemblages than do discharges (e.g. Stubbington et al. 2009). Also, the small spatial scale considered here may explain this discrepancy compared to the existing studies that often encompass regions with different stream sizes (see above for examples).

An increase in low-flow severity of 10% over 10 years seems enough to affect the local community structures significantly. Lowered species richness can directly lower the community's contributions to ecosystem productivity even if the redundancy of functional traits was present. For example, loss of *Lepidostoma unicolor* (Trichoptera: Lepidostomatidae) in an experimental setting could not be compensated for by an increased abundance of remaining species (Ruesink and Srivastava 2001). In this study, although classified under the low local extinction rate category, *L. unicolor* did not escape the increased severity, suggesting that this level of change in severity could lower the ecosystem functions of streams. Moreover, the negative impacts observed here are predicted to be more severe in reality because the complications due to species interactions (e.g. competition and predation) were not incorporated in the model. This leads to a concern for the conservation of

benthic aquatic insect communities since the future changes to low-flow events could be as high as 50% of the current level (e.g. Schneider et al. 1990).

There was no immigration allowed in all models despite the importance of refugia and recolonization sources (Fagan 2002), thus the results can only be extrapolated for a closed community and may have few direct analogies in the real world. In reality, the space created by local extinctions of some taxa allows other taxa to colonize during (Georgia et al. 2006) or after (reviews in Boulton and Lake 2008) such disturbances. In the case of headwater streams, the downstream reaches (i.e. nearby permanent reaches) can act as sources of colonization (Delucchi 1988; del Rosario and Resh 2000), especially since most species present in the intermittent stream community are also present in the permanent streams (Richardson 1992; 2001). Also, since site-specific features mediate the effects of disturbance, the small spatial scale used here is problematic for further extrapolation of the findings to larger spatial scales. For example, stream bed type affects the refugia availabilities during low-flows. When a stream bed is porous (i.e. not bedrock), pools may be maintained by hyporheic flow (Stanley et al. 1997) or springs (Dahm et al. 2003) percolating through the channel bed. In other words, a lack of perceptible surface flow does not indicate that of groundwater connectivity. If the extinction rates simulated in this study using the population models could be compared to the immigration rates during the recolonization phase, and the rates of extinction are higher than those of immigration, then the effects of summer low-flow events on headwater stream community can be thought to follow the intermediate disturbance hypothesis (Petraitis et al. 1989).

An increase in inter-annual variations of precipitation and drought (or flood) frequency is projected in the future (Hulme 2004). The observed effects of an increase in low-flow event severity by 10% on an aquatic insect community of riffles in headwater streams signal the need for immediate attention to the underlying mechanisms and implications for conservation

of lotic systems. The changes in community structures could alter the ecosystem functions (Loreau et al. 2001), especially under the influences of disturbance events (Cardinale and Palmer 2002). Additional concerns related to reduction in flows include reduced water quality (e.g. Chessman and Robinson 1987), increased concentrations of pollutants (e.g. Boulton and Lake 1990) or salts (e.g. Lind et al. 2006) and increased water temperatures (e.g. Durance and Ormerod 2009) that were not considered in this study. Therefore, in reality, the effects of increased severity in low-flow events would have much larger effects on lotic community structures.

In conclusion, the two scenarios for low-flow parameters (random vs. increased severity) showed the importance of future climate scenario with intensifying extreme events on disturbing benthic insect communities. The simulations of the developed population models showed that a trait-based approach can identify sensitivities to different scenarios through differing extinction rates of aquatic insects. Although suggested by the differences in benthic community responses towards the two low-flow event scenarios, connecting the effects of low-flow events on macroinvertebrates to the effects on ecosystem functions still requires further investigation (e.g. Castella et al. 1995; Dewson et al. 2007a; 2007b; James et al. 2008).

The importance of low-flow events on lotic community structures is now recognized (Lytle and Poff 2004; Monk et al. 2008), especially for supraseasonal droughts (Boulton and Lake 2008; Stubbington et al. 2009). However, the difficulties in studying the mechanisms that connect the reduced flow and community structures still exist, largely due to the regional differences in low-flow events and biotic responses (Boulton 2003; Demuth and Young 2004; Boulton and Lake 2008: Monk et al. 2009). These difficulties could potentially be overcome by the use of trait-based approaches in combination with the suggested river classifications by flow regime regions (Monk et al. 2008). The benefits of the trait-based approaches to the relationships between environmental conditions and biotic communities are apparent (e.g.

Statzner et al. 1997; Bonada et al. 2007), however, the approaches are not always applicable. One main problem with aquatic insect communities, in particular, is the lack of trait information at genus levels. Trait information at genus levels can be crucial as aquatic insects often show a wide range of traits within a family. The recent efforts to compile catalogues of traits for aquatic insects in Europe (e.g. Statzner et al. 2007) and North America (e.g. Vieira et al, 2006) that are accessible to the public should assist the trait-based approaches greatly, and such efforts for other regions of the world are in need. Another confounding factor is the large temporal scale required for studying the underlying mechanisms. The required temporal scale is often outside of most research projects' time frame (Lake 2003). The increasing amount of long-term monitoring projects (longer than 10 years) around the world (e.g. U.K. - Bradley and Ormerod 2001; Monk et al. 2006; U.S. - Bêche et al. 2006) should assist in furthering our understanding of such mechanisms. Although long-term studies could potentially bias towards reporting increased community variability by including more environmental variability (Bengtsson et al 1997; Haddad et al. 2002; but see e.g. Scarsbrook 2002; Woodward et al. 2002; Griswold et al. 2008).

Table 3-1. Summary of the four population models for the different life cycles. Life Cycle of D was assumed to be 2 years. Reproduction periods were divided into November-April (non-summer) and May-October (summer). N = population size, t = time in years, m = mortality rate, r = reproduction rate, g = number of generation per summer that was assumed to be 2 for simplicity, $_s$ = summer, $_w$ = winter, J_1 = first year population size and J_2 = second year population size.

LCcode	Life Cycle (year)	# generation/year	Reproduction period
A	≤ 1	1	non-summer
	$\Delta N = N_t(1-m_s)r(1-m_w)$		Equation A
B	≤ 1	1	summer
	$\Delta N = N_t(1-m_s)r_s(1-m_w)$		Equation B
C	≤ 1	>1	summer
	$\Delta N = N_t(1-m_s)r_s^g(1-m_w)$		Equation C
D	> 1	<1	summer
	$\Delta N = N_{t+1} - N_t$ $= J_{1,t+1} + J_{2,t+1} - J_{1,t} - J_{2,t}$ $= J_{2,t}(1-m_{s2})r_s(1-m_w) - J_{1,t} + J_{1,t}(1-m_{s1})(1-m_w) - J_{2,t}$		Equation D

Table 3-2. The summary of resistance classes assigned to each of the chosen trait categories. The classification was based on traits with respect to summer low-flow events: beneficial (scalar = 0.5), neutral (1) or disadvantageous (2). The resistance classes were assigned relative to each category within a trait (i.e. at least one category in a trait received the neutral effect).

Categories	Categories	Effect	Example References
Body size			Huryn and Wallace 2000
	<20mm	1	
	>20mm	2	
Dispersal modes			Boulton et al. 1992
	aquatic	1	Lytle 2008
	aerial	0.5	
Resistance modes			Hynes 1970;
	desiccation	0.5	Wiggins 1973;
	diapause.egg	0.5	Wissinger et al. 2003
	diapause.larvae/pupae	0.5	
	diapause.adult	0.5	
	none	1	
Respiration modes			Lytle 2001
	aq.dep	2	
	aq.indep	1	
Locomotion modes			Boulton 2003
	mobile	1	
	epibenthic	1	
	endobenthic	0.5	
	attached	2	

Table 3-3. The comparisons of two scenarios on the diversity indices calculated for the 10-yr simulations. S is the number of species present at year 10. D was calculated as $\sum_{i=1}^{S} p_i^2$ and H was calculated as $-\sum_{i=1}^{S} p_i \log_2 p_i$, where p_i stands for the proportion of ith species. Both D and H were calculated using the R package VEGAN (Oksanen et al. 2009).

	Species richness (S)		Simpson's (D)		Shannon (H)	
Scenario	1	2	1	2	1	2
mean	41	39	0.52	0.54	1.05	0.98
SD	2.0	2.2	0.0714	0.070	0.156	0.149
min-max	34-46	33-47	0.29-0.72	0.30-0.73	0.59-1.59	0.58-1.54
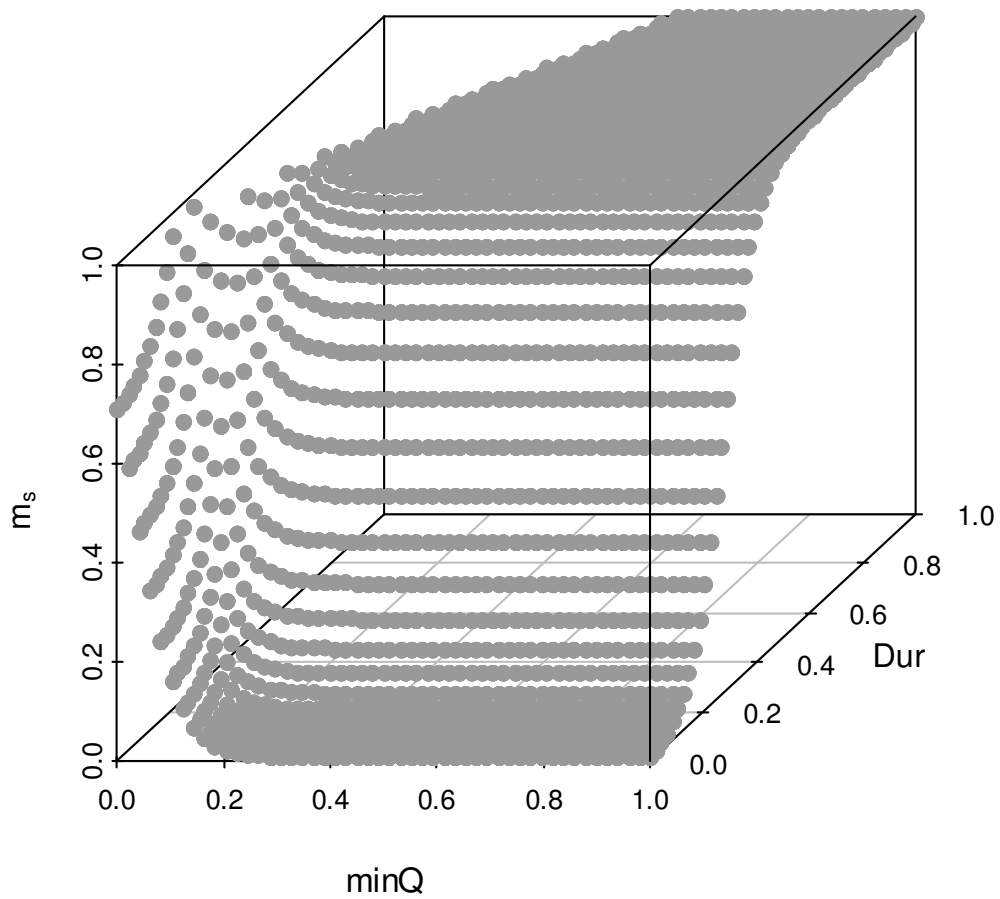
Figure 3-1. Total summer mortality (m_s) curve ranging from zero to one was used for simulations. The mortality curve of minimum discharge (m_{minQ}) and that of duration (m_{Dur}) were added to create m_s (Equations 1 to 3; Figures 3-2 and 3-3). Both minQ and Dur are unitless as they were 0-1 standardized.
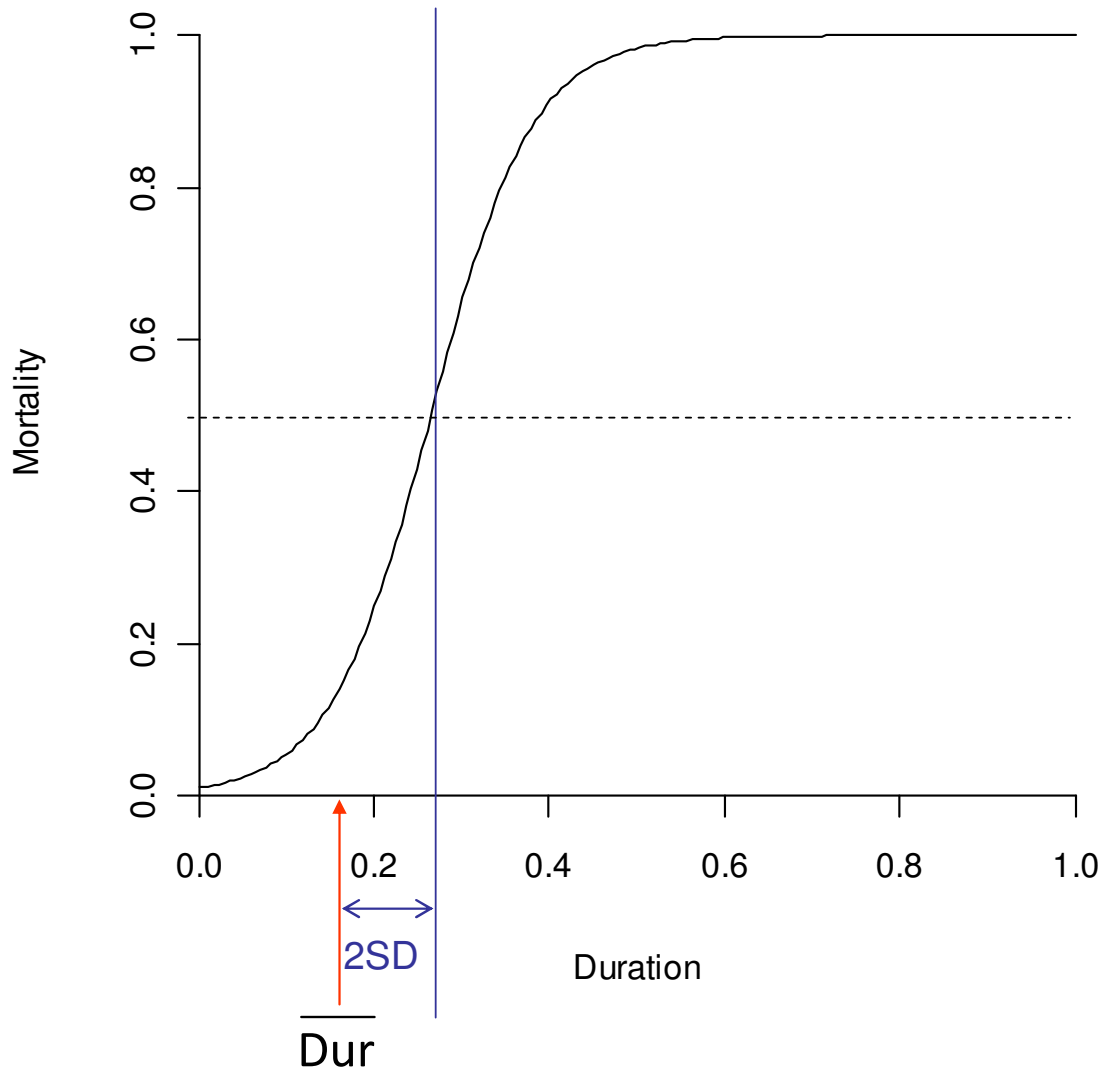
Figure 3-2. Mortality curve per generation due to the duration of the lowest flow event (mDur) used for simulations. mDur was assumed to follow a sigmoidal curve that reaches mortality of 0.5 (dotted horizontal line) at the duration of 9-year average ($\overline{\text{Dur}}$; red arrow) + 2 standard deviations (blue vertical line). See Equation 2 for the mathematical equation.
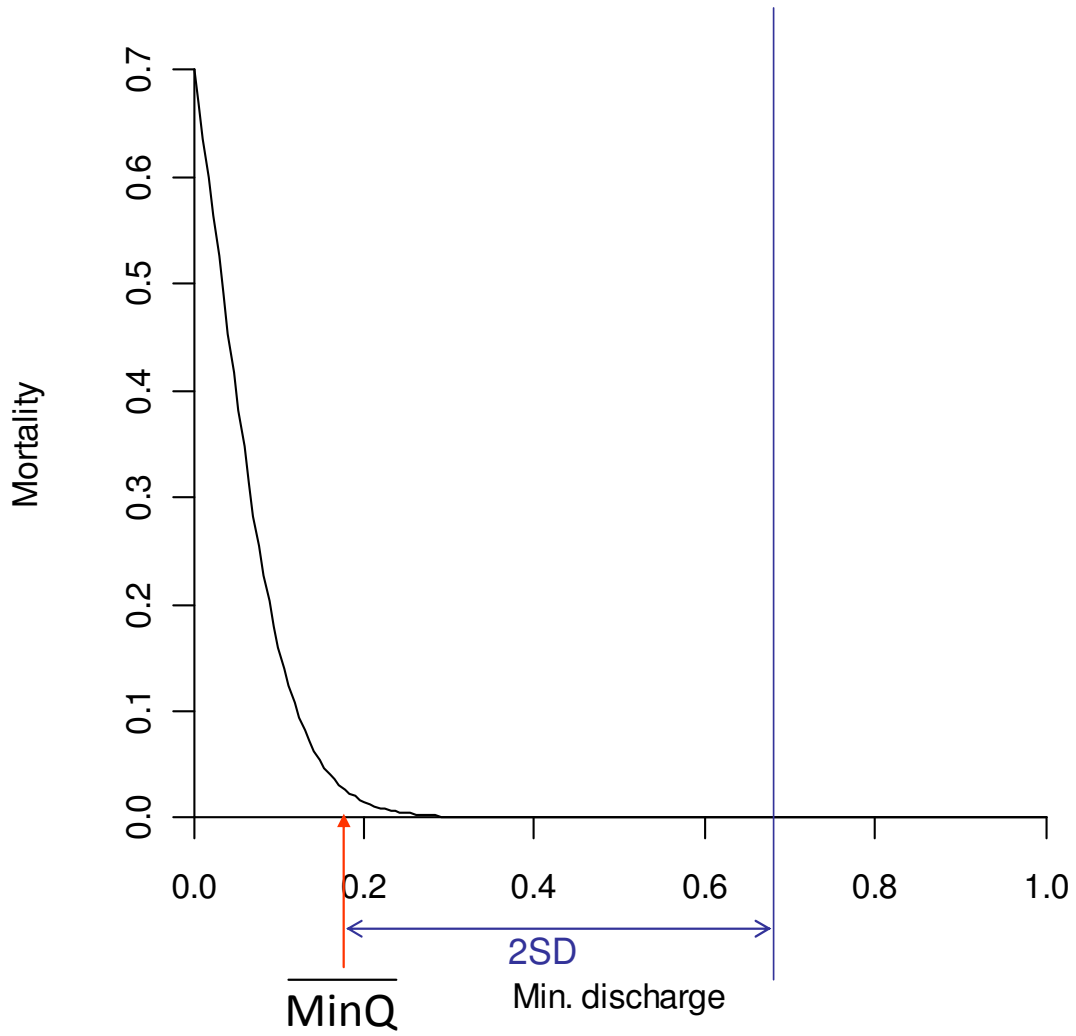
Figure 3-3. Mortality curve per generation due to minimum discharge (minQ) used for simulations. The curve was set to start increasing at the average ($\overline{\text{MinQ}}$) till it reaches mortality rate of 0.7 at the lowest discharge. See Equation 3 for the mathematical equation.
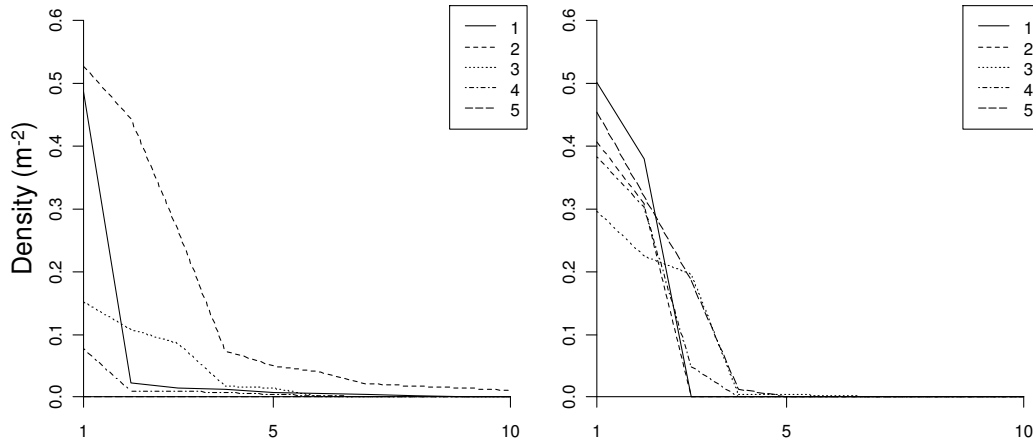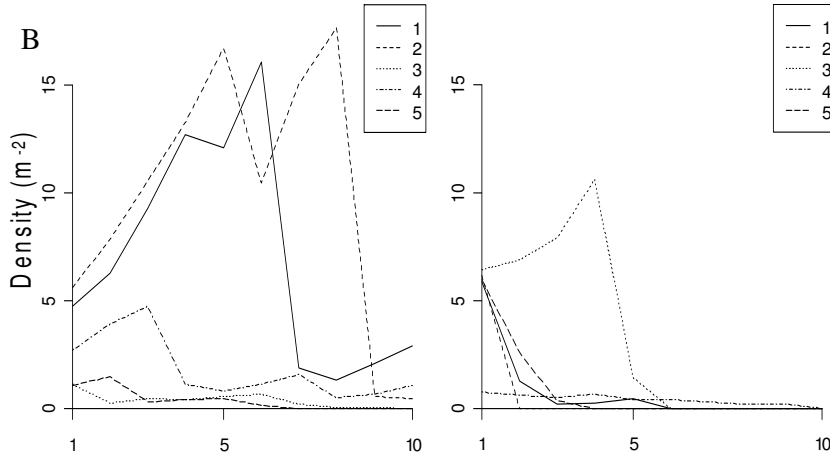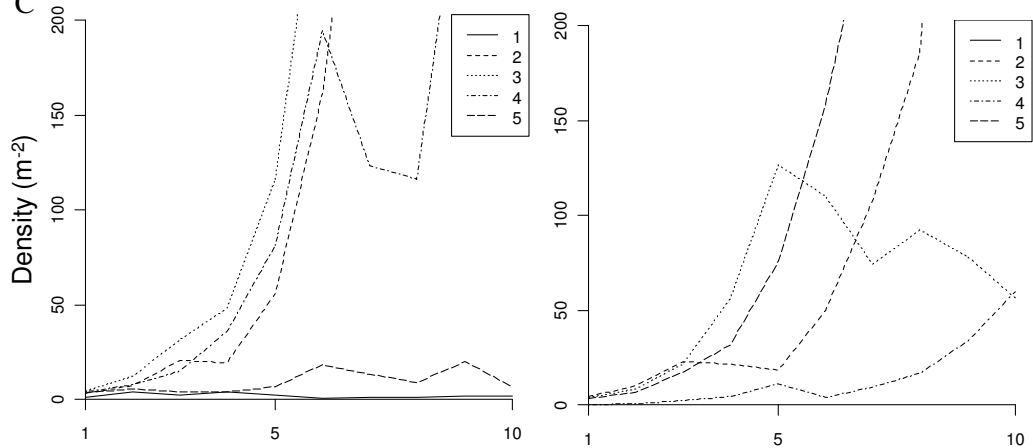
Figure 3-4. Examples of 5 simulated 10-year trends in population density for 3 taxa.
Dolophilodes spp. (Trichoptera: Philopotamidae) showed the highest extinction rate of 0.9-1
(Panel A). *Parapsyche* spp. (Trichoptera: Hydropsychidae) showed significantly different
extinction rates between the two scenarios (Panel B). *Ameletus* spp. (Ephemeroptera:
Ameletidae) showed the lowest extinction rate of 0 (Panel C).
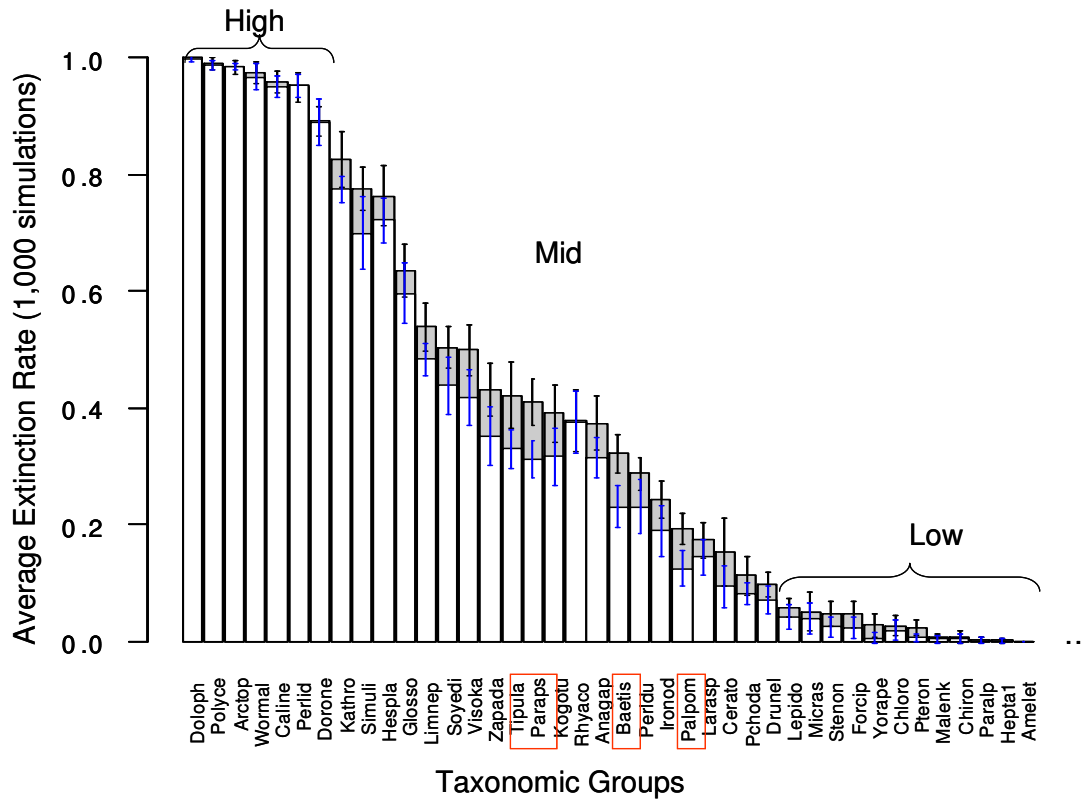
Figure 3-5. The comparison of the extinction rates between the two scenarios for all taxonomic groups. For each taxon, the grey bar is the average extinction rate over 1,000 simulations for scenario 2 (increased severity) and the white bar (scenario 1, long-term average) is overlaid on top the grey bar. Error bars indicate standard deviations. Taxonomic groups with extinction rates of zero ("Apatan", "Chelif", "Cinygm", "Crypto", "Despax", "Dicran", "Dixasp", "Dysmic", "Empidi", "Epeoru", "Hexato", "Neoher", "Neophy", "Swelts" and "Tipuli") are not shown here except for "Amelet" as an example. See Appendix A for the identities. Rectangles indicate taxonomic groups with significant differences in their extinction rates between the two future climate scenarios. High, Mid and Low indicate the arbitrary groupings created based on their extinction rates for scenario 1 (0.8<High, 0.06<Mid<0.8, Low<0.06).
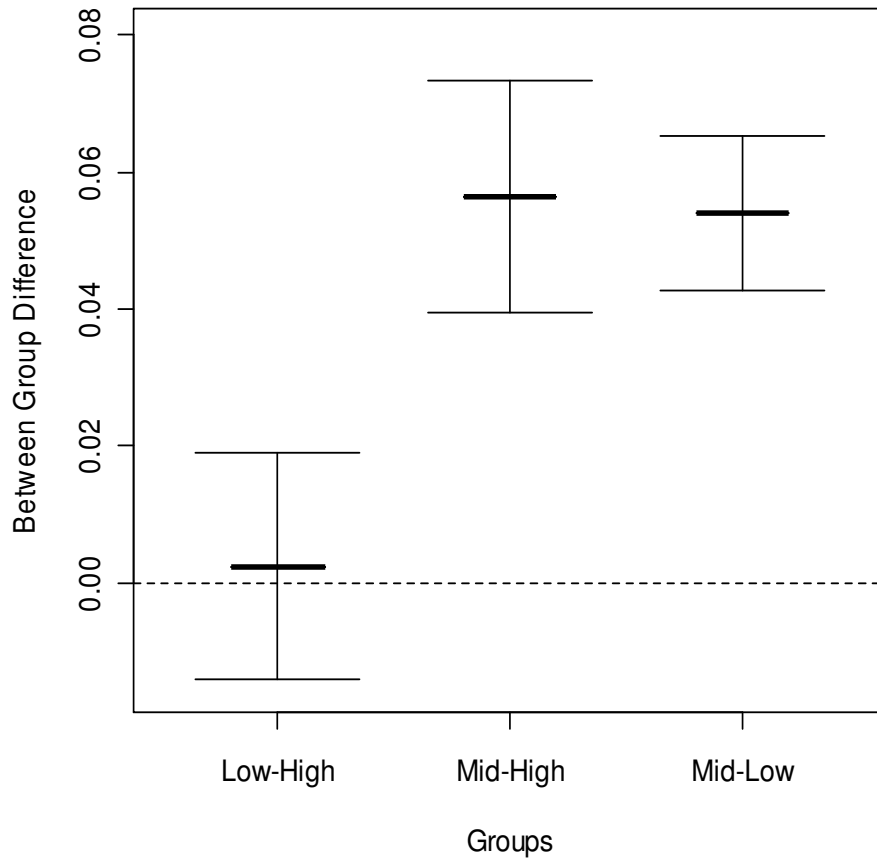
Figure 3-6. Comparing the extinction rate differences (sc2-sc1) between the three groups formed according to their extinction rates. High = groups with 0.8<sc1, Mid = groups with 0.06 <sc1 <0.8, Low = groups with sc1 <0.06. Error bars indicate the 95% confidence intervals of the differences calculated using the Tukey Honest Significant Differences (HSD). Mid group is significantly different from both High and Low groups in the extinction rate differences between two scenarios.

3.6   Literature Cited

Anderson, N.H. and J.R. Sedell. 1979. Detritus processing by macroinvertebrates in stream ecosystems. *Annual Review of Entomology*, 24:351-377

Banks, J.L., J. Li and A.T. Herlihy. 2007. Influence of clearcut logging, flow duration, and season on emergent aquatic insects in headwater streams of the Central Oregon Coast Range. *Journal of the North American Benthological Society*, 26:620-632

Bengtsson, J., S.R. Baillie and J. Lawton. 1997. Community variability increases with time. *Oikos*, 78:249-256

Bonada, N., M. Rieradevall and N. Prat. 2007. Macroinvertebrate community structure and biological traits related to flow permanence in a Mediterranean river network. *Hydrobiologia*, 589:91-106

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

Boulton, A.J. and P.S. Lake. 2008. Effects of drought on stream insects and its ecological consequences. *In* Aquatic Insects: Challenges to Populations: Proceedings of the Royal Entomological Society's 24th Symposium. J. Lancaster and R.A. Briers (eds). CABI Publishing, Cambridge, MA, pp. 81-102

Boulton, A.J., E.H. Stanley, S.G. Fisher and P.S. Lake. 1992. Over-summering strategies of macroinvertebrates in intermittent streams in Australia and Arizona. *In* Aquatic Ecosystems in Semi-arid Regions: Implications for Resource Management. R.D. Robarts & M.L. Bothwell (eds), NHRI Symposium Series 7. Environment Canada, Saskatoon, Saskatchewan, pp.227-237

Bradley, D.C. and S.J. Ormerod. 2001. Community persistence among stream invertebrates tracks the North Atlantic Oscillation. *Journal of Animal Ecology*, 70:987-996

Brown, A.V. and P.P. Brussock. 1991. Comparisons of benthic invertebrates between riffles and pools. *Hydrobiologia*, 220:99-108

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

Calow, P. 1987. Towards a definition of functional ecology. *Functional Ecology*, 1:57-61

Camargo, J.A. and G.D. de Jalón. 1990. The downstream impacts of the burgomillodo reservoir, Spain. *Regulated Rivers: Research & Management*, 5:305-317

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

Chadwick, M.A. and A.D. Huryn. 2005. Response of stream macroinvertebrate production to atmospheric nitrogen deposition and channel drying. *Limnology and Oceanography*, 50:228-236

Chessman, B.C. and D.P. Robinson. 1987. Some effects of the 1982-83 drought on water quality and macroinvertebrate fauna in the lower La Trobe River, Victoria. *Australian Journal of Marine and Freshwater Research*, 38:289-299

Chevene, F., S. Dolédec and D. Chessel. 1994. A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology*, 31:295-309

Compton, J.E., M.R. Church, S.T. Larned and W.E. Hogsett. 2003. Nitrogen export from forested watersheds in the Oregon coast range: the role of N_2-fixing red alder. *Ecosystems*, 6:773-785

Cortes, R.M.V., M.T. Ferreira, S.V. Oliveira and F. Godinho. 1998. Contrasting impact of small dams on the macroinvertebrates of two Iberian mountain rivers. *Hydrobiologia*, 389:51-61

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

Cummins, K.W. 1974. Structure and function of stream ecosystems. *BioScience*, 24:631-641

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

Daufresne, M., P. Bady and J. Fruget. 2007. Impacts of global changes and extreme hydroclimatic events on macroinvertebrate community structures in the French Rhône River. *Oecologia*, 151:544-559

Delucchi, C.M. 1988. Comparison of community structure among streams with different temporal flow regimes. *Canadian Journal of Zoology*, 66:579-586

Demuth S. and A.R. Young. 2004. Regionalization procedures. *In* Hydrological Drought: Process and Estimation Methods for Streamflow and Groundwater. L.M. Tallakse, H.A.J. Van Lanen (eds). Developments in Water Science 48, Elsevier, Amsterdam, pp. 307–343

Díaz, A.M., M.L.S. Alonso and M.R.V. Gutiérrez. 2008. Biological traits of stream macroinvertebrates from a semi-arid catchment: patterns along complex environmental gradients. *Freshwater Biology*, 53:1-21

Durance, I. and S.J. Ormerod. 2007. Climate change effects on upland stream macroinvertebrates over a 25-year period. *Global Change Biology*, 13:942–957

Durance, I. and S.J. Ormerod. 2009. Trends in water quality and discharge confound long-term warming effects on river macroinvertebrates. *Freshwater Biology*, 54:388-405

Fagan, W.F. 2002. Connectivity, fragmentation, and extinction risk in dendritic metapopulation. *Ecology*, 83:3243-3249

Gleick, P.H. 1998. The World's Water 1998-1999. Island Press, Washington D.C., 319p.

Griswold, M.W., R.W. Berzinis, T.L. Crisman and S.W. Golladay. 2008. Impacts of climatic stability on the structural and functional aspects of macroinvertebrate communities after severe drought. *Freshwater Biology*, 53:2465-2483

Haddad, N.M., D. Tilman and J.M.H. Knops. 2002. Long-term oscillations in grassland productivity induced by drought. *Ecology Letters*, 5:110-120

Hooper D.U., F.S. Chapin, J.J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J.H. Lawton, D.M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A.J. Symstad, J. Vandermeer, D.A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: a concensus of current knowledge. *Ecological Monographs*, 75:3–35

Hulme, M. 2004. Recent climate trends. *In* Climate Change and Biodiversity. T.E. Lovejoy & L. Hannah (eds). Yale University Press, Grand Rapids, Michigan. pp.31-40

Huryn, A.D. and J.B. Wallace. 2000. Life history and production of stream insects. Annual Review of Entomology, 45:83-110

Hynes, H.B.N. 1970. Ecology of Running Waters. University of Toronto Press, Toronto. 555p.

Jaag, O. and H. Ambühl. 1964. The effect of the current on the composition of biocoenoses in flowing water streams. In Advances in Water Pollution Research; Proceedings of the Second International Conference. Pergamon Press, Oxford, pp. 31-49

Intergovernmental Panel on Climate Change. 1996. Climate Change 1995: Impacts, Adaptations, and Mitigation of Climate Change. Contribution of Working Group II to the Second Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.Jongman, R. H. G., C. J. F. ter Braak, and O. F. R. van Tongeren, editors. 1995. Data Analysis in Community and Landscape Ecology. New Ed. Cambridge University Press, New York.

Lambeets, K., M.L. Vandegehuchte, J. Maelfait and D. Bonte. 2009. Integrating environmental conditions and functional life-history traits for riparian arthropod conservation planning. *Biological Conservation*, 142:625-637

Lind, P.R., B.J. Robson and B.D. Mitchell. 2006. The influence of reduced flow during a drought on patterns of variation in macroinvertebrate assemblages across a spatial hierarchy in two lowland rivers. *Freshwater Biology*, 51:2282-2295

Logan, P., and M.P. Brooker. 1983. Macroinvertebrate faunas of riffles and pools. *Water Research*, 17:263-270.

Loreau, M., S. Naeem, P. Inchausti, J. Bengtsson, J.P. Grime, A. Hector, D.U. Hooper, M.A. Huston, D. Raffaelli, B. Schmid, D. Tilman and D.A. Wardle. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, 294:804-808

Lytle, D.A. 2001. Disturbance regimes and life-history evolution. *The American Naturalist*, 157:525-536

Lytle D.A. 2008. Life-history and behavioural adaptations to flow regime in aquatic insects. *In* Aquatic Insects: Challenges to Populations: Proceedings of the Royal Entomological Society's 24th Symposium. J. Lancaster, R.A. Briers & C. Macadam (eds). CABI International, Cambridge, MA, pp.122-138

Marczak, L.B., J.S. Richardson and M.-C. Classen. 2006. Life history phenology and sediment size association of the dragonfly *Cordulegaster dorsalis* (Odonata: Cordulegastridae) in an ephemeral habitat in southwestern British Columbia, Canada. *Canadian Field-Naturalist*, 120:347-350

Matthews, W.J. 1998. Patterns in Freshwater Fish Ecology. Springer, New York, 784p.

McGill, B.J., B.J. Enquist, E. Weiher and M. Westoby. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21:178-185

Meyer, J.L., D.L. Strayer, J.B. Wallace, S.L. Eggert, G.S. Helfman and N.E. Leonard. 2007. The contribution of headwater streams to biodiversity in river networks. *Journal of the American Water Resources Association*, 43:86-103

Monk, W.A., P.J. Wood, D.M. Hannah, D.A. Wilson, C.A. Extence and R.P. Chadd. 2006. Flow variability and macroinvertebrate community response within riverine systems. *River Research and Applications*, 22:595-615

Monk, W.A., P.J. Wood, D.M. Hannah and D.A. Wilson. 2008. Macroinvertebrate community response to inter-annual and regional river flow regime dynamics. *River Research and Applications*, 24:988-1001

Muchow, C.L. and J.S. Richardson. 2000. Unexplored diversity: macroinvertebrates in coastal British Columbia headwater streams. Proceedings of a Conference on the Biology and Management of Species and Habitats at Risk, Kamloops, B.C., L.M. Darling (eds), Volume Two, pp.15-19

B.C. Ministry of Environment, Lands and Parks, Victoria, B.C. and University College of the Cariboo, Kamloops, B.C. 520pp.

Oksanen, J., R. Kindt, P. Legendre, B. O'Hara, G.L. Simpson, P. Solymos, M. Henry, H. Stevens and H. Wagner. 2009. vegan: Community Ecology Package. R package version 1.15-2. http://CRAN.R-project.org/package=vegan

Palmer, M.A., C.A. Reidy Liermann, C Nilsson, M. Florke, J. Alcamo, P.S. Lake and N. Bond. 2008. Climate change and the world's river basins: anticipating management options. *Frontiers in Ecology and the Environment*, 6:81-89

Petchey, O.L. and K.J. Gaston. 2002. Functional diversity (FD), species richness and community composition. *Ecology Letters*, 5:402-411

Petraitis, P.S., R.E. Latham and R.A. Niesenbaum. 1989. The maintenance of species diversity by disturbance. *The Quarterly Review of Biology*, 64:393-418

Poff, N.L. 1996. A hydrogeography of unregulated streams in the United States and an examination of scale-dependence in some hydrological descriptors. *Freshwater Biology*, 36:71-91

Poff, N.L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society*, 16:391-409

R Development Core Team 2007-2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Resh, V.H., A.G. Hildrew, B. Statzner and C.R. Townsend. 1994. Theoretical habitat templets, species traits, and species richness: a synthesis of long-term ecological research on the Upper Rhône River in the context of concurrently developed ecological theory. *Freshwater Biology*, 31:539-554

Řezníčková, P., P. Pařil and S. Zahrádková. 2007. The ecological effect of drought on the macroinvertebrate fauna of a small intermittent stream - an example from the Czech Republic. *International Review of Hydrobiology*, 92:514-526

Richardson, J.S. 1992. Food, microhabitat, or both? Macroinvertebrate use of leaf accumulations in a montane stream. *Freshwater Biology*, 27:169-176

Richardson, J.S. 2001. Life cycle phenology of common detritivores from a temperate rainforest stream. *Hydrobiologia*, 455:87-95

Ruesink, J.L. and D.S. Srivastava. 2001. Numerical and per capita responses to species loss: mechanisms maintaining ecosystem function in a community of stream insect detritivores. *Oikos*, 93:221-234

Scarsbrook, M.R. 2002. Persistence and stability of lotic invertebrate communities in New Zealand. *Freshwater Biology*, 47:417-431

Schneider S.H., P.H. Gleick and L.O. Mearns. 1990. Prospects for climate change. *In* Climate Change and U.S. Water Resources. P.E. Waggoner (eds). Wiley-Interscience, Toronto, pp. 41-74

Southwood, T.R.E. 1977. Habitat, the templet for ecological strategies? *The Journal of Animal Ecology*, 46:337-365

Southwood, T.R.E. 1988. Tactics, strategies and templets. *Oikos*, 52:3-18

Stanley, E.H., S.G. Fisher and N.B. Grimm. 1997. Ecosystem expansion and contraction in streams. *BioScience*, 47:427-435

Statzner,B., K. Hoppenhaus, M.F. Arens and P. Richoux. 1997. Reproductive traits, habitat use and templet theory: a synthesis of world-wide data on aquatic insects. *Freshwater Biology*, 38:109–135

Statzner,B., N. Bonada and S. Dolédec. 2007. Conservation of taxonomic and biological trait diversity of European stream macroinvertebrate communities: a case for a collective public database. *Biodiversity and Conservation*, 16:3609-3632

Stubbington, R., P.J. Wood and A.J.Boulton. 2009. Low-flow controls on benthic and hyporheic macroinvertebrate assemblages during supra-seasonal drought. *Hydrological Processes*, Published Online, doi: 10.1002/hyp.7290.

Townsend, C.R. A.G. Hildrew. 1994. Species traits in relation to a habitat templet for river systems. *Freshwater Biology*, 31:265-275

Townsend, C.R., M.R. Scarsbrook and S. Doledec. 1997. Quantifying disturbance in streams: alternative measures of disturbance in relation to macroinvertebrate species traits and species richness. *Journal of the North American Benthological Society*, 16:531-544

Vieira, N.K.M., N.L. Poff, D.M. Carlisle, S.R. Moulton II, M.L. Koski and B.C. Kondratieff. 2006. A database of lotic invertebrate traits for North America. U.S. Geological Survey, Reston, Virginia. Data Series 187. http://pubs.water.usgs.gov/ds187

Waggoner, P.E. and J. Schefter. 1990. Future water use in the present climate. *In* Climate Change and U.S. Water Resources. P.E. Waggoner (eds). Wiley-Interscience, Toronto, pp. 19-39

Ward J.V. and J.A. Stanford. 1984. The regulated stream as a testing ground for ecological theory. *In* Regulated Rivers. A. Lillehamer & S.J. Saltveit (eds). Oslo University Press, Norway, pp. 139–165

Wiggins, G.B. 1973. A Contribution to the Biodiversity of Caddisflies (Trichoptera) in Temporary Pools. Royal Ontario Museum, Life Sciences Contributions 88

Wipfli, M.S. and D.P. Gregovich. 2002. Export of invertebrates and detritus from fishless headwater streams in southeastern Alaska: implications for downstream salmonid production. *Freshwater Biology*, 47:957–969

Wipfli. M.S., J.S. Richardson and R.J. Naiman. 2007. Ecological linkages between headwaters and downstream ecosystems: Transport of organic matter, invertebrates and wood down headwater channels. *Journal of the American Water Resources Association*. 43:72-85

Wissinger, S.A., W.S. Brown and J.E. Jannot. 2003. Caddisfly life histories along permanence gradients in high-altitude wetlands in Colorato (USA). *Freshwater Biology*, 48:255-270

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

Yule, C.M., M.Y. Leong, K.C. Liew, L. Ratnarajah, K. Schmidt, H.M. Wong, R.G. Pearson and L. Boyero. 2009. Shredders in Malaysia: abundance and richness are higher in cool upland tropical streams. *Journal of the North American Benthological Society*, 28:404-415

Chapter 4 Prospects for climate change impacts on small stream ecosystems and research needs

Historical background of the study

Recently, there has been an increasing awareness about the lack of our understanding about the impacts of low-flow events on instream communities (e.g. Death 2002; Boulton 2003; Lake 2003; Boulton and Lake 2008). In the previous century, we had a relatively low understanding of at least three aspects. First, there was no accepted view on what the most appropriate hydrological measures are for investigating the impacts of low-flow events (Monk et al. 2006). Second, integration of hydrology and ecology were relatively rare (but see Richter et al. 1997). This was largely due to lack of long-term hydrological and biological data. Third, even when the data were available, quantifying the relationships between flow parameters and community indices was scarce (but see Jowett and Duncan 1990). Recent studies have attempted to fill the gaps, especially with the increased use of approaches such as ordinations and functional traits (e.g. Bêche and Resh 2007). For example, Monk et al. (2006) analyzed 83 rivers in England and Wales to determine what the most appropriate hydrological measures are, using community indices at the family level. Several recent studies utilized long-term hydrological and biological data to assess the relationships between hydrology and ecology (e.g. Bradley and Ormerod 2001; Bêche et al. 2006; Chessman 2008). However, they often encountered difficulties in pinpointing the relationship due to confounding by physicochemical attributes such as anthropogenic changes in water quality (e.g. Daufresne et al. 2007) or indirect effects of low-flow events such as increased temperature (e.g. Bogan and Lytle 2007) and salt concentration (e.g. Lind et al. 2006), rather than changes in habitat size or velocity (e.g. Miller et al. 2007). Others encountered difficulties in generalizing over stream types and sizes (e.g. Upland vs. Lowland rivers; Castella et al. 1995) as these two

factors play an important role in shaping the community structures. Also, some studies used biological data at the family level (e.g. Monk et al. 2006; Chessman 2008), which is easier for long-term monitoring but may miss some crucial ecological feature such as keystone species or key traits due to diversity within a family. The forested, headwater streams targeted in this study provided a unique opportunity to focus on the physical aspects of low-flow events and their impacts on the benthic invertebrate communities for the following reasons. The streams studied here are spring- and/or groundwater-fed (Kiffney et al. 2002), allowing for the minimum increase in water temperature with reduced flow, if any (Table 2-1), together with shading from the dense canopy cover (Kiffney et al. 2003). A similar pattern of this disconnection between discharges and temperatures was seen in experimental manipulations on small streams in New Zealand (James et al. 2008). Anthropogenic disturbances to the streams are minimal since the forest fire in 1931 as they are either the control (East and Mike Creeks) or 30-m buffer (South Creek) sites for studying the effects of forest harvesting on the streams and adjacent riparian ecosystems (Kiffney et al. 2003). Choosing small stream size allowed us to minimize the impact of reduced lateral connectivity suggested by previous studies (e.g. Bunn and Arthington 2002; Boulton 2003; Lake 2008). The MKRF riparian project has been monitoring the benthic macroinvertebrates of riffles since 1997 and samples are identified to as low as species level, providing the opportunity to explore the community response at a much finer scale. Moreover, the potential increase in competition between individuals for resources, which is an indirect effect of decreased flow (e.g. Boulton 2003; Dewson et al. 2007), seemed negligible in this study (Chapter 2). This is probably due to choosing the riffles over pools that resulted in minimizing the complexity of low-flow events (described extensively by Boulton 2003 for example).

Findings of this study

Together, the two chapters successfully answered the two proposed questions through analysis of empirical data (Chapter 2) and modelling (Chapter 3). How macroinvertebrate communities respond to the inter-annual variations in frequency, duration, intensity and abruptness of summer flow regimes in small headwater streams, and how community structure in headwater streams will change as a result of the different responses by macroinvertebrate groups towards shifts in the frequency, duration, intensity and abruptness of low discharge regimes in summer.

Chapter 2 showed a significant relationship between the summer low-flow events and benthic macroinvertebrate communities through three-table ordinations on the existing long-term monitoring data. The community structure was correlated with Pacific Decadal Oscillation (Mantua et al. 1997) through the changes in flow regimes, following the original hypothesis. The intensity and duration of low-flow events were identified to explain the observed changes in community structure, favouring r-selected traits, the most.

Chapter 3 showed the differential impacts of the two future low-flow event scenarios (random vs. increased severity of duration and minimum discharges) through modelling individual populations according to their traits. The simulations using the two scenarios identified a classification that separated aquatic insects into three groups of differing sensitivities to such scenarios. The resulting community structures for the two scenarios differed significantly over all indices considered (species richness, Shannon's diversity index, Simpson's index and relative proportions of functional feeding groups).

Limitations of this study

There are at least four limitations to this study for the results to be extrapolated and applied. First, the study could only incorporate three streams within a temperate forest, providing very

weak power for any extrapolation of its findings. Second, the extrapolation is also limited by the small spatial scale involved in this study and its uniqueness discussed above. However, the findings of this study should still be applicable as an increase in the knowledge missing to understand the mechanisms of how low-flow events affect lotic communities. The uniqueness of this system could further be utilized through an experimental approach like flow diversions (e.g. Wills et al. 2006; James et al. 2008). Third, consequences of previous years' conditions such as cumulative or lag effects (e.g. Boulton and Lake 1992) could not be assessed through the approaches taken here. For example, Bêche and Resh (2007) found that prolonged drought over years can result in increased temporal constancy of lotic communities both in dry and wet seasons. Fourth, rapid recoveries of macroinvertebrates following the low-flow events (e.g. Williams and Hynes 1977; Caruso 2002; Churchel and Batzer 2006) are likely to be underestimated in this study due to not incorporating refuge availabilities for instance.

Future directions

This research clearly indicated the importance of low-flow events on structuring the lotic macroinvertebrate community and the implications for future changes in the community due to predicted changes in hydrologic regimes as suggested by others (e.g. a recent review by Boulton and Lake 2008). With the current climate change forecasts (Hulme 2004) and increases in human need for freshwater (Poff et al. 2003), the lotic ecosystem is facing a rather strong environmental filter (Rood et al. 2008). Some argue for the need to apply the landscape ecology approach to lotic and adjacent riparian systems (Wiens 2002). Studies over large spatial and temporal scales are necessary to advance the recently founded discipline of ecohydrology (or hydroecology) and to apply for conservation and/or restoration projects.

Literature Cited

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

Bêche, L.A., E.P. McElravy and V.H. Resh. 2006. Long-term seasonal variation in the biological traits of benthic-macroinvertebrates in two Mediterranean-climate streams in California, U.S.A.. *Freshwater Biology,* 51:56-75

Bêche, L.A. and V.H. Resh. 2007. Short-term climatic trends affect the temporal variability of macroinvertebrates in California 'Mediterranean' streams. *Freshwater Biology*, 52:2317-2339

Bogan, M.T. and D.A. Lytle. 2007. Seasonal flow variation allows 'time-sharing' by disparate aquatic insect communities in montane desert streams. *Freshwater Biology*, 52:290-304

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

Boulton, A.J. and P.S. Lake. 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

Boulton, A.J. and P.S. Lake. 2008. Effects of drought on stream insects and its ecological consequences. *In* Aquatic Insects: Challenges to Populations: Proceedings of the Royal Entomological Society's 24th Symposium. J. Lancaster and R.A. Briers (eds). CABI Publishing, Cambridge, MA, pp. 81-102

Bradley, D.C. and S.J. Ormerod. 2001. Community persistence among stream invertebrates tracks the North Atlantic Oscillation. *Journal of Animal Ecology*, 70:987-996

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

Chessman, B.C. 2008. Climatic changes and 13-year trends in stream macroinvertebrate assemblages in New South Wales, Australia. *Global Change Biology*, Published Online. doi: 10.1111/j.1365-2486.2008.01840.x.

Churchel, M.A. and D.P. Batzer. 2006. Recovery of aquatic macroinvertebrate communities from drought in Georgia piedmont headwater streams. *The American Midland Naturalist*, 156:259-272

Daufresne, M., P. Bady and J. Fruget. 2007. Impacts of global changes and extreme hydroclimatic events on macroinvertebrate community structures in the French Rhône River. *Oecologia*, 151:544-559

Death, R.G. 2002. Predicting invertebrate diversity from disturbance regimes in forest streams. *Oikos*, 97:18-30

Hulme, M. 2004. Recent climate trends. *In* Climate Change and Biodiversity. T.E. Lovejoy & L. Hannah (eds). Yale University Press, Grand Rapids, Michigan. pp.31-40

James, A.B.W., Z.S. Dewson and R.G. Death. 2008. The effect of experimental flow reductions on macroinvertebrate drift in natural and streamside channels. *River Research and Applications*, 24:22-35

Jowett I.G., and M.J. Duncan. 1990. Flow variability in New Zealand rivers and its relationship to in-stream habitat and biota. *New Zealand Journal of Marine and Freshwater Research*, 24:305–317

Kiffney, P.M., J.P. Bull and M.C. Feller. 2002. Climatic and hydrologic variability in a coastal watershed of Southwestern British Columbia. *Journal of the American Water Resources Association*, 38:1437-1451

Kiffney, P.M., J.S. Richardson and J.P. Bull. 2003. Responses of periphyton and insects to experimental manipulation of riparian buffer width along forest streams. *Journal of Applied Ecology*, 40:1060-1076

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

Lind, P.R., B.J. Robson and B.D. Mitchell. 2006. The influence of reduced flow during a drought on patterns of variation in macroinvertebrate assemblages across a spatial hierarchy in two lowland rivers. *Freshwater Biology*, 51:2282-2295

Mantua, N.J., S.R. Hare, Y. Zhang, J.M. Wallace and R.C. Francis. 1997. A pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society*, 78:1069-1079

Miller, S.W., D. Wooster and J. Li. 2007. Resistance and resilience of macroinvertebrates to irrigation water withdrawals. *Freshwater Biology*, 52:2494-2510

Monk, W.A., P.J. Wood, D.M. Hannah, D.A. Wilson, C.A. Extence and R.P. Chadd. 2006. Flow variability and macroinvertebrate community response within riverine systems. *River Research and Applications*, 22:595-615

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

Richter B.D., J.V. Baumgartner, R. Wigington and D.P. Braun. 1997. How much water does a river need? *Freshwater Biology*, 37:231–249

Rood, S.B., J. Pan, K.M. Gill, C.G. Franks, G.M. Samuelson and A. Shepherd. 2008. Declining summer flows of Rocky Mountain rivers: changing seasonal hydrology and probable impacts on floodplain forests. *Journal of Hydrology*, 349:397-410

Wiens, J.A. 2002. Riverine landscapes: taking landscape ecology into the water. *Freshwater Biology*, 47:501-515

Wills, T.C., E.A. Baker, A.J. Nuhfer and T.G. Zorn. 2006. Response of the benthic macroinvertebrate community in a northern Michigan stream to reduced summer streamflows. *River Research and Applications*, 22:819-836

Williams, D.D. and H.B.N. Hynes. 1976. The ecology of temporary streams I: the faunas of two Canadian streams. *Internationale Revue der gesamten Hydrobiologie und Hydrographie*, 61:761-787

Appendix A. Taxonomic group codes used throughout the thesis.

taxacode	Phylum	Class	Order	Family	Genus
Acarin	Arthropoda	Arachnida	Acari		
Amelet	Arthropoda	Insecta	Ephemeroptera	Ameletidae	Ameletus
Anagap	Arthropoda	Insecta	Trichoptera	Glossosomatidae	Anagapetus
Apatan	Arthropoda	Insecta	Trichoptera	Apataniidae	Apatania
Arctop	Arthropoda	Insecta	Trichoptera	Hydropsychidae	Arctopsyche
Baetis	Arthropoda	Insecta	Ephemeroptera	Baetidae	Baetis
Caline	Arthropoda	Insecta	Plecoptera	Perlidae	Calineuria
Cerato	Arthropoda	Insecta	Diptera	Ceratopogonidae	
Chelif	Arthropoda	Insecta	Diptera	Empididae	Chelifera
Chiron	Arthropoda	Insecta	Diptera	Chironomidae	
Chloro	Arthropoda	Insecta	Plecoptera	Chloroperlidae	
Cinygm	Arthropoda	Insecta	Ephemeroptera	Heptageniidae	Cinygma
Crypto	Arthropoda	Insecta	Trichoptera	Limnephilidae	Cryptochia
Despax	Arthropoda	Insecta	Plecoptera	Leuctridae	Despaxia
Dicran	Arthropoda	Insecta	Diptera	Tipulidae	Dicranota
Dixasp	Arthropoda	Insecta	Diptera	Dixidae	Dixa
Doloph	Arthropoda	Insecta	Trichoptera	Philopotamidae	Dolophilodes
Dorone	Arthropoda	Insecta	Plecoptera	Perlidae	Doroneuria
Drunel	Arthropoda	Insecta	Ephemeroptera	Ephemerellidae	Drunella
Dysmic	Arthropoda	Insecta	Megaloptera	Corydalidae	Dysmicohermes
Empidi	Arthropoda	Insecta	Diptera	Empididae	
Epeoru	Arthropoda	Insecta	Ephemeroptera	Heptageniidae	Epeorus
Forcip	Arthropoda	Insecta	Diptera	Ceratopogonidae	Forcipomyia
Glosso	Arthropoda	Insecta	Trichoptera	Glossosomatidae	Glossosoma
Hepta1	Arthropoda	Insecta	Ephemeroptera	Heptageniidae	
Hespla	Arthropoda	Insecta	Plecoptera	Perlidae	Hesperoperla
Hetero	Arthropoda	Insecta	Trichoptera	Calamoceratidae	Heteroplectron
Hexato	Arthropoda	Insecta	Diptera	Tipulidae	Hexatoma
Ironod	Arthropoda	Insecta	Ephemeroptera	Heptageniidae	Ironodes
Kathro	Arthropoda	Insecta	Plecoptera	Chloroperlidae	Kathroperla
Kogotu	Arthropoda	Insecta	Plecoptera	Perlodidae	Kogotus
Larasp	Arthropoda	Insecta	Coleoptera	Elmidae	Lara
Lepido	Arthropoda	Insecta	Trichoptera	Lepidostomatidae	Lepidostoma
Limnep	Arthropoda	Insecta	Trichoptera	Limnephilidae	
Malenk	Arthropoda	Insecta	Plecoptera	Nemouridae	Malenka
Micras	Arthropoda	Insecta	Trichoptera	Brachycentridae	Micrasema
Nemato	Nematoda				
Neoher	Arthropoda	Insecta	Megaloptera	Corydalidae	Neohermes
Neophy	Arthropoda	Insecta	Trichoptera	Uenoidae	Neophylax
Oligoc	Annelida	Clitellata	Oligochaeta		
Ostrac	Arthropoda	Ostracoda			
Palpom	Arthropoda	Insecta	Diptera	Ceratopogonidae	Palpomyia

Appendix A (continued).

taxacode	Phylum	Class	Order	Family	Genus
Paralp	Arthropoda	Insecta	Ephemeroptera	Leptophlebidae	Paraleptophlebia
Paraps	Arthropoda	Insecta	Trichoptera	Hydropsychidae	Parapsyche
Pchoda	Arthropoda	Insecta	Diptera	Psychodidae	Psychoda
Perldu	Arthropoda	Insecta	Plecoptera	Perlodidae	
Perlid	Arthropoda	Insecta	Plecoptera	Perlidae	
Planar	Platyhelminthes	Turbellaria	Tricladida	Planariidae	
Polyce	Arthropoda	Insecta	Trichoptera	Polycentropidae	Polycentropus
Pteron	Arthropoda	Insecta	Plecoptera	Pteronarcyidae	Pteronarcys
Rhyaco	Arthropoda	Insecta	Trichoptera	Rhyacophildae	Rhyacophila
Simuli	Arthropoda	Insecta	Diptera	Simuliidae	Simulium
Soyedi	Arthropoda	Insecta	Plecoptera	Nemouridae	Soyedina
Stenon	Arthropoda	Insecta	Ephemeroptera	Heptageniidae	Stenonema
Swelts	Arthropoda	Insecta	Plecoptera	Chloroperlidae	Sweltsa
Tipula	Arthropoda	Insecta	Diptera	Tipulidae	Tipula
Tipuli	Arthropoda	Insecta	Diptera	Tipulidae	
Visoka	Arthropoda	Insecta	Plecoptera	Nemouridae	Visoka
Wormal	Arthropoda	Insecta	Trichoptera	Philopotamidae	Wormaldia
Yorape	Arthropoda	Insecta	Plecoptera	Peltoperlidae	Yoraperla
Zapada	Arthropoda	Insecta	Plecoptera	Nemouridae	Zapada

Appendix B. Fuzzy coded species traits (Q).

taxacode	a1	a2	b1	b2	b3	c1	c2	c3	d1	d2	e1	e2	e3	e4	e5	f1	f2
Acarin	1	0	0	0.25	0.75	0.33	0.33	0.33	1	0	0	0.17	0.17	0.39	0.28	1	0
Amelet	1	0	0	0.75	0.25	0.5	0.5	0	0.57	0.43	0	0.31	0.12	0.12	0.44	1	0
Anagap	1	0	0	1	0	0.5	0.5	0	1	0	0	0	0.5	0	0.5	1	0
Apatan	1	0	0	1	0	0.5	0.5	0	0.5	0.5	0	0.17	0.39	0.17	0.28	1	0
Arctop	0	1	0.25	0.75	0	0.5	0.5	0	0.75	0.25	0	0	0.5	0	0.5	1	0
Baetis	1	0	0	0.4	0.6	0.5	0.5	0	0.86	0.14	0	0.25	0	0	0.75	1	0
Caline	0.25	0.75	1	0	0	0.5	0.5	0	0.6	0.4	0	0	0	0	1	1	0
Cerato	1	0	0	0.46	0.54	0.25	0.75	0	0.57	0.43	0	0	0	0.17	0.83	1	0
Chelif	1	0	0	0.6	0.4	0	1	0	0.67	0.33	0.03	0.14	0.12	0.12	0.59	1	0
Chiron	0.86	0.14	0	0.25	0.75	0	1	0	0.6	0.4	0	0.1	0.23	0.1	0.57	0.8	0.2
Chloro	0.73	0.27	0.22	0.67	0.11	0.5	0.5	0	0.77	0.23	0	0.09	0.09	0.09	0.73	1	0
Cinygm	1	0	0	1	0	0.5	0.5	0	0.5	0.5	0	0	0	0	1	1	0
Crypto	1	0	1	0	0	0	1	0	0.5	0.5	0.5	0	0	0	0.5	1	0
Despax	1	0	0.5	0.5	0	0.5	0.5	0	0.67	0.33	0	0.5	0.21	0.21	0.07	1	0
Dicran	1	0	0	0.75	0.25	0.33	0.67	0	0.75	0.25	0	0.25	0.12	0.12	0.5	0.25	0.75
Dixasp	1	0	0	1	0	0.5	0.5	0	0.8	0.2	0	0.5	0.25	0.25	0	0	1
Doloph	1	0	0	0.4	0.6	0.5	0.5	0	0.5	0.5	0	0	0	0	1	1	0
Dorone	0.4	0.6	1	0	0	0.5	0.5	0	0.5	0.5	0	0	0	0	1	1	0
Drunel	1	0	0	1	0	0.5	0.5	0	0.49	0.51	0	0	0	0	1	1	0
Dysmic	0	1	1	0	0	0	1	0	0.33	0.67	0.5	0	0	0	0.5	1	0
Empidi	1	0	0	0.5	0.5	0	1	0	0.67	0.33	0.03	0.14	0.12	0.12	0.59	0.83	0.17
Epeoru	1	0	0	1	0	0.5	0.5	0	0.5	0.5	0	0.3	0.1	0.1	0.5	1	0
Forcip	1	0	0	0.33	0.67	0	1	0	0	1	0	0	0	0.5	0.5	1	0
Glosso	1	0	0	0.25	0.75	0.5	0.5	0	0.5	0.5	0	0	0.5	0	0.5	1	0
Hepta1	1	0	0	0.71	0.29	0.5	0.5	0	0.52	0.48	0	0.15	0.03	0.03	0.78	1	0
Hespla	0.4	0.6	1	0	0	0.5	0.5	0	0.33	0.67	0	0	0	0	1	1	0
Hetero	0	1	0.33	0.67	0	0.5	0.5	0	0.33	0.67	0	0	0	0	1	1	0
Hexato	1	0	0	0.75	0.25	0.33	0.67	0	0.5	0.5	0	0.25	0.12	0.12	0.5	0.25	0.75
Ironod	1	0	0	0.5	0.5	0.5	0.5	0	0.4	0.6	0	0	0	0	1	1	0
Kathro	0	1	0.5	0.5	0	0.5	0.5	0	0.67	0.33	0	0	0	0	1	1	0
Kogotu	1	0	0.25	0.75	0	0.5	0.5	0	0.67	0.33	0	0	0	0	1	1	0
Larasp	1	0	1	0	0	0.5	0.5	0	0.75	0.25	0	0	0	0	1	1	0
Lepido	1	0	0	0.75	0.25	0.5	0.5	0	0.6	0.4	0	0	0	0	1	1	0
Limnep	0	1	0	1	0	0.4	0.6	0	0.6	0.4	0	0.25	0.5	0.25	0	1	0
Malenk	1	0	0	1	0	0.5	0.5	0	0.8	0.2	0	0.2	0.1	0.1	0.6	1	0
Micras	1	0	0	1	0	0.5	0.5	0	0.25	0.75	0	0	0	0	1	1	0
Nemato	1	0	0.25	0.5	0.25	0.5	0.17	0.33	0.75	0.25	0	0.07	0.04	0.03	0.87	1	0
Neoher	0	1	1	0	0	0	1	0	0.33	0.67	0.5	0	0	0	0.5	1	0
Neophy	1	0	0	0.75	0.25	0.5	0.5	0	0.25	0.75	0	0.25	0.5	0.25	0	1	0
Oligoc	0	1	0	0	1	0.33	0.33	0.33	1	0	0.03	0.09	0.09	0.09	0.7	1	0
Ostrac	1	0	0	0.5	0.5	0.33	0.33	0.33	0	1	0.5	0.5	0	0	0	1	0
Palpom	1	0	0	0.5	0.5	0.33	0.67	0	0.67	0.33	0	0	0	0	1	1	0
Paralp	1	0	0	1	0	0.5	0.5	0	0.43	0.57	0	0	0	0	1	1	0
Paraps	0.8	0.2	0.25	0.75	0	0.5	0.5	0	0.75	0.25	0	0.1	0.37	0.23	0.3	1	0
Pchoda	1	0	0	0.25	0.75	0.5	0.5	0	0.8	0.2	0	0	0	0	1	0	1
Perldu	0.5	0.5	0	1	0	0.5	0.5	0	0.5	0.5	0	0.11	0.05	0.05	0.79	1	0
Perlid	0.25	0.75	1	0	0	0.5	0.5	0	0.6	0.4	0	0	0	0	1	1	0
Planar	1	0	0	1	0	0.33	0.33	0.33	0.49	0.51	0.5	0.38	0	0.13	0	1	0
Polyce	0	1	0	0.25	0.75	0.5	0.5	0	0.5	0.5	0	0.25	0.25	0.12	0.38	1	0
Pteron	0	1	1	0	0	0.5	0.5	0	0.25	0.75	0	0.43	0.2	0.2	0.17	1	0
Rhyaco	0.25	0.75	0	1	0	0.5	0.5	0	0.71	0.29	0	0.23	0.1	0.1	0.57	1	0
Simuli	1	0	0	0.4	0.6	0.4	0.6	0	0.43	0.57	0	0.28	0.17	0.17	0.39	1	0
Soyedi	1	0	0	1	0	0.5	0.5	0	1	0	0	0	0	0	1	1	0
Stenon	1	0	0	0.75	0.25	0.5	0.5	0	0.5	0.5	0	0	0	0	1	1	0
Swelts	1	0	0	1	0	0.5	0.5	0	0.8	0.2	0	0.2	0.2	0.2	0.4	1	0
Tipula	0	1	0.25	0.75	0	0.5	0.5	0	0.5	0.5	0	0.22	0.12	0.12	0.53	0.5	0.5
Tipuli	0.88	0.12	0.03	0.79	0.18	0.39	0.61	0	0.48	0.52	0	0.18	0.09	0.09	0.63	0.29	0.71
Visoka	1	0	1	0	0	0.5	0.5	0	1	0	0	0	0	0	1	1	0
Wormal	1	0	0	0.4	0.6	0.5	0.5	0	0.75	0.25	0	0	0	0	1	1	0
Yorape	1	0	1	0	0	0.5	0.5	0	0.5	0.5	0	0	0	0	1	1	0
Zapada	1	0	0.25	0.75	0	0.5	0.5	0	1	0	0	0	0	0	1	1	0

Appendix B (continued).

taxacode	g1	g2	g3	g4	h1	h2	h3	i1	i2	j1	j2	j3	k1	k2	k3
Acarin	0.63	0.25	0.13	0	0	0	1	0	1	0	0	1	0	0.67	0.33
Amelet	1	0	0	0	0.56	0.44	0	0.29	0.71	0	1	0	0.75	0.25	0
Anagap	0.75	0	0	0.25	0.25	0.75	0	0.2	0.8	0	1	0	0	1	0
Apatan	1	0	0	0	0.2	0.8	0	0	1	0	1	0	0	1	0
Arctop	0.6	0	0	0.4	0.43	0	0.57	0.14	0.86	0	1	0	0	0.75	0.25
Baetis	0.88	0	0.13	0	0.44	0.56	0	0.2	0.8	0	1	0	0.75	0.25	0
Caline	1	0	0	0	0	0	1	0	1	1	0	0	0	0.75	0.25
Cerato	0.55	0.45	0	0	0.12	0.35	0.54	0.18	0.82	0	1	0	0.17	0.55	0.28
Chelif	0.33	0.5	0.17	0	0	0.17	0.83	0.18	0.82	0	1	0	0.17	0.55	0.28
Chiron	0.56	0.22	0.11	0.11	0.55	0.27	0.18	0.4	0.6	0	1	0	0.25	0.5	0.25
Chloro	0.59	0	0.41	0	0.14	0.1	0.76	0.14	0.86	0.86	0.14	0	0	0.63	0.37
Cinygm	0.67	0	0.33	0	0.5	0.5	0	0	1	1	0	0	0.75	0.25	0
Crypto	0.6	0.4	0	0	1	0	0	0	1	0	1	0	0	1	0
Despax	0.67	0	0.33	0	1	0	0	0	1	0	1	0	0	1	0
Dicran	0.4	0.6	0	0	0	0	1	0.2	0.8	0	1	0	0.17	0.55	0.28
Dixasp	1	0	0	0	0.3	0.4	0.3	0.18	0.82	0	1	0	0.17	0.55	0.28
Doloph	0.4	0	0	0.6	0.5	0.33	0.17	0	1	0	1	0	0	1	0
Dorone	1	0	0	0	0	0	1	0	1	0.33	0.67	0	0	1	0
Drunel	1	0	0	0	0.57	0.29	0.14	0	1	0.25	0.75	0	1	0	0
Dysmic	1	0	0	0	0	0	1	0	1	0.25	0.75	0	0	0.75	0.25
Empidi	0.4	0.4	0.2	0	0	0.17	0.83	0.18	0.82	0	1	0	0.17	0.55	0.28
Epeoru	1	0	0	0	0.33	0.67	0	0.14	0.86	1	0	0	1	0	0
Forcip	0.67	0.33	0	0	0.17	0.83	0	0.18	0.82	0	1	0	0.17	0.55	0.28
Glosso	0.75	0	0	0.25	0.25	0.75	0	0.5	0.5	0	1	0	0.67	0.33	0
Hepta1	0.85	0.15	0	0	0.49	0.51	0	0.16	0.84	1	0	0	0.7	0.3	0
Hespla	1	0	0	0	0	0.14	0.86	0.25	0.75	0.67	0.33	0	0	1	0
Hetero	0.75	0.25	0	0	1	0	0	0.2	0.8	0	1	0	0	0.33	0.67
Hexato	0.4	0.6	0	0	0.17	0	0.83	0.18	0.82	0	1	0	0.17	0.55	0.28
Ironod	1	0	0	0	0.83	0.17	0	0.33	0.67	1	0	0	1	0	0
Kathro	0.4	0	0.6	0	0.2	0.2	0.6	0.2	0.8	0.67	0.33	0	0	1	0
Kogotu	1	0	0	0	0	0.17	0.83	0	1	0.5	0.5	0	0	1	0
Larasp	0.5	0.5	0	0	1	0	0	0	1	0.25	0.75	0	0.67	0.33	0
Lepido	1	0	0	0	0.57	0.14	0.29	0	1	0	1	0	0	0.75	0.25
Limnep	0.75	0	0	0.25	0.29	0.57	0.14	0.17	0.83	0	1	0	0	1	0
Malenk	0.71	0.29	0	0	0.71	0.14	0.14	0.33	0.67	1	0	0	0.25	0.75	0
Micras	0.75	0	0	0.25	0.33	0.67	0	0	1	0	1	0	0	1	0
Nemato	0.6	0	0.4	0	0	0.14	0.86	0.18	0.82	0	1	0	0.17	0.55	0.28
Neoher	1	0	0	0	0	0	1	0	1	0.25	0.75	0	0	0.75	0.25
Neophy	0.67	0	0	0.33	0.43	0.57	0	0.3	0.7	0	1	0	0	0.6	0.4
Oligoc	0.33	0.67	0	0	0.8	0.2	0	0.18	0.82	0	1	0	0.17	0.55	0.28
Ostrac	0.57	0.14	0.29	0	0.57	0.29	0.14	0.25	0.75	0.5	0	0.5	0.17	0.55	0.28
Palpom	0.5	0.5	0	0	0.1	0.2	0.7	0.18	0.82	0	1	0	0.17	0.55	0.28
Paralp	0.83	0.17	0	0	0.75	0.25	0	0.17	0.83	0.67	0.33	0	0.4	0.6	0
Paraps	0.6	0	0	0.4	0.33	0	0.67	0.13	0.88	0	1	0	0	1	0
Pchoda	0.25	0.75	0	0	0.6	0.3	0.1	0.18	0.82	0.33	0.67	0	0.17	0.55	0.28
Perldu	0.83	0	0.17	0	0.13	0.23	0.64	0.34	0.66	0.88	0.13	0	0.27	0.73	0
Perlid	1	0	0	0	0	0	1	0	1	1	0	0	0	0.75	0.25
Planar	1	0	0	0	0	0	1	0.18	0.82	1	0	0	0.17	0.55	0.28
Polyce	0.5	0	0	0.5	0.17	0.25	0.58	0	1	0	1	0	0	1	0
Pteron	1	0	0	0	0.86	0.14	0	0.4	0.6	0	1	0	1	0	0
Rhyaco	0.75	0	0	0.25	0	0.13	0.88	0.25	0.75	0	1	0	0	0.5	0.5
Simuli	0.33	0	0	0.67	0.6	0.2	0.2	0.18	0.82	0	1	0	0.17	0.55	0.28
Soyedi	1	0	0	0	1	0	0	0.4	0.6	0	1	0	0	1	0
Stenon	0.75	0.25	0	0	0.25	0.75	0	0	1	1	0	0	0.75	0.25	0
Swelts	0.67	0	0.33	0	0	0	1	0.17	0.83	1	0	0	0	0.67	0.33
Tipula	0.2	0.8	0	0	0.5	0.25	0.25	0.18	0.82	0	1	0	0.17	0.55	0.28
Tipuli	0.33	0.64	0	0.02	0.52	0.17	0.32	0.15	0.85	0	1	0	0.17	0.55	0.28
Visoka	1	0	0	0	1	0	0	0.43	0.57	0	1	0	0	1	0
Wormal	0.4	0	0	0.6	0.67	0.33	0	0.33	0.67	0	1	0	0	0.5	0.5
Yorape	1	0	0	0	1	0	0	0.14	0.86	0.5	0	0.5	0.5	0.5	0
Zapada	1	0	0	0	0.71	0.29	0	0.6	0.4	0	1	0	0	1	0

Appendix C. Sample identifications and summer low-flow variables (R).

ID	Site	Year	Season	Fre	Dur	minQ	Int	Abr
E.98.S	East	1998	Spring	7	59	0.258	6.56	0.014
E.00.S	East	2000	Spring	5	41	0.781	9.03	0.009
E.01.S	East	2001	Spring	7	20	1.073	5.04	0.422
E.01.F	East	2001	Fall	7	20	1.073	5.04	0.422
E.02.S	East	2002	Spring	6	54	0.509	3.49	0.008
E.03.S	East	2003	Spring	5	56	0.116	1.56	0.102
E.04.S	East	2004	Spring	4	68	0.178	8.04	0.012
E.04.F	East	2004	Fall	4	68	0.178	8.04	0.012
E.05.S	East	2005	Spring	5	73	0.385	6.90	0.043
E.05.F	East	2005	Fall	5	73	0.385	6.90	0.043
E.06.S	East	2006	Spring	4	99	0.000	5.49	0.146
E.06.F	East	2006	Fall	4	99	0.000	5.49	0.146
E.07.S	East	2007	Spring	5	66	0.004	4.56	4E-04
E.07.F	East	2007	Fall	5	66	0.004	4.56	4E-04
M.98.S	Mike	1998	Spring	7	59	0.168	3.78	0.009
M.00.S	Mike	2000	Spring	5	41	0.508	5.63	0.006
M.00.F	Mike	2000	Fall	5	41	0.508	5.63	0.006
M.01.S	Mike	2001	Spring	7	16	0.697	2.55	0.275
M.01.F	Mike	2001	Fall	7	16	0.697	2.55	0.275
M.02.S	Mike	2002	Spring	6	45	0.331	1.55	0.005
M.02.F	Mike	2002	Fall	6	45	0.331	1.55	0.005
M.03.S	Mike	2003	Spring	5	53	0.075	0.13	0.066
M.03.F	Mike	2003	Fall	5	53	0.075	0.13	0.066
M.04.S	Mike	2004	Spring	4	68	0.116	4.68	0.008
M.04.F	Mike	2004	Fall	4	68	0.116	4.68	0.008
M.05.S	Mike	2005	Spring	5	73	0.250	3.87	0.028
M.05.F	Mike	2005	Fall	5	73	0.250	3.87	0.028
M.06.S	Mike	2006	Spring	4	102	0.000	2.90	0.095
M.06.F	Mike	2006	Fall	4	102	0.000	2.90	0.095
M.07.S	Mike	2007	Spring	5	66	0.002	2.98	3E-04
M.07.F	Mike	2007	Fall	5	66	0.002	2.98	3E-04
So.00.S	South	2000	Spring	5	34	0.078	6.30	0.003
So.00.F	South	2000	Fall	5	34	0.078	6.30	0.003
So.01.S	South	2001	Spring	6	16	0.159	3.81	0.215
So.01.F	South	2001	Fall	6	16	0.159	3.81	0.215
So.02.S	South	2002	Spring	6	47	0.024	2.58	0.002
So.03.F	South	2003	Fall	5	24	0.078	6.30	0.003
So.04.S	South	2004	Spring	4	70	0.000	5.34	0.024
So.04.F	South	2004	Fall	4	70	0.000	5.34	0.024
So.05.S	South	2005	Spring	5	76	0.001	4.73	2E-04
So.06.S	South	2006	Spring	4	92	0.000	3.57	1E-03
So.06.F	South	2006	Fall	4	92	0.000	3.57	1E-03
So.07.S	South	2007	Spring	4	66	0.000	2.96	4.058
So.07.F	South	2007	Fall	4	66	0.000	2.96	4.058

Appendix D. Species abundance table

ID	Acarin	Amelet	Anagap	Apatan	Arctop	Baetis	Caline	Cerato	Chelif	Chiron	Chloro	Cinygm	Crypto	Despax	Dicran	Dixasp	Doloph	Dorone	Drunel	Dysmic	Empidi
E.98.S	0.0337	0	0	0	0	0.0332	0.0049	0.0037	0.0061	0.2746	0.1832	0	0	0.0037	0	0	0	0	0.0025	0	0.0037
E.00.S	0.0333	0	0	0	0	0.0243	0.0019	0.0103	0	0.3285	0.0161	0.0029	0	0.0048	0.0033	0	0	0	0.0026	0	0
E.01.S	0	0	0	0	0	0.0612	0.0025	0.0223	0.0124	0.2312	0.0439	0.0149	0	0.0869	0.0041	0	0	0	0	0	0.0041
E.01.F	0.0767	0	0	0.0064	0	0.0241	0.0017	0.0017	0	0.0206	0	0.0071	0	0	0	0	0	0.0098	0	0.0241	0
E.02.S	0.0291	0	0	0	0	0.0702	0	0	0	0.1805	0.0333	0	0	0.018	0	0	0	0	0	0	0
E.03.S	0.0144	0	0	0	0	0.0319	0.0083	0.0205	0.0671	0.3441	0.0083	0	0	0	0.0061	0	0	0	0	0	0
E.04.S	0.0051	0	0	0	0	0.034	0.004	0.0115	0.0027	0.3561	0.1709	0.004	0	0.031	0.003	0	0	0	0	0	0.0013
E.04.F	0.0094	0	0	0	0	0.021	0.0257	0.0409	0.0032	0.0471	0.1412	0.0235	0	0.0868	0	0.0026	0	0.0036	0	0	0
E.05.S	0.008	0.0047	0	0	0	0.0227	0.0054	0.0054	0.0024	0.2204	0.1248	0	0	0.03	0.0023	0	0	0.0024	0	0	0.0031
E.05.F	0.0273	0.0019	0.0289	0	0	0.0082	0.0182	0.0239	0.0139	0.0749	0.1491	0.0034	0	0.0328	0.0019	0.0034	0.0066	0.0051	0.0051	0	0.0097
E.06.S	0.0102	0.0068	0	0	0	0.0221	0	0.0069	0.0542	0.2347	0.0828	0	0	0.0103	0	0	0	0	0	0	0.015
E.06.F	0.0258	0.0126	0.0499	0	0	0.0013	0.0007	0.0189	0.0026	0.0722	0.0802	0.0007	0	0.0799	0.01	0	0.0075	0	0	0	0.0025
E.07.S	0.0269	0.0013	0	0	0	0	0	0.0141	0	0.2064	0.0555	0.0013	0	0.0478	0.0024	0	0.0013	0	0	0	0
E.07.F	0.0076	0.0056	0.0522	0	0	0.0113	0	0.039	0	0.0957	0.1287	0.0042	0	0.0322	0.0067	0.001	0.001	0	0	0	0.001
M.98.S	0.0159	0	0	0	0	0.0092	0	0.0327	0	0.0928	0.0348	0.0606	0	0.0042	0.0056	0	0	0	0	0	0
M.00.S	0.0288	0	0.0012	0	0.0024	0.0139	0	0.0275	0	0.1629	0.0344	0.0115	0	0.0011	0.0034	0	0	0	0	0.0024	0
M.00.F	0	0	0.0051	0.0172	0	0.0099	0	0.0074	0	0.0555	0	0.0406	0	0	0	0	0	0	0	0.0075	0
M.01.S	0.0034	0	0.0012	0	0.0024	0.0461	0	0.0043	0	0.1376	0.0496	0.0272	0	0.0015	0.0013	0	0	0	0	0.0071	0
M.01.F	0.0227	0	0	0	0	0	0	0.0206	0	0.161	0.0412	0.0133	0	0.0135	0.0052	0.0037	0	0	0	0.0011	0
M.02.S	0.099	0	0	0	0	0	0	0	0	0.1265	0.0238	0.0183	0	0.0275	0	0	0	0	0	0	0
M.02.F	0.0166	0	0	0	0	0	0	0.0204	0	0.0756	0.0545	0.009	0	0	0.0054	0	0	0	0	0.0038	0
M.03.S	0.0188	0	0	0	0	0.0027	0	0.0134	0	0.1347	0.0685	0.0255	0.0014	0	0.0114	0.0014	0	0	0	0.0014	0
M.03.F	0.0739	0	0	0	0	0	0	0.018	0	0.0045	0	0	0	0	0	0	0	0	0	0	0.0045
M.04.S	0.0803	0	0	0	0	0	0	0.024	0	0.0798	0.0328	0.027	0.0057	0	0.0116	0.0058	0	0	0	0	0
M.04.F	0.021	0	0	0	0	0	0	0.033	0	0.0598	0.0909	0	0.0015	0.004	0.006	0.003	0	0	0	0	0
M.05.S	0.0014	0	0	0	0	0.0014	0.0128	0.0142	0.0014	0.1773	0.0944	0	0	0.017	0.0056	0	0	0	0	0	0.0014
M.05.F	0.0145	0.0007	0.0015	0	0	0.0015	0.0029	0.0186	0.0056	0.149	0.1315	0.0045	0.0015	0.0151	0.0027	0.0007	0	0.0007	0	0	0
M.06.S	0.0128	0	0	0.0065	0	0.0013	0.0169	0.026	0.0065	0.1227	0.1109	0	0	0.0107	0	0	0	0	0	0.0013	0
M.06.F	0.0183	0	0.0429	0	0	0.0023	0.0088	0.0222	0.0012	0.1156	0.1002	0.001	0	0.037	0.0071	0	0	0.001	0	0	0
M.07.S	0.0219	0	0.074	0	0.0135	0.0036	0.009	0.0326	0.0094	0.0978	0.0593	0	0	0.0036	0.0085	0	0	0	0	0	0
M.07.F	0.0105	0	0	0	0	0.1103	0.015	0.0117	0	0.158	0.1098	0.0058	0.0031	0.0053	0.016	0.0047	0	0	0	0	0
So.00.S	0.0117	0	0.0136	0	0	0.0057	0.0013	0.009	0	0.1196	0.1203	0.0035	0	0.0114	0.0006	0	0	0.0039	0	0	0.0013
So.00.F	0.0199	0	0.0031	0	0	0.0019	0	0.0123	0	0.1775	0.0343	0.1094	0.0016	0.0342	0.0335	0.0016	0	0	0	0	0
So.01.S	0.0198	0	0	0	0	0.005	0.0008	0.0082	0	0.1067	0.129	0.0276	0	0.0034	0.0089	0	0	0.0008	0	0	0
So.01.F	0.025	0.002	0	0	0	0.0082	0.0024	0.0136	0.0027	0.2554	0.1232	0.042	0	0.0076	0.0094	0	0	0	0	0	0
So.02.S	0.0047	0	0	0	0	0.0083	0	0.0189	0	0.1494	0.1777	0.0167	0	0.0167	0	0	0	0	0	0	0
So.03.F	0.0714	0	0	0	0	0	0	0.1607	0	0.2589	0.0179	0	0	0	0	0	0	0	0	0	0.0089
So.04.S	0	0	0	0	0.0051	0.0151	0	0.0243	0	0.1063	0.0816	0.0142	0	0.0071	0.0071	0	0	0	0	0.0116	0
So.04.F	0.0392	0	0	0	0	0	0.0083	0.0108	0	0.0413	0.0613	0.0053	0	0.0027	0.0027	0	0	0.008	0	0.022	0
So.05.S	0.0063	0	0	0	0	0.0022	0	0.0044	0	0.0343	0.1426	0	0	0.0234	0	0	0	0	0.0022	0.1458	0
So.06.S	0.0044	0.0027	0	0	0	0	0	0.111	0.0017	0.0437	0.1887	0.0071	0	0.0081	0.0034	0	0	0	0	0	0
So.06.F	0.0287	0.0093	0	0	0	0.0112	0.0058	0.0138	0.0064	0.2189	0.1447	0.0016	0	0.024	0.0064	0	0	0	0.0016	0	0
So.07.S	0.0409	0.0033	0.0033	0	0	0	0.0033	0.0049	0.0016	0.1744	0.1369	0.0167	0	0.05	0.0016	0	0	0	0	0.0016	0
So.07.F	0.0274	0	0	0	0	0.0102	0.01	0.0033	0	0.1716	0.2914	0	0	0.0033	0.0067	0	0	0	0	0	0

Appendix D (continued).

ID	Epeoru	Forcip	Glosso	Hepta1	Hespla	Heterl	Hexato	Ironod	Kathro	Kogotu	Larasp	Lepido	Limnep	Malenk	Micras	Nemato	Neoher	Neophy	Oligoc	Ostrac	Palpom
E.98.S	0	0	0	0.0037	0	0.0442	0	0.0074	0.0312	0	0.0012	0.0012	0	0.0049	0.0061	0	0	0.0037	0.1281	0	0.0025
E.00.S	0.0231	0	0.0023	0.0038	0	0.0228	0	0.01	0	0	0.0023	0.0038	0	0.0088	0.0099	0.0047	0.001	0.005	0.0088	0.0047	0
E.01.S	0.0124	0	0	0.005	0	0.0397	0	0.0364	0.005	0	0	0.0025	0	0.0488	0.0083	0.0025	0	0.0066	0.0654	0	0
E.01.F	0.04	0.0017	0	0.0064	0.0088	0	0	0	0.1687	0	0	0.01	0.0494	0	0	0	0.1034	0	0	0	0
E.02.S	0.0616	0	0	0	0.018	0	0	0	0	0	0	0	0	0.0248	0.0454	0	0	0	0.0983	0.0735	0
E.03.S	0.0083	0	0	0	0	0.0486	0	0	0	0	0	0.0083	0	0	0.0091	0	0	0.0197	0.0183	0.003	0.0061
E.04.S	0.0044	0	0.0017	0.0013	0	0.0498	0.0013	0.0017	0.004	0	0.0013	0.0192	0	0	0.0175	0	0	0.0027	0.0102	0.0017	0
E.04.F	0	0	0.0385	0.0082	0	0.0827	0.0018	0.0394	0.0089	0	0	0.0096	0	0	0.0091	0	0	0	0.1207	0.0176	0
E.05.S	0.0135	0	0.0024	0.0023	0	0.0254	0	0.0093	0.0117	0	0	0.0093	0	0.0068	0.0073	0.0031	0	0.0111	0.0158	0.0114	0.0024
E.05.F	0	0	0	0.0348	0.0085	0.0334	0.0074	0.0114	0.0037	0	0	0.0091	0	0	0.0191	0	0	0	0.057	0.007	0
E.06.S	0.0306	0	0	0.0076	0	0.011	0	0.0598	0.0056	0	0.0028	0.0165	0	0.017	0.0117	0.0014	0	0.0294	0.0187	0	0
E.06.F	0	0	0	0.0962	0	0.0139	0	0.0964	0	0	0.0039	0.0094	0	0	0.0026	0.0007	0	0	0.0137	0.0105	0.0049
E.07.S	0.0098	0	0	0.0222	0	0.0141	0	0.0061	0.0027	0	0.0061	0.0229	0	0.0761	0.0067	0	0	0.005	0.0424	0	0
E.07.F	0	0.0056	0	0.0128	0.001	0.0341	0.0024	0.0378	0	0	0.0091	0.0355	0	0	0.0072	0.0019	0	0	0.0596	0.0024	0
M.98.S	0.0033	0	0	0.061	0	0	0.0042	0	0	0	0	0.0188	0	0.0149	0	0.0455	0	0	0.3824	0	0
M.00.S	0.0036	0	0	0.0061	0	0	0	0.0009	0.0122	0	0	0.057	0.0012	0.0181	0.0031	0.0026	0.0949	0	0.0213	0	0
M.00.F	0.005	0.005	0	0	0.0025	0	0	0	0.0477	0	0	0.0962	0.0125	0	0	0	0.0968	0	0	0	0
M.01.S	0.0106	0.0012	0	0.0162	0	0	0.0012	0	0.0415	0	0	0.0142	0.0024	0.0433	0.0222	0.0044	0.0047	0	0.2197	0	0.0024
M.01.F	0.0011	0	0	0.0157	0	0	0.0011	0	0	0	0.0087	0.0156	0	0.0047	0.0091	0.0757	0	0	0.2833	0.0014	0.0021
M.02.S	0	0	0	0	0	0	0	0	0	0	0.022	0	0	0.0221	0	0.0183	0	0	0.1102	0.011	0
M.02.F	0	0	0	0.0209	0	0	0	0	0	0	0	0	0	0.0242	0	0.0036	0	0	0.4517	0	0.0038
M.03.S	0	0	0	0.0716	0	0	0	0	0	0.0027	0.0014	0.0041	0	0.102	0	0	0	0	0.1914	0	0
M.03.F	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.009	0	0	0.6429	0	0.009
M.04.S	0	0	0	0.0029	0	0	0	0	0	0	0.0028	0	0	0.0291	0	0.0029	0	0	0.4038	0	0.0028
M.04.F	0	0	0	0.0039	0	0	0	0	0	0	0.0095	0.0015	0	0.019	0.0267	0	0	0	0.2856	0	0
M.05.S	0	0	0	0	0	0.0369	0.0014	0	0	0	0.0056	0.0183	0	0.0042	0	0.017	0	0.0014	0.0435	0	0
M.05.F	0	0	0.0174	0.0015	0	0.0396	0.0029	0.0015	0	0	0.0046	0.0172	0.0015	0.001	0.0029	0.0094	0	0.001	0.0977	0	0.0044
M.06.S	0	0	0.0326	0	0	0.0229	0	0.0026	0	0	0.0013	0.013	0	0.0026	0	0	0	0	0.0203	0	0
M.06.F	0	0	0	0.0278	0	0.0205	0.0025	0	0	0	0.0072	0.0038	0	0.0055	0.0025	0.0181	0	0.001	0.022	0.0038	0
M.07.S	0	0	0	0.0182	0	0.0144	0.0018	0.02	0	0	0.0108	0.0067	0.0009	0.0009	0.0117	0.0317	0	0	0.0726	0.0009	0
M.07.F	0.0016	0	0	0.0053	0	0	0.0021	0.0188	0	0	0	0.0016	0	0.0403	0	0.0084	0	0.008	0.0094	0	0.0047
So.00.S	0	0	0	0.0151	0	0.0075	0.0012	0.0222	0	0	0	0.0176	0.0044	0.0263	0.0077	0.0073	0	0.0013	0.1604	0.0018	0
So.00.F	0	0	0	0.0031	0	0	0.0069	0	0	0	0	0.0035	0	0.0139	0	0.0016	0	0	0.1271	0.0031	0
So.01.S	0	0	0	0.027	0	0.0578	0.0155	0	0	0.0017	0.0017	0.0025	0	0.0059	0.0017	0.0051	0	0.0008	0.2414	0	0.0032
So.01.F	0	0	0	0.0049	0	0.0445	0.0064	0	0	0.0007	0	0.0204	0.0013	0.0093	0	0.0065	0	0.0011	0.1026	0	0
So.02.S	0	0	0	0.0047	0	0.0475	0.0083	0	0	0	0	0	0	0.0167	0	0	0	0	0.0555	0	0
So.03.F	0	0	0	0	0	0	0	0	0	0	0.0179	0.0179	0	0	0.0089	0.0804	0	0	0.1161	0.0268	0
So.04.S	0	0.0116	0	0	0	0.0142	0.0035	0	0.1815	0	0	0.0035	0	0	0	0	0.0152	0	0.0426	0	0.0065
So.04.F	0	0.0083	0.0027	0	0	0.0453	0.008	0	0.0634	0	0.008	0	0.0028	0	0	0.0027	0.0496	0	0.3206	0	0
So.05.S	0	0	0	0.0127	0	0	0	0	0	0	0	0	0	0.0065	0.0218	0.0042	0.1042	0	0.1099	0	0.0208
So.06.S	0	0	0	0.0137	0	0.0259	0	0	0	0	0.0034	0	0	0	0	0.0249	0	0	0.1206	0	0
So.06.F	0	0	0	0	0	0.0213	0	0.0016	0	0	0.0016	0.0164	0	0.0016	0.0032	0.0064	0	0	0.1055	0	0.0103
So.07.S	0	0	0	0.0033	0	0.0216	0	0	0	0	0.0088	0.0275	0	0	0.0144	0.0016	0	0	0.081	0	0
So.07.F	0	0	0	0	0	0.0333	0	0	0	0	0.0068	0	0	0.0068	0	0.0167	0	0	0.1168	0	0

Appendix D (continued).

ID	Paralp	Paraps	Pchoda	Perldu	Perlid	Planar	Polyce	Pteron	Rhyaco	Sialis	Simuli	Soyedi	Stenon	Swelts	Tipula	Tipuli	Visoca	Wormal	Yorape	Zapada
E.98.S	0.0209	0	0	0.0049	0.0049	0	0.0263	0	0.0061	0	0.0025	0	0	0	0	0	0.0074	0.0258	0.0111	0.0258
E.00.S	0.0447	0.0023	0	0.0209	0.0048	0	0	0.0057	0.0312	0	0.0047	0	0	0	0	0	0.0086	0.0067	0.0309	0.1865
E.01.S	0.0745	0.0108	0	0.0174	0.0083	0	0	0.005	0.0108	0	0.0066	0	0	0	0	0	0	0.0091	0.0215	0.0041
E.01.F	0.0604	0	0.0017	0.021	0	0	0	0.0046	0	0.0017	0	0	0.0594	0	0	0.0054	0.0313	0	0.0175	0.0135
E.02.S	0.0967	0	0	0	0.018	0.0137	0.0522	0.0274	0.0068	0	0.0068	0	0	0	0	0	0	0.0342	0.0111	0.0111
E.03.S	0.1502	0	0	0.0472	0	0	0	0.003	0.0152	0	0.0061	0	0	0	0	0	0	0	0.0213	0.1057
E.04.S	0.0452	0	0	0.024	0.0257	0.0017	0.0085	0.0017	0.0243	0	0	0	0	0	0	0	0.0034	0	0.0323	0.0223
E.04.F	0.0254	0.0177	0	0.0018	0.0196	0	0.0026	0.0068	0.0277	0	0	0.0036	0	0	0	0	0	0.025	0.0044	0.0292
E.05.S	0.0904	0.0087	0	0.0629	0.0049	0.0073	0.0023	0.0062	0.008	0	0	0	0	0	0	0	0.0047	0.0278	0.0486	0.0246
E.05.F	0.0331	0.0051	0	0	0.0398	0.0074	0	0.0083	0.0273	0	0	0.0036	0	0.0291	0	0.0034	0.0142	0.0068	0.0376	0.0108
E.06.S	0.0255	0.0062	0	0.0014	0.0253	0.0238	0	0.0144	0.0595	0	0.0082	0	0	0	0	0.0042	0.0069	0.0014	0.0304	0.0256
E.06.F	0.1003	0.0012	0	0	0.0326	0.0197	0	0.0054	0.0143	0	0	0.002	0	0	0.0013	0	0.0064	0.0204	0.0033	0.0114
E.07.S	0.0495	0.0013	0	0	0.0216	0.0087	0.0013	0.0121	0.072	0	0.0024	0	0	0	0	0.0013	0	0.0098	0.0061	0.0394
E.07.F	0.0828	0.0039	0	0	0.0497	0.0217	0.0014	0.0048	0.0119	0	0	0	0	0	0	0.0039	0.0057	0.011	0.0327	0.0727
M.98.S	0.0207	0	0	0	0	0	0	0	0.0083	0	0.0007	0	0	0	0	0	0.0141	0	0.0042	0.1014
M.00.S	0.0212	0.0017	0.0085	0.0036	0.0009	0	0.0021	0	0	0	0.0009	0	0	0	0	0	0	0.0517	0.0045	0.2855
M.00.F	0.0548	0	0.0224	0.01	0	0	0.0074	0	0	0	0	0	0.0252	0	0	0.0174	0.0254	0	0.0051	0.0936
M.01.S	0.0383	0.0009	0	0.0024	0	0	0.0178	0	0	0	0.0024	0	0.0083	0	0	0	0.0012	0.0304	0.0231	0.0509
M.01.F	0.0799	0	0	0	0	0	0.0147	0	0.0023	0	0.0041	0.0415	0	0	0	0.0011	0	0.003	0.0142	0.0425
M.02.S	0.0496	0	0	0	0	0	0.033	0	0	0	0	0.022	0	0	0	0	0	0	0.0221	0.2113
M.02.F	0.0411	0	0	0	0	0	0	0	0	0	0.0076	0.0233	0	0	0	0	0	0.0074	0.0125	0.0961
M.03.S	0.0617	0	0	0	0	0	0	0.0027	0.0041	0	0.0046	0	0	0	0	0	0.023	0.0931	0.0306	0.0195
M.03.F	0	0	0	0	0	0	0	0	0.0465	0	0	0	0	0	0	0	0	0	0	0
M.04.S	0.089	0	0	0	0	0	0	0	0.0114	0	0.0029	0	0	0	0	0.0034	0	0.0028	0.0097	0.0181
M.04.F	0.0774	0	0	0	0.0143	0.0905	0.0095	0	0.0359	0	0	0.037	0	0	0	0	0	0.0134	0.0234	0.0574
M.05.S	0.0721	0	0	0	0	0.2681	0.0069	0	0	0	0.0028	0	0	0	0	0.0028	0	0.0294	0.0464	0.0327
M.05.F	0.0551	0	0	0	0.0186	0.0098	0.0007	0	0.0059	0	0.001	0.0164	0	0	0.0007	0	0.0061	0.0322	0.0367	0.0607
M.06.S	0.0435	0.0013	0	0	0.0146	0.0042	0.0013	0	0.0047	0	0	0.0091	0	0	0	0.0039	0.0161	0.131	0.0359	0.2039
M.06.F	0.0795	0	0	0.0082	0.0061	0.0025	0	0	0.0013	0	0.0032	0.0013	0	0.0025	0	0.0051	0.0052	0.0355	0.0709	0.2297
M.07.S	0.0724	0.0151	0	0	0	0.0079	0	0	0.0111	0	0.0088	0	0.0009	0	0	0	0.0018	0.0825	0.1595	0.0297
M.07.F	0.058	0.0016	0	0	0	0.0047	0	0	0.0074	0	0.0021	0	0	0	0	0.0016	0.0021	0.0121	0.0809	0.018
So.00.S	0.0452	0.0031	0	0.0114	0.008	0.0136	0	0	0.0138	0	0.0069	0	0	0.0012	0	0	0	0.0455	0.0699	0.0791
So.00.F	0.0695	0.0173	0	0	0	0	0.0019	0	0.013	0	0	0	0	0	0	0	0	0.0417	0.0178	0.1221
So.01.S	0	0	0	0.0068	0	0.0008	0	0	0.0075	0	0	0	0	0	0	0	0	0	0.0059	0.1508
So.01.F	0.0248	0	0	0.0063	0.0016	0.0236	0.0013	0	0.0127	0	0	0.0016	0	0.0016	0	0	0	0.0038	0	0.0714
So.02.S	0.0178	0.0142	0	0	0.0047	0.0236	0	0	0.033	0	0.0083	0	0	0	0	0	0	0.0047	0.0355	0.1975
So.03.F	0.0179	0	0	0	0	0	0	0	0	0	0.0268	0	0	0	0	0	0	0	0.0179	0
So.04.S	0.0333	0	0	0	0	0	0.0051	0	0	0	0.0051	0	0	0	0	0.0035	0	0	0.0131	0.2641
So.04.F	0.0136	0	0.0193	0	0	0	0	0	0.0027	0	0.0196	0	0	0	0	0	0.0165	0	0.0163	0.016
So.05.S	0.0258	0.0065	0	0.0125	0	0.0153	0.0042	0	0.0127	0	0.0044	0	0	0	0	0	0	0.0214	0.0973	0.047
So.06.S	0.0224	0	0	0.0565	0.0207	0.0071	0	0	0	0	0	0	0	0.0142	0.0051	0.0095	0	0	0.0146	0.02
So.06.F	0.0106	0	0	0.0177	0	0.0016	0	0	0.0026	0	0	0	0	0	0.0016	0	0	0.0081	0.0756	0.1146
So.07.S	0.0413	0.0049	0	0.0056	0.017	0.0033	0.0111	0	0.0154	0	0.0056	0	0	0	0	0	0	0.0416	0.0327	0.0841
So.07.F	0.017	0	0	0	0.0205	0.0342	0	0	0.0204	0	0.0137	0	0	0	0	0.0033	0	0.0274	0.0341	0.0474

Appendix E. The R script used to simulate the population models (Chapter 3).

```r
sim <- function(codes, type = 1, trials = 5, times = 10){
  #parameters
  mw  <- 0.2
  mwc <- 1 - mw
  r   <- 2
  gen <- 2
  res <- 'res'

  #Mortality and reproduction rate equations
  mD <- function(Dur, a=17.35, C=0.01){ C * exp(a*Dur)  / (C*exp(a*Dur) +1-C) }
  mQ <- function(minQ, a=-25, C=0.7){ C * exp(a*minQ) / (C*exp(a*minQ)+1-C) }
  #ms <- function(x, y){ mQ(minQ=x) + mD(Dur=y) }
  mr <- function(x, y){ 1 - (mQ(minQ=x) + mD(Dur=y)) * res }
  rs <- function(r, x, y){ r * exp(x*-y) }
  severity <- function(t=11){
      A = numeric(t)
      A[1] = 0.01
      for(i in 2:t){
      A[i] = A[i-1]*i^0.1524
      }
      return(A)
  }
  sev <- severity()
  lflow = switch(type,
    function(i){
     x <- rnorm(1, mean=0.2808, sd=0.35596) / 1.5
     y <- rnorm(1, mean=28.45, sd=8.151) / 169
     c(ifelse(x>0, x, 0), ifelse(y>0, y, 0))
    },
    function(i){
       x <- rnorm(1, mean=(0.2808*(1-sev[i])), sd=0.35596) / 1.5
       y <- rnorm(1, mean=(28.45*(1+sev[i])), sd=8.151) / 169
       c(ifelse(x>0, x, 0), ifelse(y>0, y, 0))
    })
  #Population dynamics
```

```r
equations <- list(
  A = function(N, x, y){ N * mr(x, y) * r * mwc },
  B = function(N, x, y){ N * mr(x, y) * rs(r, x, y) * mwc },
  C = function(N, x, y){ N * (mr(x, y) * rs(r, x, y))^2 * mwc },
  D = function(N, x, y){
    mrmwc <- mr(x, y) * mwc
    N*0.2 * mrmwc * rs(r, x, y) + N*0.8 * mrmwc
  }
)
#Output structure
nrows <- nrow(codes)
out   <- array(
  dim = c(times, nrows, trials),
  dimnames = list(1:times, codes$taxacode, paste('Trial', 1:trials, sep='')))

#Simulation
for(k in 1:trials) for(j in 1:nrows){
  res <- codes$rescode[j]
  N   <- codes$N.zero[j]
  eq  <- equations[[codes$LCcode[j]]]
  v   <- rep(0, times)
  for(i in 1:times){
    p <- lflow(i)
    N <- eq(N, p[1], p[2])
    if(N <= 0) break
    v[i] = N
  }
  out[,j,k] <- v
}
out
}
#Reading the code table
codes <- read.table('codes.csv', header=T, sep=",", as.is=T, na.strings=" ")
result1 <- sim(codes, type = 1, trials = 1000) #Scenario 1 Simulation (1,000 trials)
result2 <- sim(codes, type = 2, trials = 1000) #Scenario 2 Simulation (1,000 trials)
```

Appendix F. Preliminary analyses - two-table ordinations

F.1   Methods

To answer the first question, the empirical data from the three sites at MKRF (East, Mike and South Creeks; see site descriptions in Chapter 2 for details) were used: the insect abundance data (L; see Appendix D) and low-flow parameters (R; see Table F-1 for the definitions of each parameters and Appendix C for the data). Here, the relationships between abundance and low-flow parameters were analyzed without the trait information of taxonomic groups (for analysis in which the traits were incorporated, see Chapter 2). Both L and R were $\log(x+1)$ transformed to correct for extreme numbers. The relationship was investigated using two two-table ordination approaches: Canonical correspondence analysis (CCA ter Braak 1987; ter Braak, and Prentice 1988; Jongman et al. 1995) and Co-inertia analysis (CoIA; Dolédec and Chessel 1994; Dray et al. 2004) by the package ade4 (Dray and Dufour 2007) in Program R 2.7.0-2.9.0 (R Development Core Team 2009). The differences between these two-table ordination methods are the limiting conditions of the demonstration of any pertinent structure. In CCA, the number of environmental variables must be small with respect to the sample size to explain species data while there is no limit to the numbers in CoIA (Dolédec and Chessel 1994). Here the number of environmental variables is small relative to the sample size (5 vs. 44; Appendix B).

113

CCA is a technique to select linear combination of environmental variables that maximizes the dispersion of the species scores (e.g. Jongman et al. 1995). The corresponding eigenvalue equals the maximized dispersion of the species scores along the axis (i.e. a measure of how much variation in the species data is explained by the low-flow variables). Canonical coefficients refer to the best weights after the final regression in the iteration process. The multiple correlation of the final regression is called the species-environment correlation (i.e. correlation between the site scores that are weighted averages of the species scores and the site scores that are a linear combination of the environmental variables). The species-environment correlation measures the association between species and low-flow events. The potential arch effect may be removed by removing the superfluous environmental variables (that have high correlation with second axis). In the CCA biplot approximating the weighted averages of each species with respect to low-flow variables, the arrow head and projection point lying on the same side of the origin indicates that the inferred weighted average is higher than the non-weighted average.

CoIA searches for a common structure between two tables (here, species abundance and low-flow variables), utilizing PCA ordination of each table (Dray et al. 2007). The RV coefficient calculated by the function 'coinertia' in the package ade4 (Dray and

Dufour 2007) measures global similarity between R and L. The RV coefficient is between 0 and 1, and the similarity is greater when the coefficient is closer to 1. The repeated Monte-Carlo tests (10,000 times) on the total eigenvalues were performed based on 1,000 replicates to analyze the simulated p-values.

F.2   Results

Co-inertia analysis on the relationship between species abundance and low-flow variables (L and R, respectively) showed that minimum discharge and duration best explains the variances in the changes of relative abundance between Spring and Fall populations (Figure F-1). The first two CoIA axes explained 88% of the total variance observed (Table F-1). The RV coefficient of 0.24 showed a weak similarity between R and L. However, the CoIA result of the relationship between L and R was not significant after 10,000 repetition of Monte-Carlo test based on 1,000 replicates (average simulated p=0.17).

The first two axes of CCA on R and L could explain 85% of the variance explained by those of non-constrained PCA (Table F-2). The CCA result showed that minimum discharge and duration best explained the variances in the changes of relative abundance between Spring and Fall populations (Figure F-2).

In both ordination analyses, intensity also showed relatively high explanatory values. Intensity correlated strongly with the second ordination axis in both cases, while the correlation with the first axis was weak. Since second ordination axes are known to often imply an arch effect (ter Braak 1987), intensity was not included in the later modelling processes.

From the results of CCA and CoIA, the two best low-flow variables were chosen to be minimum discharge (minQ) and duration (Dur), as seen in previous studies (e.g. Monk et al. 2006). The observed relationship between the two variables with respect to low-flow events showed no clear correlation pattern. So, the effects of summer low-flows on mortality and reproduction rates in the model were calculated as additive effects of minimum discharge and duration in constructing the population models.

F.3   Literature Cited

Braak, C. J. F. ter, and I. C. Prentice. 1988. A theory of gradient analysis. *Advances in Ecological Resarch*, 18:271-313.

Braak, C. J. F. ter, and P. Šmilauer. 1998. CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4). Microcomputer Power, Ithaca, NY, 352p.

Dolédec, S. and D. Chessel. 1994. Co-inertia analysis: an alternative method for studying species-environment relationships. *Freshwater Biology*, 31: 277–294.

Dray, S., D. Chessel and J. Thioulouse 2003. Co-inertia analysis and the linking of the ecological data tables. *Ecology*, 84:3078–3089

Jongman, R.H.G., C.J.F. ter Braak and O.F.R. van Tongeren. 1995. Data Analysis in Community and Landscape Ecology. New Ed. Cambridge University Press, NY, 290p.

Monk, W.A., P.J. Wood, D.M. Hannah, D.A. Wilson, C.A. Extence and R.P. Chadd. 2006. Flow variability and macroinvertebrate community response within riverine systems. *River Research and Applications*, 22:595-615

R Development Core Team 2007-2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Austria. www.R-project.org.

Table F-1. Summary of the first two axes obtained from co-inertia analysis of species abundance (L) and low-flow variables (R). Correlation refers to the correlation coefficients between L and R.

		Variance		Covariance		Correlation	
	Total	1	2	1	2	1	2
Fall-Spring	21.9	13.8 (63)	5.4 (25)	3.72	2.32	0.81	0.93

Table F-2. The summary of canonical correspondence analysis of species-site and environment-site tables (L and R Tables). The absolute ("iner") and cumulative ("inercum") contributions of the decomposition of inertia; absolute ("inerC") and cumulative ("inercumC") variances of the projections; the "ratio" between inercumC and "inercum"; the square coefficient of correlation ("R^2") and the eigenvalues (lambda).

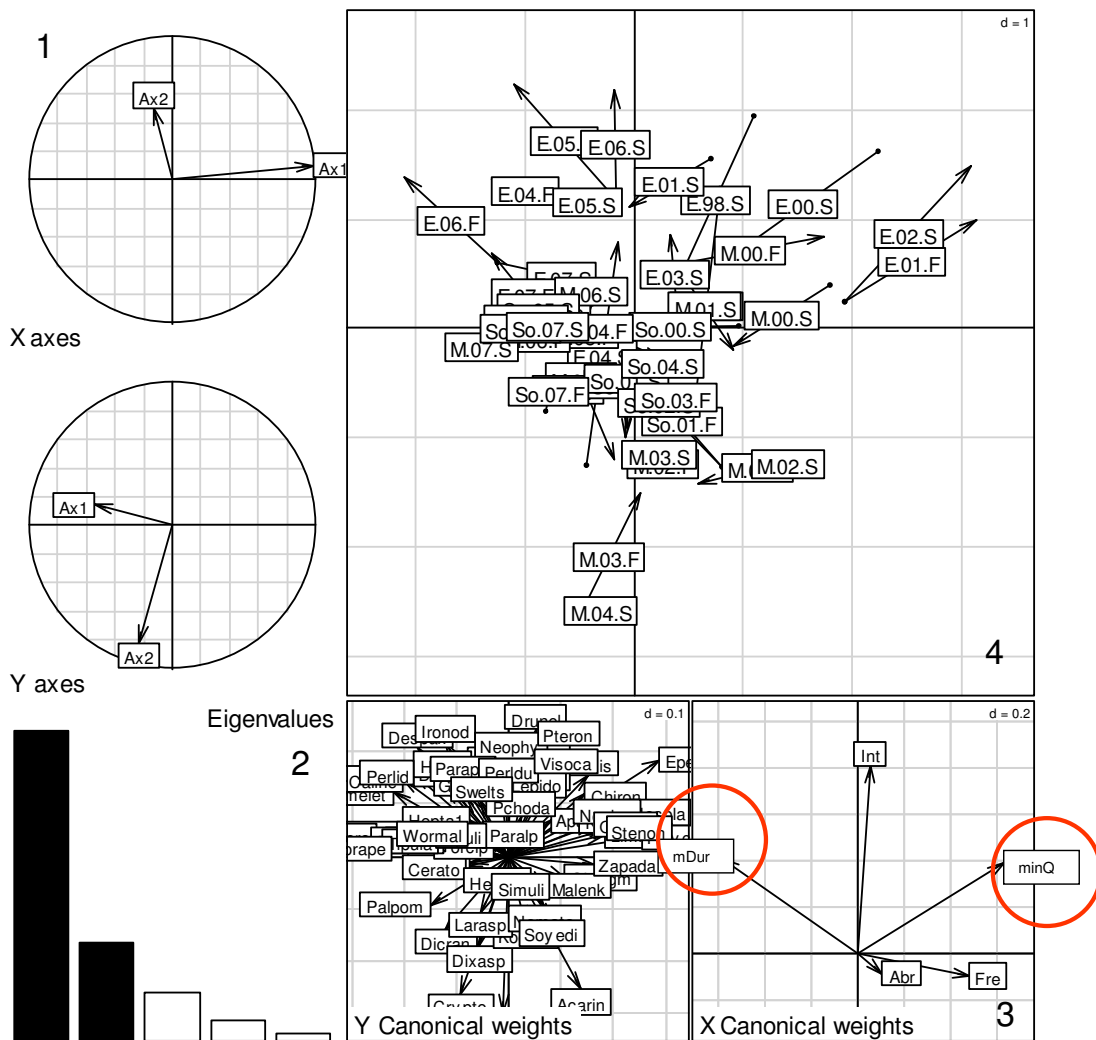| Axis	iner	inercum	inerC	inercumC	ratio	R^2	λ
1	0.00152	0.00152	0.00082	0.00082	0.539	0.636	0.000521
2	0.00091	0.00243	0.00125	0.00207	0.852	0.372	0.000466

Figure F-1. Co-inertia analysis of log(x+1)-transformed species abundance table (L) and environmental table containing low-flow parameters (R). L consisted of the difference between Fall and Spring populations of each species in proportion while R contained frequency, duration, intensity, abruptness and minimum discharge (see Chapter 2 for details). 1) projection of the principal axes of the two tables (species and environment) on co-inertia axes, 2) eigenvalues screeplot, 3) canonical weights of species and environmental variables, and 4) joint display of the sites with predictions by regression (arrow tips). The distance scale (d) indicates the length of a side of grey squares in CA scales.
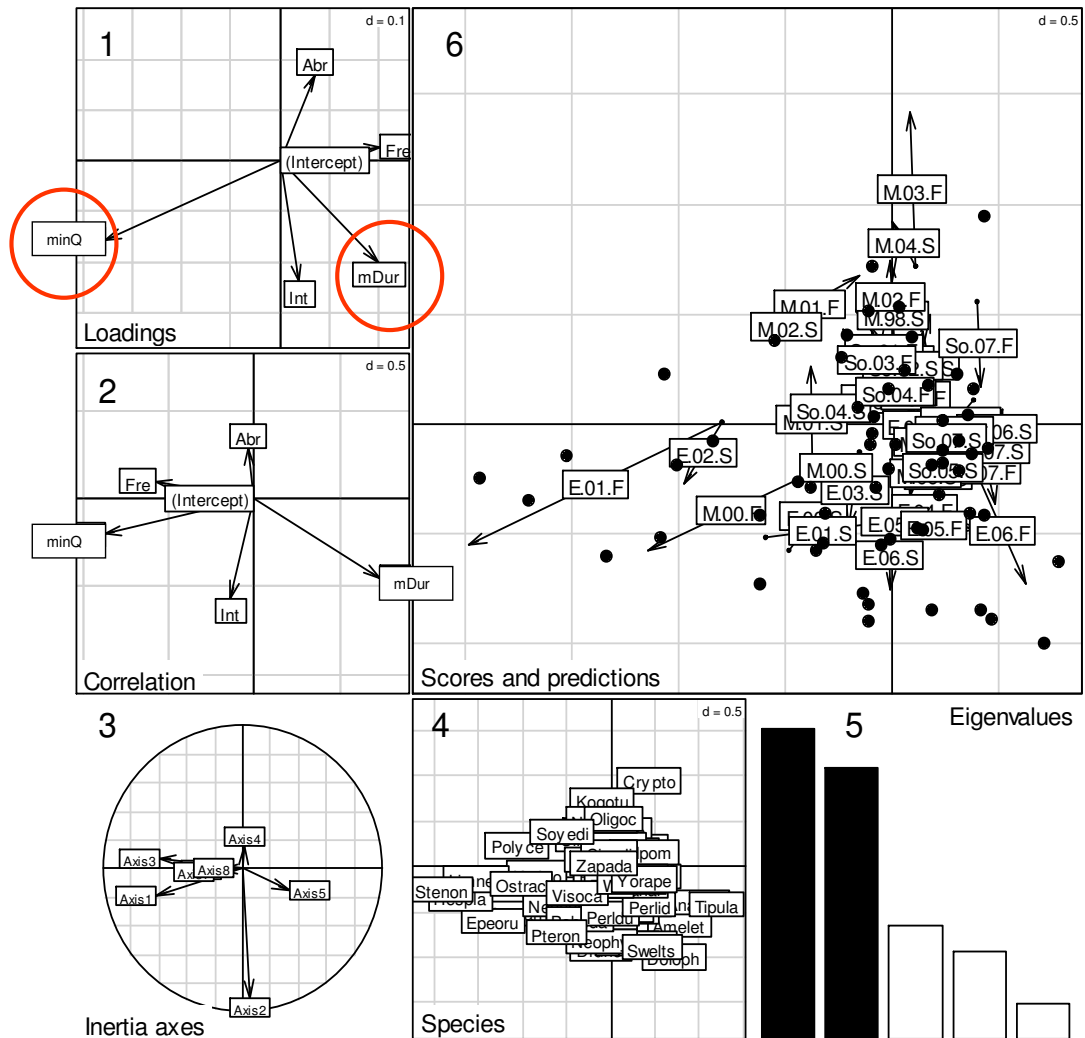
Figure F-2. The summary plot of canonical correspondence analysis of log(x+1) transformed species abundance table (L) and environmental table containing low-flow parameters (R). L contained the difference between Fall and Spring populations of each species in proportion while R contained frequency, duration, intensity, abruptness and minimum discharge (see Chapter 2 for details). 1) canonical weights of low flow variables, 2) correlations between low flow variables and CCA axis, 3) inertia axes projected on PCAIV axis, 4) canonical weights of species. The distance scale (d) indicates the length of a side of grey squares in CA scales.

Appendix G. The list of codes used to simulate the population models in Chapter 3.

taxacode	LCcode	rescode	N.zero.m2
Amelet	C	0.565	19
Anagap	C	0.94	105
Apatan	C	0.48	11
Arctop	A	1.84	9
Baetis	D	0.76	241
Caline	B	1.4	65
Cerato	D	0.72	357
Chelif	C	0.005	76
Chiron	D	0.68	2448
Chloro	B	0.77	1480
Cinygm	C	0.625	209
Crypto	A	0.125	6
Despax	A	0.37	302
Dicran	C	0.41	80
Dixasp	C	0.225	11
Doloph	D	1.2	6
Dorone	A	1.2	13
Drunel	C	0.745	5
Dysmic	A	0.125	87
Empidi	C	0.005	21
Epeoru	C	0.565	87
Forcip	D	0.375	13
Glosso	D	0.705	37
Hepta1	C	0.675	205
Hespla	B	1.065	15
Hexato	C	0.35	30
Ironod	D	0.7	145
Kathro	B	1.165	223
Kogotu	C	0.835	2
Larasp	A	0.875	54
Lepido	C	0.8	204
Limnep	C	1	30
Malenk	C	0.72	230
Micras	C	0.78	112
Neoher	A	0.125	178
Neophy	C	0.415	37
Palpom	C	0.835	33
Paralp	C	0.715	816
Paraps	A	0.955	47

Pchoda	D	0.45	20
Perldu	C	0.92	130
Perlid	B	1.4	145
Polyce	D	1.545	80
Pteron	A	0.735	41
Rhyaco	C	1.47	223
Simuli	D	0.825	61
Soyedi	C	1	64
Stenon	C	0.75	35
Swelts	C	0.525	19
Tipula	A	0.86	3
Tipuli	A	0.45	26
Visoka	A	1	76
Wormal	D	1.4	340
Yorape	A	0.75	500
Zapada	A	1	1270