SPATIOTEMPORAL DYNAMICS OF A REGULATED ALPINE RIVER ECOSYSTEM

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The candidate confirms that the work submitted is his/her own and that appropriate credit has been given where reference has been made to the work of others.

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ABSTRACT

The contributions of glacier-melt, snowmelt, and groundwater to stream flow in alpine catchments result in characteristic discharge regimes and unique stream habitats. The year-round dynamics of alpine floodplain ecosystems are however, poorly understood, in particular the effects of flow regulation on alpine stream ecosystems have not been assessed. Fieldwork was undertaken over two summer melt-seasons (2008/2009) and the intervening winter season within the Eisboden catchment, Austrian Alps. The application of a novel diurnal statistical hydrograph classification technique to analyse flow dynamics at six stream sites elucidated the varying influences of precipitation, ablation, and groundwater contributions on spatiotemporal flow dynamics. Although a clear ablation driven seasonal progression in river flow was evident, rainfall also exerted a dominant influence altering the melt-signal during both summer seasons. Water temperature time series, monitored at 23 sites across the catchment revealed year-round spatiotemporal variability in flow permanency, and high thermal heterogeneity, amongst streams. Benthic macroinvertebrate communities were found to be associated predominately with variations in stream temperature and channel stability during the summer melt-season. However, the communities of mixed water source floodplain sites were found to be highly dynamic and considerably more diverse than expected with respect to existing conceptual models of alpine streams. Macroinvertebrate community structure differed markedly during the winter; the assemblage diversified at glacial-fed and mixed sites both in terms of taxonomic and functional diversity. Anthropogenic flow regulation from the Weiβsee hydropower storage reservoir had a large impact on the discharge and thermal regimes of streams but the macroinvertebrate community was relatively resistant in flow regulation disturbances. This finding suggests alpine stream macroinvertebrates inhabiting proglacial river systems are well adapted to the harsh and dynamic physicochemical conditions. Current hydrological and ecological conceptual models of alpine stream systems are evaluated with respect to new insights from the Eisboden and future research directions suggested.

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ABBREVIATIONS

AFDM	Ash-Free Dry Mass
ANOSIM	Analysis of similarity
ANOVA	Analysis of variance
AWS	Automatic Weather Station
BACI	Before-After-Control-Impact experimental design
BF	Baseflow
CCF	Cross-Correlation Function
CLSR	Crawler Locomotion and Substrate Relation
d_{ij}	Dissimilarity between taxa *i* and *j*
DF	Deposit Feeder
dGPS	Differential Global Positioning System
DV	Diurnal Variability
EC	Electrical Conductivity
EPT	Ephemeroptera, Plecoptera and Trichoptera
F	F-value
FD	Dendrogram based functional diversity
FLM	Food; Living Microphytes
GI	Glaciality Index
GMT	Greenwich Mean Time
HCA	Hierarchical Clustering Analysis
m.a.s.l.	Meters above sea level
N	Number of time steps
n	Number of days
n_s	Number of individuals in sub-sample
NMDS	Non Metric multi-Dimensional Scaling
NRF	No Resistance Form
OLS	Ordinary Least Square

p	p-value
p_i	Relative abundance of species *i*
PCA	Principal Components Analysis
PFAN	Pfankuch index
POM	Particulate Organic Matter
Ppn	Precipitation
r	r-value
r^2	Coefficient of determination
RDA	Redundancy Analysis
S	Total species richness
SFH	Scraper Feeding Habit
ShFH	Shredder Feeding Habit
SIMPER	Similarity percentage
SSC	Suspended sediment concentrations
SV	Semi-Voltine
T_{air}	Air Temperature
T_{max}	Maximum water temperature
$t_{p,av}$	Mean time at peak-flow
T_{range}	Daily water temperature range
$\bar{T}$	Mean daily water temperature
ΔT	Thermal heterogeneity
UV	Univoltine
Q	Discharge
$\bar{Q}$	Mean weekly discharge
Q_{amp}	Flow amplitude
Q_{ampstd}	Standardised flow amplitude
Q_b	Morning baseflow
Q_{mean}	Mean daily flow
Q_p	Peakflow
Q_{std}	Discharge standard deviation
QE	Rao’s Quadratic Entropy
x	Site grouping for thermal heterogeneity analysis
σ	Standard Deviation

CHAPTER 1: INTRODUCTION

1.1. RESEARCH CONTEXT

The hydrology, geomorphology, and biota of river ecosystems are highly sensitive to environmental change across a wide range of spatial and temporal scales (Ward, 1989; Poff, 1997; Wiens, 2002). Environmental conditions fluctuate naturally, but direct human impacts including flow regulation, water pollution, fishing, introduction of invasive species and channel alteration can be large factors driving changes to river ecosystems (Karr & Chu, 2000; Moilanen et al., 2008). Human impacts on river ecosystems worldwide, and particularly in less economically developed countries, are predicted to increase in response to future global population and development trends (Meybeck, 2004). Furthermore global climate change will serve as a continuous pressure on river ecosystems (Robinson et al., 2003; Durance & Ormerod, 2007; IPCC, 2007; Vaughan et al., 2007; Whited et al., 2007; Vörösmarty et al., 2010).

Conservation of river ecosystems is vital given their importance for biodiversity, nutrient cycling, freshwater supply, and provision of food (Postel & Carpenter, 1997; Karr & Chu, 2000; Aylward et al., 2006; Brown et al., 2009a). However, predicting and managing the effects of contemporary human impacts, and assessing local-scale implications of global environmental change on river ecosystems present considerable challenges to researchers, resource managers, and conservationists (Nel et al., 2009; Vörösmarty et al., 2010). Aside from logistical, political and financial constraints associated with mitigating anthropogenic impacts to river systems, there has been insufficient integrated research on river ecosystem structure to underpin conservation and management strategies. In fact, it has been clearly stated that current research outputs are not meeting the needs of river managers and conservationists (Petts et al., 2006; Ormerod et al., 2007). Therefore, there is an urgent need for more integrated research to investigate how climatic, geomorphic, hydrological and ecological processes interact to control river ecosystem processes.

Alpine stream systems are of particular importance in a global context from both (i) a water supply perspective as alpine catchments act as ’natural water towers’ providing storage and distribution of a critical water supply to extensive surrounding areas (Viviroli & Weingartner, 2004b; Viviroli et al., 2007) and, (ii) a conservation perspective because of the diverse and unique ecosystems that alpine streams host (Milner & Petts, 1994; Füreder, 1999; Brittain & Milner, 2001; Brown et al., 2003; Hieber et al., 2005; Brown et al., 2006d). However, the hydrology and ecology of alpine streams are predicted to be affected significantly even under the most conservative estimates of climate change (Barnett et al., 2005; Stahl et al., 2008; Milner et al., 2009), and increasing water supply demand, particularly by hydropower storage schemes, will place a further substantial pressure on the ecosystems of alpine catchments (McGregor et al., 1995; Wehren et al., 2010b). Further research is therefore urgently required to develop a better understanding alpine stream hydrology and ecology and to develop appropriate conservation strategies for alpine ecosystems (Hannah et al., 2007a).

1.2. RESEARCH AIMS AND THESIS STRUCTURE

This thesis aims to examine the spatiotemporal dynamics of an alpine proglacial floodplain ecosystem that is impacted by anthropogenic flow regulation. To this end the study had four key objectives:

(i) To use an objective hydrograph classification technique to analyse the hydrological functioning of an alpine floodplain stream system.

(ii) To investigate year-round flow permanency and thermal dynamics of streams across the floodplain and more widely across the basin.

(iii) To examine the spatiotemporal dynamics of the macroinvertebrate floodplain community with respect to physicochemical habitat conditions.

(iv) To analyse the biological and functional trait characteristics of floodplain macroinvertebrate assemblages.

The thesis structure is outlined in Figure 1.1. Chapter 2 provides: (i) a rationale for the focus of this thesis on an alpine stream system impacted by anthropogenic flow regulation; (ii) an integrated review of hydrological-geomorphologic-ecological research relevant to alpine stream systems; (iii) a review of studies relevant to an alpine context that have assessed the impacts of anthropogenic flow regulation on stream ecosystems, and; (iv) an outline of some of the most pertinent research gaps that this thesis seeks to address. Chapter 3 details the study area and overall data collection strategy. The hydrological functioning of the catchment is investigated in Chapter 4 using an objective statistical hydrograph classification approach. Chapter 5 examines the spatiotemporal dynamics of catchment stream temperature and flow permanency. Chapter 6 considers the year-round dynamics of macroinvertebrate assemblage structure in relation to stream environmental conditions, and Chapter 7 investigates assemblage-environment patterns further by analysing macroinvertebrate communities from a biological trait and functional diversity perspective. The final chapter synthesises the key findings from previous chapters, discusses the implications of this research for current conceptual ideas of how alpine stream ecosystems are structured and function year-round, and proposes future research directions.

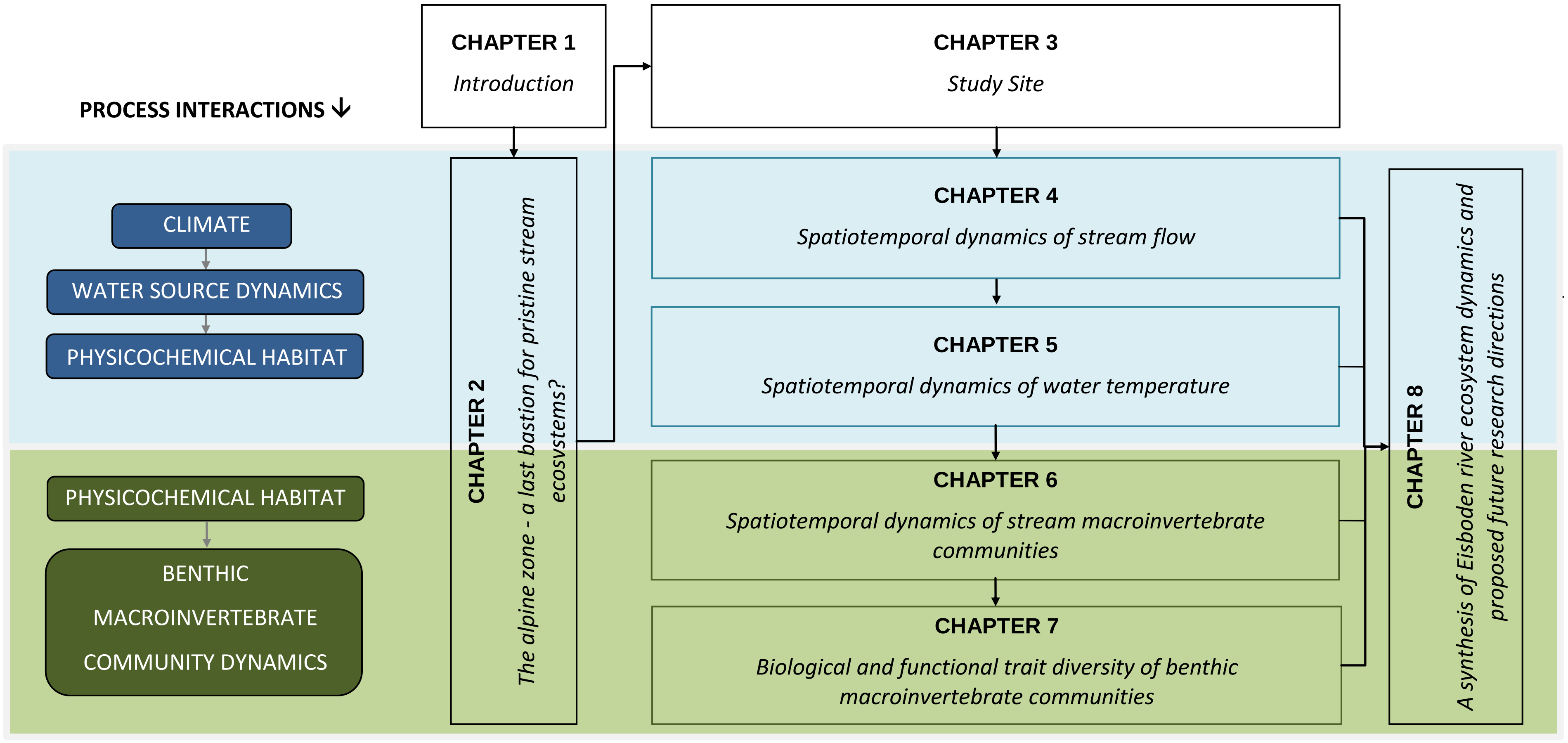

Figure 1.1 - *Schematic thesis structure.*

CHAPTER 2: THE ALPINE ZONE - A LAST BASTION FOR PRISTINE STREAM ECOSYSTEMS?

2.1 INTRODUCTION

This chapter provides a rationale for the focus of the thesis on an alpine stream system impacted by anthropogenic flow regulation. It begins by providing an overview of anthropogenic pressures on alpine stream systems and discussing the importance of alpine stream systems from conservational and water resources perspectives (Section 2.2). Further context for the thesis is provided through an integrated review of hydrological-geomorphological-ecological literature (Section 2.3). The review provided in Section 2.3 is not intended to be exhaustive, as more specific detailed reviews are integrated into the introductory material of chapters 4-7. The impact of anthropogenic flow regulation on alpine stream ecosystems is considered by reviewing the available research on alpine streams subject to flow regulation, and additionally by considering the transferability of findings from previous research into the impacts of flow regulation in lower altitude ‘sub-alpine’ river reaches (Section 2.4). A synthesis of key findings (Section 2.5) precedes a discussion of substantial research gaps that this thesis aims to address (Section 2.6).

2.2 PRESSURES ON THE ALPINE ZONE AND ALPINE WATER RESOURCES

The alpine-zone lies above the natural tree-line in mountainous areas between the Arctic and Antarctic regions (McGregor et al., 1995; Körner, 2003; Brown et al., 2007c). Contributions of glacier melt, snowmelt, and groundwater to stream flow in the alpine zone results in characteristic discharge regimes and provides unique physicochemical conditions for stream habitats (Milner & Petts, 1994; Füreder, 1999; Brittain & Milner, 2001; Brown et al., 2003; Hieber et al., 2005; Brown et al., 2006d). However, the quality of many alpine stream habitats is potentially compromised by widespread anthropogenic regulation for water supply, hydropower, irrigation, and nutrient enrichment from grazing livestock (Füreder et al., 2002; Wehren et al., 2010b). Additionally, runoff in recent decades has been subject to more indirect anthropogenic modifications such as snowpack alteration by artificial snow generation and ski piste formation, and by pollution from ski-resorts (Schiermeier, 2004; Wemple et al., 2007; Pintar et al., 2009; Wehren et al., 2010b). It is therefore perhaps surprising that little work has been done to quantify either the spatiotemporal extent or the consequences of anthropogenic impacts on alpine stream ecosystems. The current status of alpine zones as largely supporting ‘relatively pristine ecosystems’ (Hannah et al., 2007a) is therefore questionable, particularly in the European Alps where anthropogenic pressures are intense. Furthermore, there is considerable uncertainty regarding the response of alpine stream ecosystems in the face of predicted anthropogenic climate change (IPCC, 2007).

Alpine stream systems are particularly sensitive to climate change because of their position at a climatic extreme where a strong coupling exists between atmospheric forcing, snowpack/glacier mass-balance, flow source components and physicochemical habitat (Williams et al., 1996; Braun et al., 2000; Viviroli & Weingartner, 2004a; Oerlemans, 2005; Brown et al., 2007c; Hannah et al., 2007a; Milner et al., 2009). Alpine stream ecosystems are thus considered likely to provide early indications of hydrological and ecological responses to climate change. They are therefore important as global change indicators and from both natural resources and conservation, management perspectives (McGregor et al., 1995; Brown et al., 2009b). For example; (i) if predicted shifts in seasonal peak runoff time (Barnett et al., 2005) occur this could have serious implications for water supply to surrounding regions, and (ii) a reduction in meltwater inputs is predicted to lead to the loss of some endemic species and reduced biodiversity, particularly gamma (regional) diversity (Brown et al., 2007a; Milner et al., 2009).

Managing the balance between habitat conservation and resource utilisation in alpine catchments presents a considerable challenge. From a conservation perspective, alpine stream systems are particularly fragile (McGregor et al., 1995) because they (i) provide unique habitats (Füreder, 2007), (ii) are important hot-spots of biodiversity (Bundi, 2010), and (iii) host many endemic species (Brown et al., 2009a). In stark contrast, alpine catchments are considered ‘natural water towers’ from a natural resources perspective because over-one sixth of the world’s population is reliant on the discharge from glaciers and seasonal-snowpacks for water supply (Viviroli & Weingartner, 2004b; Viviroli et al., 2007). At a regional scale, the proportion of discharge in lowland areas sourced from mountainous catchments can be as high as 95% (e.g. in the Aral Sea watershed, Central Asia; Liniger et al., 1998). In those countries with extensive mountainous regions that produce large quantities of runoff, water is also used in hydropower schemes to provide a large proportion of gross electrical energy production. For example, in Austria and Switzerland approximately 55-60% of gross electrical energy production comes from hydropower (Wehren et al., 2010b). It has been suggested that as electrical power consumption continues to increase and thus that as renewable energy resources provide an increasingly significant share of the energy market, hydropower will become increasingly important. Not least because unlike most other renewable supplies, storage hydropower can meet daily or seasonal surges in demand and is not reliant on immediate weather conditions to maintain supply (compare to for example wind and solar power) (Fette et al., 2007). Unfortunately, hydropower schemes, particularly storage power plants, abstract, store, re-route and re-flux large volumes of water and thus significantly alter the natural runoff characteristics of source and sink rivers (Wehren et al., 2010b). For example, the Enzingerboden storage hydropower station, which is the upper of three hydropower stations in the Stubach valley, Austrian Alps, draws water from seven alpine basins resulting in downstream flow reduction and irregular flow-peaks from reservoir overtopping (Figure 2.1). Water is re-routed from the WeiBsee reservoir and the Wurfbach (stream) to the Tauernmoose reservoir via rivers resulting in hydropeaking and a seasonal shift hydrological functioning.

McGregor et al. (1995), Brown et al. (2007a) and Milner et al. (2009) have provided reviews to include perspectives on the impacts of climate change and associated hydrological response to alpine stream ecosystems. Nonetheless, a detailed review on the impacts of flow regulation in alpine systems is severely lacking. It is specifically the effect of flow regulation on stream ecosystems that forms the focus of this review chapter, since flow regulation exerts a particularly large and direct influence on catchment runoff characteristics. A recent extensive review by Poff & Zimmerman (2010) attempted to evaluate statistical links between flow regulation and ecological response by considering 165 studies conducted world-wide on a range of stream types. They suggested that the currently available global literature is not sufficient to develop general transferable models that link flow alterations to ecological response. While the risk of ecological impacts increases with the level of flow regime regulation, the specific characteristics of ecological responses to changes in flow regime remain unclear. Macroinvertebrates populations when considered as a group exhibited particularly mixed responses to flow alterations; in contrast to fish populations which consistently declined. It is clear that in order to more precisely assess the response of macroinvertebrate communities to flow regulation consideration is required of: (i) the environmental context of the impacted system (Carlisle et al., 2010b); (ii) more refined taxonomic groups, and (iii) the specific nature/severity of flow alteration (Göran & Böjrn, 1996; Acreman & Dunbar, 2004; Carlisle et al., 2010a; Carlisle et al., 2010b; Poff & Zimmerman, 2010). This review chapter therefore firstly provides contextual information on relationships between alpine hydrological functioning, stream physicochemical characteristics and ecological characteristics of 'naturally' functioning alpine stream systems. It then focuses on the evidence for how different forms of flow regulation can impact alpine stream systems. In summation this review chapter identifies a series of notable research gaps which are expanded on in this thesis.

2.3 CHARACTERISTICS OF ALPINE STREAM SYSTEMS

The physicochemical habitat conditions of alpine stream systems exhibit considerable variability both spatially and temporally through a multitude of scales (Milner & Petts, 1994; Füreder, 1999; Brittain & Milner, 2001; Hieber et al., 2005; Brown et al., 2006d). Some examples of variations in environmental conditions at different scales are shown in Figure 2.2, i.e. variations in (i) snow cover at the seasonal scale, (ii) discharge, channel stability and turbidity at the reach scale; and (iii) substratum and vegetation at the patch scale.

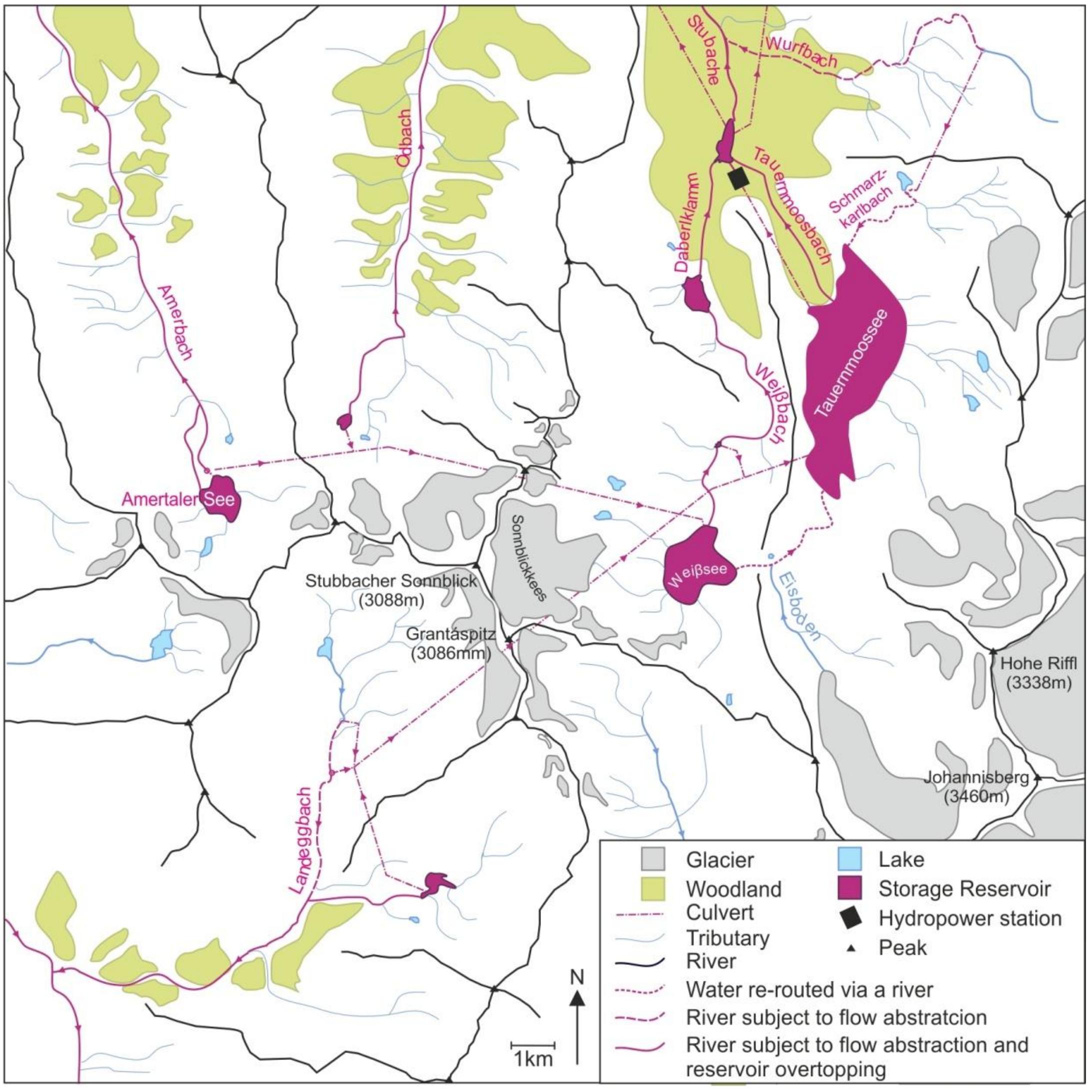

Figure 2.1 - *Alpine rivers affected by regulation for hydropower in the Granatspitzgruppe, Austrian Alps.*

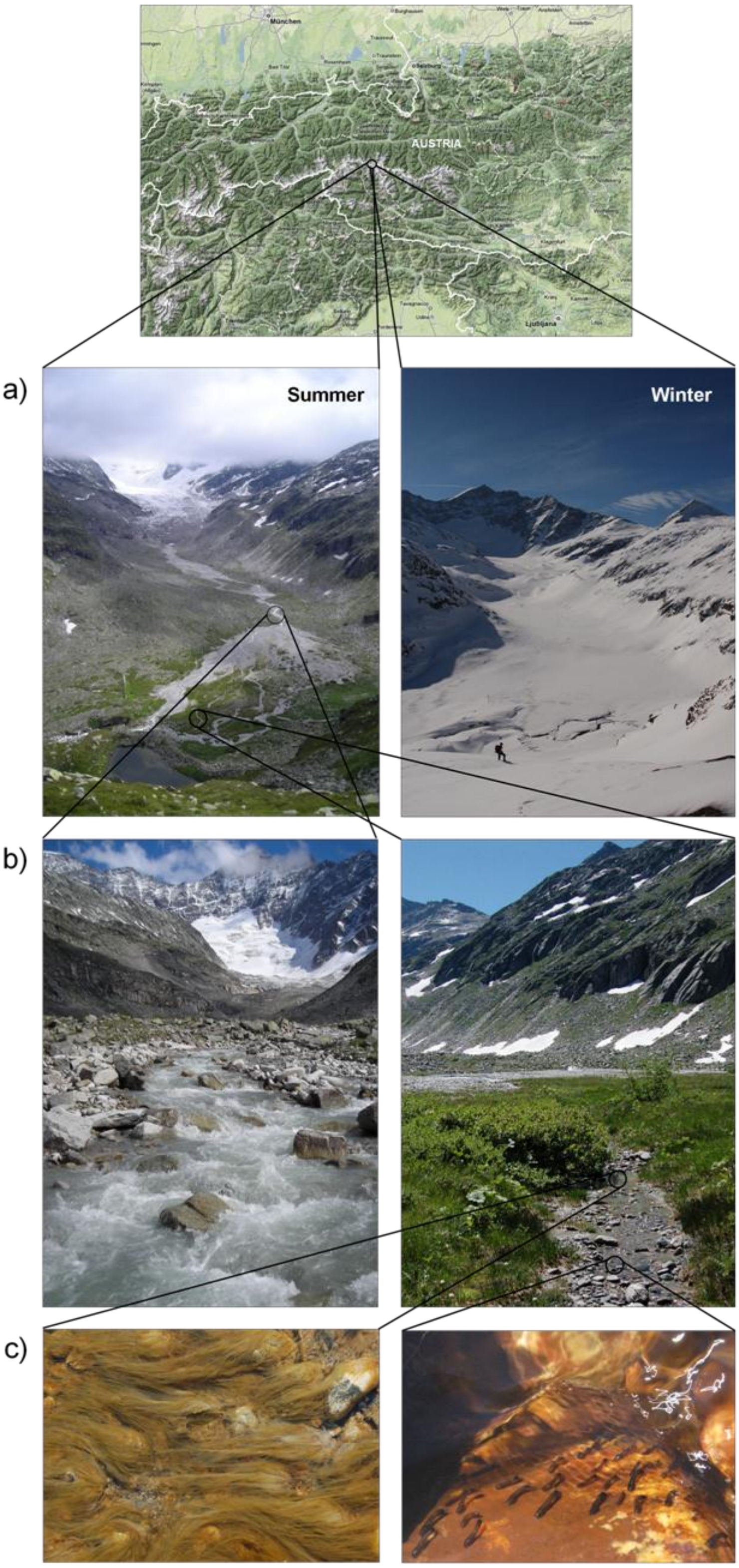

Figure 2.2 - *Examples of spatiotemporal variations in environmental conditions at different scales in the Eisboden Catchment, Austria; a) seasonal variations in snow cover; b) reach-scale physicochemical characteristics of a glacial (left) versus groundwater (right) fed stream; c) Patch-scale substratum and biota variations.*

Habitat spatiotemporal dynamics in alpine streams are governed by a complex cascade of processes (Smith et al., 2001; Hannah et al., 2007a) (Figure 2.3). At the top of the cascade climatic processes influence the volume of precipiation inputs and melt water generation at the catchment scale. The resulting proportions of snowmelt, icemelt and groundwater contributions that mix to comprise the stream water in any particular reach are key determinants of in-stream physicochemical habitat conditions which influence the functioning and structure of benthic macroinvertebrates communities. Anthropogenic activities can potentially impact this cascade at a number of levels; some examples are given in Figure 2.3. The response of stream ecosystems at a very local scale (e.g. patch, reach) to an anthropogenic activity is dependent on the linking cascade of processes. Localised anthropogenic impacts such as groundwater contamination by pollution from mountain huts or agriculture (Reischer et al., 2008) may affect physicochemical habitat conditions by the contamination of a water source, whereas the impact of global climate change (IPCC, 2007) is at the top of the cascade and its impact on stream ecosystems is throughout the whole cascade of interacting processes. This serves to illustrate that a local scale response to anthropogenic impacts higher up the cascade may vary greatly from reach-to-reach, catchment-to-catchment and from region-to-region (McGregor et al., 1995).

2.3.1 Water source contributions and runoff characteristics

Snowmelt, icemelt, groundwater and runoff from rainfall are the four principal water sources that generate distinct spatiotemporal variations of physicochemical stream properties in alpine basins. The timing, duration and magnitude of these water source contributions are key factors that characterise stream habitat conditions due to the distinct physicochemical characteristics of each water source (Brown et al., 2003). A distinct characteristic of alpine streams fed by snow/ice melt is the diurnal pulsing of flow which is driven by the influence daily radiation flux on melt. The form and timing of diurnal peaks, and the base flow above which diurnal flow-peaks occur depend upon; (i) climatic conditions; (ii) the availability of water stores, and; (iii) the effectiveness of drainage pathways; all of which exhibit considerable seasonal variation (Swift et al., 2005).

2.3.1.1 Spring and summer - melt season flow dynamics

The start of the melt season in alpine basins is marked by an increase in snowmelt stimulated by an increase in atmospheric energy inputs. However, a somewhat subdued and lagged diurnal stream-flow response to radiation during this period (Paterson, 1994; Hannah et al., 2000; Swift et al., 2005) is caused by relatively inefficient early-season flow routing through snow-packs (Colbeck, 1976) and poorly developed glacial drainage systems (Röthlisberger & Lang, 1987; Paterson, 1994; Jansson et al., 2003; Fountain et al., 2005). Snowmelt discharge in alpine basins tends to peak in mid-late spring, and in non-glacierized basins peak snow-melt typically marks the start of a general decline in basin discharge (McGregor et al., 1995; Füreder et al., 2001; Lafrenière & Sharp, 2005). However, dry winter seasons, summers with high precipitation, and the presence of permafrost are factors that can result in no distinct seasonal discharge peak as observed by Woo (1994) in the Cirque Basin, located in the Chinese Tianshan In Xinjiang Uigur Autonomous Region.

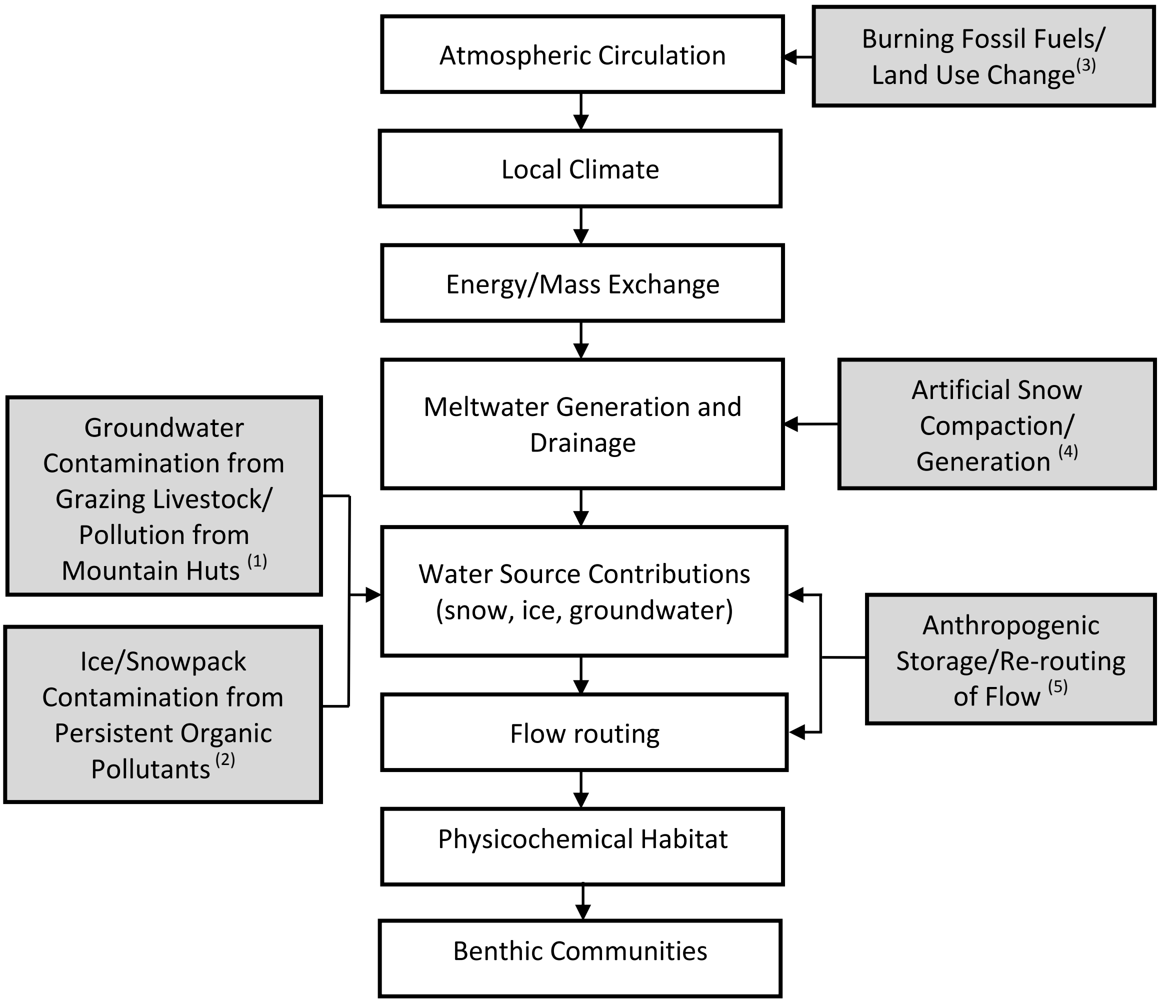

Figure 2.3 - *Hypothesised process cascade showing climatic-hydrological-ecological links in an alpine, glacierized catchment and examples of potential anthropogenic processes influencing the cascade (shaded boxes). Adapted from Hannah et al. (2007a) See (1)(Kralik, 2001; Reischer et al., 2008), (2)(Blais et al., 2001; Caruso, 2002; Bogdal et al., 2009), (3)(McGregor et al., 1995; Brown et al., 2007a; Milner et al., 2009), (4)(Schiermeier, 2004; Wemple et al., 2007; Pintar et al., 2009; Wehren et al., 2010b), (5)(Petts & Bickerton, 1994; Fette et al., 2007; Wehren et al., 2010b).*

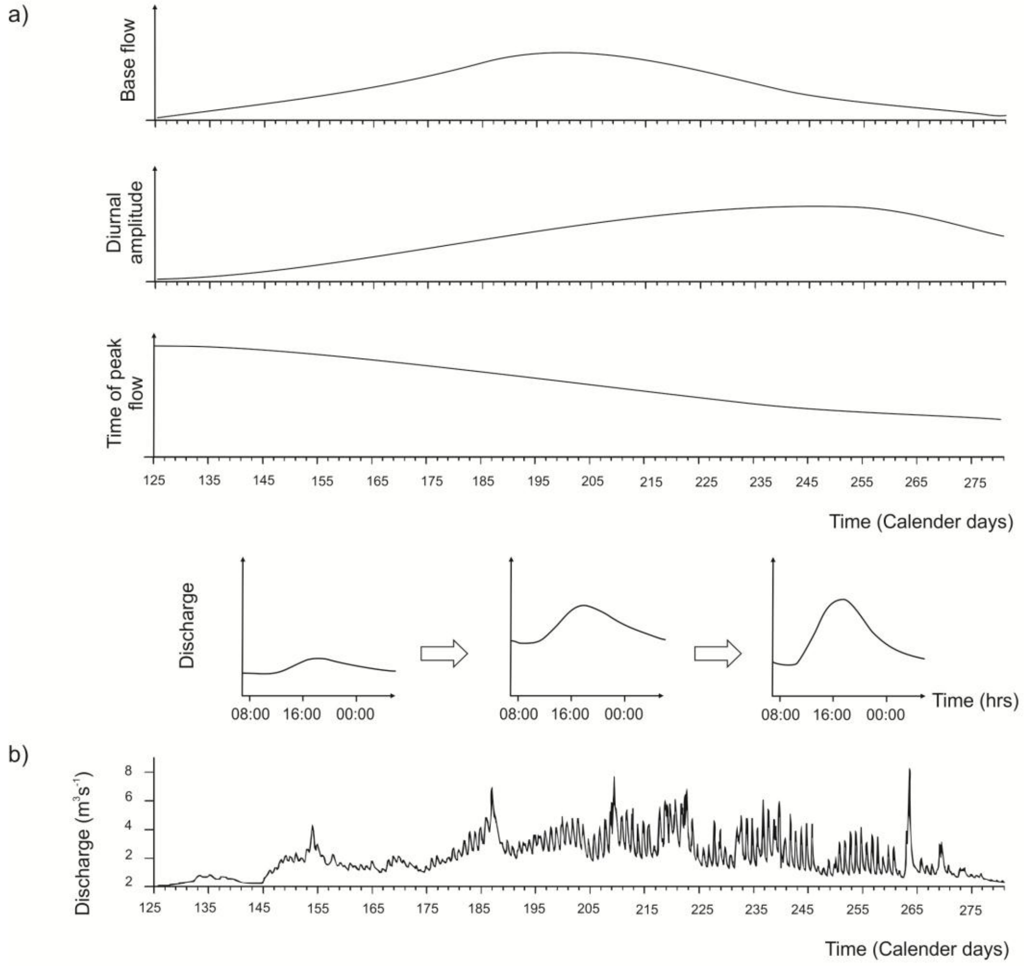

Figure 2.4 - *Evolution of a proglacial stream hydrograph through the melt season; a) conceptual representation in the seasonal evolution of; base-flow, diurnal amplitude, time of peak flow, and diurnal hydrograph form, and; b) an example hydrograph of a proglacial stream hydrograph during the melt season (Haut-Glacier de Arolla, 1999; Swift et al., 2005).*

Figure 2.4 illustrates the typical summer evolution of hydrograph form of a proglacial stream. In glacierized basins, as snowpacks recede and the ablation zones of glacier surfaces are increasingly exposed from mid-spring into summer, ice-melt becomes a more dominant flow source and flow routing becomes more efficient through the expansion of en- and sub-glacial drainage systems (Paterson, 1994; Malard et al., 1999; Hannah et al., 2000; Swift et al., 2005). This typically leads to a gradual reduction in base flow, but also to more pronounced diurnal variations; a shortening of lag times between peak daily incoming radiation and peak stream flow results in earlier peak flow times (Milner & Petts, 1994; Hannah et al., 2000; Swift et al., 2005).

Unlike snow and icemelt contributions to stream flow, groundwater contributions do not exhibit strong diurnal oscillations. Thus, groundwater contributions maintain base flow and dampen diurnal oscillations driven by melt flow components. Although groundwater is ultimately sourced from melt or rainfall, subsurface aquifers substantially modify the physicochemical properties of groundwater (Malard et al., 1999; Tranter et al., 2002; Brown et al., 2006c). Annual variations in groundwater contributions to stream flow are not as a strongly defined as melt components (Malard et al., 1999; Brown et al., 2007b). Brown et al. (2006c) utilised an end member mixing approach to examine stream flow components in the Taillon-Gabiétous basin, French Pyrénées and found groundwater contributions to increase in response to substantial recharging of aquifers: (i) at the beginning of the melt season, and; (ii) after prolonged precipitations events. The influence of groundwater on proglacial stream discharge regimes and physicochemical characteristics tends to increase with distance from the glacial margin as meltwater is increasingly diluted by groundwater (Malard et al., 1999; Brown et al., 2006c; Brown et al., 2009b). The influence of groundwater also varies markedly between basins. In unglacierized basins such as the Königsbach, Austria, groundwater constitutes the sole baseflow component once seasonal snowpacks have melted (Füreder et al., 2001). Brown et al. (2007b) found that during summer seasons ground water contributed ~55, 25 and 15% to total stream flow with 2, 4 and 6% glacierized catchment areas respectively in the Taillon and Gabiétous catchments, French Pyrénées. In more heavily glacierized catchments, the proportional contributions of groundwater are likely to be further reduced (e.g. Smith et al., 2001).

Precipitation events are common in alpine regions and can punctuate underlying seasonal trends in catchment discharge. The impact of rainfall events on discharge regimes is influenced by the seasonal evolution of catchment drainage systems. During spring, snowpacks act as buffers delaying the hydrological response after rainfall but as snowpacks are reduced and glacial drainage pathways evolve (Lavandier & Décamps, 1985; Röthlisberger & Lang, 1987; Paterson, 1994; Jansson et al., 2003; Fountain et al., 2005) hydrological response to rainfall can be more dramatic. In catchments with relatively small glacierized areas, rainfall can be key driver of major flow events (Lavandier & Décamps, 1985; Hannah et al., 2000; Brown & Hannah, 2007). Conversely, summer snowfall events may act to reduce the efficiency of flow pathways (Collins, 1998), although the associated reduction in atmospheric energy inputs may also be a significant factor reducing discharge during summer cold periods (Woo et al., 1994).

2.3.1.2 Autumn and winter - recession flows and dormancy

Although the active hydrological driving processes and flow characteristics in alpine basins have been relatively well studied during the spring and summer melt season, alpine basins have been less well studied in autumn and winter seasons (Brittain & Milner, 2001; Brown et al., 2007c). Extreme weather conditions, access difficulties and the build up of a deep snow pack covering many stream networks (Schütz et al., 2001) make it logistically challenging to monitor stream flow or to conduct water sampling. It is evident from discharge records of lower reaches of proglacial rivers (e.g. van der Weijden & Middelburg, 1989; Arscott et al., 2002; Chalise et al., 2003; Dery et al., 2009) that flow contributions from alpine catchments are extremely reduced during the winter months compared to summer. The few studies that have recorded year-round stream flow in glacierized headwater basins have shown that (i) close to a glacier margin winter reductions in mean daily discharge can be extreme and (ii) that mean reductions in discharge during winter are also associated with the stabilisation of diurnal fluctuations as radiation flux is reduced and drainage pathways become blocked by snow (Schütz et al., 2001; Robinson et al., 2002). A key study by Malard et al. (1999) investigated the hydrology of the upper floodplain of the Roseg River, Switzerland and used hydrochemistry analysis to provide insight into dynamics of water source contributions during winter months. They found that a twelve-fold decrease in discharge occurred though the autumn, that a substantial en-glacial flow component was evident into October, that sub-glacial drainage provided surface flow to the floodplain until January, and that from January-March groundwater was the dominant water source. Some surface flow of glacial origin was found at the entry to the floodplain although this down-welled into the sediment before re-emerging in the lower portion of the floodplain; thus all emerging downstream flow was groundwater fed.

2.3.2 Physicochemical habitat

Alpine stream habitats exhibit large physicochemical variations over a range of spatiotemporal scales. The water source type is a key factor that pre-determines aspects of its physicochemical habitat; indeed several attempts to classify and characterise alpine stream habitats by water source have been made (Steffan, 1971; Ward, 1994; Brown et al., 2003).

Ward (1994) proposed a three-fold classification model which distinguished ‘kryal’, ‘rhithral’ and ‘krenal’ stream segments with the assumption that streams are dominated by one particular water source which defines its characteristics. These stream three types are characterised in the following paragraphs to give a flavour of the expected physicochemical characteristics where a singular water source dominates.

Kryal segments are considered to be sourced from the melting of glacier ice. Kryal discharge is characterised during a summer melt season by elevated base flow and large diurnal discharge fluctuations, and during the winter by dramatically reduced and stable discharge (Schütz et al., 2001; Robinson et al., 2002; Swift et al., 2005). Water temperature increases longitudinally downstream but close to a glacier margin water temperature is extremely low (<2^{o}C) (Ward, 1994; Uehlinger et al., 2003b; Brown & Hannah, 2008). Kryal channels are characteristically highly unstable and a braided planform is common although channel stability generally increases with distance from the glacial margin (Milner & Petts, 1994; Gurnell et al., 1999). The glacier margin acts as a major source of sediment supply in glacierized catchments by releasing frequent pulses of suspended sediment into Kryal stream segments (Hodson et al., 1998; Richards & Moore, 2003; Orwin & Smart, 2004). During a melt season background suspended sediment concentration is generally high but during pulses concentrations can exceed 500 mgL^{-1} (Gurnell, 1987; Warburton, 1990; Gurnell, 1995). Subglacial chemical weathering leads to the enrichment of kryal waters with sulphates and carbonates (Tranter et al., 2002) although conductivity is typically low (Malard et al., 2000; Füreder et al., 2001).

Rhithral segments are considered to be fed by snowmelt. Rhithral discharge exhibits large diurnal and seasonal variation. Seasonally, rhithral discharge typically peaks earlier in the melt season than in Kryal segments. Discharge reduces significantly later in the season as annual snowpacks disappear and snowmelt contributions remain very subdued until spring despite snowpack replenishment during autumn due to insufficient atmospheric energy inputs to drive melt (Malard et al., 1999). Water temperatures at snowpack margins are extremely low. However rhithral waters tend to flow into the main basin stem via small streams, thus strong longitudinal thermal gradients may arise in these small streams and waters may be significantly warmed by the time they flow into the main basin stem (Ward, 1994; Brown et al., 2006a; Brown & Hannah, 2008). Suspended sediment concentration in snowmelt streams is generally very low although when discharge is elevated sufficiently by rapid melt, turbidity and suspended sediment concentrations can increase as a result of stream bed and bank erosion (Milner & Petts, 1994; Richards & Moore, 2003). The hydrochemistry of snow melt is not temporally stable as SO_4^{2-}, NO_3^- and Cl^- are preferentially eluted early in the melt season. The ionic compositions of snowpack's also vary throughout the year, for example concentrations of HCO_3^- and Ca^{2+} are low in late winter but significant enrichment occurs by early spring (Malard et al., 1999).

Krenal streams are considered to be groundwater fed and to represent the most stable of alpine stream habitats. Flow conditions are relatively stable at diurnal and seasonal scales and are only attenuated by precipitation events (Ward, 1994). Brown et al. (2006b) suggested that some krenal stream sections may freeze during winter. Thermal variation at source is low; water temperature is typically 'summer cool' and 'winter warm' relative to the ambient climate but warm relative to Kryal segments. Turbidity is low (Füreder, 1999; Ward et al., 1999a) and hydrochemistry is dependant on underlying geology although electrical conductance tends to be high (Fenn, 1987; Ward et al., 1999a; Robinson & Matthaei, 2007).

Ward’s (1994) model is useful for characterising streams of a relatively distinct origin close to the source, but it fails to reflect that fact that alpine streams typically comprise of a temporally dynamic mix of water sources. To address this short-coming, Brown et al. (2003) suggested a temporally dynamic, nine-fold classification model to better account for spatiotemporal physicochemical variations by considering the ratio of contributions from Kryal, Rhithral and Krenal water sources at a point in time. Despite this improvement, it remains that an inherent limitation of classification models based on water source is that physicochemical properties of stream waters undergo significant change in a longitudinal dimension (Ward, 1989) and this cannot be accounted for by considering only the mixing of water sources. This limitation is particularly salient to characterising the thermal properties of stream habitats based on water sources as local climate, distance from source and flow-routing also exert a large influence (Caissie, 2006). Thus, in addition to water source mixing it is also necessary to consider longitudinal gradients arising as a result of energy/matter exchange which are discussed in the following section.

2.3.3 Gradients and discontinuities along the longitudinal dimension

Changes in physicochemical conditions along the longitudinal dimension of alpine streams are well studied during summer melt seasons (e.g. Milner, 1994; Gíslason et al., 2001; Lods-Crozet et al., 2001; Malard et al., 2001; Milner et al., 2001b; Snook & Milner, 2001). In proglacial streams strong longitudinal gradients exist in habitat conditions. Water temperature (Uehlinger et al., 2003b; Brown & Hannah, 2008), channel stability (Nicholas & Sambrook-Smith, 1998) and food resources (Zah & Uehlinger, 2001) for example, tend to increase downstream whilst suspended sediment concentration (Orwin & Smart, 2004) and diurnal (Swift et al., 2005) discharge fluctuation decrease downstream. Overall, therefore reaches close to a glacier margin are considered to represent the harshest of alpine stream habitats and habitat conditions are considered to ameliorate downstream (Milner et al., 2001a; Ilg & Castella, 2006). A prominant driver for these longitudinal gradients is the increasing proportion of groundwater water source contributions downstream relative to melt-water contributions (Malard et al., 1999; Brown et al., 2006c; Brown et al., 2009b) i.e. in proglacial streams glacial and snowmelt influence on stream conditions is reduced downstream and in non-glacierized catchments snow-melt influence is reduced (Füreder et al., 2001; Finn & Poff, 2006). Indeed, as illustrated in Plate 2.1, mixing of contrasting waters at tributaries can lead to large longitudinal discontinues in physicochemical properties (Knispel & Castella, 2003; Ilg & Castella, 2006; Brown et al., 2007b). However, alpine stream physicochemical properties are also subject to modification along stream flow paths due to inputs and losses of energy and matter from the atmospheric, streambed and riparian interfaces. For example, atmospheric radiative inputs raise stream temperature (Caissie, 2006; Webb et al., 2008), deposition of transiently stored sediment generally occurs downstream as stream gradient reduces reducing suspended sediment concentration (Warburton, 1990) and allochthonous inputs although low near the glacial margin increase downstream due to inputs from riparian vegetation (Zah & Uehlinger, 2001). Conversely, during winter the routing of flow under thick seasonal snow packs can insulate streams from sub-zero air temperatures, which minimises spatiotemporal thermal variation (Schütz et al., 2001; Brown et al., 2006b).

Landscape, hydrological and local geomorphic controls can lead to discontinuities in longitudinal patterns of physicochemical characteristics. For example, small shallow channels in braided stream systems increase thermal exchange at the surface-atmosphere interface and thereby amplify longitudinal thermal gradients (cf. single thread channels) (Mosley, 1983; Caissie, 2006). However, in a study by Uehlinger et al. (2003b) on the Val Roseg floodplain, Switzerland, increased atmospheric warming due to braiding was found to a have only a modest effect on longitudinal temperature (<0.2°C) over ~ 2.8 km because, despite a substantial expansion of wetted area during summer, more than 80% of the discharge was still carried by the main channel. Hyporheic exchange is another mechanism that influences the magnitude and timing of diurnal temperature pattern along braided river sections (Acuña & Tockner, 2009). Acuña and Tockner (2009) observed both positive and negative net temperature change arising from hyporheic exchange along a braided headwater reach of the Tagliamento River, Italy and noted a dampening effect on diurnal temperature oscillations of surface flows.

The presence of lentic water bodies in alpine stream networks can have a particularly large influence on longitudinal gradients of physicochemical properties. Higher maximum daily water temperatures and lower diurnal temperature fluctuations are typical of alpine lake outlets compared to; (i) inlet temperatures, and (ii) to the expected temperature change over an equivalent non-lentic stream length (Hieber et al., 2002; Uehlinger et al., 2003b; Robinson & Matthaei, 2007). For example, in a snowmelt and ground water fed lake, in the North Macun Basin, Switzerland, Robinson and Matthaei (2007) observed temperature increases of > 10 °C from lake inlet to outlet over a distance of < 0.25 km although the influence of lower altitude lakes on stream thermal characteristics was less pronounced. Robinson and Matthaei (2007) also suggested that the presence of lakes in the North Macun catchment may have helped to sustained stream flow in the absence of snowmelt in late summer and that lakes throughout the Macun catchment exerted a significant influence on stream hydrochemistry. Uehlinger et al. (2003b) observed that the Roseg proglacial lake, Switzerland increased temperatures in the oulet stream by 2 – 4 °C compared to expected longitudinal temperature increases. From mid-autumn to early-spring this longitudinal thermal discontinuity was particularly large relative to the longitudinal thermal stream gradient as temperature then decreased downstream of the lake outlet. Glacial outburst floods from proglacial lakes can also cause major periodic disturbances to the discharge regime and these are reviewed by Tweed and Russell (1999) and Ghimire (2004-2005).

Plate 2.1 - *The mixing of contrasting waters at groundwater tributaries in the glacierized Taillon-Gabiétous basin, French Pyréneés. The relatively high turbidity of the glacial melt waters is clear from the contrast in opaqueness between; the glacial stem (left image; on right, right image; on left) and the clearer groundwater tributaries.*

2.3.4 Stream ecology

The heterogeneous physicochemical habitats of alpine streams support a diverse range of flora and fauna (Milner et al., 2009). Distributions of benthic macroinvertebrates communities, particularly during the melt-season, have been relatively well studied over the last two decades, not least because benthic macroinvertebrates are highly sensitive to physicochemical stream characteristics and thus are powerful indicator organisms of habitat quality and habitat change over time (McGregor et al., 1995; Robinson et al., 2007; Milner et al., 2009). A diverse range of macroinvertebrate taxa are typically found in any alpine stream system, which is in contrast to other taxa groups such as fish that are only present in a relatively small number of alpine streams (Milner & Petts, 1994). Recent research into alpine macroinvertebrate benthic community distribution has primarily focused on investigating; (i) longitudinal trends in community composition with distance from the glacial margin; (ii) community composition in streams of varying water source contributions, and; (iii) temporal variations in community composition. The respective findings from these three central research themes are critically discussed below.

2.3.4.1 Longitudinal gradients of biota along proglacial streams

Investigating longitudinal trends in macroinvertebrate community distributions has been a major focus of ecological research on alpine stream systems (Milner, 1994; Burgherr & Ward, 2001; Gíslason et al., 2001; Lods-Crozet et al., 2001; Malard et al., 2001; Milner et al., 2001a; Milner et al., 2001b; Snook & Milner, 2001; Ilg & Castella, 2006; Brown et al., 2007c). Almost all of this research stems from the influential work of Milner and Petts (1994) who proposed, and later refined (Milner et al., 2001a; see Figure 2.6) a conceptual model which proposed that general longitudinal trends in macroinvertebrate community compositions during the summer melt season can be attributed to the variation of two key variables: (i) water temperature and (ii) channel stability. The premise of this model is that because of the harshness of alpine stream systems, the disturbance regime and low temperatures override the significance of other variables in controlling macroinvertebrate community structure and biomass. Typically, during a summer melt season in European proglacial streams, the chironomidae genus *Diamesa* dominates macroinvertebrate assemblages close the glacier snout were maximum water temperatures (T_{max}) are low (< 2 ^{o}C) and channel banks and beds are very unstable (Pfankuch Index of 40-60); although other Diamesinae (e.g. *Pseudodiamesa* and *Pseudokiefferiella*) may also be present. Close to the glacial margin, T_{max} is the primary constraint on the presence of Orthocladiinae, but where T_{max} increases above 2 ^{o}C some Orthocladiinae begin to colonise regardless of low channel stabilities. Some species of Oligochaeta and Tipulidae are also tolerant to T_{max} in the 2 - 4^{o}C range although channel stability is a constraint in very unstable sections (Pfankuch Index of > 40). Further downstream, where T_{max} rises above 4 ^{o}C and channels become more stable Perlodidae, Taeniopterygidae, Baetidae, Simuliidae and Empididae can be expected in benthic assemblages. Limnephilidae are typically found in channels of further enhanced stability with increased supply of allochthonous material where stream temperatures are > 6 ^{o}C. Neumoridae, Leuctridae, Heptageniidae, Rhyacophilidae and Chironominae will colonise streams where temperatures >8 ^{o}C and channel stability is high. In addition to variations in macroinvertebrate community structure increases in algal biomass, bryophyte biomass, chlorophyll a, and diatom taxonomic richness generally occur with distance from the glacial margin as stream conditions ameliorate (Gíslason et al., 2001; Lods-Crozet et al., 2001; Hieber et al., 2005; Brown et al., 2007c).

Longitudinal discontinuities in physicochemical habitat and thus in biological communities may arise in proglacial streams at major tributaries as water sources mix, or due to stream-flow routing (see Section 2.3). Milner et al.'s (2001a) model attempted to account for longitudinal habitat discontinuities by using the direct physicochemical habitat indicators of water temperature and channel stability, rather the indirect indicator; distance from the glacial margin. Indeed, findings from studies of several Swiss alpine lake outlets by Hieber et al. (2002, 2005) and Robinson et al. (2007) broadly conformed to Milner et al.'s (2001a) model. Although large longitudinal thermal discontinuities were observed at lake outlets, no significant changes in invertebrate community structure were evident as channel stability still acted as major constraint. However, a study by Knispel & Castella (2003) suggested that community composition around tributaries may depart from the predictions of Milner et al. (2001a). Knispel & Castella (2003) found that a relatively small tributary to the Rhone river acted to enrich the species pool both upstream and downstream of its confluence, despite having only a minimal impact on physicochemical conditions. Species found to be enriching confluence diversity where physicochemical conditions would be expected to be too harsh for their presence (Milner et al., 2001a) are however thought to be unable to complete their life-cycles in these harsher habitats (Saltveit et al., 2001; Knispel & Castella, 2003).

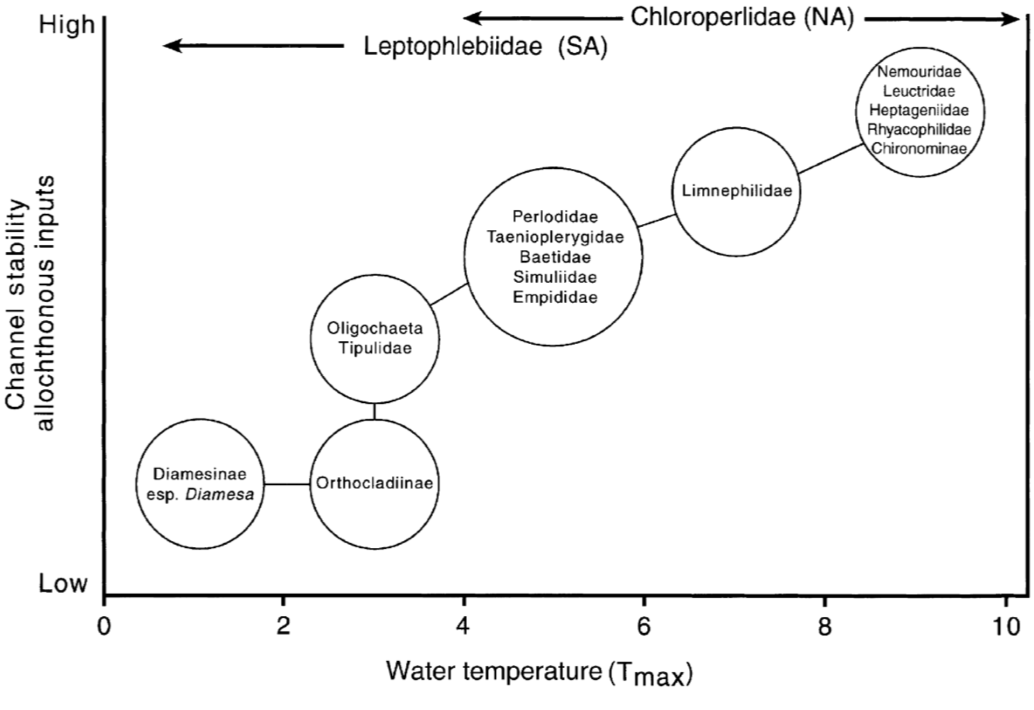

Figure 2.5 - *Conceptual model describing the likely first appearance of macroinvertebrate taxa along an upstream-downstream continuum from the glacier margin with increasing water temperature and channel stability during the melt season for European glacier-fed rivers. Arrows indicate taxa that may be found across this temperature range in other geographical areas; SA = South America, NA = North America (From Milner et al., 2001a).*

Milner et al.'s (2001a) model is appealing as a tool to assess the likely implications of flow regulation on the distribution of biota given the likely effects of such discontinuities on channel stability and thermal regime. However, the form of Milner et al.'s (2001) model is limited as it does not account for seasonal temporal variations in stream community composition (see

Section 2.3.3.3). This is a particularly salient limitation for streams subject to winter flow regulation as impacts to winter community distribution cannot be assessed and furthermore winter disturbances may also have antecedent implications for summer community structure as predicted by the model (see Tockner et al., 2010). More work is also required to generalise the model for alpine regions globally, particularly in the southern-hemisphere (Gíslason et al., 2001; Milner et al., 2001a; but see Milner et al., 2001b; Cadbury et al., 2010; Jacobsen et al., 2010).

Although most research investigating longitudinal trends has taken a taxa based approach to investigating gradients in community structure, a few recent studies have adopted a traits based approach in an attempt to obtain a more mechanistic understanding of ecosystem functioning (see Snook & Milner, 2002; Ilg & Castella, 2006; Füreder, 2007). In contrast to a taxa based approach which looks directly for correlations between taxa abundance and environmental gradients, a traits based approach examines the relationships between functional attributes or traits of taxa (for example feeding habit, life-cycle characteristic, or size) and environmental gradients. Traits based studies have shown that close to the glacial snout of a proglacial river, where glacial influence is strongest, physicochemical conditions place severe constraints on the ability of taxa to colonise and persist meaning that only a very select group of taxa with specific functional traits can survive (Snook & Milner, 2002; Ilg & Castella, 2006; Füreder, 2007). Further downstream, as habitat conditions ameliorate, a broader range of functional characteristics can be expected amongst taxa. There are however disagreements regarding which traits represent beneficial adaptations to survival in harsh alpine streams. For example, Ilg & Castella (2006) suggest that an ability to adopt a semi-voltine life cycle may constitute an advantage in harsh glacial streams whereas Finn & Poff (2006) suggested that semi-voltinism is a trait primarily associated with benign habitats, and that long-life cycles may be a disadvantage in harsh environments. It is clear that more research is required to clarify longitudinal trait gradients and that a functional approach, whilst yet to be tested, may yield enlightening insights on the structure and function of macroinvertebrate communities in non glacier-fed alpine streams (but see Finn & Poff, 2006) and also to the year-round trends in community structure and function.

2.3.4.2 Biotic composition of non-glacial alpine streams

Investigating macroinvertebrate community structure amongst streams of varying water source contributions has been another important theme of alpine ecological research. Compared to proglacial streams, groundwater-fed streams are expected to exhibit weaker longitudinal gradients in faunal composition because physicochemical habitat conditions are typically more similar along their length (Lavandier & Décamps, 1985; Füreder et al., 2001;

Gíslason et al., 2001; Snook & Milner, 2001; Füreder et al., 2002). A comparison of the proglacial Rotmoosache stream and predominately groundwater fed Königsbach stream in Austria revealed that at similar altitudes to the Rotmoosache glacial margin, abundance and taxonomic richness were far greater in the spring-fed stream (8x and 3x respectively; Füreder et al., 2001). However, at lower altitude (distance from glacial margin) abundance and taxonomic richness of the two streams became more similar (Füreder et al., 2002). Small groundwater streams and mixed stream networks that occur at braided floodplain reaches along proglacial river corridors can also support high algal biomass and rich zoobenthic assemblages not found in the main proglacial channel where stream conditions are too harsh (Uehlinger et al., 1998; Burgherr et al., 2002). It can be concluded from these studies that a holistic understanding of community distributions for all stream types is important for assessing the implications of flow regulation as flow regulation may occur in non-glacierized basins or impinge upon groundwater or mixed habitats in glacierized catchments.

2.3.4.3 Seasonal temporal dynamics.

A major limitation of the Milner et al. (2001a) model is that it only applies to the summer melt season (Saltveit et al., 2001; Füreder et al., 2002). During the summer melt season, conditions in proglacial streams are particularly harsh due to maximum glacial water source contributions driving low water temperatures and regular disturbances to the benthos (Malard et al., 1999). Outside of the melt season, during spring and to a greater extent autumn, physicochemical conditions are typically more benign as rhithral and krenal water sources are respectively more dominant (Lavandier & Décamps; Robinson et al., 2001; Saltveit et al., 2001; Schütz et al., 2001; Burgherr et al., 2002). The limited number of studies that have been conducted during these periods suggest that community structure in cold proglacial streams may diversify during spring and autumn (Füreder et al., 2001; Saltveit et al., 2001; Burgherr et al., 2002) and that this diversification is associated with increases in benthic organic matter when channels are open, particularly supported by the growth of golden alga, *Hydrurus foetidus* (Füreder et al., 2001; Robinson et al., 2001; Schütz et al., 2001). Burgherr et al. (2002) found Ephemeroptera and Plecoptera along the main glacial channel of the Val Roseg floodplain, Switzerland during late autumn/early winter in stream reaches where T_{max} did not exceed 4 ^{o}C. Conversely, abundances were found to be significantly lower in side channels during October as the floodplain contracted and some channels were left dry. Salveit et al. (2001) also reported finding Plecoptera close to the glacial margin in the Dalelva River, Norway despite cold temperatures in both Spring (May) and Autumn (October) but not during summer. Burgherr et al. (2002) postulated that shifts in water source contributions to the hyporheic layer and associated steep thermal hyporheic gradients may explain the diversification of proglacial channels outside of the summer melt season, because by moving within the substrate taxa are able to limit their exposure temperatures.

Ecological surveys during mid-winter when much of the alpine zone and many streams are covered by a thick snowpack have rarely been conducted (but see Lavandier & Décamps, 1985; Schütz et al., 2001). Schütz et al. (2001) provided a novel insight into mid-winter macroinvertebrate distributions along the partially snow covered proglacial Rotmoosache stream, Austria, during winter. Schutz et al. (2001) found elevated abundances (during winter cf. summer) of several taxonomic groups including Ephemeroptera and Plectoptera, and 4% of all taxa recorded were only found during winter. The finding of *Capnia vidua* (Plecoptera) was particularly significant as they had not been previously described in glacial streams above 2000m, probably because only early in-stars are present during summer and emergence occurs early in spring (Schütz et al., 2001). A number of predatory taxa were also found (*Clinocera* sp., Dicranota sp., *Dictyogenus fontium*, *Perlodes* sp., Hydracarina) during winter which are atypical of cold-glacial streams (Milner et al., 2001b). Generally, abundances and diversity were significantly lower under the observed snow-covered channel compared to the open channel but other physicochemical variables, and distance from the glacial margin was not controlled for. Schütz (2001) considered that growth and development under snow cover were very low, which is in general agreement with the findings of Lavandier and Décamps (1985) who suggested growth of macroinvertebrates is nil or negligible under snow cover in the Estaragne, French Pyréneés which a non-glacial-fed alpine stream.

Collectively, these ecological studies conducted outside of the summer melt-season suggest that (i) community structure may be markedly different for most of the year compared to that documented by the majority of studies undertaken during the summer melt season, and; (ii) physicochemical conditions during winter months clearly play an important role in the life-cycle strategies of biota that have adapted to survive in these extreme environments (see also Robinson et al., 2010). These findings highlight that the implications of flow regulation for ecosystems may exhibit considerable seasonality (Tockner et al., 2010) and that Milner et al's conceptual model (2001b) does not provide a sufficient basis with which to consider the impacts of flow regulation on abundance and biodiversity year-round.

2.4 FLOW REGULATION IN ALPINE STREAMS

Flow regulation is wide-spread across the European Alps and pressures on the water resources of the alpine zone are expected to increase globally, particularly for storage hydropower schemes which lead to the abstraction, storage, re-routing and re-fluxing of large volumes of water from source and sink rivers (Wehren et al., 2010b). Flow regulation of alpine streams varies through a spectrum of severity but can be classified into four main forms (cf. Brittain & Saltveit, 1989): (i) mean flow reduction (or cessation), (ii) hydropeaking and short term flow pulses, and (iii) seasonal flow constancy (the dampening of natural seasonal fluctuations), and (iv) mean flow increase; see Figure 2.6. The next section reviews the potential impacts of each of these flow regime modifications on alpine stream habitats and macroinvertebrate communities. Flow regulation alters the hydrological dynamics of stream systems but a typical feature of flow regulation systems is that they involve the storage of water in reservoirs. As a pretext to the discussion of stream flow regulation effects on stream ecosystems, the impacts of reservoir storage on flooded basins and the physicochemical characteristics of out-flowing water are first considered.

2.4.1 Effects of reservoir storage on water physicochemical characteristics

Dam construction and the associated flooding of river basins leads to a radical transformation of flooded river reaches. Flooded areas undergo a complete change from lotic to lentic habitats and running water biota are replaced with biota adapted to life in standing freshwater (Walker, 1985; Friedl & Wuest, 2002). The drastic impact of damming on flooded river reaches is of course immediately apparent visually. However, storage of water in reservoirs and its subsequent release also has large implications for downstream habitats (e.g. Maiolini et al., 2003; Mannes et al., 2008; Bruno et al., 2009b). Reservoirs are distinct from other natural hydrological stores (e.g. snowpacks, glaciers, groundwater systems and lakes) as (i) discharge from reservoirs is typically managed and not directly governed by melt or precipitation and, (ii) storage in reservoirs significantly alters the physicochemical properties of out flowing water. Therefore reservoirs in alpine catchments can be considered as distinct modifiers of icemelt, snowmelt and groundwater sources to stream-flow (Figure 2.3).

High alpine reservoirs are typically cold monomictic (unstratified) with maximum water temperatures below 4 ^{o}C (Hutchinson & Loffler, 1956; Dake & Harleman, 1969). In some deep alpine reservoirs thermal stratification may occur where mixing of surface and profundal water is slow and radiative inputs are sufficient (Maiolini et al., 2003; Wehren et al., 2010b). Water temperature in the deep hypolimnetic layer of stratified alpine reservoirs is close to 4^{o}C throughout the year (Dake & Harleman, 1969). Reservoir outlet valves are typically positioned at depth (Maiolini et al., 2003; Wehren et al., 2010b; Zolezzi et al., 2010) and discharged water temperature is $\leq 4^{o}$ C. When full, water can also be discharged from reservoirs by overspill. When overspill occurs, reservoirs serve to act as thermal modifiers to receiving streams in a similar way as a natural lake would, generally causing a longitudinal thermal discountinuity where warming is increased (Brittain & Saltveit, 1989; Robinson & Matthaei, 2007). In addition to affecting water temperature, reservoirs may also have a marked effect on suspended sediment concentrations and hydrochemistry. Suspended sediment settles in reservoirs due to the very low flow velocities and thus vastly reduced flow competence in comparison to tributary streams (Petts & Bickerton, 1994; Anselmetti et al., 2007; Wehren et al., 2010b; Wüest, 2010). Biochemical processes within a reservoir can cause hydrochemical alterations to stored water including depletion of dissolved oxygen, reductions of nitrate, iron (hydro)oxides, manganese (hydro)oxides and sulphates, and the accumulation of reduced toxic products such as Mn(II), Fn(II), NH_4^+ and H_2S (Friedl & Wuest, 2002).

2.4.2 Flow reduction and cessation

Mean flow reduction can be caused by anthropogenic regulation for either (i) a clearly defined stream length, for example where water is diverted through a turbine run for hydro-electric generation or; (ii) an indefinite stream length, for example when water is re-routed from one catchment to another to regulate levels in storage reservoirs (Wehren et al., 2010b). In the second of these examples flow is most severely reduced in residual reaches but a significant mean flow reduction may also extend into lower catchments (Acreman & Dunbar, 2004; Wehren et al., 2010b; Wüest, 2010). In extreme cases, streams can completely dry-out leading to the complete loss of a stream habitat (Petts & Bickerton, 1994; Dewson et al., 2007; Wüest, 2010). In these extreme cases the impacts on stream habitat are drastic. In contrast, alterations to habitat conditions may be more subtle where streamflow is reduced but persistently low and the implications for in-stream macroinvertebrate communities thus more difficult to predict.

2.4.2.1 Impact of flow reduction/cessation on stream physicochemical habitat

Flow reduction generally leads to decreases in flow velocity, flow depth, and wetted width of streams, although exactly how these parameters scale with a reduction of flow depends on a channel cross-section (Dewson et al., 2007). The link between discharge and wetted width is particularly important in meltwater-fed braided river systems, where increased ablation during summer drives an expansion phase which results in a large increase in stream habitat and increased habitat heterogeneity (Malard et al., 2000; Arscott et al., 2002; Malard et al., 2006). A reduction in flow can potentially limit or prevent floodplain expansion phases (Lavandier & Décamps, 1985; Ward & Stanford, 1995). Several studies have evidenced this effect in rivers in sub-alpine reaches (e.g. Pautou et al., 1997; Brunke, 2002; Zolezzi et al., 2010). For example, Brunke (2002) examined two floodplains along the Brenno River, Switzerland and found that a 27% reduction in mean discharge had resulted in decreased lateral connectivity and a shift from ecosystems controlled by allogenic (i.e. frequent flooding) processes to slower autogenic processes (i.e. succession of plant communities). Indeed, Bertoldi et al. (2009) identified quantitative critical stage thresholds upstream of braided river sections along the Tagliomento, Italy for downstream hydrological connectivity, geomorphic change and floodplain/riparian flow-vegetation interactions.

No published case-studies have explicitly examined the effects of anthropogenic flow reduction on floodplain habitats in the alpine zone. However, Petts and Bickerton (1994) and Gurnell et al. (1990) both noted that reaches subject to flow reduction for the Grande Dixence hydropower scheme in the Val de Arolla, Switzerland were narrower, more deeply incised, and a meandering single thread (*vs.* braided) when compared with un-regulated reaches. These findings agree with those of Surian (1999) and Brunke (2002) who observed that flow-reduction in sub-alpine floodplains resulted in more deeply-incised and stable channels due to a deficit of sediment supply and due to a reduction in ‘channel-forming’ or ‘bank-full’ discharge. Formation of debris fans and scree slopes extending into the river channels, colonisation of floodplains and gravel banks by woody vegetation, and clogging of interstitial voids in coarse substrate material by embedded fine sediments, have all also been noted to be a consequence of severely reduced flows (~88%) along sub-alpine reaches of the River Spöl, Switzerland (Mürle et al., 2003; Uehlinger et al., 2003a).

Mean stream temperature and variability is typically increased by a reduction in flow because of the reduced heat capacity of the water body (Caissie, 2006; Dewson et al., 2007; Webb et al., 2008), especially in river sections of gradual slope (Meier et al., 2003). However, flow regulation schemes commonly alter the balance of water source contributions to a stream reach and this can have an additional affect on stream temperature. For example, the abstraction of glacial meltwater in the Val d’Arolla, Switzerland, increases the relative contribution of groundwater and snowmelt to stream flow resulting in higher stream temperatures (~1-2^{o}C) (Petts & Bickerton, 1994). Reduced stream flow is also common downstream of reservoir outlets, in which case releases of stored reservoir water may have large effect on stream temperature (Robinson et al., 2004) (see Section 2.4.1).

2.4.2.2 Impact of flow reduction/cessation on stream biota

To my knowledge, only one peer-reviewed study has specifically examined the effects of flow reduction on stream ecosystems in the alpine zone: Petts and Bickerton (1994) found that immediately downstream of abstractions (0.4km from the glacial margin) where flows were intermittent and frequent high turbidity purging flows common, the Borgne d'Arolla, Switzerland was devoid of fauna. *Diamesa* started to colonise ~1.6 km below the abstraction point and Simulidae were found a little further downstream. At 2.3 km below the abstraction point a tributary sustained permanent flow and due to the abstraction of all major glacial melt inputs to the stream was characterised by groundwater and snowmelt inputs from this point. A diverse range of macroinvertebrate families (e.g. Chironomidae, Simuliidae, Baetidae, Nemouridae, Limnephilidae and Chloroperlidae) were thus able to colonise the stream relatively close (2.7-3.2km) to the glacial margin. However, it is difficult to generalise from Petts and Bickerton's (1994) results because the effects of flow reduction on physicochemical habitats depend on antecedent habitat conditions, the severity and timing of flow reduction, and the nature of changes to water source contributions.

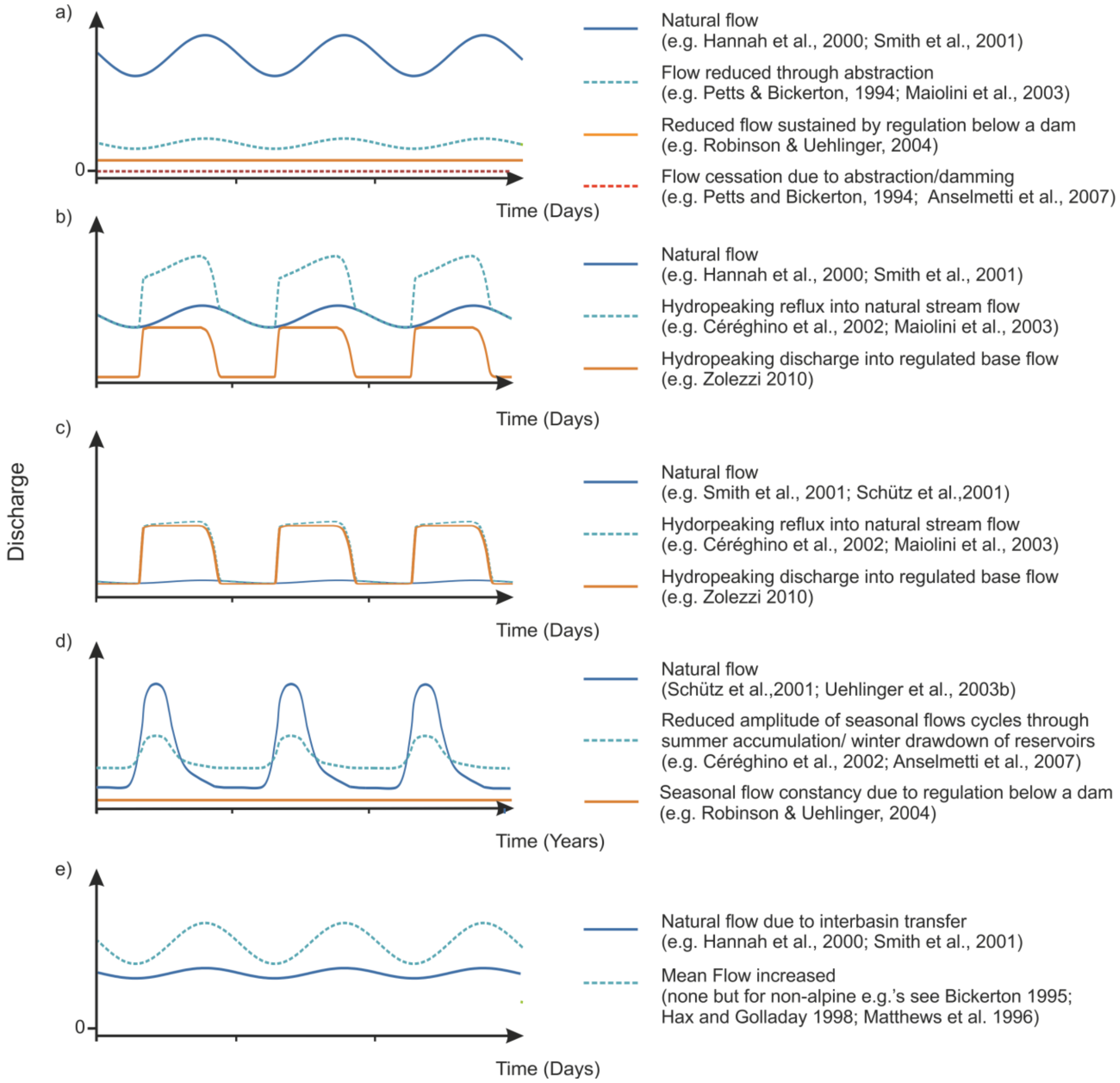

Figure 2.6 - *Schematic representations of modifications to melt driven flow regimes subject to; a) flow reduction, b) hydropeaking during summer, c) Hydropeaking during winter, d) reductions in seasonal flow amplitudes, and e) mean-flow increase.*

Suren and Riis (2010) suggested that in streams with a poor resource supply and low stability (typical proglacial stream conditions), flow reduction will cause little or no change to a diatom-dominated stream plant community as this community is primarily structured by top-down grazing pressure and as a consequence the macroinvertebrate community will experience little change. However, the studies that form the evidence basis of Suren and Riis's (2010) model (Caruso, 2002; Suren et al., 2003; James et al., 2008; James & Suren, 2009) investigated the effects of comparatively short low-flows (< 3 months) relative to the long-term / indefinite flow-reductions that can result from anthropogenic regulation. At longer timescales, and as noted in Section 2.4.2.1, channel stability can increase with reduced flow (Petts & Bickerton, 1994; Surian, 1999; Brunke, 2002; Bertoldi et al., 2009), thus potentially enabling the colonisation of more diverse and abundant flora (Uehlinger et al., 2003a) and a significant change in macroinvertebrate community composition (Milner et al., 2001a). Indeed, even at relatively short time scales (< 3 months) during autumn/winter/spring, reductions in flow disturbance from glacial-melt and storm pulses have been found to stimulate the growth of flora, to increase benthic organic matter (Robinson et al., 2001; Schütz et al., 2001) and to lead to a shift in macroinvertebrate community composition (Robinson et al., 2001; Saltveit et al., 2001; Schütz et al., 2001; Burgherr et al., 2002). Changes in the thermal regime caused by flow reduction or by the associated change in storage may also suit some taxa (Milner et al., 2001a). It seems likely that if flow reduction is significant enough in proglacial streams (i.e. below significant biogeomorphic change thresholds; see Bertoldi et al., 2009) then a shift towards increased zoobenthic biomass and more diverse fauna as predicted by higher channel stabilities in Milner and Pett's (2001a) model should occur at the expense of highly specialised taxa adapted to extreme proglacial river conditions (Petts & Bickerton, 1994). However, this diversification and increase in abundance could potentially be constrained or inverted if either (i) base flow reduction is extreme or, (ii) disturbance inducing floods are completely eliminated.

Where flow abstraction leads to extremely reduced base flow or to temporally intermittent flow, species diversity may be considerably reduced due to the intolerance of many taxa to drought conditions. The effect of drought conditions on macroinvertebrate communities in non-alpine streams is relatively well studied (e.g. Brittain & Saltveit, 1989; Boulton, 2003; Lake, 2003, 2007) and some generic lessons from these studies may well be applicable to alpine systems exhibiting severe low flows; but they require testing. For example, large bodied organisms are generally most vulnerable to drought; species able to survive desiccation using a diapause strategy or are able to migrate rapidly may recover rapidly after drought but other species may take some time to re-colonise and although drought may generally act as a ramp disturbance critical water supply thresholds may exist which trigger severe impacts rapidly if exceeded.

In the Borgne d'Arolla, close to the glacial margin, Petts and Bickerton (1994) observed the presence of no fauna where flow pulses were only intermittent and highly turbid due to the abstraction scheme. The lack of sufficient flow to induce expansion at floodplain and braided reaches would also be expected to lead to a reduction in benthic habitat area. At the event scale, during period’s drought densities of biota may increase as populations become more concentrated as habitat area contracts (Malard et al., 2006). At longer time scales, a general homogenisation of habitats resulting in reduced biotic diversity would be expected in the event of a lack of disturbance inducing flows (Pautou et al., 1997; Malard et al., 1999; Brunke, 2002). High flow disturbance is also important to flush-out accumulations of fine-sediments which otherwise clog interstitial voids in the substrate (Céréghino et al., 2002; Robinson & Uehlinger, 2007). Accumulation of clogging sediments which can result from flow reduction can severely effect macroinvertebrate community composition, particularly constraining grazers, filter feeders and organisms that inhabit the interstices between coarse sediments (Wood & Armitage, 1997; Bo et al., 2007).

2.4.3 Hydropeaking and short-term flow pulses

Extreme flow fluctuations are a common feature of streams downstream of hydropower storage reservoirs where sharp, turbid pulses of water are discharged at least daily to meet surges in power demand. The resulting highly transient and variable flow pattern is a phenomenon known as hydropeaking (Céréghino et al., 2002; Cortes et al., 2002; Bruno et al., 2009b). Sediment purging pulses of abstraction systems are another cause of anthropogenically induced flow pulses (Petts & Bickerton, 1994). Hydropeaking events are known to have a large effect on faunal composition (Bruno et al., 2009b) although most streams subject to hydropeaking events already have an anthropogenically reduced base stream-flow and so the antecedent flow conditions cannot be considered ‘natural’ (see also Céréghino et al., 2002). Most studies that have investigated the impacts of hydropeaking have focused on investigating impacts to fish populations in temperate streams/rivers. Only a few studies have evaluated the impacts of hydropeaking on stream ecosystems in alpine zones, and these have almost exclusively focused on sub-alpine stream reaches (but see Petts & Bickerton, 1994).

2.4.3.1 Impact of hydropeaking and short-term flow pulses on stream physicochemical habitat

Hydropeaking events that have been investigated in sub-alpine stream reaches vary from fairly modest releases, (e.g. typically <50% of base flow in the Noce Bianco stream, Italy; Maiolini et al., 2003) to much larger releases (e.g. ~11-fold increases during Summer/Winter in the River Oriège, Pyrénées; Céréghino et al., 2002). In the Spöl River, Switzerland, the impacts of experimental flow releases of up to 35 x baseflow have been investigated (Robinson & Uehlinger, 2007). Increased bed scour and the flushing of fine mineral particles are commonly associated with hydropeaking (Céréghino et al., 2002; Mürle et al., 2003), but it has been demonstrated that high magnitude floods of short-duration generally do less geomorphic work than elevated discharge maintained over longer durations (Surian, 1999; Tockner et al., 2010). Mürle (2003) observed that a sharp 7-fold experimental flow increase (up to 10 m^3s^{-1}) mobilised fine bed sediments and caused bank erosion in the Spöl River, but to cause significant bed scouring and mobilise coarser bed sediments (> 2 mm) a 21-fold flow increase (up to 30 m^3s^{-1}) was required.

In many streams subject to hydropeaking, base flow is sustained by catchment runoff and peak flows are generated by releases from the hypolimnetic waters of reservoirs. Hydropeaking is therefore commonly associated with sharp variations in water temperature , which is known as thermopeaking, see Figure 2.7; warm thermopeaking is typical during winter (~ 2 – 3 ^{o}C increase) and cold thermopeaking during summer (Webb & Nobilis, 1995; Céréghino et al., 2002; Maiolini et al., 2003; Carolli et al., 2008; Toffolon et al., 2010; Zolezzi et al., 2010). Where a base-flow is sustained by hypolimnetic water, thermopeaking does not occur and stream temperatures remain relatively constant during hydropeaks (Robinson & Uehlinger, 2007).

2.4.3.2 Impact of hydropeaking and short-term flow pulses on stream biota

Macroinvertebrate communities respond to hydropeaking in the short-term by catastrophic drift (i.e. drift stimulated by an abiotic disturbance; Davies & Cook, 1993; Gibbins et al., 2007b). Catastrophic drift can arise with relatively small increases in discharge where minimal bed scouring occurs, as well as during larger bed mobilisation events (Brittain & Eikeland, 1988; Bosco & Perry, 2000; Gibbins et al., 2007a; Gibbins et al., 2007b). In an experimental flume study, Gibbins et al. (2007a,b) found a shear stress threshold (90 $\mu N.cm^{-2}$) above which the agitation, but not mobilisation of coarse bed-substrata, instigated catastrophic drift. Bruno et al. (2009b) studied catastrophic drift responses to non-scouring hydropeaking (7-fold increase in discharge up to 7 m^3s^{-1}) in the Adige River, Italy, and found that a hydropeak wave caused a 9-fold increase in drifting biota occurring at sampling stations near to the release point and 8 km downstream. Taxa that exhibited strong drift responses included Chironomidae, Plecoptera, Ephemeroptera, Baetidae and Psychodidae. Harpacticoida and Nematoda, which are associated more with hyporheic habitats, were more resistant to hydropeaking. Over longer time-scales, regular drift-inducing hydropeak events may be a factor in the depletion of benthic macroinvertebrates from habitats (Céréghino et al., 2002; Bruno et al., 2009b).

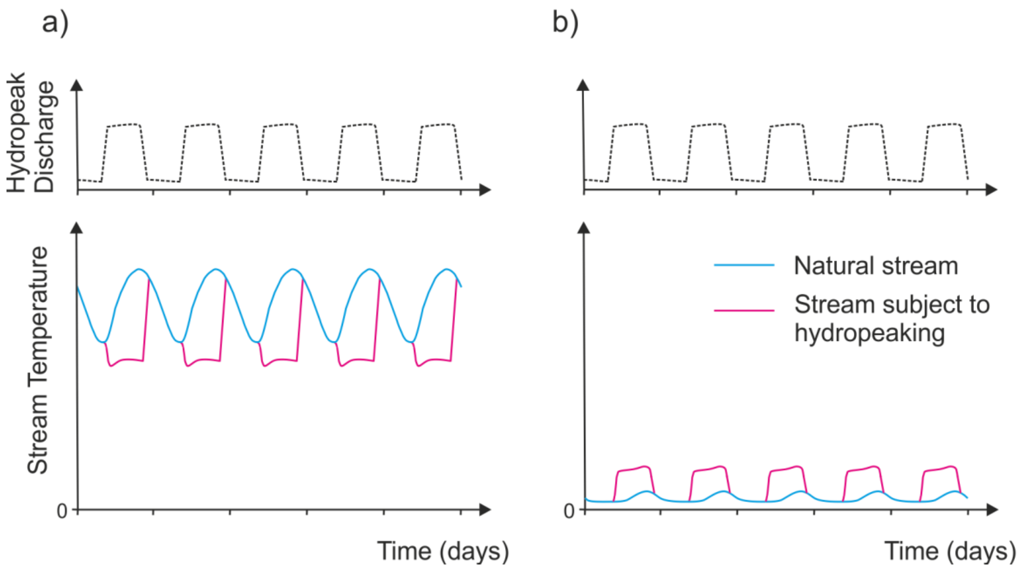

Figure 2.7 - *Schematic representation of a) 'summer cool' and b) 'winter warm' thermopeaking.*

The long-term effects of hydropeaking on stream community structure depend on the antecedent habitat conditions prior to the commencing of hydropeaking cycles. Céréghino et al. (2002) examined the longitudinal impacts of hydropeaking on a sub-alpine reach of the River Oriège, French Pyrénées, between 920 and 819 m.a.s.l. The Oriège's natural flow regime is impacted by hypolimnetic hydropeaking discharged from a conduit at 912 m.a.s.l. Céréghino et al. (2002) found a negative longitudinal discontinuity occurred below the conduit due to the harsh and unstable habitat conditions. Dramatic decreases in the benthic abundance of most species occurred downstream of the conduit outlet and some species disappeared from the assemblage altogether (e.g. *Baetis muticus*). Taxa with flattened (*Rhithrogena, Ecdyonurus*) or cylindrical bodies (*Esolus, Limnius, Limoniidae*, Empididae, Chironomidae), or crawlers and clingers (e.g. some Trichoptera), were more tolerant of hydropeaking flows or able to move towards refugia (see Bruno et al., 2009b). Abundance recovered to reference levels in the Oriège (monitored above the conduit outlet) between 700 - 2500m downstream.

Hydropeaking impacts on macroinvertebrate communities in the Oriège (Céréghino & Lavandier, 1998a,b; Céréghino et al., 2002) would generally be considered overall to be negative as they have altered the 'natural' antecedent stream ecosystem. However, hydropower reservoir releases have been proposed as 'artificial' disturbances to partially restore the ecological integrity of regulated rivers (Cortes et al., 2002; Robinson & Uehlinger, 2007). After a period 30 years of reduced flow (88 % mean annual reduction), a series of experimental flow releases in the River Spöl, Switzerland, were found to invigorate the ecosystem by: removing accumulations of fine sediment (Mürle et al., 2003); substantially reducing periphyton, particularly dense algal mats (Uehlinger et al., 2003a); helping to reestablish the macroinvertebrate community composition that would have been expected prior to flow regulation (Robinson et al., 2003), and improving habitat conditions for brown trout (Ortlepp & Mürle, 2003).

Despite the recent increase in research attention on sub-alpine regulated rivers, no studies have specifically examined the effects of anthropogenic flood pulses on ecosystems at higher altitudes in alpine basins. Taxa found in proglacial channels during the summer melt-season are well adapted to regular melt pulses and sharp disturbance floods, so the overall summer assemblage may potentially be less severely affected by cold flood pulses than in sub-alpine reaches. Outside of the summer season when a more diverse range of taxa may be found (Saltveit et al., 2001; Burgherr et al., 2002) the consequence of flow pulses from reservoirs are difficult to predict. Regular flow pulses causing substrate disturbance and preventing periphyton growth (Robinson et al., 2001; Schütz et al., 2001) may be a constraint to many taxa. However, flow pulses may ameliorate some aspects of the physicochemical habitat , for example by maintaining flow during ecosystem contraction phases (cf. Malard et al., 2006) preventing snowpacks forming over channels and increasing water temperature.

2.4.4 Reduced amplitude of seasonal flow cycles

Flow regulation for water supply (particularly for hydropower; Wehren et al., 2010b), disrupts the natural seasonality of many rivers because water demand is not synchronous with natural seasonal runoff cycles. Water is allowed to accumulate in storage reservoirs during the spring and summer to provide a supply during autumn and spring. Thus, natural stream-flow is reduced during spring/summer and then during autumn/winter mean flow is increased as this water is routed down from high altitude reservoirs to lower reservoirs in streams rather than conduits (Anselmetti et al., 2007; Wüest, 2010), or refluxed into streams below hydropower generators (Wehren et al., 2010b). The net result is that the amplitude of seasonal peak flows is reduced (Anselmetti et al., 2007; Fette et al., 2007; Wehren et al., 2010b).

2.4.4.1 Impact of reduced amplitude of seasonal flow cycles on stream physicochemical habitat

A reduction in the amplitude of seasonal flow cycles is associated with reduced seasonality in physicochemical variables. Since the early 1930s, seasonal sediment budgets of the River Aire, Switzerland, between 2300 and 560 m.a.s.l have been dampened by reduced seasonal flow amplitude (Anselmetti et al., 2007). Anselmetti (2007) found that 21 % of annual catchment runoff is now discharged in the winter (Nov-Mar), compared to just 10 % before the construction of three large reservoirs close to the glacial margin. The increase in winter discharge was associated with an increase in total sediment transport during winter from ~3 kt to 14 kt. Seasonal water temperature trends were also dampened due to the influence of hypolimnetic waters. In a sub-alpine reach (217 m.a.s.l) of the Noce River, Italy, Zolezzi et al. (2009; 2010) noted this effect, with mean monthly water temperature increased by 1.2 ^{o}C during November but then decreased by 1.9 ^{o}C in May. In proglacial stream reaches at higher altitudes where base stream temperatures are lower, it can be hypothesised that hypolimnetic waters will reduce summer temperatures less significantly but in winter the increase would be expected to be larger. In braided reaches, a dampening of seasonal flow amplitude potentially could also be expected to reduce the extent of seasonal expansion/contraction cycles (Malard et al., 1999; Malard et al., 2006).

2.4.4.2 Impact of reduced amplitude of seasonal flow cycles on stream biota

The potential impacts of reduced flow during summer have been discussed at length in Section 2.4.2, but the impacts of year-round flow regulation on alpine stream ecosystems are poorly studied. In a reach of the River Oriège, Pyrénées, subject to supplementary hydropeaking discharges from a conduit (5 m^3s^{-1} during spring melt season and 10 m^3s^{-1} during summer/winter), Céréghino and Lavandier (1998b) and Céréghino et al. (1997) observed slight modifications in hatching and/or emergence period, and the growth of several species of Trichoptera and Ephemeroptera. For example, *Rhithrogena semicolorata, Rhyacophila occidentalis* and *Drusus rectus* grew throughout the winter downstream of the conduit, most likely in response to increased temperatures (by ~ 2 - 3 °C) whereas growth was minimal upstream of the conduit. In contrast, temperature fluctuations were found to have little effect on the life history of Plecoptera as they were able to complete larval development during periods when stream temperature was not greatly raised by supplementary discharges (Céréghino & Lavandier, 1998a). Céréghino et al. (2002) also noted during autumn (October) when the difference between natural and peak flows was the greatest, both catastrophic drift and the recovery distance of populations from the point of discharge supplementation were maximum.

In alpine basins, particularly close to the glacial-margin where seasonal variability in stream conditions is large (Schütz et al., 2001), a seasonal shift in flow regime due to regulation can be expected to have even greater implications for macroinvertebrate community distribution, structure and function. A major research gap exists because no studies have assessed year-round anthropogenic impacts in high alpine basins.

2.4.5 Mean flow increase

Anthropogenic inter-basin transfer of water results in a mean flow decrease (see Section 2.4.2) in donor basins but may also result in a mean flow increase in recipient basins if flow is channelled into open river sections (see Figure 2.6). This type of alteration to the flow regime is likely to occur in combination with another form of anthropogenic impact, for example, in recipient catchments; hydropeaking or, a reduction in the amplitude of seasonal variation, and in donor catchments; flow reduction. No studies have specifically examined the impacts of anthropogenic regulation resulting in mean flow increase in alpine catchments, however the following section considers the applicability of findings from studies in more temperate catchments to an alpine context.

2.4.5.1 Impact of mean flow increase on stream physicochemical habitat

Where water is transferred directly from one river to another via a conduit and regulated by the river flow in the donor basin, (e.g. from to Wurfbach to the Schmarzkarlbach in the Granatspitzgrupper region of the Austrian Alps; see Figure 2.1), a habitat discontinuity in the recipient river can be hypothesised as similar to that observed downstream of river confluence in a natural river (Knispel & Castella, 2003; Ilg & Castella, 2006; Brown et al., 2007b). The timing and magnitude of flow attenuation, and the associated discontinuity in physicochemical characteristics in the recipient river will be dependent on the characteristics flow from both the donor catchment and recipient catchment. However purely as a result of increased flow, increased floodplain expansion and increased sediment mobilisation can be expected (Gurnell, 1987; Gurnell et al., 1990; Warburton, 1990; Gurnell, 1995). In cases where flow is re-routed to a reservoir and the stored prior to transfer, for example from the Weiβsee reservoir into the Eisboden river, Granatspitzgrupper region (see Figure 1.1), in addition to an overall increase in flow, the controlled release of water may result in a drastic change in hydrograph form, such as hydropeaks, or a reduction in the amplitude of seasonal flow peaks. In these cases, impacts of hydropeaking and a reduction in the amplitude on stream flow to stream physicochemical habitat may also be relevant (see Sections 2.4.3.1, 2.4.4.1).

2.4.5.2 Impact of mean flow increase on stream biota

Very few studies have examined the effects of mean flow increases from inter-basin transfer on biota. Of the 165 studies of anthropogenic regulation reviewed by Poff and Zimmerman (2010), only five examined mean flow increases due to inter-basin transfer and none of these focused on alpine streams. Of these five studies, four (Golladay & Hax, 1995; Matthews et al., 1996; Hax & Golladay, 1998; Gibbins et al., 2000) examined impacts over a relative short period after the initiation of transfer (<14 days). Matthews (1996) and Gibbins et al. (2000) observed species specific increases/decreases in abundances whilst, Hax and Golladay (1998) observed 56-90% decreases in macroinvertebrate abundances and Golladay and Hax (1995); 85-98% decreases in meiofauna abundances in response to relatively large increases in discharge (up to 1000X). However, these studies focussed on the relatively short term disturbances to biota from increases in discharge (similar to those discussed in Section 2.4.3), rather than long term implications for ecosystems of a mean flow increase. In contrast, Bickerton (1995) investigated likely implications of inter-basin transfer to the River Glen, Lincolnshire, England, based on long-term (18 years) macroinvertebrate community-to-discharge correlations observed in the river. Bickerton (1995) found that that the responses of communities were likely to be site specific, and that species specific responses were expected to reflect habitat preferences of species. It can be hypothesied that the findings of Bickerton (1995) will be relevant to an alpine context, i.e. that macroinvertebrate responses would be species and site specific. However, the strong links between stream water source and the structure of alpine stream ecosystems means that the response of species are unlikely to be predictable from the volume of flow increase alone (as assumed by Bickerton, 1995). In an alpine context, the difference between the physicochemical characteristics of the recipient and donor streams water would also be an important consideration.

2.5 CONCLUSIONS

Alpine river ecosystems are controlled by a complex cascade of processes that drive considerable spatiotemporal habitat heterogeneity. Understanding the links between processes is essential to underpin models of ecosystem functioning and distribution that are necessary for informing conservation and management decisions relating to anthropogenic flow regulation and climate change (Brown et al., 2009b). A significant amount of research over the past two decades has greatly advanced knowledge of alpine river systems. However, this review has shown that knowledge remains insufficient to predict with confidence, particularly in quantitative terms, the impacts of flow regulation on alpine river basins.

This review chapter has revealed that more research is required to address the following three key themes:

i) *Year-round river ecosystem dynamics – Whilst alpine stream ecosystems have been relatively well studied during the summer melt season, little is known about the structure or functioning of alpine ecosystems outside of this period, or of the antecedent significance of seasonal heterogeneity for subsequent summer distributions.*

ii) *Anthropogenic impacts – Most research in alpine basins has focused on relatively pristine river systems that have minimal obvious anthropogenic impact. At regional to global scales there has been very little quantification of the extent of anthropogenic regulation in alpine basins, and even at sub-basin scales there has been very little* *assessment of how specific regulation practices impact upon stream habitats and ecological communities.*

iii) *Multiple processes – To predict in a mechanistic sense how ecological communities are likely to respond to anthropogenic or climate pressures, it is essential to consider holistically the process cascade between the pressure and community response. Due to the multi-disciplinary nature of cascade processes (e.g. hydrological, geomorphic and ecological), research is likely to most effective if an interdisciplinary approach is taken (Hannah et al., 2007a; Hannah et al., 2007b).*

2.6 RESEARCH GAPS

This thesis addresses its central aim stated in Chapter 1 by investigating the year-round hydrological and ecological dynamics of an anthropogenically impacted alpine proglacial river system. Each of the following chapters of this thesis addresses one of the four objectives identified in Chapter 1 which link respectively to the following specific research gaps that have been identified in this literature review chapter. Research gaps are elaborated upon in more detail in the introductory sections of each specific chapter, but here can be summarised to comprise;

i) *Statistical hydrograph classification techniques have been demonstrated to be an effective tool for characterising diurnal hydrograph forms and identifying under-lying trends in runoff processes in proglacial rivers (Hannah et al., 2000; Swift et al., 2005). If the diurnal hydrograph classification approach of Hannah et al. (1999) could be successfully used to compare stream types within a catchment it would provide a valuable tool for examining spatial hydrological functioning. Potentially the application of these techniques to multiple stream types, both laterally and longitudinally distributed within a catchment, may help to unpick catchment scale processes by isolating water source contributions (Brown et al., 2006c; Brown & Hannah, 2007), elucidate channel connectivity and braiding dynamics (Malard et al., 1999; Nicholas, 2003) and classify the spatial heterogeneity of habitats. Furthermore, statistical classification techniques may also provide a method for quantitatively and objectively assessing the impact of reservoir releases on river flow regimes.*

ii) *A quantification of year-round stream temperatures and flow permanency is required to provide a full picture of the thermal regime of alpine river systems and to inform ecological distributional studies. Although the spatiotemporal variability of water temperature in alpine basins during the summer melt-season is relatively well* *understood, year-round thermal dynamics have been poorly studied. Inferences of flow permanency and water surface conditions made from stream temperature records (e.g. Brown et al., 2006b) have not been validated with direct field observations. The effects of flow regulation from reservoirs on the thermal regime of high alpine basins have also been poorly studied.*

iii) *Although longitudinal trends in physicochemical habitat and biota along proglacial rivers are relatively well studied (Milner et al., 2001a), the lateral dimension and the temporal dimension (see Ward, 1989), of alpine ecosystem dynamics, particularly year-round, has been largely neglected. Thus little is known about the year-round functioning of alpine ecosystems. A more comprehensive understanding of the spatiotemporal dynamics of alpine ecosystems is essential to assess the implications of anthropogenic pressures as well as more observational studies focused on impacted basins (e.g. Petts & Bickerton, 1994).*

iv) *Many studies have shown that macroinvertebrate assemblages in alpine streams are sensitive to the influence of water source contributions and that specific habitats arising from water source contributions tend to host a predictable array of macroinvertebrates (Milner et al., 2010). However the underpinning links between the functional characteristics (traits) of taxa and stream ecosystems in which they are found are poorly understood. Functional trait analysis has the potential to provide valuable insight into alpine stream ecosystem structure and functioning, but few alpine studies have adopted this approach (Snook & Milner, 2002; Finn & Poff, 2006; Ilg & Castella, 2006) and none have focused on examining the lateral and temporal dimensions of alpine stream systems.*

CHAPTER 3: STUDY SITE

3.1 INTRODUCTION

This chapter firstly provides a rationale for the selection of the Eisboden catchment as the focus of this study (Section 3.2), before secondly providing a detailed description of the Eisboden catchment (Section 3.3). Descriptions of the six main stream monitoring sites used are given along with a rationale for the selection of these sites (Section 3.4). Further details of instrumentation installed, and of flow-gauging and sampling techniques implemented at stream monitoring sites are given where relevant to the analysis in chapters (4 to 7) along with details of laboratory and statistical techniques used. A description of meteorological monitoring methods is given (Section 3.5) and finally a summary of the sampling/monitoring strategy from June 2008 through to September 2009 is given (Section 3.6).

3.2 STUDY SITE SELECTION CRITERIA

To achieve the central aims of this thesis (Chapter 1.2) it was necessary to work within a catchment that met the following four criteria:

1. Located within the alpine zone with glacial, snowmelt, groundwater water sources.
2. Containing a range of stream habitats including a main proglacial channel, predominantly groundwater-fed streams, and mixed floodplain channels.
3. Subject to anthropogenic flow regulation.
4. Accessible for year-round sampling.

The Eisboden catchment in the Granatspitzgruppe of the Austrian Alps conformed to each of these four criteria, and the details are discussed herein.

3.3 STUDY SITE CHARACTERISTICS

The Eisboden catchment is located on the edge of the Hohe Tauern National Park in the Central Austrian Alps at 47°07’W, 12°38’W (Figure 3.1, Plate 3.1). The catchment lies above the tree-line and spans an altitudinal range of 2110-3460 m from the most downstream main monitoring site (Site B). Access is relatively straightforward during the summer tourist season (June – September) and winter ski season (December–April), not least because a gondola operates from Enzingerboden to the Rudolfshütte Berghotel. The Rudolfshütte is situated at 2315 m.a.s.l and is a 1.5 km walk from the Eisboden study site (2120 m.a.s.l). When the gondola is not running, access is also possible from Enzingerboden (1468 m.a.s.l) via a 7.0 km walk.

Twenty-three percent of the total 11.7 km^2 catchment area (above Site B) is occupied by the Ödenwinkelkees glacier, the much smaller Rifflkees glacier and permanent snow packs (Figure 3.1). The Eisboden flows from the Ödenwinkelkees glacier snout (2194 m.a.s.l.) down a steep-sided (30 - 60°) north-facing glacially-deepened valley into the Tauernmoossee reservoir (2023 m.a.s.l) where it terminates. Three distinct floodplains where substantial lateral braiding occurs exist along the Eisboden between more geomorphically stable reaches (see Figure 2.1). These floodplains are referred to as (i) The Upper Eisboden Braidplain; situated between the Ödenwinkelkees snout and a point 960 m downstream (2194 – 2147 m.a.s.l); (ii) The Central Eisboden Braidplain; situated between 1030 and 1420m's from source (2135 – 2114 m.a.s.l.) and; (iii) The Lower Eisboden Braidplain; situated between 1620m -1820m from source (2105 m.a.s.l – 2099 m.a.s.l). The geology of the valley is predominantly of feldspathic rocks, mica schist and gneiss, and soils are Leptic Regosols within the glacial foreland (above the Lower Braidplain) and Eutric Regosols further down-valley (Bardgett et al., 2007; Philippot et al., 2010). The valley sides are predominantly bedrock mantled with shallow soils and vegetation colonising the moraine fills and scree down-valley of the Ödenwinkelkees glacier.

Plate 3.1 - *The Eisboden catchment viewed from the Mittleree Schafbichl in July (left) and April (right).*

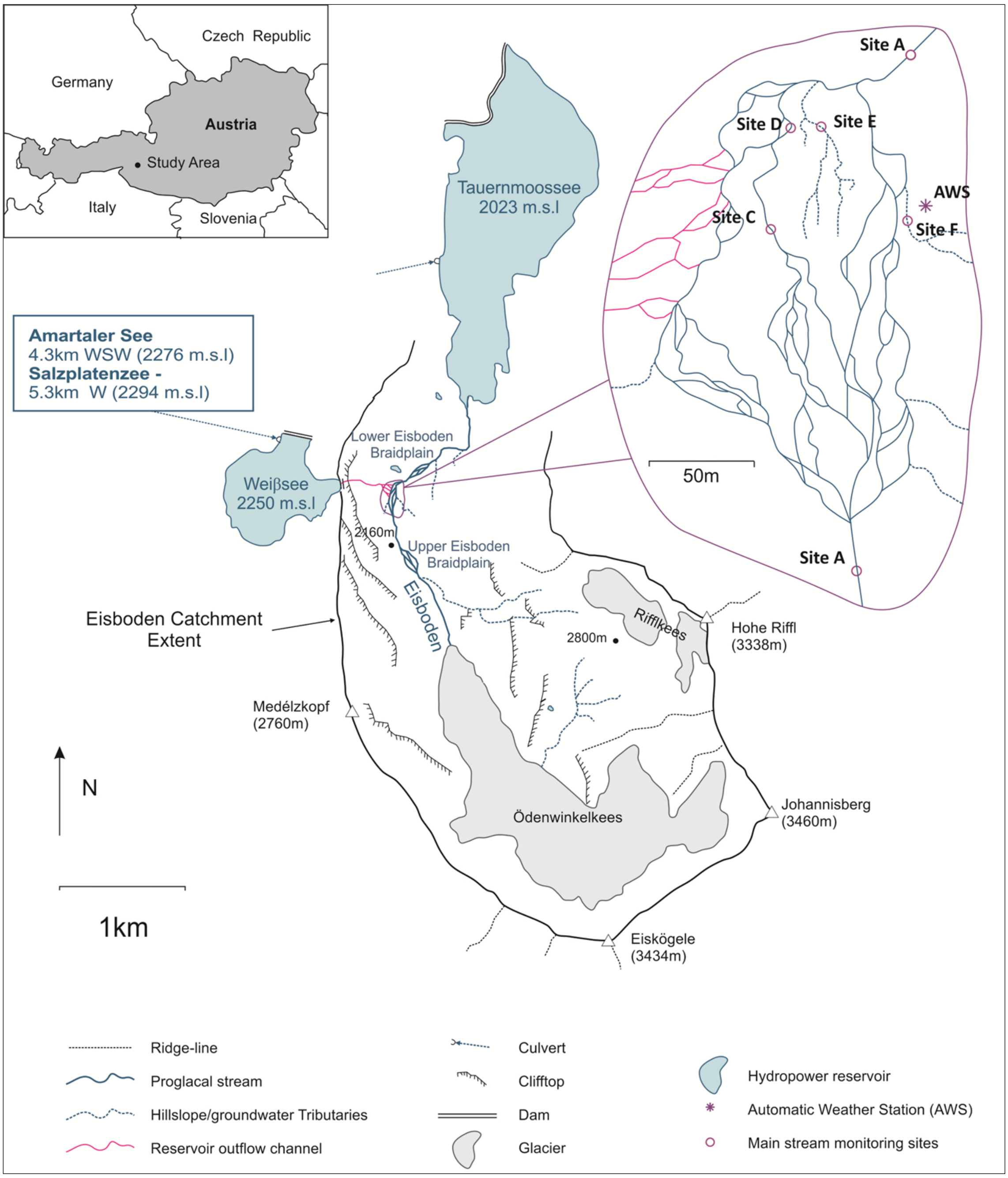

Figure 3.1 - *Map of study area.*

3.3.1 Hydrological sources and pathways

The Eisboden catchment contains five distinct and highly dynamic hydrological sources/pathways: (i) the Ödenwinkelkees and Rifflkees glaciers, (ii) seasonal snowpacks, (iii) an alluvial groundwater system, (iv) hillslope groundwater streams, and (v) overspill or regulated drawdown flows from the Weißsee reservoir.

The Ödenwinkelkees (Plates 3.2 and 3.3) faces NW and now covers 9.8 km^2 but has retreated 1.5 km at an average rate of 10 myr^{-1} since 1850, when it was at its maximum neo-glacial extension reaching to the outlet of the Central Eisboden Braidplain (Slupetzky, 2000; Bardgett et al., 2007). The Eisboden emerges at its terminus which is now 1030m upstream of the Central Eisboden Braidplain. The Rifflkees is a much smaller WNW facing hanging glacier (0.8 km^2). The proglacial stream system of the Rifflekees intermittently flows through sediments before emerging as a continuous small stream approximately 200 m from its confluence with the main Eisboden stem; 430 m downstream of the Ödenwinkelkees snout.

Snow cover across the Eisboden catchment usually lasts from mid-October until late-June though summer snowfall is not uncommon (Tscherko et al., 2003). During the summer snow-packs recede and the surface of the Ödenwinkelkees glacier is gradually exposed. Small permanent snow-packs exist throughout the catchment but are more numerous and substantial at higher altitudes on the slopes of the Medélzkopf, Eiskögele, Johannisberg and Hohe Riffl.

The Weißsee reservoir is located to the west of the Eisboden catchment and provides water storage for hydropower generation in Enzingerboden at a plant which is the upper of three hydropower stations owned by The Federal Austrian Railways (ÖBB) in the Stubach valley. The Weiβsee fills through the melt-season accumulating runoff from the glacierized Schotterbachboden basin and through an underground culvert linked to two other reservoirs (the Amertaler See and Salzplattensee) in valleys to the west. In late summer when the Weißsee reaches maximum capacity it overspills into the Central Eisboden floodplain (Plate 3.4). Periodic drawdown from the Weiβsee occurs from mid-autumn until late-winter to transfer accumulated water to the Tauernmoosee reservoir from which water is drawn to supply the ÖBB Enzingerboden hydropower station. The underground culverts linking the Amertaler See, Salzplattensee and Weißsee are part of a wider scheme across the Granatspitzgruppe engineered to supply the Tauernmoosee, all of which combined together affect the hydrological functioning of seven alpine basins across the region (see Figure 2.1).

Plate 3.2 - *The Ödenwinkelkees glacier.*

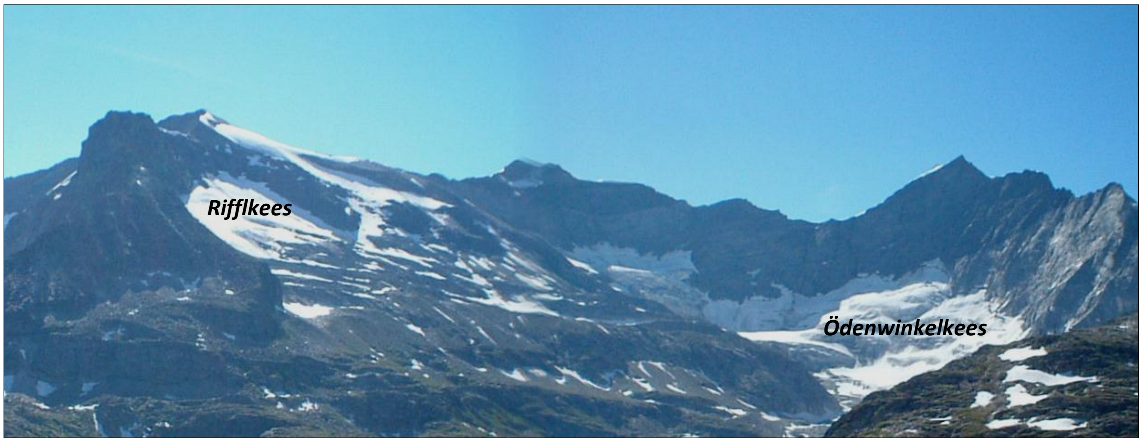

Plate 3.3 - *The Ödenwinkelkees and Rifflkees glaciers*

Plate 3.4 - *Views of overtopping flows (top) and drawdown flows (below), from the Weiβsee cascading into mixed channels on the west side of the Eisboden braidplain.*

3.4 OVERALL MONITORING STRATEGY

Distinct differences in the characteristics of streams across the Eisboden catchment result from differences in the proportions of flow contributions from hydrological sources/pathways. Physicochemical habitat characteristics and benthic sampling were conducted at six main stream monitoring across the Central Eisboden Braidplain (Figures 3.1 and 3.3, Plates 3.5 and 3.6) that were selected to represent (i) two main glacial-stem habitats, and (ii) two mixed stream habitats, that are only intermittently connected with the main glacial stem, but otherwise fed by alluvial groundwater and hill-slope tributaries; and (iii) two predominately groundwater fed stream that are rarely effected by flow from the main glacial stem. Of each pair of sites, one was anticipated to be effected by anthropogenic flows from the Weiβsee (see Figures 3.2, 3.3). Stage was measured continuously at each site and used to estimate a continuous (15 minute resolution) discharge record. Detailed descriptions of stage monitoring instruments and flow gauging techniques are given in Chapter 4.2. Stream temperature was monitored continuously at Sites A to F (15 minute resolution). Spot measurements of water temperature, flow velocity, conductivity, stream depth and snow depth were made at each site on macroinvertebrate sampling days and water samples were collected and analysed for suspended sediment concentration. Further details of instrumentation, field and laboratory techniques used for physicochemical habitat and ecological monitoring are given in chapter 6.2. In addition to the six main stream monitoring sites (A to F), stream temperature was monitored at an additional 17 sites to investigate the broader catchment wide thermal characteristics of streams; these are described in detail in Chapter 5.2.

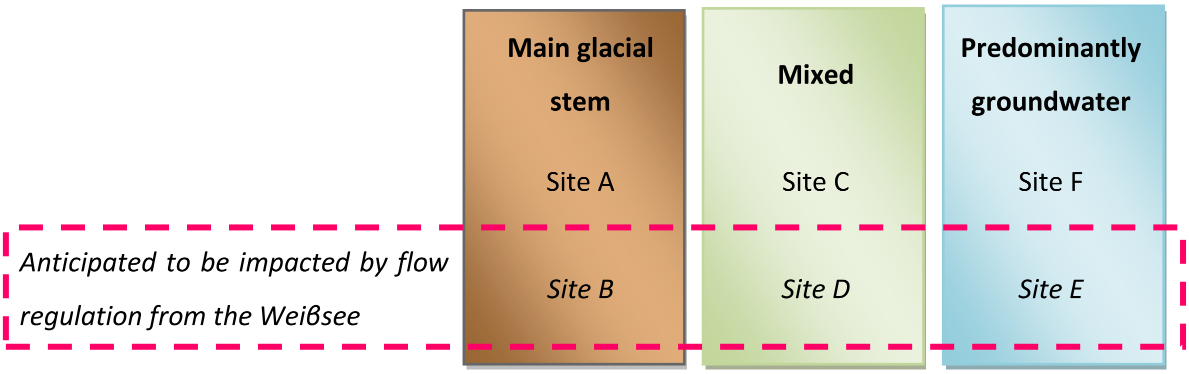

Figure 3.2 - *Stream types of each sampling site.*

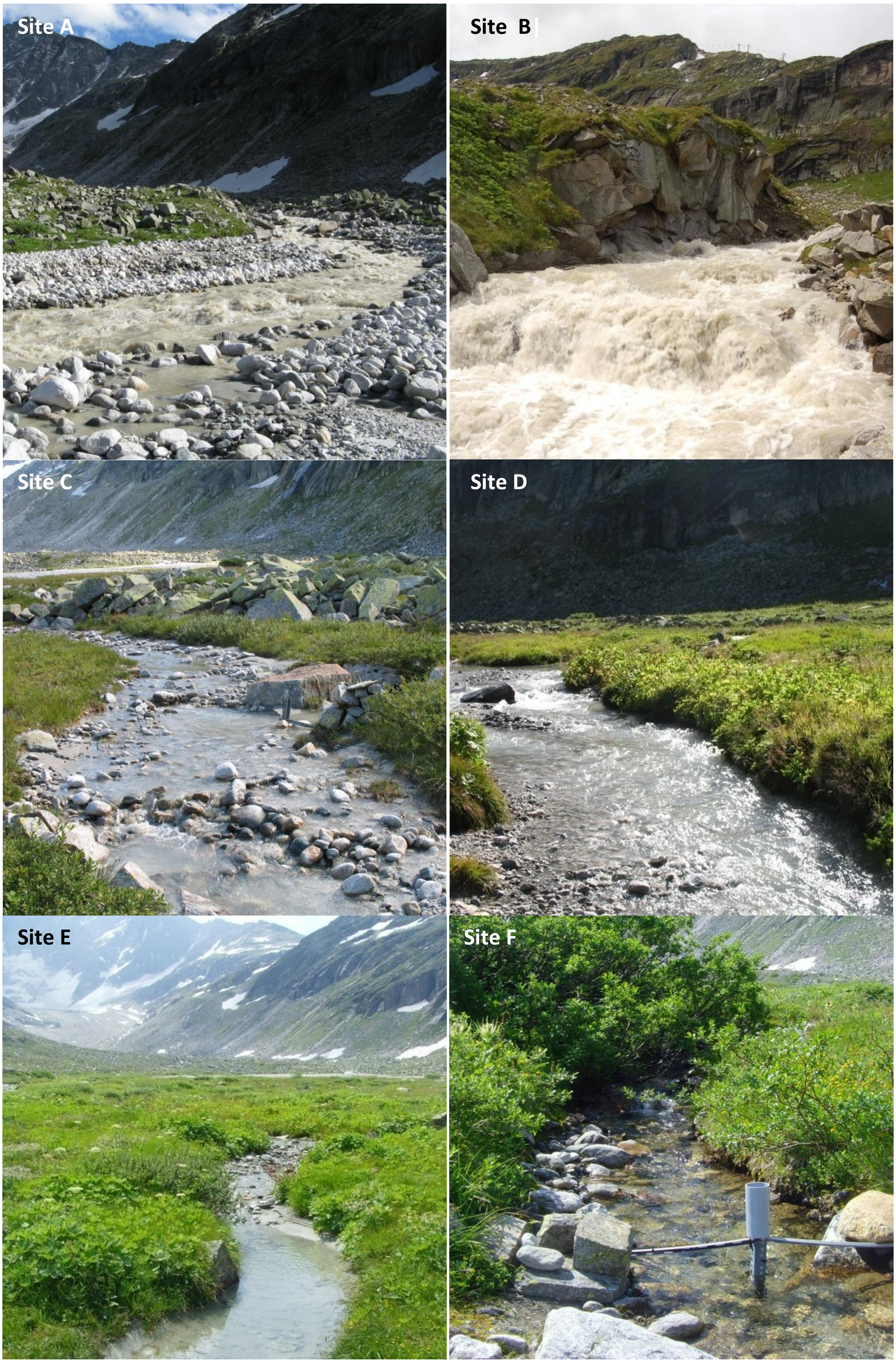

Plate 3.5 - *Main stream monitoring sites.*

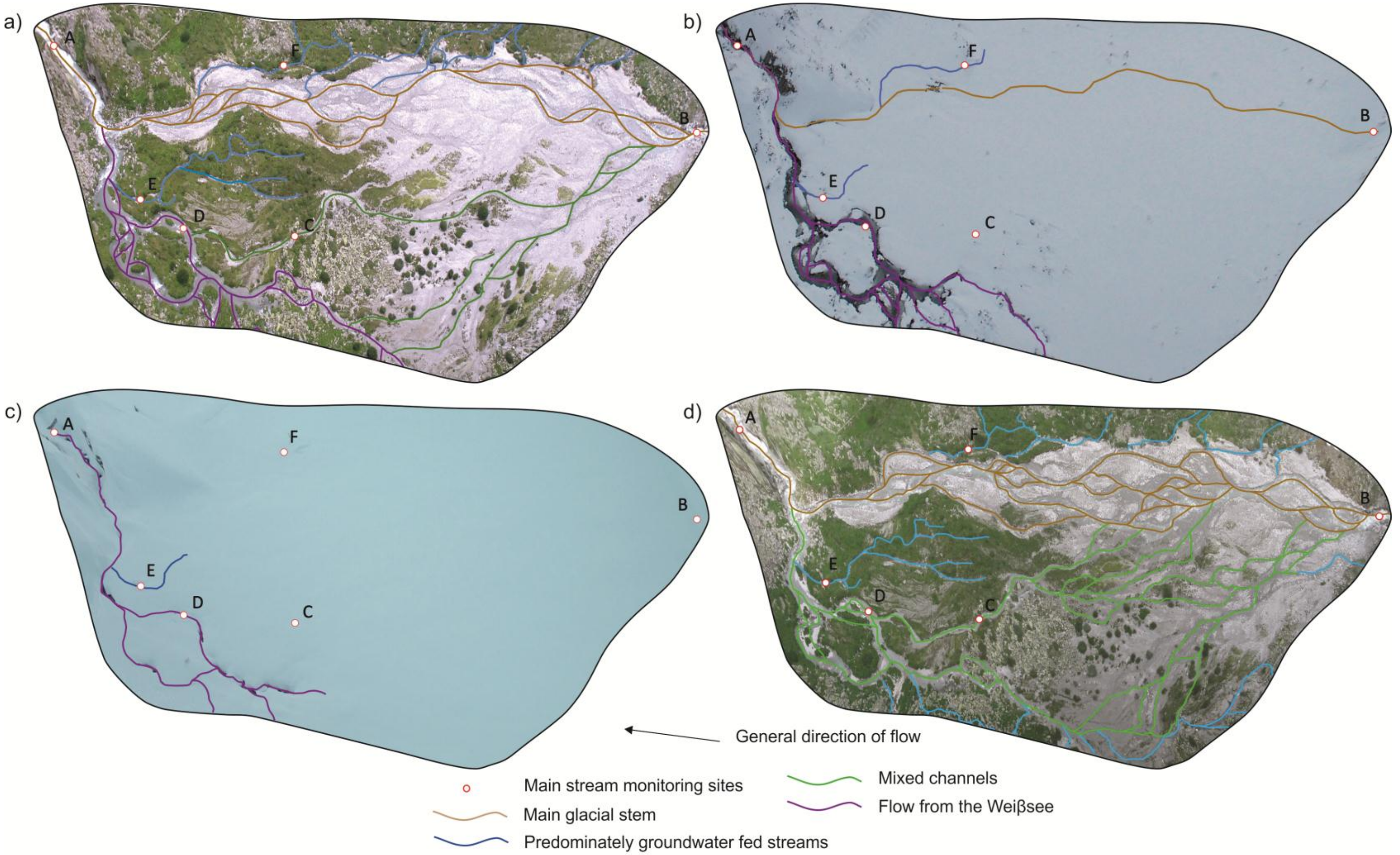

Figure 3.3 - *Orthoimages of the Central Eisboden Braidplain showing the main monitoring sites and streams observed to be flowing in; a) August 2008, b) December 2008, c) March 2009 and, d) June, 2009.*

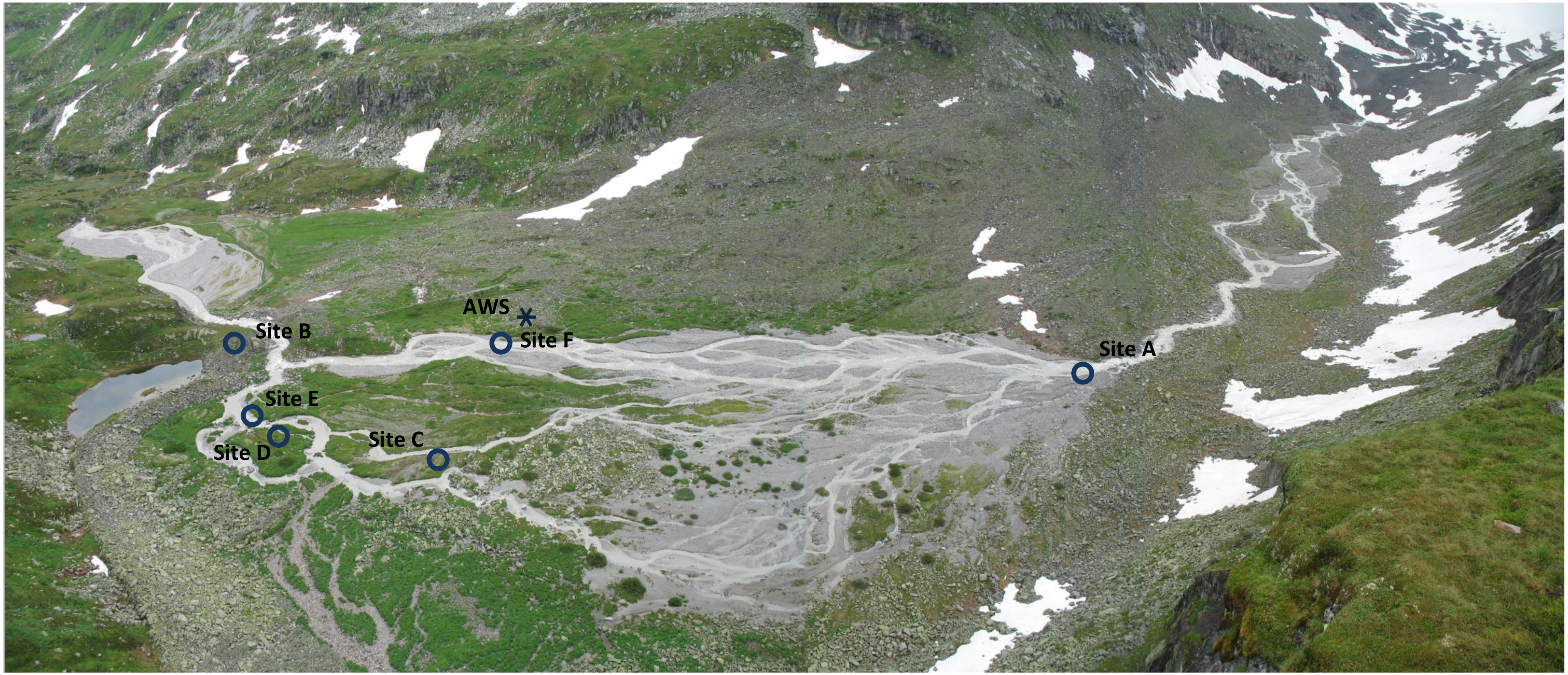

Plate 3.6 - *Panoramic view of the Central Eisboden Braidplain showing main stream monitoring sites and Automatic Weather Station (AWS) locations.*

3.5 METEOROLOGICAL MONITORING

Air temperature, incoming shortwave radiation and precipitation were monitored using an Automatic Weather Station (AWS) situated adjacent to the floodplain (Figure 3.1, Plate 3.7). AWS measurements were logged using a Campbell Scientific CR200 datalogger. Air temperature (T_{air}) was measured using a CS215 temperature/humidity probe. Incoming shortwave radiation was measured using a SP1110 pyranometer. Rainfall was measured at ground level using an ARG100 tipping bucket gauge (0.2 mm resolution). Following snowfall events snow was not cleared from the gauge but was allowed to melt into the tipping bucket. Precipitation data from during and shortly following snowfall periods (see sections 4.3.2 and 5.4.1) should therefore be treated with caution. All dataloggers were synchronised prior to installation and internal clocks checked regularly. All sensors were scanned at 10 s intervals and data was logged at 15 min. intervals.

3.6 SAMPLING PERIOD AND TEMPORAL RESOLUTION

The AWS and dataloggers at Site B were installed prior to day 126, 2008 and left in-situ at the end of the monitoring period enabling the hydrological analysis of two complete melt seasons at Site B (2008/2009) and the intervening winter period (see Chapter 4). Dataloggers were installed on or prior to calendar day 182, 2008 and removed on day 247, 2009 at the other five main stream monitoring sites (Site A and C to F) to enable consecutive analysis across two summer melt seasons and the intervening winter season. Temperature loggers at an additional 15 other sites were installed prior to day 182, 2008 to enable concurrent thermal analysis, and two additional temperature loggers were installed on day 182, 2009. Further details and rationale of the installation of temperature loggers is given in Chapter 5. Physicochemical habitat and benthic macroinvertebrate sampling was conducted monthly during summer field campaigns lasting from the end of June through until the beginning of September (2008 and 2009). Thus, each of the six sites was sampled three times each summer (see section 6.2 for precise dates). Samples were also collected during winter field visits in early December, 2008 and early March, 2009 (see section 6.2). Flow gauging to construct stage-discharge rating curves was carried out throughout each summer season and on winter field visits.

Collecting un-interrupted year-round time series data in alpine catchments is challenging (Schütz et al., 2001; Brown et al., 2006b). For example, keeping loggers fixed in place in unstable channel sections, ensuring a continuous power supply despite extremely cold winter temperatures, preventing animals eating through electrical cables, avoiding dewatering around probes due to changes in channel cross-section and locating loggers during winter when covered in a thick snowpack all presented considerable challenges in this study. In 2009, gaps arose in incoming shortwave radiation data (days 116 and 145 - 181), precipitation data (days 145-181) and in the air temperature time series (days 168 - 170, 185 - 187) due to cable damage from animals at the AWS. Details of any gaps arising in discharge and water temperature time series data are described in Chapters 4 and 5 respectively.

CHAPTER 4: SPATIOTEMPORAL DYNAMICS OF STREAM FLOW

4.1 INTRODUCTION

Alpine catchments act as 'natural water towers' providing a supply of water for drinking, irrigation and hydropower generation that is essential to sustain the demands of over one-sixth of the world's population (Barnett et al., 2005; Viviroli et al., 2007; Wehren et al., 2010b). The temporal availability and total water-supply from alpine catchments is predicted to be significantly affected even under the most conservative estimates of climate change (Barnett et al., 2005; Stahl et al., 2008) which would lead to widespread regional water-supply problems. Hydrographs can reveal trends in catchment runoff that are important for water-management and provide an empirical evidence base for changes in regional hydrological functioning. Furthermore, the analysis of hydrograph form and magnitude aids an examination of the processes driving catchment hydrological functioning (Hannah et al., 2000).

Hydrograph classification methods have the potential to distil large high resolution time series into discrete classifications of runoff records exhibiting similar form and magnitude (Hannah et al., 1999; Bower et al., 2004). The overall aim of these techniques is to make the original data set more manageable and interpretable, while still maintaining an integral representation of the original data. Hydrograph classifications can be derived for a variety of time scales from annual (e.g. Kansakar et al., 2002; Bower et al., 2004; Moon et al., 2004; Monk et al., 2007) down to diurnal periods (e.g. Hannah et al., 2000; Swift et al., 2005). The resultant classifications can be used to examine: (i) catchment scale processes governing hydrological outputs (e.g. Hannah et al., 2000; Bower et al., 2004; Moon et al., 2004; Swift et al., 2005), and (ii) relationships between stream hydrographs and linked geomorphic (Orwin & Smart, 2004) or ecological processes (Harris et al., 2000; Monk et al., 2006).

Proglacial stream hydrographs typically exhibit strong diurnal fluctuations during spring and summer due to the presence of melt-water flow components that are inextricably linked to daily cycles of incoming solar radiation (Röthlisberger & Lang, 1987; Jansson et al., 2003). Classifying hydrographs at the diurnal scale is therefore of interest so that these diurnal pulses can be compared both within and between systems, and incorporated in related studies examining alpine hydrological, geomorphic or ecological processes (Smith et al., 2001; Richards & Moore, 2003; Orwin & Smart, 2004; Swift et al., 2005). Traditionally, studies that classified proglacial hydrographs based on diurnal data did so using relatively subjective methods. For example, some studies relied purely on the judgement of the analyst examining the data to define time blocks where hydrographs appeared to have similar characteristics (e.g. Gurnell et al., 1994; Hodson et al., 1998). Other studies have applied hydrological indices such as maximum and minimum discharge (e.g. Gurnell et al., 1992) to provide some objectivity to the temporal discretisation of the data set, but the definition of class boundaries still remains subjective with this approach.

Hannah et al. (1999; 2000) suggested that whilst subjective techniques may work well in ablation-dominated glacier basins more objective approaches are required in other systems. Hannah et al. (1999; 2000) therefore developed a two-fold statistical procedure for hydrograph classification to address the aforementioned lack of objectivity. In essence, a monitoring period is divided into diurnal hydrographs and then each diurnal hydrograph is classified by its form (shape) and magnitude. This technique has subsequently been tested on a handful of glacial catchments (see Hannah et al., 1999; Hannah et al., 2000; Swift et al., 2005) but these sites have all had strong ablation-driven diurnal meltwater pulses and the suitability of the technique for more chaotic hydrological functioning is yet to be fully tested. The application of the diurnal-hydrograph technique has also been limited to single gauging sites or sites along a single channel (see Hannah et al., 2000) and it remains to be tested in proglacial systems where multiple streams are sourced from distinct water sources (e.g. glacial, snowmelt, groundwater and combinations of these; Brown et al., 2003; Malard et al., 2006);i.e. where streams have a range of hydrological behaviours.

The hydrological functioning of multiple stream types, both laterally and longitudinally distributed within a catchment can help to unpick catchment scale processes by isolating water source contributions (Brown et al., 2006c; Brown & Hannah, 2007), elucidate channel connectivity and braiding dynamics (Malard et al., 1999; Nicholas, 2003) and classify the spatial heterogeneity of habitats (Tockner et al., 2000; Smith et al., 2001; Monk et al., 2006; Brown et al., 2009b). If the diurnal hydrograph classification approach of Hannah et al (1999) could be successfully used to compare stream types within a catchment, it would provide a valuable tool for examining spatial hydrological functioning.

This chapter analyses the suite of hydrographs recorded at the six main monitoring sites (Figure 3.1) across the Eisboden braidplain between the spring of 2008 and autumn 2009. The aims of this chapter are: (i) to characterise the hydrological functioning of different stream types across a proglacial braidplain with respect to water sourcing and climatic conditions, and (ii) to assess the potential of an objective statistical hydrograph classification technique for analysing different stream types within a single catchment. The analyses are presented in two sections so that the specific application of statistical techniques can be explained in the context of the results. Each section contains specific details of the statistical methods and of the corresponding results. Firstly the hydroclimatological regimes of Site B are analysed and hydrographs are statistically classified to characterise *temporal* catchment functioning from the start of the melt season (early May) through until 3rd September for both 2008 and 2009. Secondly, concurrent hydrographs at all six main monitoring sites are analysed for July and August (2008, 2009) using the same approach to consider *spatial* dynamics and further unpick catchment hydrological controls.

4.2 FIELD METHODS

The configuration of the six main monitoring sites across the Ödenwinkelkees braidplain that were maintained through 2008 and 2009 capture a complex stream network fed by five highly dynamic and spatially variable hydrological sources/pathways: (i) the Ödenwinkelkees and Rifflkees glaciers; (ii) seasonal snowpacks; (iii) an alluvial groundwater system; (iv) hillslope groundwater systems and; (v) overspill or regulated flows from Weißsee reservoir (see Chapter 3.3). River stage was monitored continuously at Site B from day 319, 2007 and subsequently at all sites from day 176, 2008 through to day 247, 2009 using Trafag DL/N-70 pressure transducers mounted in stilling wells. Stage-discharge curves were constructed to provide continuous estimates of flow. Curves were established from salt-dilution gauging measurements using both ‘in solution’ (Moore, 2005) and ‘dry’ (Fraser, 2005) slug injection methods at a range of flows during 2008 and 2009. Sensors were cross-calibrated to ensure comparable datasets (Brown et al., 2006a). Gaps in the discharge time series are summarised in Table 4.1. These gaps resulted primarily from sediment deposited in stilling wells following high flow events. This was a particular problem in the shallow groundwater streams (Sites E, F) and the extremely variable mixed streams (Sites C, D) where the logger had to be mounted near to the bed to avoid the stream level dropping below the sensor. Other instances of missing discharge data at Site B were attributable to logger power failure (days 180-183; 2008) and marmots chewing through the logger cables during spring 2009 (logger re-instated day 176). Air temperature, incoming shortwave radiation and precipitation were monitored at the AWS as described in Chapter 3.5.

4.3 TEMPORAL (MELT SEASON) HYDROGRAPH DYNAMICS AT SITE B

4.3.1. Methods

To characterise the general hydrological functioning of the Eisboden catchment, and to assess the suitability of statistical hydrograph classification techniques for the river regimes in this catchment, unregulated periods of flow at Site B were selected for analysis. The stream flow record at Site B is a product of all catchment input, transport and storage processes making it the best choice of sites to examine aggregated catchment-scale trends and dynamics in hydrological processes. Discharge data sets (15 min resolution) from day 126, 2008 and the equivalent calendar day (125) in 2009 were used to define the start of the melt season (Nb. 2008 was a leap year). Data beyond day 230, 2008 and day 218, 2009 were not included as flows at Site B were significantly modified by overspill from the Weißsee reservoir.

Table 4.1 - *Summary of statistical analysis.*

		Single site analyses	**Multiple site analyses**					
Time period analysed	**2008**	126-230	183-247					
	2009	125-218	182-246					
Sites used		*Site B*	*Site A*	*Site B*	*Site C*	*Site D*	*Site E* *	*Site F*
Days with Incomplete data	**2008**	157-164,174, 183-185,	-	184,185, 234	-	-	196,197, 198,208, 209,211, 212,220-223,233, 234,236, 237	196,197, 198,208, 209,211, 212,220-222
	2009	177-182,	-	182	-	207,208, 218-220, 230,231	200-203	182,183, 200-203
Total days removed due to incomplete data		20	0	4	0	7	15	16
No. of PCs retained		3	3		3		4	
Variance explained by retained PCs		87.4%	87.0%		87.1%		67.4%	
Number of shape clusters derived		4	3		5		3	
Number of magnitude clusters derived		6	5		5		5	

**Site E was excluded from the analysis in 2009 (see text).*

4.3.2 Hydroclimatological context

Air temperature, radiation and precipitation time series collected at the AWS throughout the 2008/2009 melt seasons are presented in Figure 4.1, alongside discharge monitored at Site B to compare trends in discharge and key hydrological drivers within and between seasons. The discharge record was summarised in the form of mean monthly flows (Figure 4.2). The mean monthly flow record at Site B was extrapolated through August based on a linear regressions of the mean daily flows of the 30 days prior to overspill with Site A ($r^2 = 0.80$, $p < 0.001$; 2008 and, $r^2 = 0.88$, $p < 0.001$; 2009). This extrapolation gives an approximation of the start of the declining limb of the seasonal hydrograph at Site B that would have been observed if the flow regime was not modified by flows from the Weißsee reservoir and thus reflects only natural hydrological processes. A single peak regime with a maximum in July can therefore be inferred for both years (see Figure 4.2). However, the underlying seasonal hydrological regime hides a complex series of cycles linked to precipitation events and summer snow accumulation and melt (Figure 4.1).

In 2008, discharge increased gradually during a cloudless period (day 128 - 137) with consistently high incoming daily radiation totals at the beginning of the spring melt period (Figure 4.1). A fall in shortwave radiation and daily air temperatures was then associated with reduced melt until day 146. Thereafter, a marked rise in daily air temperature was accompanied by a significant build in the seasonal hydrograph, culminating in a series of sharp diurnal peaks (days 148, 149, 150). Following a period of missing discharge data between days 157-164 the air temperature time series was punctuated by a significant dip below zero. Succeeding this dip (from day 168) air temperature steadily increased and there was an associated increase in discharge and the diurnal flow dynamics in response to increased melt water inputs culminating in a series of melt-dominated days (175 - 178) with strong diurnal variation. The seasonal hydrograph (Figure 4.2) indicates that mean discharge continued to rise into July although more gradually than in June, before receding in August. From day 175, discharge records (Figure 4.1) reflected several building and recession cycles as energy inputs varied significantly throughout the rest of the summer season. For example, daily air temperature dropped below freezing on days 204, 205 and 229, which suppressed melt and thus discharge. However, snow fall events renewed the snow packs fuelling increased melt water supply on subsequent days. Precipitation was a very significant hydrological driver throughout the summer of 2008 and the extreme frequency of occurrence of precipitation events (see Figure 4.1) suppressed the seasonal melt signal in the discharge record. Successive periods of clear days where energy inputs were high and where clear melt driven building could be observed in the hydrograph were few (e.g. days 223, 224 and 225).

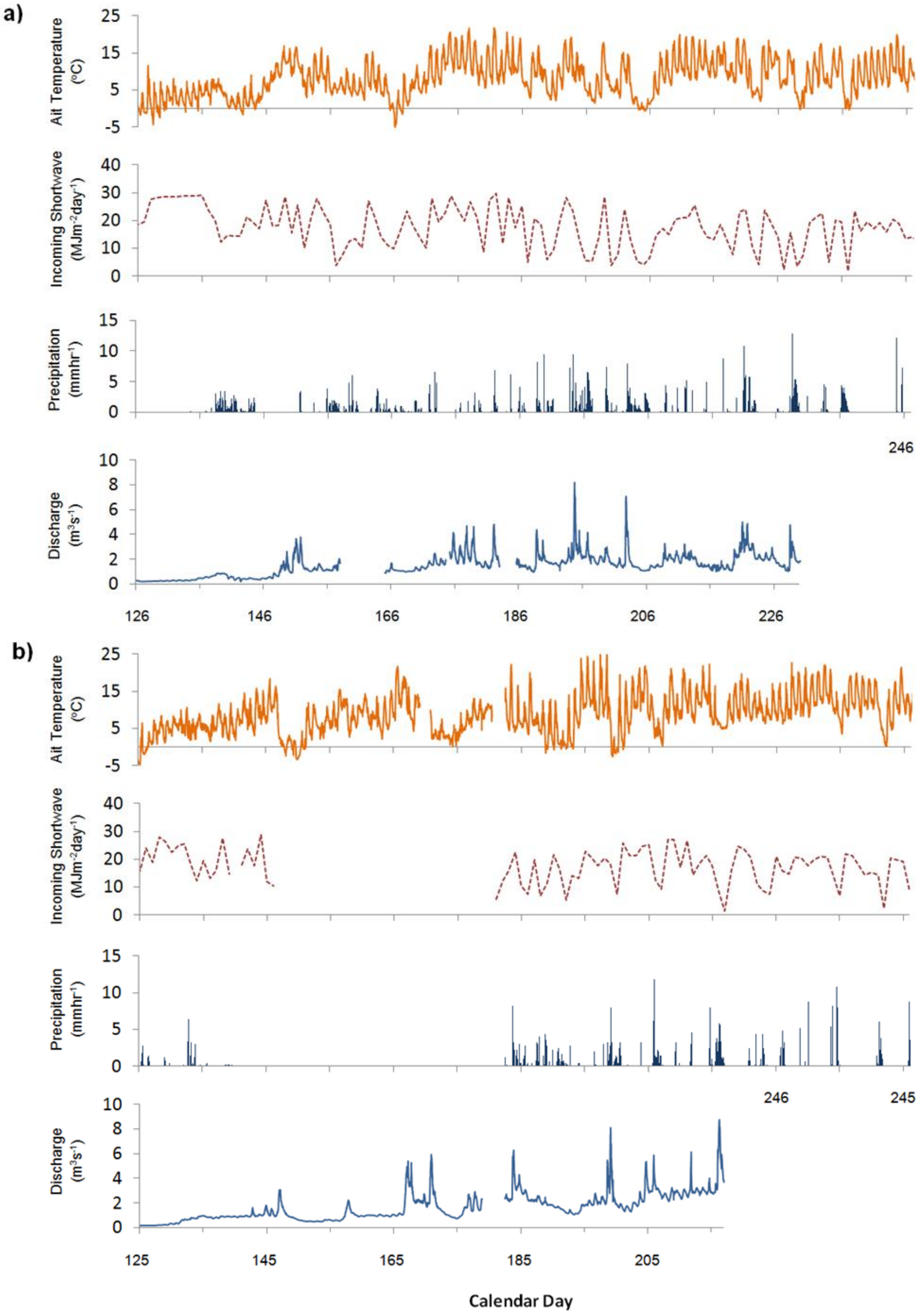

Figure 4.1 - *Air temperature, incoming shortwave radiation, precipitation and discharge at Site B during spring/summer; (a) 2008, (b) 2009.*

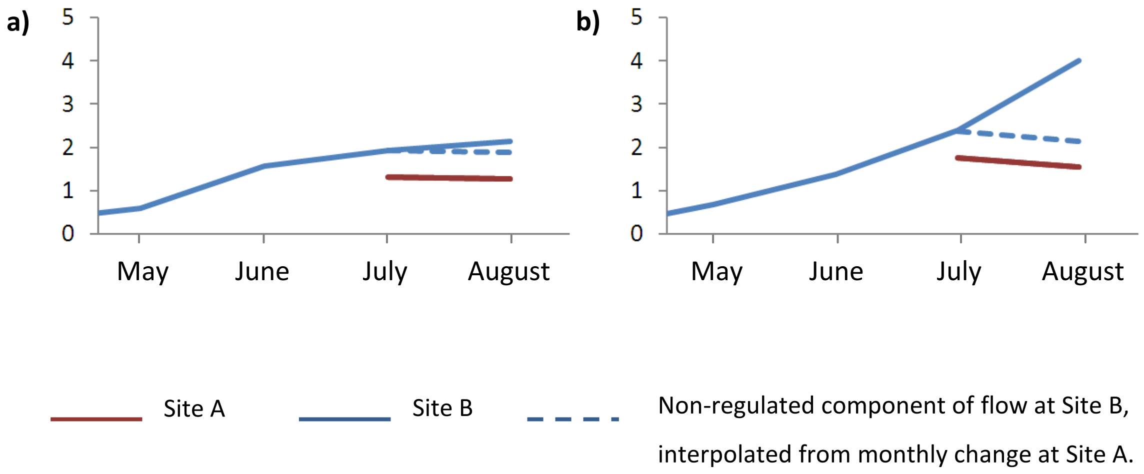

Figure 4.2 - *Mean monthly hydrographs; (a) 2008, (b) 2009.*

The start of the melt season in 2009 was marked by a sustained rise in mean daily air temperature above 0^{o} C from day 127, when shortwave radiation was high. Discharge rose gradually into the summer in a similar manner to 2008 with several cycles of building and recession flows (see Figure 4.1). Unfortunately, a lack of climatic data during late spring makes it difficult to make inferences about the hydrological drivers for this period. In contrast to 2008, precipitation events during the summer of 2009 were slightly less common (Dickson et al., 2010) and discharge trends could be more discernibly associated with incoming shortwave energy fluxes which followed several cycles through the summer. For example, a substantial cold period with snow fall on days 188, 189 and 191 resulted in recessional flow days with subdued diurnal dynamics. A rise in energy inputs then resulted in a series of building hydrographs which exhibited strong diurnal melt signals (days 196, 197 and 198). This building phase culminated in two extreme precipitation events on 198 and 199 where flows were extreme. These were immediately followed by another period of low energy inputs and recessional flows (days 200 and 201) that signalled the start of another cycle.

4.3.3 Shape Classification

Diurnal hydrographs were classified by using a two-stage statistical classification procedure (Hannah et al., 1999; Hannah et al., 2000; Swift et al., 2005); first by conducting a Principal Components Analysis (PCA) and secondly by a Hierarchical Clustering Analysis (HCA). Prior to the PCA, the following five steps were taken to prepare the discharge record. (1) Seven and a half minute resolution data points were linearly interpolated from the 15 min record to produce a PCA input matrix with more columns (time steps, N) than rows (days, n) and thus avoid algebraic problems in the computation of the covariance matrix (Hannah et al., 1999). (2) Based on the results of a preliminary PCA (conducted after preparing a data set in the same manner described but without this step) the data set was offset by 8 hours, 22 minutes so that ‘hydrological days’ were defined from 08:22 GMT. This offset was calculated from the minima of the first principal component’s factor scores to align the data sets’ diurnal cycles to a more hydrologically meaningful datum than 24:00 GMT (cf. Hannah et al., 1999; Hannah et al., 2000). A comparison with results obtained using 24:00 GMT as a temporal datum indicated that the offset method explained a greater proportion of variance using fewer Principal Components (PCs). Additionally, the resultant clusters obtained from HCA were more readily interpretable. (3) Days with incomplete data were removed from the data set (see Table 4.1) to avoid missing values in the input matrix. (4) The same physical processes are likely to have controlled hydrological functioning between each year, thus datasets from the two summers were amalgamated into a single matrix so that only one set of classifications would be computed enabling direct between year comparisons. (5) The data was restructured into an input matrix containing 192 time steps per day (N) by 180 days (n) and standardised using z-scores (Swift et al., 2005).

The PCA was run incorporating a VARIMAX orthogonal rotation to maximise loadings on variables and simplify data structure. The first three PCs were retained from the PCA based on the physical interpretability of PCs (Jolliffe, 1990, 1993) and these cumulatively explained 87.5 % of the total variance in the data set. A HCA was conducted on the component loadings of the retained PC scores. This is an agglomerative clustering method where cluster sizes are progressively increased by first aggregating similar cases, then similar clusters. The average linkage method using a Euclidean distance measure was used as this was found to give the most structured dendrogram (cf. Swift et al., 2005) and physically interpretable clusters (cf. Orwin & Smart, 2004). Four distinct clusters were evident from the dendrogram (Figure 4.3) which can be interpreted from empirical analysis of the diurnal hydrograph as follows;

(i) Recessional Hydrograph. This cluster contained 40 days (21 from 2008, 19 from 2009) that exhibited overall recessional flows. Where present, diurnal flow peaks were small relative to the overall recessive trend but in most cases flow peaking was subdued.

(ii) Peaked Hydrographs. This was the largest cluster containing 51 days from 2008 and 48 from 2009 days. The mean z-score plot (Figure 4.3) reflected a late afternoon flow peak (mean time at peak ($t_{p,av}$) = 18:52) characteristic of predominately melt-driven discharge regimes (Röthlisberger & Lang, 1987; Paterson, 1994; Raymond et al., 1995). However, a more detailed examination of these hydrographs revealed that this cluster contained a large number of precipitation days (65% of days where precipitation was recorded) indicating that precipitation would have been a significant hydrological driver alongside melt.

(iii) Building/Late Peaking Hydrographs. This cluster grouped 35 days (19 from 2008, 17 from 2009) which were characterised by extended building hydrographs peaking either shortly before 06:22GMT or into the next day ($t_{p,av}$ = 03:07).

(iv) Erratic/Dipped Hydrograph. This cluster contained one day (174; 2009) when flow exhibited a pronounced dip throughout the afternoon and evening before rising overnight.

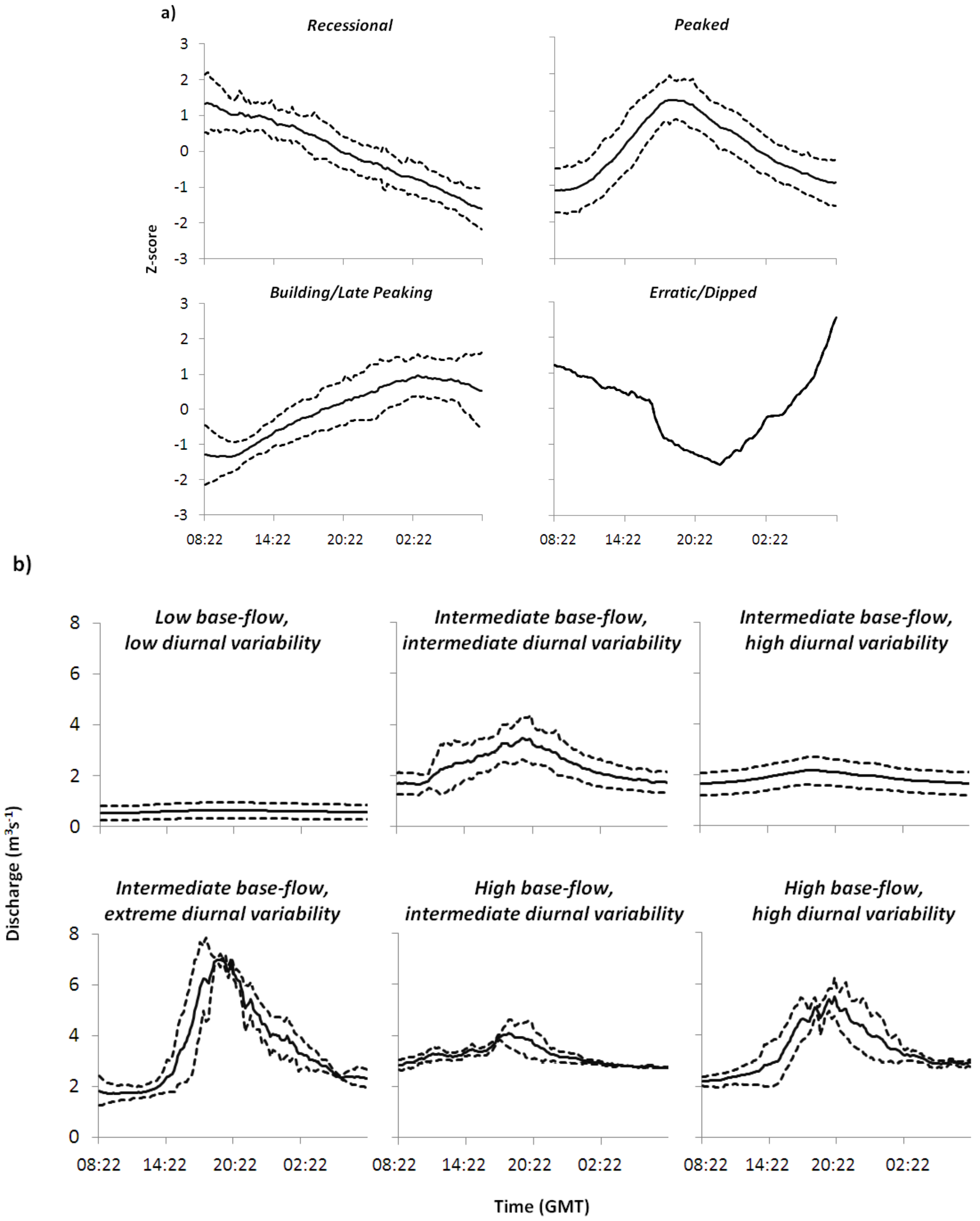

Figure 4.3 - *(a) Representative hydrograph shapes for Site B, and (b) representative magnitude classifications for peaked days at Site B. Z-scores and discharge are plotted for 7.5 min resolution data. Broken lines represent ±1 standard deviation about the mean.*

4.3.3 Magnitude Classification

Hydrographs were classified by magnitude based on a standard group of indices and using the same HCA technique as employed in the shape classifications (Hannah et al., 1999; Hannah et al., 2000; Swift et al., 2005). Only peaked hydrographs were considered for magnitude classification (Swift et al., 2005) as the lack of a clear diurnal signal in clusters 1, 3 and 4 made it difficult to interpret the physical significance of magnitude classifications based on indices defined by diurnal characteristics. Furthermore, in preliminary analyses the inclusion of non-peaked hydrographs in the magnitude HCA was found to significantly compromise the interpretability of clusters assigned to peaked hydrographs, because of the dominance of the extreme indices arising from hydrographs contained in non-peaking clusters. In contrast to the approach of Hannah et al. (1999; 2000), days that were affected by significant volumes of rainfall were not excluded from the analysis for three reasons; (i) Excluding data based on judgement compromises the objectivity of the analysis, (ii) There was no reliable precipitation data for the early melt season hydrographs making an accurate assessment of potentially affected flows difficult, and (iii) During the summer months, precipitation events were extremely frequent and storm events not clearly defined. Thus, it is difficult to make a clear distinction of which days to exclude. Six diurnal magnitude indices were calculated for each of the 102 peaked hydrographs that were selected to reflect, baseflow, bulkflow and diurnal components (Hannah et al., 1999; Swift et al., 2005) as follows;

(i) Mean daily discharge (Q_{mean}). To reflect aggregated snow, ice and groundwater flow outputs from the catchment.

(ii) Morning Baseflow (Q_b). Calculated as the flow minimum occurring prior to the flow maximum (cf. Hannah et al., 1999; Hannah et al., 2000; Orwin & Smart, 2004) to represent the magnitude of long residence-time flow components (i.e. groundwater).

(iii) Peakflow (Q_p). The peak runoff from all flow sources**.**

(iv) Flow Amplitude (Q_{amp}). The difference between Q_p and Q_b, representing the magnitude of the diurnal signal produced by medium/short residence time flow components (generated by melt/precipitation, respectively).

(v) Standardised Flow Amplitude (Q_{ampstd}). Q_{amp} expressed as a proportion of Q_b (Q_{amp}/Q_b). This provided an index that minimises the representation of underlying super-diel scale flow trends that Q_{amp} may be subject to.

(vi) Discharge Standard Deviation (Q_{std}). Indicative of the aggregate variation of flow about the mean rather than just the diurnal variation expressed by Q_p, Q_{amp} and Q_{ampstd}.

All indices were standardised using z-scores calculated for the aggregated 2008/2009 peaked flow data set prior to HCA. Six distinct clusters were evident from the dendrogram (Table 4.2) which can be interpreted as representing the following;

(i) *Low base-flow, low diurnal variability.* This cluster contained 31 days (13 from 2008, 18 from 2009) exhibiting relatively low flow days with low diurnal variability (contained the minimum mean for all indices)

(ii) Intermediate base-flow, intermediate diurnal variability. This cluster was the largest and grouped 51 days (27 from 2008, 24 from 2009).This cluster had the second lowest mean Q_{mean}, Q_p and Q_{range} although Q_b was slightly lower than that for magnitude cluster iii.

(iii) Intermediate base-flow, high diurnal variability. This cluster of 8 days was exclusively comprised of days from 2008. Members exhibited a clear diurnal signal but the mean Q_b of this cluster was the second lowest.

(iv) Intermediate base-flow, extreme diurnal variability. This cluster contained just two days from 2008, which exhibited extreme diurnal variability (highest Q_{mean} Q_p, Q_{amp} $Q_{ampstd,}Q_{std}$) from a intermediate Q_b.

(v) High base-flow, intermediate diurnal variability. This cluster contained just two days from 2008 and a single day in 2009 when Q_b was relatively high (highest mean) but the relative diurnal variability was low (Q_{ampstd} is second lowest).

(vi) High base-flow, high diurnal variability. This cluster contained four days (all from 2009) and contrasted with cluster iv in that it had slightly lower diurnal variability but from a higher Q_b, resulting in a slightly lower Q_{mean} (3.34 cf. 3.54 m^3s^{-1})

Table 4.2 - *Mean indices calculated for magnitude clusters (all in m^3s^{-1}) with one standard error in parenthesis.*

Cluster	Q_{mean}	Q_b	Q_p	Q_{amp}	Q_{ampstd}	Q_{std}	n
(i) Low base-flow, low diurnal variability.	0.59 (0.054)	0.53 (0.052)	0.64 (0.057)	0.11 (0.015)	0.27 (0.050)	0.03 (0.004)	31
(ii) Intermediate base-flow, Intermediate diurnal variability.	1.94 (0.065)	1.51 (0.058)	2.56 (0.083)	1.06 (0.053)	0.76 (0.037)	0.28 (0.014)	51
(iii) Intermediate base-flow, High diurnal variability.	2.38 (0.160)	1.37 (0.116)	4.14 (0.245)	2.78 (0.211)	2.14 (0.254)	0.72 (0.058)	8
(iv) Intermediate base-flow, extreme diurnal variability.	3.54 (0.267)	1.66 (0.345)	7.64 (0.569)	5.99 (0.224)	3.75 (0.647	1.73 (0.053)	2
(v) High base-flow, Intermediate diurnal variability.	3.20 (0.103)	2.69 (0.023)	4.38 (0.258)	1.70 (0.280)	0.63 (0.110)	0.42 (0.086)	3
(vi) High base-flow, High diurnal variability.	3.44 (0.105)	2.15 (0.120)	5.92 (0.203)	3.76 (0.188)	1.77 (0.150)	1.06 (0.140)	4

4.3.4 Temporal sequencing of hydrograph shape and magnitude classifications

Peaked hydrographs were the dominant shape class throughout the melt seasons of 2008 and 2009 (Figure 4.4). During 2008, *building/late peaked hydrographs* were more common early in the melt season and *recessional hydrographs* more common later in the season. During 2009, this pattern was not as clear although a phase where *building/late peaked hydrographs* were dominant (days 127 - 136) was evident early in the season but seven days later than the first building phase in 2008 (days 134 - 141). A clear temporal shift was evident in magnitude classifications from *low base-flow, low diurnal variability* early in the season to higher discharge magnitude classifications, most commonly I*ntermediate base-flow, intermediate diurnal variability* hydrographs later in the season (Figure 4.4). The final *low base-flow, low diurnal variability* day occurred 18 days earlier in 2008 (day 147) than 2009 (day 165). However, some *intermediate base-flow, intermediate diurnal variability* days occurred before day 166 in 2009 (days 142, 144, 145 and 157) in contrast to the final low base-flow day in 2008 which ended a period of exclusively low base flow-days. Following approximately day 166 in both seasons (2008/2009), the magnitude class *intermediate base-flow, intermediate diurnal variability* came to dominate (n=27; 2008 and, n=24; 2009) and in 2008 *intermediate base-flow, high diurnal variability* days were also fairly common (n=8) although none occurred in 2009. *Peaked* days, classified with high base-flow and either; intermediate or high diurnal variability, occurred fairly infrequently (1 in 2008 and 6 in 2009) and these were associated with large precipitation events when base-flow was already relatively high. *Intermediate base-flow, extreme diurnal variability* characterised two days in 2008 (194 and 202) when extreme afternoon storm events attenuated rising meltwater flows. There were two clear differences in the distribution of the magnitude classifications between 2008 and 2009 (Figure 4.4); (i) there were no *high base-flow, high diurnal variability* days in 2008; (ii) There were no days classified with only intermediate base flow but high to extreme diurnal variability in 2009.

4.4 SPATIAL HYDROGRAPH DYNAMICS

Hydrographs from all six main monitoring sites were analysed in order to; (i) characterise and compare the hydrological functioning of stream 'types' across the Eisboden braidplain over the 2008 and 2009 summer melt seasons, and (ii) assess the suitability of diurnal hydrograph classification techniques for analysing multiple monitoring sites subject to a wide range of flows from varying sources, some of which may not exhibit a strong diurnal pulse (i.e. groundwater; Ward et al., 1999a; Brown et al., 2003). The summer monitoring period was defined for all sites from day 183 - 247, 2008 and day 182 - 246, 2009 (NB. 2008 was a leap year) to allow the analysis of equivalent time periods in both years.

4.4.1 Spatial Hydrological Regimes

The hydrological regime of Site B, which was a product of all catchment scale hydrological processes, and the Eisboden's climatic dynamics have been described up to day 230, 2008 and day 218, 2009 whereafter Weiβsee overspills commenced (Section 4.3.1). The previous analysis provides a basis with which to contrast the flow regimes of the other sites.

4.4.1.1 Spatial Hydrological Regimes - Sites A and B

Site A, which was situated at the upstream main glacial channel inlet to the braidplain, exhibited broadly similar diurnal hydrograph form and magnitude trends to Site B during the unregulated periods though absolute discharge was consistently less (mean difference = 0.65 m^3s^{-1} in 2008 and 0.70 m^3s^{-1} in 2009; see Figure 4.5). During the latter part of the 2008 monitoring period when Site B was affected by flows from the Weiβsee, shortwave energy inputs into the catchment were relatively high and precipitation events infrequent (days 234, 237, 246, 247 are exceptions). During the same period Site A experienced relatively distinct diurnal variations in flow but a consistent base-flow; the mean monthly discharged dropped only slightly during August (1.26 vs. 1.30 m^3s^{-1} in July; Figure 4.2). Site B in contrast experienced an increase in mean monthly discharge (2.14 in August vs. 1.93 m^3s^{-1} in July; Figure 4.1). This resulted from overspill form the Weiβsee which was particularly prolific on days 230, 234, 239 and 244 (Figure 4.5). Overspill increased both the diurnal flow range at Site B relative to Site A (Figure 4.5), and also the base flow. On precipitation free days (e.g. 237-242, 2008) peak overspill flow discharged from the Weiβsee typically lagged peak meltwater flows at Site A, resulting in a secondary flow peak at Site B later in the evening (see Dickson et al., 2010).

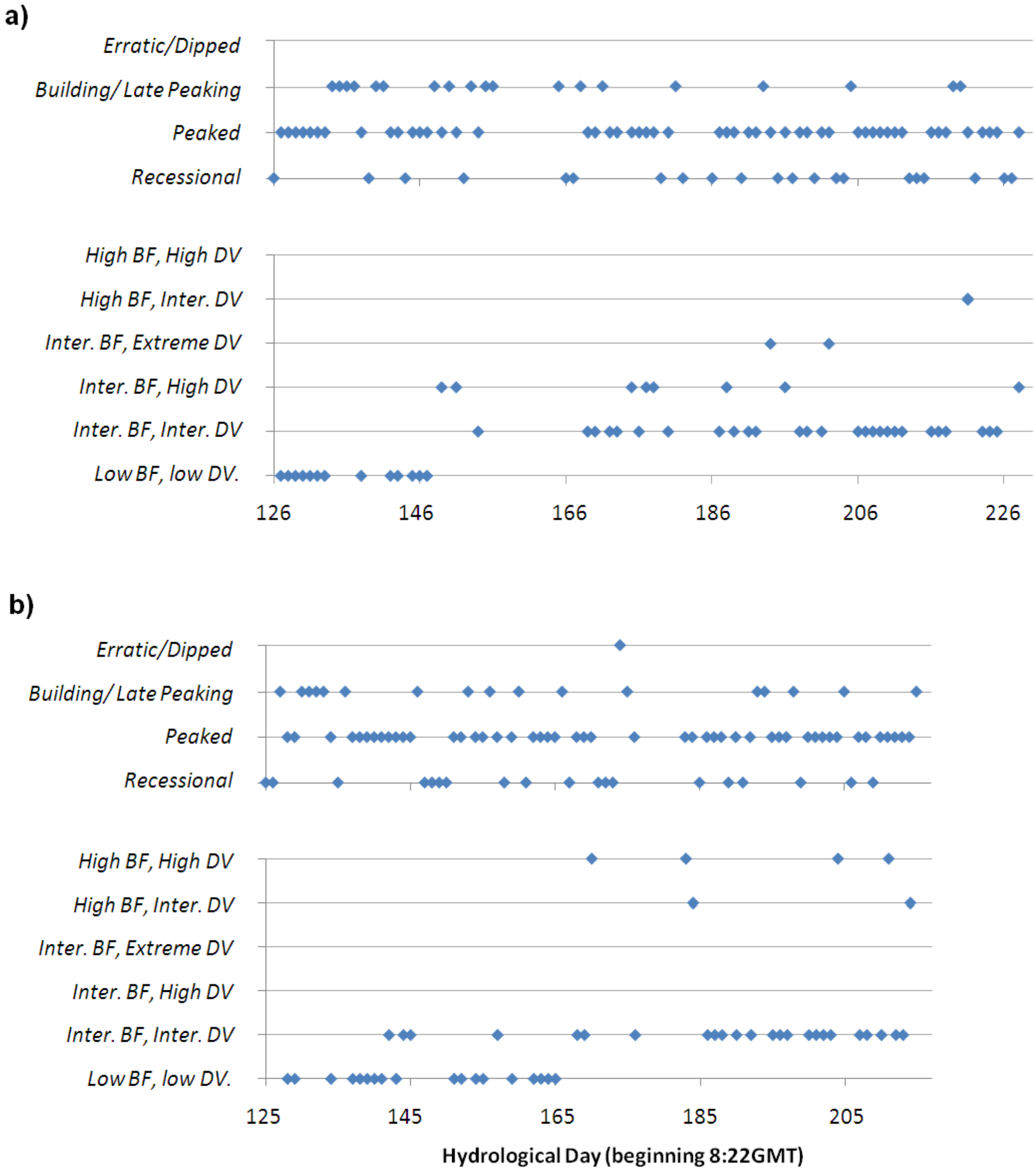

Figure 4.4 - *Temporal sequencing of shape and magnitude classifications (for 'peaked' hydrographs only) from the start of the melt-season up until the overspill of the Weiβsee during (a) 2008, and (b) 2009. [BF=base-flow, DV=diurnal variability].*

The climatic conditions of the catchment during the 2009 period of overspilling (days 218-247) were similar to the overspilling period in 2008 (Figure 4.1); precipitation events were relatively infrequent and atmospheric energy inputs into the catchment relatively high. Site A, characterised by only natural flows, had a strong diurnal melt signal and relatively stable base flow during this period (see Figure 4.5). On average, daily overspill in 2009 discharged more water into the Eisboden catchment than in 2008, and began 11 days earlier (day 218 in 2009 cf. day 230 in 2008). The overspills in 2009 resulted in a large increase in the mean monthly flow at Site B relative to both; the mean-monthly flow at Site A, in July (4.00 *vs.* 1.53 m^3s^{-1}) and the mean-monthly flow at Site B in August 2008 at (2.14 m^3s^{-1}; Figure 4.2).

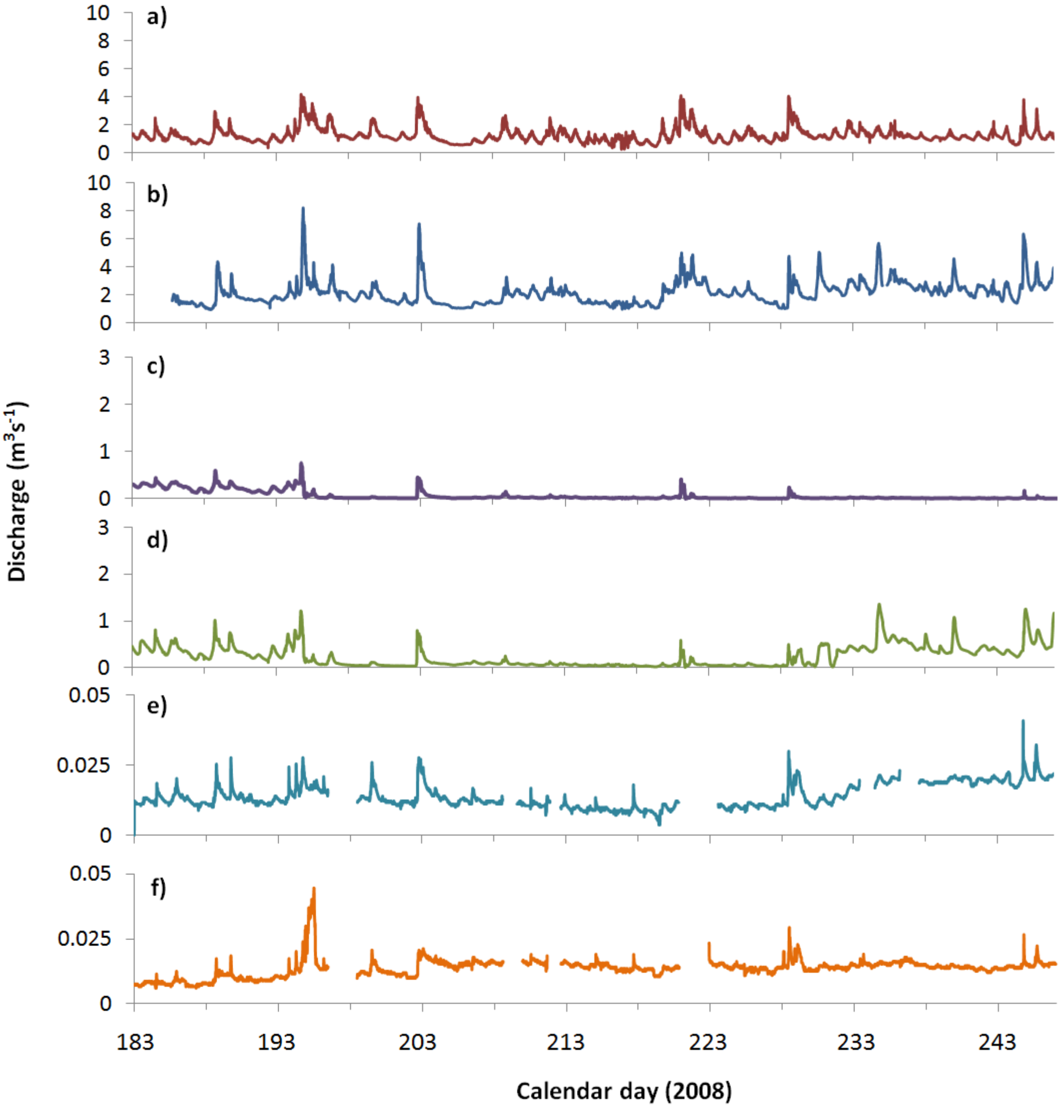

Figure 4.5 - *Discharge time series during July-August 2008. Figures (a)-(f) correspond to Sites A-F*.

4.4.1.2 Spatial Hydrological Regimes - Sites C and D

Discharge at Site C during both 2008 and 2009 melt seasons was heavily influenced by the routing of the main glacial channel and the extent to which braiding occurred. When connected to the main glacial stem diurnal variability and base flow of Sites C and D increased dramatically (e.g. days 183 - 195 in 2008; see Figure 4.5). In addition to connectivity Site D was also majorly affected by overspill from the Weiβsee. Early in the 2008 monitoring period (days 183 - 195), Site C and D received a significant proportion of glacial melt flows routed from the main channel and consequently diurnal hydrograph shapes at Sites C and D were broadly similar to Sites A and B. From day 195 in 2008 through to the end of the 2008 monitoring period, the base flow at Site C dropped dramatically when glacial flows were primarily routed down the east side of the Eisboden braidplain. Major periodic inundations occurred only on days 202, 222 and 228 in 2008 when flows at Site A were attenuated by rainfall. Site D followed a similar pattern as Site C until day 230 in 2008 when diurnal variability and base flow were increased by flows from the Weiβsee. Flow, on average, was greater at Sites C and D during 2009 than in 2008 (Site C: 0.25 *vs*. 0.068 m^3s^{-1}; Site D: 1.01 *vs.* 0.25 m^3s^{-1}). Early during the 2009 monitoring period, base flow and diurnal variability gradually undulated between relatively low and medium levels with the exception of day 197, 2009 at Site C and days 201, 202 and 203, 2009 at both Sites C and D when major inundations from the main glacial channel occurred. From day 215, 2009, base flow at both Sites C and D remained high for the remainder of the monitoring period due to a substantial re-routing of flows across the braidplain towards the West side. Discharge at Site D was further increased from day 218, 2009, by flows from the Wei*β*see.

4.4.1.3 Spatial Hydrological Regimes - Sites E and F

Throughout the 2008 monitoring period, Sites E and F were predominantly groundwater-fed and this produced a lack of diurnal flow pulses in the time-series (Figure 4.5). Distinct peaks in the times-series of both Sites E and F were observed during major precipitation events and at Site E on days 194 and 195, 2008 when the main glacial channel overflowed into the channel of Site E. From day 230, 2008, Site E experienced a gradual increase in flow and exhibited stronger diurnal variability as overspill from the Weiβsee recharged the groundwater system around the site. Site F exhibited similar behaviour throughout the summer monitoring period of 2009 (Figure 4.6) but there were no inundation events from the main channel and mean flow discharge decreased slightly compared with 2008 (0.13 vs. 0.14 m^3s^{-1}). In contrast, the character of Site E varied markedly over time in 2009, with an increase in hydrological connectivity to a mixed side channel downstream of Site C resulting in higher base flows and increased diurnal variability for much of the summer (Figure 4.6). Several often extended events, where the stream was connected to a larger side channel (days 184-185, 199-200, 206-213, 215-236, 241-243 and 247;, 2009), resulted in marked increases in discharge.

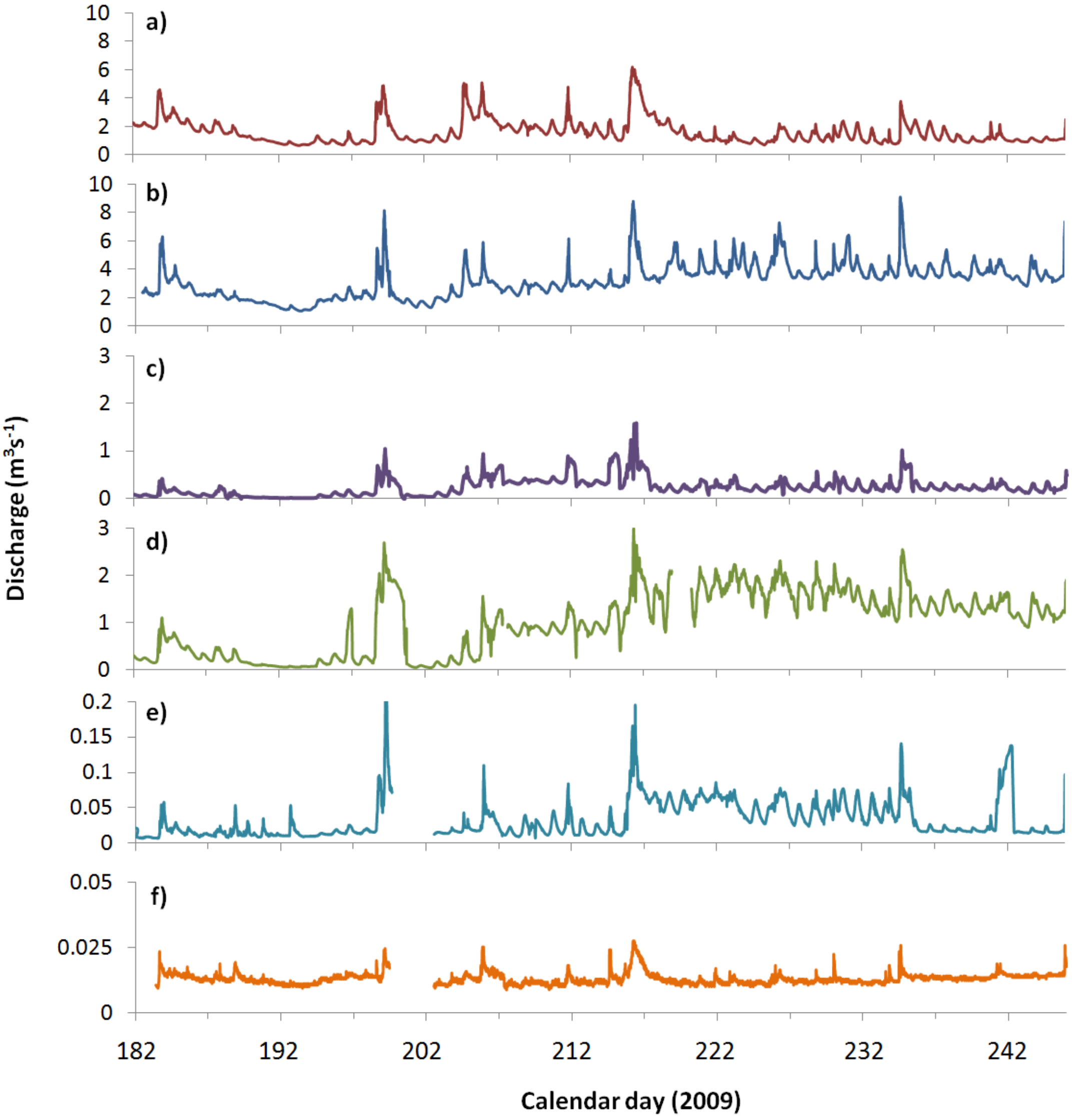

Figure 4.6 - *Discharge time series during July-August 2009. Figures (a)-(f) correspond to Sites A-F.*

4.4.2 Shape Classification

The two stage PCA and HCA classification procedure described in section 4.2.2 was used to derive shape classifications but the way in which the data was prepared was adapted (see Table 4.1) with the following three considerations. (1) Hydrological 'days' were defined from (7:04 GMT) for all sites and based on the results of a preliminary PCA analysis of Site A. As Site A was situated at the input to the braidplain, it was considered to contain the greatest melt-water component proportional to its discharge. Thus, it was judged to provide the most appropriate time datum linked to diurnal flow dynamics. (2) Prior to classification, the entire dataset was not aggregated to avoid the loss of site-specific patterns and nested hydrological complexity. Data from site pairs A and B (main melt-water channel), C and D (braided side channels), and E and F (groundwater tributaries) were however combined across the two years (except in the case of Site E, see below) to avoid generating an excessive number of different classifications. The flow sources and physical mechanisms controlling each of these pairs of sites were considered to be relatively similar and so any loss of interpretability of the results is minimised by these pairings (cf. Swift et al., 2005). The level of aggregation was based on preliminary analyses and judged to provide a balance between either excessively and inappropriately compressing the initial dataset leading to a loss of detail in the resultant classifications, or under-compressing the initial data set resulting in the derivation of an excessive number of classifications that do not optimally aid the interpretation of the results, particularly between sites. Data from 2009 recorded at Site E were omitted from the analysis due to the marked departure in hydrological functioning from Site F (2008/2009) and Site E (2008) (Figure 4.6) which resulted from a new connection with the main glacial channel. (3) The interpolation of five minute data steps was necessary to provide valid input matrices containing data sets from each site pair across the two seasons. Further details of each analysis are given in Table 4.1.

Three sets of shape classifications were interpreted from the Site A and B paired dataset (Figure 4.7a*);* ***(i) recessional hydrographs*** (n = 42); ***(ii) peaked hydrographs*** (n = 191); ***(iii) building/late peaking hydrographs*** (n = 16). These clusters had the same general characteristics to those described for Site B through the full spring/ summer melt season (section 4.3.2), although the shape of each classification differed slightly (Figures 4.3 vs. 4.7). Five shape clusters were identified for Sites C and D (Figure 4.7b): ***(i) recessional hydrographs*** (n = 35); ***(ii) peaked hydrographs*** (n = 145); ***(iii) building/late peaking hydrographs*** (n=41); (***iv) double peaked hydrographs*** (n = 5), containing clusters with two well defined peaks; ***(v) recessive/peaked hydrographs***, containing a single overall recessional day but with a well defined late peak (Site C; day 239, 2008). Sites E and F yielded three shape clusters: ***(i) recessional hydrographs*** (n = 39); ***(ii) peaked hydrographs*** (n = 12), and; ***(iii) late peaked hydrographs*** (n = 110). Variance explained by the three retained PC's for Sites E and F (67.4 %) was less than the three PC's retained from the PCA of Site B (Section 4.3.2: 87.4 %), Sites A and B (87.0 %), and Sites C and D (87.1 %). The mean standardised plots for shape clusters at Sites E and F (Figure 4.7) exhibited greater 'noise' than those for Sites A and B, and C and D.

4.4.3 Magnitude Classification

The magnitude classification procedure as described for Site B (Section 4.3.3) was applied to the peaked days from Sites A and B, and D and E, and to the peaked and late peaked days from Sites E (2008) and F (2008/2009). Indices were standardised using z-scores calculated for the aggregated 2008/2009 *peaked flow* days data set for each site pair (A+B, C+D, E+F) prior to HCA to emphasise variations in space. Five distinct clusters were evident from each of the three HCAs (Figure 4.8). The mean indices values, and a qualitative interpretation of each of these clusters, are given in Table 4.3.

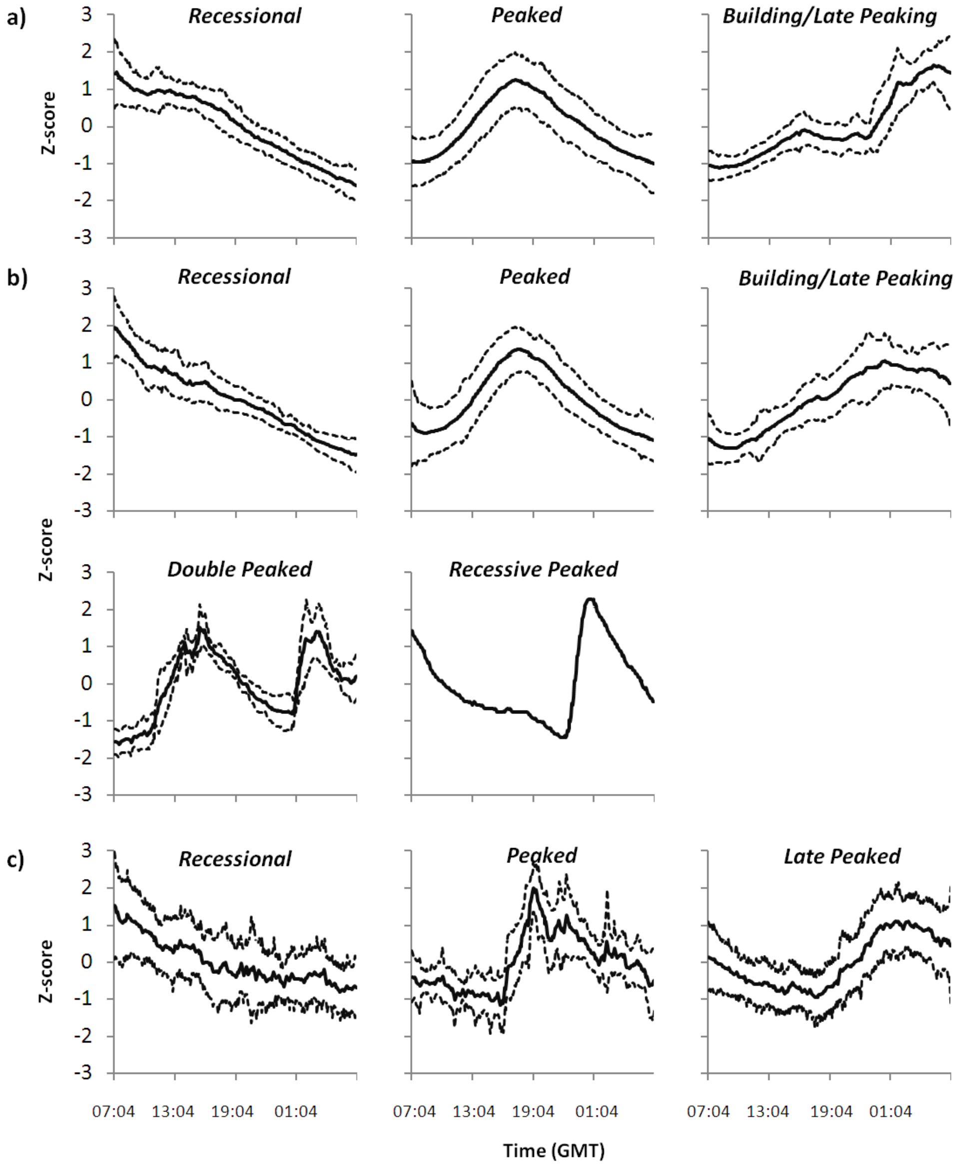

Figure 4.7 - *Representative hydrograph shapes for: (a) Site A & B, (b) Site C & D, (c) Site E (2008 only) & F. Mean Z-scores of classified hydrographs are plotted at 5 min intervals. Broken lines represent ±1 standard deviation about the mean.*

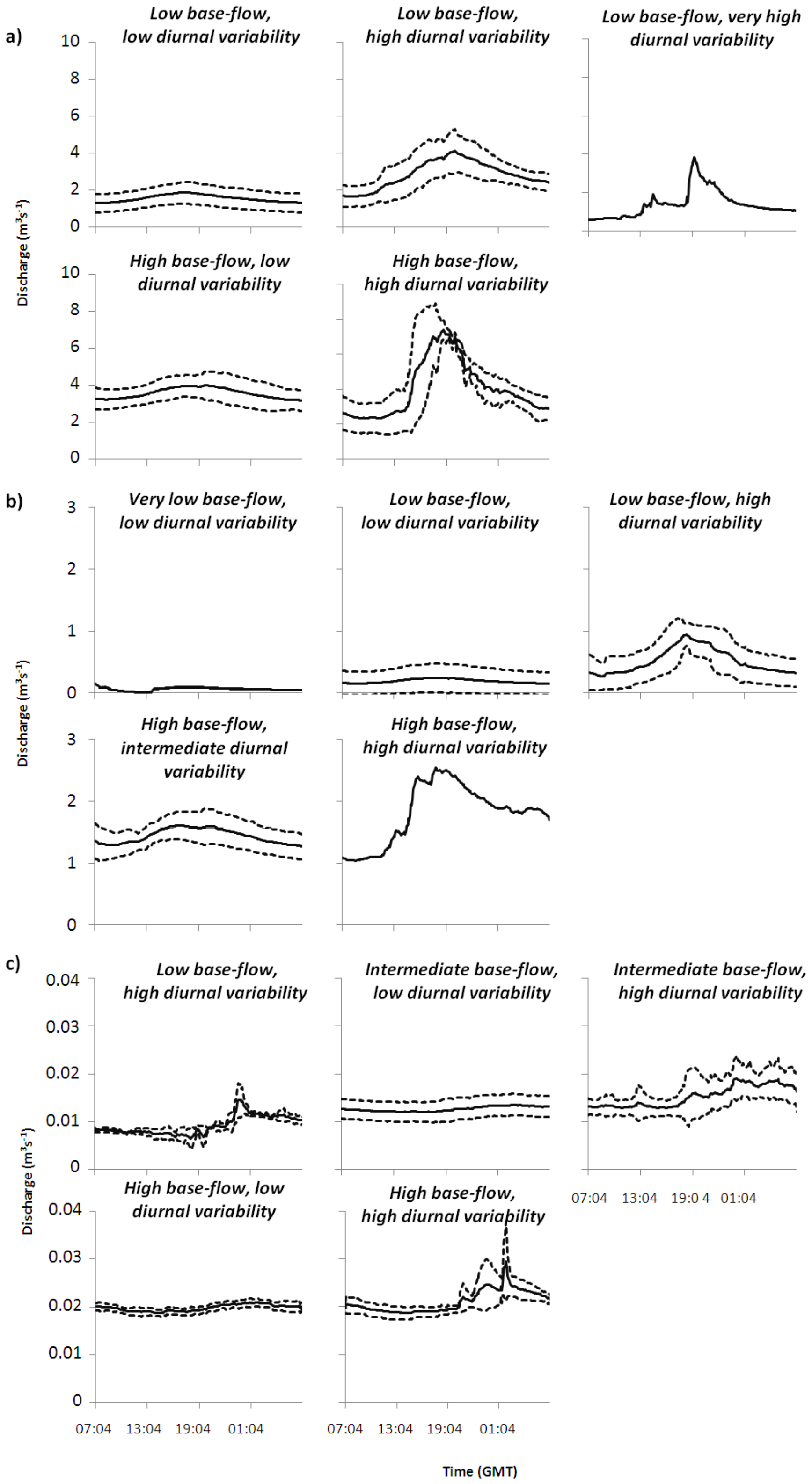

Figure 4.8 - *Representative magnitude classifications for (a) Site A & B, (b) Site C & D, and (c) Site E (2008 only) & F. Mean discharge of classified hydrographs are plotted at 5 min intervals; Dashed lines represent the standard deviation about the mean. Note that the cluster interpretation is only relative to each site pair, and there is a dramatic difference in the discharge magnitudes between each site pair.*

Table 4.3 - *Mean indices calculated for magnitude clusters (all in m^3s^{-1}) with 1 standard error in parenthesis.*

	Cluster Interpretation	Q_{mean}	Q_b	Q_p	Q_{amp}	Q_{ampstd}	Q_{std}	n
Sites A,B (2008,2009)	**Low base-flow, low diurnal variability.**	1.55 (0.04)	1.26 (0.04)	2.08 (0.05	0.82 (0.04)	0.79 (0.06)	0.24 (0.01)	141
	Low base-flow, high diurnal variability.	2.86 (0.13)	1.62 (0.15)	5.01 (0.21)	3.38 (0.15)	2.36 (0.23)	0.94 (0.06)	17
	Low base-flow, very high diurnal variability.	3.20 -	2.69 -	4.38 -	1.70 -	0.63 -	*0.42* -	1
	High base-flow, low diurnal variability.	3.59 (0.10)	3.18 (0.09)	4.58 (0.16)	1.40 (0.14)	0.45 (0.05)	0.41 (0.04)	29
	High base-flow, high diurnal variability.	4.04 (0.63)	2.22 (0.62)	8.12 (0.58)	5.90 (0.16)	3.09 (0.81)	1.75 (0.03)	3
Sites C,D (2008,2009)	**Very low base-flow, low diurnal variability.**	0.058 -	0.000 -	0.144 -	0.143 -	357.975 -	0.027 -	1
	Low base-flow, low diurnal variability.	0.192 (0.02)	0.145 (0.02)	0.270 (0.02)	0.126 (0.01)	2.685 (0.63)	0.038 (0.00)	136
	Low base-flow, high diurnal variability.	0.513 (0.07)	0.251 (0.07)	1.025 (0.07)	0.773 (0.06)	10.775 (5.70)	0.272 (0.03)	10
	High base-flow, intermed. diurnal variability.	1.436 (0.05)	1.221 (0.04)	1.710 (0.07)	0.489 (0.06)	0.411 (0.05)	0.153 (0.01)	17
	High base-flow, high diurnal variability.	1.809 -	1.028 -	2.549 -	1.521 -	1.480 -	0.477 -	1
Site E (2008), F (2008,2009)	**Low base-flow, High diurnal variability.**	0.009 (0.00)	0.006 (0.00)	0.016 (0.00)	0.010 (0.00)	1.667 (0.18)	0.002 (0.00)	93
	Intermediate base-flow, low diurnal variability.	0.013 (0.00)	0.012 (0.00)	0.015 (0.00)	0.004 (0.00)	0.359 (0.02)	0.001 (0.00)	16
	Intermediate base-flow, high diurnal variability.	0.015 (0.00)	0.012 (0.00)	0.026 (0.00)	0.014 (0.00)	1.227 (0.08)	0.003 (0.00)	3
	High base-flow, low diurnal variability.	0.020 (0.00)	0.019 (0.00)	0.021 (0.00)	0.003 (0.00)	0.137 (0.02)	0.001 (0.00)	8
	High base-flow, high diurnal variability.	0.021 (0.00)	0.018 (0.00)	0.037 (0.00)	0.018 (0.01)	1.034 (0.39)	0.004 (0.00)	2

4.4.4 Temporal sequencing of hydrograph shape and peaked hydrograph magnitude

Flow records from all sites indicated some spatial conformity to temporal trends in diurnal hydrograph shapes (Figure 4.10) but the degree to which this occurred varied through the summer seasons of 2008 and 2009.

4.4.3.1 Temporal sequencing of hydrograph shape and peaked hydrograph magnitude- Sites A and B

Aggregated catchment trends observed in the diurnal shape classifications of Site B (Figure 4.10) were very similar to those at Site A, particularly through the first half of the monitoring period in 2008 and most of 2009. The main difference that occurred between Sites A and B was that, occasionally, hydrographs at Site A were classified as peaked while hydrographs at Site B were classified as recessive. Closer examination of the discharge time series (Figure 4.5, 4.6) for these occurrences revealed that both sites exhibited an overall diurnal recession, but flows at Site A exhibited a more dominating diurnal peak.

During the unregulated periods of 2008 and 2009, peaked days were most commonly classified at both Sites A and B as *low base-flow, low diurnal-variability.* During these periods, most diurnal hydrographs allocated to a different magnitude classification from Sites A and B were associated with heavy precipitation events. The single exception was day 204, 2009; however, the rapidity and magnitude of the flow increases at Sites A–E suggests that there may either have been a heavy localised precipitation event not recorded by the rain gauge, or an outburst from the glacier. Where days at Site B were classified as *high base-flow*, or *high diurnal variability*, the extra volume of water entering the Eisboden between Sites A and B was reflected in the difference between the classifications of Site A and B (e.g. days 188, 194, 196, 202, 221, 2008 and 184-185, 2009). An exception to this occurred on day 205, 2009, when the diurnal hydrograph at Site A was classified as *high base-flow*, *low diurnal variability* whilst Site B was classified as *low-base-flow, high diurnal variability* which implies that the base-flow decreased downstream. However, an examination of the discharge time-series (Figure 4.6) revealed that the form of the diurnal hydrographs for day 205, 2009 at Sites A and B was similar but Site B had a higher base flow (2.87 *vs.* 2.50m^3s^{-1}). Higher Q_p, Q_{amp} and Q_{std} at Site B also led to a *high diurnal variability* classification. Once the Weiβsee began to overspill into the Eisboden in 2008, there was an increase in the number of peaked days classified with *High base-flow* (38.5 %), *High diurnal variability* (18.8 %) or both. This increase was more dramatic in 2009 (100 % vs. 38.5 %), and an increase in the base flow at Site B was particularly evident (Figure 4.11).

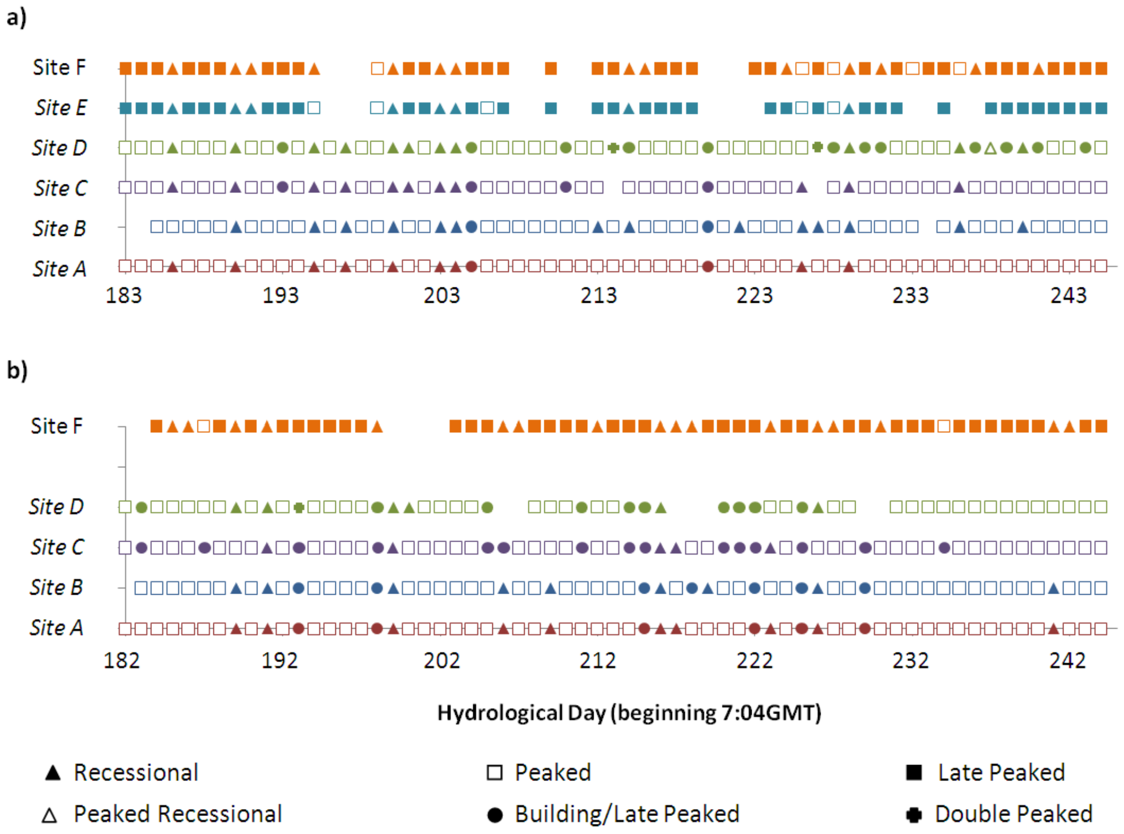

Figure 4.9 - *Temporal comparison of shape classifications for July-August; (a) 2008, (b) 2009. Note that the exact form of shape classifications differs between site pairs (A+B, C+D, and E+F) as site pairs where analysed separately.*

4.4.4.1 Temporal sequencing of hydrograph shape and peaked hydrograph magnitude - Sites C and D

Shape classifications at Sites C and D during 2008 were broadly similar to those at Sites A and B up until day 226. Where differences between shape classifications of Sites A and B, and C and D did occur, examination of the discharge time series revealed that they were predominantly associated with the difference between classification groups that arose from the PCA/HCA analysis conducted on the separate site pairs, rather than a marked difference in hydrological functioning. For example, the *peaked* group from the analysis of Sites A and B was more encompassing than the *peaked* group for Sites C and D and so occasionally (e.g. days 193, 211 and 214) diurnal hydrographs from Sites C and D were classified as *late peaking/building*, *double peaking* or *recessional* whilst the same day at Sites A and B was classified only as *peaked*.

A marked difference in classification occurred on day 215, 2008 (hydrographs at Sites A and C classified as *peaked*, Site B; *recessive* and Site D; *late peaking/building*), associated with a change in channel configuration which resulted in more flow through Site D than C. A systematic change in the classification of diurnal hydrographs at Site D compared to Site C was evident from day 226 in 2008 (Figures; 4.8, 4.9) which was associated with two factors, namely; (i) channel reconfiguration resulting in an increased amount of meltwater flow, and (ii) additional flows after day 230 in 2008 from the Weiβsee. Magnitude classifications of diurnal hydrographs at Sites C and D for 2008 suggested that there was little temporal variation in base-flow. Apart from three isolated days when large precipitation events caused high flow events at all sites, and a single day (234, 2008) at Site D during the Weiβsee overspill period, all days at Sites C and D were classified as *low base-flow, low diurnal variability*.

Figure 4.10 - *Temporal sequencing of magnitude classifications of peaked hydrographs for July-August 2008, (a)-(f); Site's A-F respectively. (BF=base-flow, DV=diurnal variability).*

Shape classifications at Sites C and D prior to overspill of the Weiβsee in 2009 were broadly similar to those at Sites A and B. Differences in hydrological function between Sites C and D, and A and B, caused by channel overspilling and restructuring (e.g. days 189, 206, 209, 211, 214 and 217 in 2009) and the influence of flow from the Weiβsee (e.g. days 223, 225 and 229, 234 in 2009) were evident in the shape classifications (Figures 4.8). Cross-examination of the discharge time series (Figure 4.5) confirmed that these differences in shape classifications reflected differences in hydrological functioning. Differences in hydrological functioning between Sites C and D due to flow routing were also evident in magnitude classifications. Site D exhibited several days classified as having higher diurnal variability than Site C prior to the overspill from the Weiβsee, and during the overspill period (from day 218 in 2009) all days were classified as having high-base flow (cf. no high base-flow days at Site D).

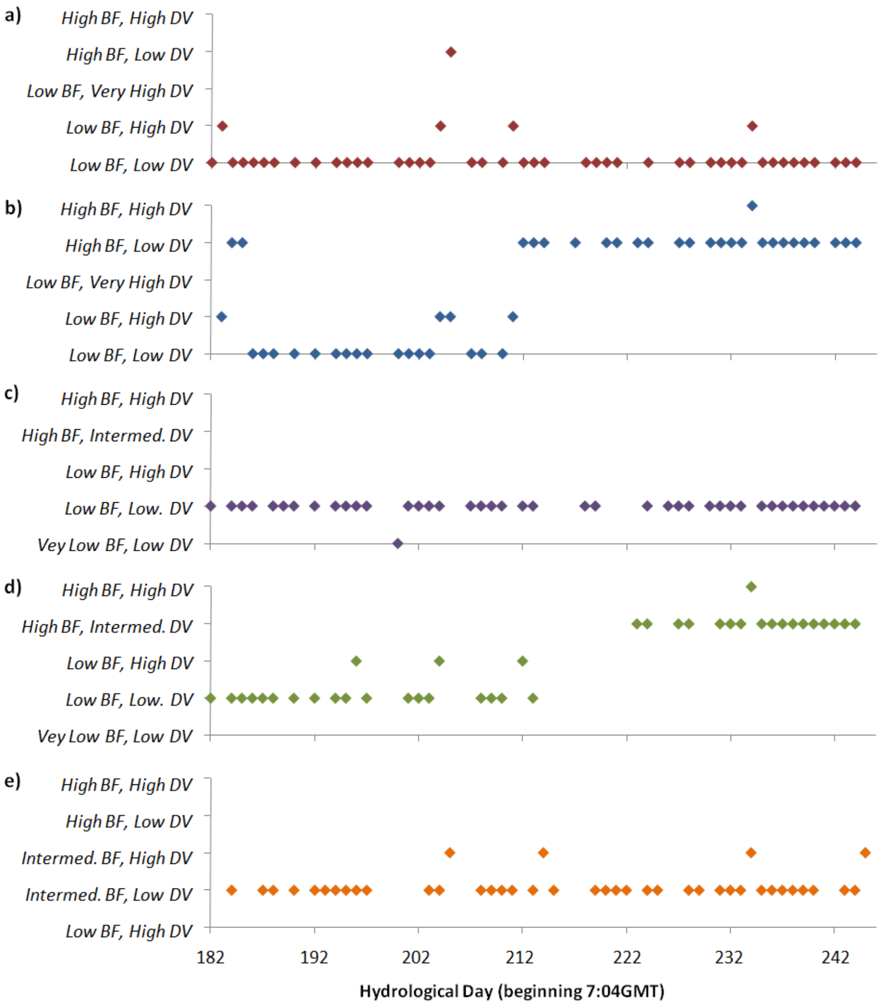

Figure 4.11 - *Temporal sequencing of magnitude classifications of peaked hydrographs for July-August 2009, (a)-(e); Site's A,B,C,D,F respectively. (BF=base-flow, DV=diurnal variability).*

4.4.4.1 Temporal sequencing of hydrograph shape and peaked hydrograph magnitude- Sites E and F

Shape classifications of predominately groundwater fed streams (Sites E and F) differed markedly from the other sites on most days of the monitoring period, with the majority of days classified as *late peaked days* (68.3 %, n = 161) with flow peaking on average at 03:09 GMT (Figure 4.9). This was in contrast to the other four sites where 70.6 % of the total days (n = 476) were classified as *peaked* with mean peaks at 17:19 GMT (Sites A and B) and 17:49 GMT (Sites C and D). Recessional classifications of Sites E and F commonly coincided with recessional days across Sites A-D (e.g. days 186, 190, 203, 204 and229, 2008, and 189, 191, 216 and 226, 2009. *Late peaked* and *peaked* days were typically associated with high diurnal variability at both sites during storm events (days 188, 194, 202, 228, 245 and 246 in 2008 and at Site F only on days 205, 214, 234 and 245 in 2009). During the overspill period in 2008 when there was no channel connectivity between Site E and the mixed side channels inundated by flow from the Weiβsee, recession flow characteristics were observed in the shape classifications of two days at Site E, and Sites D and B (days 236 and 240 in 2008; Figure 4.9). However, the recessional characterisation of Site E lagged Sites B and D by a day (e.g. on days 237 and 241, 2008). Classification of flow magnitude at Site E was more varied than at Site F through 2008 (Figure 4.10). An increase in base-flow at Site E was clear when the Weiβsee was overspilling (235-246; 2008) although intermediate base-flows on days 230 - 232 in 2008 suggested that there was a lag between the Weiβsee overspilling (day 230) and a significant increase in base-flow at Site E.

4.5 DISCUSSION

This study has extended previous applications of a statistical hydrograph classification at the diurnal scale to examine, (i) the temporal evolution of catchment runoff through two melt seasons (2008 - 2009) in a proglacial stream heavily influenced by rainfall events which confounded the rhythm of seasonal and diurnal ablation, and (ii) spatiotemporal patterns of hydrological functioning within a single catchment across six streams with various water source contributions (i.e. snow- and ice-melt, groundwater, reservoir overspill) subject to both regulated and unregulated flow conditions. The subsequent discussion considers the findings from each of these novel applications of statistical diurnal hydrograph classification in turn.

4.5.1 Temporal dynamics of runoff at the catchment outlet

The only previous studies that have used a statistical classification procedure to classify diurnal hydrographs have analysed data sets from the Taillon Glacier in the French Pyrénées (Hannah et al., 1999; Hannah et al., 2000) and Haut Glacier d'Arolla in Switzerland (Hannah et al., 2000; Swift et al., 2005). In contrast to these studies, the hydrological functioning of the Eisboden catchment during the melt seasons of 2008/2009 was found to be less well controlled by a glacial/snowpack melt signal and influenced rather more strongly by alluvial and hillslope groundwater, and periodically by the overspilling of the Weiβsee. This was evident in the relative weakness of the diurnal signal throughout the melt-season at Site B. Precipitation events were both heavier and more frequent relative to those observed during the aforementioned studies (Hannah et al., 1999; Hannah et al., 2000; Swift et al., 2005) and caused 'interference' in the diurnal meltwater runoff signal. The combined effect of a relatively weak diurnal melt signal and the interference from precipitation meant that patterns of diurnal hydrograph form and function were not readily distinguishable from the discharge record and the need for an objective approach to classify hydrograph forms was particularly pertinent. Although similar statistical classification procedures have been used with success in more temperate, non-glacierized catchments where precipitation is relatively frequent (e.g. Harris et al., 2000; Moon et al., 2004; Monk et al., 2007), these have been focussed at monthly-annual time scales and not classified diurnal hydrographs.

Three main categories of shape classification were identified from the melt-season analysis of Site A: (i) *recessional*, (ii) *peaked,* and (iii) *building/late peaking*. The quantitative details of derived classifications cannot be directly compared between previous studies that have used a statistical classification procedure because numerical procedures and both shape-based PCs and magnitude clusters have differed between studies. For example, differences occur in the way hydrological days are defined and data is standardised pre-PCA (cf. Hannah et al., 2000; Swift et al., 2005, this study). Additionally, there have been no standardisation between studies in the retention criteria for either PCs, or for clusters (cf. Hannah et al., 2000; Kansakar et al., 2002; Moon et al., 2004; Swift et al., 2005; Monk et al., 2006). However, the same three shape categories of diurnal hydrograph as identified herein have emerged from statistical classification of proglacial hydrographs by Hannah et al. (1999; 2000) and Swift et al. (2005), thereby indicating general similarities in diurnal hydrological functioning between the Odenwinkelkees, Haut Glacier d'Arolla and Taillon Glacier.

A short phase where *building / late peaking* was evident early in both melt seasons (days 134-141, 2008; 127-133, 2009) when melt increased in response to increased atmospheric energy inputs into the catchment, which resulted in increased base-flow and late diurnal peaking. The timing of the diurnal peaks during these periods can be inferred to indicate the presence of a relatively inefficient flow routing system due to meltwater flow through-snowpacks, and a relatively inefficient glacial drainage system during early summer (Röthlisberger & Lang, 1987; Paterson, 1994; Fountain & Walder, 1998; Fountain et al., 2005; Swift et al., 2005). This early melt-season hydrographical pattern has been observed in other proglacial streams (Paterson, 1994; but see Raymond et al., 1995) and was objectively identified in the Haut Glacier d'Arolla (Hannah et al., 2000; Swift et al., 2005). However, Raymond et al. (1995) observed no such progressive change in the timing of the diurnal discharge cycle for the Fels and Black Rapids catchments in Alaska but it was hypothesised that such a change may have concluded before the start of their monitoring periods (late May). Indeed in the Eisboden, the *building / late peaking* phases concluded around mid May in both years. Analysis of discharge trends at Haut Glacier d'Arolla, Switzerland in 1989 (Hannah et al., 2000) and 1998 - 1999 (Swift et al., 2005) indicated that a shift to *peaked* hydrographs forms occurred much later (day 165-185). This suggests a difference in the hydrological behaviour of the Eisboden and Arolla catchments perhaps because; (i) the Ödenwinkelkees snout (2194 m.a.s.l.) is approximately 400 m lower than the Glacier d'Arolla snout (2600 m.a.s.l) resulting in an earlier retreat of in-efficient snowpacks; (ii) the Eisboden was monitored ~1.5 km downstream of the snout resulting in a greater melt water supply from melting snowpacks which is not routed through a relatively in-efficient early season sub-glacial drainage system, and (iii) differences in local climate between catchments existed, for example the greater influence of rainfall events on hydrological characteristics in the Eisboden. However, because the statistical classification technique has not been standardised between studies, caution needs to be attached to drawing firm conclusions from the direct comparison of classifications.

In common with studies by Swift et al. (2005) and Hannah et al. (1999; 2000), *peaked* days were the most common classification across both years and were assumed to be characterised by two key flow components: (i) a base-flow component resulting from flow through relatively inefficient pathways including snowpacks (Colbeck, 1976), a hydraulically inefficient sub-glacial system (Röthlisberger & Lang, 1987; Paterson, 1994; Raymond et al., 1995) and an alluvial groundwater system (Morrice et al., 1997; Ward et al., 1999a), (ii) a dynamic meltwater component, resulting from rapidly-routed meltwater including supraglacial flow, flow through an efficient channelized sub-glacial drainage system (Röthlisberger & Lang, 1987; Paterson, 1994; Raymond et al., 1995) and rapid runoff from precipitation events over/through exposed bedrock, scree slopes and shallow soils (Orlandini et al., 1999; Brown & Hannah, 2007). The second of these two assumptions is in contrast to Swift et al. (2005), who assumed that peaked days were predominantly characterised by meltwater components, and that precipitation wasn't a major flow driver on peaked days.

Six classes of magnitude were identified from the classification procedure applied to the single floodplain outlet site analysis (Site B). The relatively large number of magnitude classes derived (cf. Hannah et al., 2000; Swift et al., 2005) was consistent with Hannah et al's (1999) analysis of the Taillon Glacier catchment (1995/1996) which also experienced fairly frequent precipitation events. Large flow events driven by precipitation tended to be more distinct relative to each other than melt-driven flow peaks, or indeed flow peaks driven by smaller precipitation events, and this was reflected in the number of relatively small clusters derived from the HCA.

The Eisboden catchment experienced a clear evolution in diurnal hydrograph magnitude characteristics during the spring. A seasonal transition from low flow in the winter to higher flows in the spring is a typical feature of alpine catchments. This seasonal transition is caused by a shift from freezing conditions in the winter through to snowmelt in the spring in response to increased atmospheric energy inputs, and then to predominant glacier-melt in summer as snow packs retreat and ice surfaces are exposed (Raymond et al., 1995; Malard et al., 1999; Hannah et al., 2000; Verbunt et al., 2003; Swift et al., 2005; Robinson & Matthaei, 2007). *Low base-flow, low diurnal variability* days were interpreted as representing days when inefficient melt-flow pathways (i.e. the presence of a thick snowpack and poorly developed sub-glacial channelization; Röthlisberger & Lang, 1987; Raymond et al., 1995; Nienow et al., 1998), resulted in a very a weak diurnal signal. *Low base-flow, low diurnal variability days* characterised the early melt-season up until day 165, 2009 when a shift to classifications characterised by higher base-flows and diurnal variability occurred. In 2008, the last *low base-flow, low diurnal variability* day occurred on day 147, 18 days earlier than 2009. However, this was not assumed to represent a marked difference in catchment functioning between years as 15 out of the 18 days between day 147 and 166; 2008 were not classified by magnitude; eight days contained missing data and so were excluded from the analysis altogether and 7 days were not classified as *peaked* and so were not included in the magnitude classification analysis.

Peaked days *classified as* either (1) *intermediate base-flow, intermediate diurnal variability* or; *(*2) *intermediate base-flow, high diurnal variability,* were not distinctly associated with either melt-driven or precipitation driven flow events. Therefore for a large number of days during the monitoring periods, predominate hydrological drivers could not be predicted with confidence from the classifications alone (cf. Swift et al., 2005). For example, an examination of the climatic data on the eight days classified with *intermediate base-flow, high-diurnal variability* that occurred occasionally in 2008 revealed that melt was the dominant hydrological driver on days 149, 175, 177 and day 178 whilst large precipitation events on days 151, 198 and 196 attenuated flow. Therefore the *intermediate base-flow, high-diurnal variability* classification was only found to delineate an empirical distinction in hydrograph magnitude between 2008 and 2009 but did not appear to characterise the functioning of any specific hydrological drivers.

The association of major flow events (*intermediate base-flow, extreme diurnal variability*; *high base-flow, intermediate diurnal variability*; or *high base-flow, high diurnal variability*) with major precipitation events indicates that precipitation is a key hydrological driver behind major flow events in the Eisboden, which is contrary to other studies that have found the most major flow events to be driven by melt, for example by Verbunt et al. (2003) in the Aletsch Basin, central Switzerland , Swift et al. (2005) in the Haut d'Arolla catchment, Switzerland. This may reflect the smaller glacierized area of the catchment (23 % vs. 69 % of the Aletsch Basin and 51 % in the Haut d'Arolla catchment), indeed the role of precipitation as driver in major flow events was evident in a study by Brown and Hannah (2007) in the Taillon–Gabiétous basin, French Pyrénées (5 % glacierized).

4.5.2 Spatiotemporal hydrological functioning of the Eisboden braid-plain and groundwater streams.

To my knowledge, this study is the first to statistically classify diurnal hydrographs of multiple stream types within a single catchment. The degree of complexity in raw hydrological data sets was particularly high due to the inclusion the of; (i) groundwater streams with a weak diurnal signal (Sites E and F), (ii) mixed channels (Sites C and D) with highly variable discharge regimes typically associated with braided systems (Mosley, 1983; Malard et al., 2006), and (iii) time periods in late summer when the flow regime of the catchment was altered by flow regulation from the Weiβsee. Classifications of hydrographs at Sites A and B similar during unregulated flow periods indicated similar diurnal hydrological patterns at the inlet and outlet of the central Eisboden braidplain. An disparity in magnitude classifications on day 205 in 2009, where the diurnal hydrograph at Site A was classified as *high base-flow, low diurnal variability* whilst Site B is classified as *low-base-flow, high diurnal variability,* was misleading in that it implied that base-flow decreased downstream. This disparity highlights the need for careful interpretation of magnitude clusters. Descriptive titles assigned to clusters offer a simplified interpretation of cluster characteristics, which broadly aids the interpretation of results (Hannah et al., 2000; Swift et al., 2005). It is acknowledged that qualitative cluster titles did not always accurately distinguish the classification of two diurnal hydrographs as simplistic titles may not summarise the relationships between all of the magnitude indices that define the cluster.

The effects of the Weiβsee on river discharge at Site B were more clearly visible from the systematic change in magnitude classifications in 2009 than in 2008, which can be attributed to mean daily flows being higher during the overspill period of 2009 than any other period. However, mean daily discharge increased more between unregulated and overspill periods in 2008 than 2009 (72 % increase vs. 63 %, respectively). A key strength of the statistical classification technique used is that it is objective (Hannah et al., 2000). However, it is important to consider that the procedure only identifies empirical distinctions between hydrographs and that differences in resultant classifications will not necessarily be tangible to any direct change in hydrological drivers. This consideration is especially salient where hydrological drivers are multiple and complex such as in the case of the Eisboden, particularly when subject to flows from the Weiβsee. Although a change in hydrological drives at Site B compared to Site A during overspill periods was evident from differences in the diurnal classifications between Sites A and B, a specific diurnal signature at Site B associated with overspills from the Weiβsee was not identified by the statistical classification procedure.

Comparing shape classifications of Sites A and B with Sites C and D during natural flow periods indicated (i) little spatial difference in hydrograph shapes between the Eisboden main stem and mixed braided sites, and ii) similar times of flow maxima in *peaked* hydrograph classifications (17:49 GMT at Sites A and B vs. 17:34 GMT at Sites C and D). These findings suggest that Sites C and D maintained some upstream connectivity with the main Eisboden stem throughout the unregulated monitoring periods, and that the glacial melt signal dominated the hydrograph shapes over contributions from alluvial up-welling and hill-slope aquifers. Upstream hydrological connectivity with melt sources is a key driver in riverscape habitat heterogeneity as melt-waters prevent the homogenisation effects of groundwater on, for example, turbidly and specific conductance (Ward et al., 1999a; Malard et al., 2000; Arscott et al., 2002; Ward et al., 2002). However, the proportions of flow contributions are also important to the physicochemical habitat characteristics of mixed streams (Malard et al., 1999, 2000; Arscott et al., 2002; Malard et al., 2006; Brown et al., 2007b; Milner et al., 2009). Comparing the discharge records of mixed sites (C and D) both with each other, and with the main glacial channel and groundwater sites, it was evident that the relative contributions of flow sources varied greatly both spatially and temporally throughout the summers. No studies have examined spatial discharge dynamics across a braidplain at the temporal resolution considered in this study, although Malard et al. (2006) examined the expansion/contraction cycles in the Val Roseg based on the presence/ absence of flow in channels and others have used a similar approach to examine sub-alpine floodplain dynamics (e.g. Kollmann et al., 1999; Tockner et al., 1999; Arscott et al., 2002; Karaus, 2004; Paillex et al., 2007). These sub-alpine studies have highlighted three key scales of flow routing dynamism: (i) erosive flooding at the annual to inter-annual scale can lead to geomorphic change and the restructuring of channel networks affecting floodplain landscapes (Kollmann et al., 1999; Tockner et al., 2000; Ward et al., 2002), (ii) the extent and pattern of flow routing at the seasonal scale is driven by snow and ice melt cycles; for example expansion in spring is driven by increased flow from snow/glacial melt (Malard et al., 1999; Arscott et al., 2002), and (iii) expansion at the event scale is driven by high discharges from peak diurnal melt or storm events (Tockner et al., 2000; Ward et al., 2002). Discharge records from the Eisboden braidplain indicated that between the seasonal and event scale, discharge in specific channels can vary greatly independently of catchment discharge, which implies that relatively stochastic geomorphic processes exert a dominant influence on flow routing at sub- seasonal scales (see Murray & Paola, 1994), which is consistent with some large sub-seasonal geomorphic changes observed in the field.

Statistical classification of diurnal hydrographs of Sites C and D was not sensitive to magnitude variations at the appropriate scale to identify much of the variation in discharge that took place at Sites C and D except during large episodic flood events. For example, in 2008 the dramatic reduction in diurnal hydrograph magnitudes after day 195 at Site C that was evident in the discharge records was not evident in the magnitude classification time series. This is a limitation of the objective statistical approach used where the sensitivity of the analysis occluded nested complexity that was of interest.

Hydrograph shape analysis revealed that there was only minimal data ‘structure’ in the time series from groundwater Sites E (2008 only) and F. A lower amount of variance was explained by fewer PCs and standardised plots were more erratic (Figure 4.7c cf. 4.7a,b). This was firstly a function of the weaker diurnal flow dynamics at Sites E (2008) and F (2008/20009) relative to the base flow due to the flow attenuation/damping imposed by the groundwater system. Secondly, precipitation events resulted in a generally more erratic discharge time-series compared to meltwater influenced streams (Röthlisberger & Lang, 1987; Hannah et al., 2000; Swift et al., 2005; Brown et al., 2006c; Robinson & Matthaei, 2007). Hydrograph shape analysis did however elucidate that Sites E and F exhibited diurnal fluctuations relative to the base flow, although these were of weaker amplitude than flows at Sites A, B, C and D, and with a later peak (~ 02:00 GMT vs. ~17:45 GMT, respectively). The later diurnal peaks may have arisen from a combination of two factors: (i) a lag between maximum alluvial down-welling when flow in the main glacial stem was at a maximum (~ 17:45 GMT) and alluvial upwelling at the stream source; (ii) a lag between maximum ablation of hillslope snowpacks and percolation of water through scree and soils into the stream. The location of Site E in the centre of the braidplain suggests that a time lag in alluvial down-welling and upwelling is likely the dominant cause here which was supported by analysis of stream thermal regimes (see Chapter 5). At Site F, the lack of any seasonal progression in hydrograph shape despite snowpack recession also implied that alluvial seepage from the main glacial channel into Site F must be an active process. Shallow hyporheic seepage was evident into a groundwater site running parallel with the main glacial channel from temperature analysis (see Chapter 5, S22), supporting this assertion.

4.5 CONCLUSIONS

Analysis of outflow hydrographs can yield a wealth of information about catchment inflow, storage and drainage processes (Hannah et al., 1999; Hannah et al., 2000). However, the more numerous and the more complex the drivers are for these processes, the more difficult their relative influence is to unpick from the outflow hydrograph. This study has demonstrated the utility of a statistical hydrograph classification approach for unpicking complex hydrological processes by investigating the hydrological functioning of a range of alpine floodplain streams in a catchment heavily influenced by precipitation and subject to reservoir over-spilling. Cross-examination of the form, magnitude and sequencing of hydrograph classifications with hydrological, geomorphological and meteorological field evidence yielded a wealth of information about the Eisboden catchment hydrological functioning; (i) the temporal dynamics of melt, and seasonal evolution of melt-water drainage pathways, (ii) the large impact of precipitation events on the timing and magnitude of catchment runoff, (iii) the role of geomorphologic process in controlling the hydrological dynamics of mixed floodplain streams, (iv) the temporal dynamics of groundwater yield, and (v) the impacts of overspill from the Weiβsee reservoir on the hydrological characteristics streams.

Understanding hydrological functioning of alpine catchments is of critical importance to managing the future water supply of surrounding regions (Barnett et al., 2005; Viviroli et al., 2007; Wehren et al., 2010b). It has been argued that projected increases in global temperature (IPCC, 2007) will significantly affect the timing and magnitude of runoff from snowmelt and glacier melt dominated catchments; at the inter-annual time scale it is expected that in alpine catchments experiencing glacial shrinkage (which is the vast majority), net runoff from ablation will initial increase in response to increased energy inputs and then in the longer term decrease in response to exhaustion of glacial water stores (Jansson et al., 2003; Barnett et al., 2005; Stahl et al., 2008; Milner et al., 2009). However, there is less certainty regarding the influence of climate change on precipitation in alpine catchments (Barnett et al., 2005). Indeed there is little agreement of the magnitude or even the direction of regional precipitation changes (Giorgi et al., 2001; Giorgi & Bi, 2005; Dai, 2006). Given the large impact of precipitation on the hydrological functioning at event to seasonal scales observed in for example; the Eisboden catchment (23 % glacierized), and the Taillon Glacier catchment (41% glaciated; Hannah et al., 2000), it seems that predicted changes in hydrological functioning in some alpine catchments may be heavily dependent on changes to rainfall as well as on glacial mass balance and snow pack dynamics. Without better regional precipitation models it is not possible to say how changes in rainfall may manifest and there is therefore considerable uncertainty regarding how the hydrological functioning of these catchments will respond to climate change (McGregor et al., 1995; Barnett et al., 2005).

CHAPTER 5: SPATIOTEMPORAL DYNAMICS OF WATER TEMPERATURE

5.1 INTRODUCTION

Water temperature is of critical importance to freshwater ecosystems because of its direct influence on metabolic rates, physiology and life-history traits of aquatic organisms, and indirect effects on other water quality determinants such as dissolved oxygen and nutrient recycling (Woodward et al., 2010). Additionally, water temperature has an economic significance due to the water quality requirements of agriculture, industry and recreation. Understanding the thermal characteristics and processes of stream systems is therefore a common concern for freshwater resource managers (Poole & Berman, 2001; Webb et al., 2008). Temporal fluctuations in water temperature stimulate distributional and behavioural responses in many benthic macroinvertebrates including life cycle duration (Céréghino et al., 1997; Füreder, 1999), insect emergence (Hogg & Williams, 1996), drift (Brittain & Eikeland, 1988) and mortality (Cox & Rutherford, 2000).

In alpine streams, water temperature is one of the key physicochemical properties that influences the spatial distribution and diversity of benthic macroinvertebrate (Milner & Petts, 1994; Füreder et al., 2002; Brown et al., 2007a; Milner et al., 2009), whole stream metabolism (Acuña et al., 2008; Robinson et al., 2008) and biogeochemical cycles (Tockner et al., 2002). An understanding and quantification of the processes driving water temperature fluctuations is therefore fundamental for the assessment and prediction of ecological patterns and processes in alpine environments.

Alpine water temperature research has to date largely focused on characterising the thermal regimes of streams that have been subject to minimal or no anthropogenic impact. Key natural drivers of water temperature are considered to be climatological conditions, water source (meltwater, groundwater, precipitation) and basin characteristics such as aspect and altitude (Arscott et al., 2001; Uehlinger et al., 2003b; Brown et al., 2006b; Brown & Hannah, 2007; Brown & Hannah, 2008). However natural fluctuations in water temperature can be confounded by anthropogenic influences (e.g. flow regulation, deforestation, and land use modifications; see Malcolm et al., 2004; Carolli et al., 2008; Webb et al., 2008; Zolezzi et al., 2010). In particular, many alpine river systems are impacted by anthropogenic modification due to widespread flow regulation for hydropower, water supply and irrigation (Füreder et al., 2002; Wehren et al., 2010b). Clearly, effective conservation and management of alpine stream ecosystems requires the effects of anthropogenic activities, such as flow regulation, on thermal regimes to be adequately quantified.

The heterogeneous effects of flow-regulation on sub-alpine river temperature regimes are well understood. Thermopeaking occurs daily in many sub-alpine rivers as hypolimnetic reservoir waters are periodically discharged when hydropower stations are activated to meet daily surges in electricity demand (Webb & Nobilis, 1995; Céréghino et al., 2002; Maiolini et al., 2003; Carolli et al., 2008; Toffolon et al., 2010; Zolezzi et al., 2010). Hypolimnetic water pulses that are typically ~4 °C year-round can thermally contrast greatly with background stream temperatures, thereby leading to ’summer cool’ and ‘winter warm’ thermopeaking. For example, Lagarrigue et al. (2002) recorded on average 6 °C water temperature decreases and 2 °C increases during respective summer and winter thermopeaking events in the River Oriège, Pyrénées at 912 m.a.s.l.. The net effect of daily thermopeaking events is that mean water temperature is reduced during summer and elevated during winter. For example, Zolezzi et al., (2010) noted that in a sub-alpine reach (217m.a.s.l) of the Noce River, Italy mean monthly water temperature was increased by 1.2 °C during November and decreased by 1.9 °C in May due to thermopeaking. A number of studies have focused on peaking and abstraction from controlled, predictable turbine runs in sub-alpine river reaches (see Céréghino et al., 2002; Carolli et al., 2008; Zolezzi et al., 2010). However, there remains a lack of understanding of how flow peaks generated by overspill, and of how controlled water movement through streams down from high altitude storage reservoirs (see Anselmetti et al., 2007; Dickson et al., 2010) alters river thermal dynamics in alpine basins.

Research into anthropogenic thermal modification has largely been constrained to the longitudinal (upstream-downstream) dimension of rivers and is typically restricted to large spatial scales at low spatial and temporal resolution. However, the large spatial complexity of water temperature at sub-basin scales in unmodified catchments has been evidenced by several studies (Arscott et al., 2001; Uehlinger et al., 2003b; Brown & Hannah, 2008) and this is considered to be an important feature for supporting biodiversity (Malard et al., 2006). At the basin scale, alpine stream mean daily temperature ranges up to 14.2 °C have been reported between sites influenced by different water sources and landscape factors (Brown & Hannah, 2008). In the face of high thermal complexity at the basin scale, more research is necessary to assess the spatial impacts of flow regulation in high alpine systems. To be effective this research must consider year-round dynamics because anthropogenic regulation occurs year round (Wehren et al., 2010b). However, due to difficulties of access and conducting field work in high alpine catchments during the winter, a focus has been placed to date on analysing stream temperature dynamics during summer (Brown & Hannah, 2007; Brown & Hannah, 2008). While some studies have inferred winter flow permanency based on alpine stream temperature records (Uehlinger et al., 2003b; Brown et al., 2006b; Robinson & Matthaei, 2007), these findings have not been validated by field observations. Clearly, ascertaining flow permanency is a pre-requisite to meaningful analysis of stream temperature records during winter.

This chapter reports on a detailed study of water temperature across 23 sites in the Eisboden basin, central Austrian Alps, which is subject to flow regulation from the Weiβsee Reservoir. The aims of this study were to (i) characterise thermal and flow permanency dynamics at nested spatial (reach - basin) and temporal scales (event - inter-annual) with respect to hydroclimatological conditions, (ii) determine the magnitude and spatial extent of thermal modification resulting from flow-regulation from the Weiβsee reservoir, and (iii) explore the utility of water temperature records as indicators of flow permanency during winter.

5.2 FIELD METHODS

Water temperature was monitored at 23 sites located within the Eisboden catchment between the Ödenwinklkees snout at 2197 m.a.s.l. and the outlet of the lower braidplain, 1.8km downstream at 2099 m.a.s.l. (Figure 5.1; Table 5.1). Sites were chosen to examine a range of stream types; six were located in predominantly melt-water (snow and ice melt) streams, six were in streams fed by hillslope groundwater springs, three in streams fed predominantly by an alluvial groundwater system and eight in mixed braided channels. Dataloggers at S1, S3, S20 and S23 (Figure 5.1) were installed at locations where the relative stability of channel sections allowed the fixing of dataloggers to examine longitudinal thermal trends along a ~2 km length of the Eisboden river. Unfortunately, the stream banks at S1 suffered recurrent major erosion during the monitoring period and after the loss of three temperature dataloggers all attempts to maintain a monitoring site close to the Ödenwinklkees snout were abandoned. However, spot stream water temperature readings were taken occasionally at S1 using a Hach HQ40d meter and these were considered representative of most time periods as there were only minimal stream temperature fluctuations due to the close proximity of this site to the glacier. S2 was located on a major tributary to the Eisboden fed by the Rifflkees glacier. The majority of sites were concentrated on and around the Central Eisboden Braidplain (Figure 5.1) to analyse thermal heterogeneity across a small braidplain (~ 0.16 km^2) at high resolution. Sites S5 - S10 were positioned to form a lateral transect across the upper half the braidplain and across to a groundwater tributary (S10). Sites S15 - S18 were situated to form a secondary lateral transect across the lower half. Sites S3, S12, S14, S16, S19 and S20 were located at physicochemical habitat monitoring and benthic sampling Sites A, C, F, D, E and B respectively (see Chapters 3, 4, 6 and 7).

Temporal changes in channel structure, flow connectivity and discharge levels meant that some of the sites featured intermittent flow; in particular active braidplain Sites S5-10, S15, S18 and S23. A Eulerian (spatially-fixed) monitoring approach was maintained; dataloggers were not moved to another location when a site was observed without flow for three reasons; (i) moving dataloggers to a new location would compromise the integrity of the data sets for temporal analysis as spatial variations in water temperature can be large even over small distances (Brown et al., 2005; Caissie, 2006), (ii) checking each datalogger on a daily basis throughout the monitoring period (particularly outside of the summer season) would have been impractical, and (iii) there were often no alternative stable channel sections where dataloggers could be moved to. For example, an anchoring point where the datalogger at S23 could be fixed was provided by bedrock on the east channel side. When flow diverted away from the east side of the channel (days 203 - 221 and 289 - 319 in 2008, and days 183 - 201 in 2009) there was no other suitable location to move the datalogger to as the centre and west channel side were extremely unstable. Periods where dataloggers were left exposed to air are detailed in Table 5.1. In addition data were not recorded at S3 (day 155 - 181 in 2009) as the datalogger cable running to the logger was severed by a marmot, and at S20 (179 - 183 in 2009) where power was lost to the datalogger.

Water temperature was monitored continuously (1 min. sensor and 15 min. logged resolution) using a combination of Gemini Tinytag data loggers, Trafag DL/N 70 integrated pressure transducer/temperature probes and a Campbell Scientific CS547A conductivity/temperature sensor linked to a CR1000 datalogger. All temperature sensors were mounted in open-ended white radiation shields which were fixed to the stream bed as close to the stream thalweg as practically possible. At the majority of sites, dataloggers were installed on or prior to day 182 in 2008 and removed on day 247 in 2009. Dataloggers at S21 and S11 were installed on day 182 in 2009. Prior to installation in the field, datalogger timestamps were synchronised and sensors were cross-calibrated to ensure comparable datasets (Brown et al., 2006a). Manufacturer's reported error ranges for all water temperature sensors were ± 0.2°C. Air temperature, incoming shortwave radiation and precipitation were monitored at the nearby AWS (see Section 3.5 and Figure 5.1). Altitude, position and distance from source of site were recorded using a dual phase Leica GPS500 differential Global Positioning System (dGPS) (± 5 cm horizontal, ± 10 cm vertical accuracy).

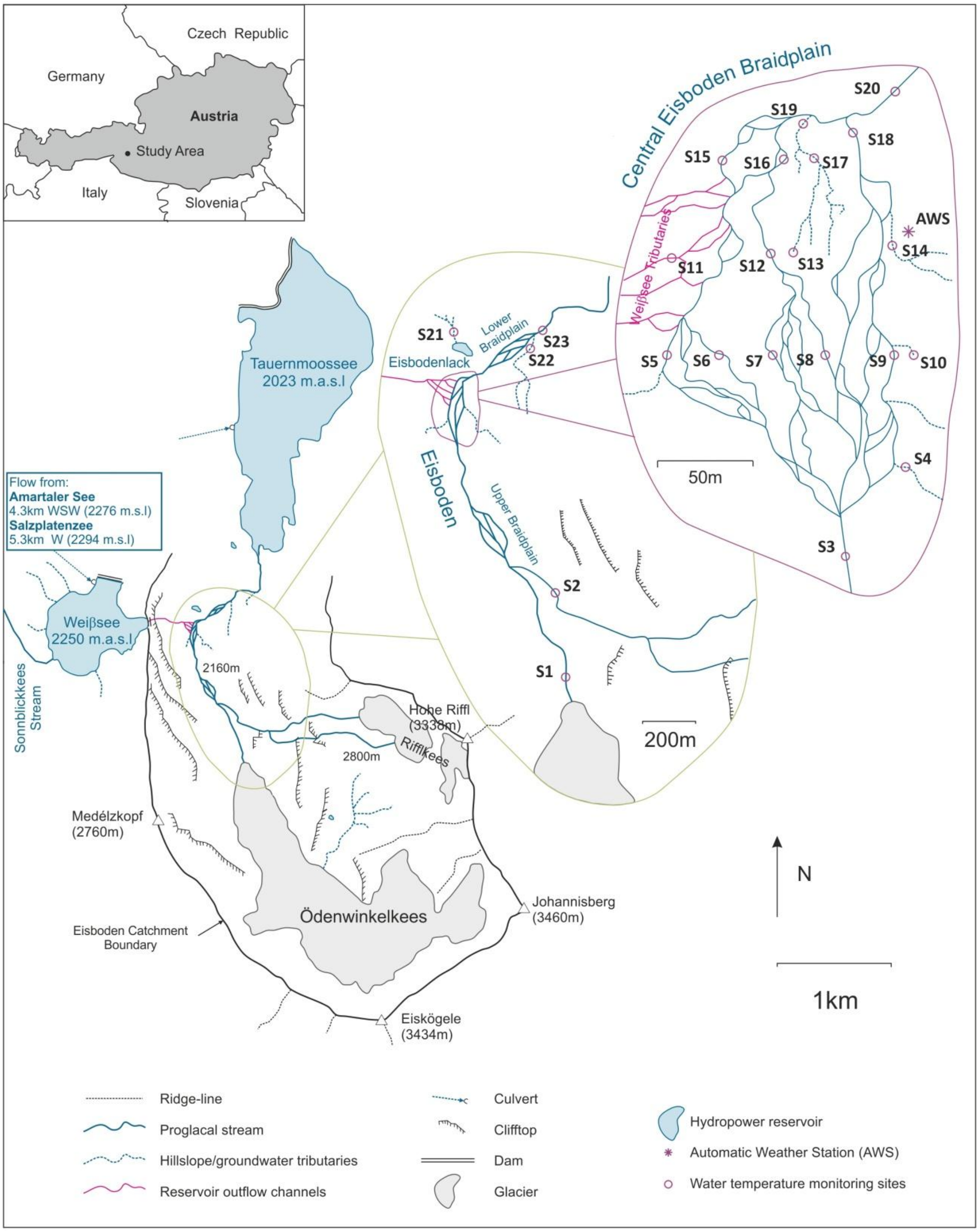

Figure 5.1 - *Stream water column temperature monitoring site locations*

During mid-winter site visits on days 344 in 2008 and day 65 in 2009, Sites S3, S12, S14, S16, S19 and S20 were located using the dGPS stake-out facility. A cross-section of the channel at these sites was excavated several meters downstream of the logger location (to minimise disturbance to logged water temperature records) to measure snow depth, water discharge and stream water temperature. Flow velocities were measured using a SENSA RC2 electromagnetic velocity probe and water temperature was measured using a Hach HQ 40d meter (0.1^{o}C resolution). The streambed was also checked for evidence of hyporheic flow near to the streambed surface by digging down ~20cm.

5.3 DATA ANALYSIS

Water temperature records were firstly scrutinised for evidence of dewatering (no stream flow around the logger sensor; Constantz et al., 2001). Where there was no snow cover at sites it was clear from the temperature time-series that probes were no longer submersed as temperature records became very closely associated with air temperature (cf. Brown et al., 2006b). Where this occurred for part or all of a day, data for that day were removed from further analysis. Sites were grouped according to primary water sourcing prior to thermal heterogeneity analysis (Brown & Hannah, 2008). Siz site groupings were defined: (i) all sites with dataloggers installed from day 182, 2008 to day 247, 2009 (i.e. excluding S1, S11 and S21), (ii) hillslope groundwater tributaries (S4, S10, S14 and S22) with dataloggers installed from day 182 in 2008 up to day 247 in 2009, (iii) alluvial groundwater stream sites (S13, S17 and S19), (iv) main-stem sites along the Eisboden (S3, S20, S23), (v) sites located on the Central Braidplain (S3, S5-9, S12, S13, S15-20), and (vi) invertebrate sampling sites (S3, S12, S14, S16, S19, S20). Thermal heterogeneity (ΔT) was calculated by:

$$\Delta\mathrm{T} = max\,\bar{T}_x - \,min\,\bar{T}_x$$

Were $\bar{T}_x$ is the mean daily water temperature at an individual site, and x refers to site groupings of data (Brown & Hannah, 2008).

Pearson's product moment correlation coefficients (r) were calculated using 15 min. resolution datasets to assess associations between; (i) air and water temperature, (ii) incoming solar radiation and water temperature, (iii) incoming solar radiation and the difference in water temperature between S3 and S20, and (iv) air temperature and the difference in water temperature between S3 and S20. To compare the strength of correlations (i) and (ii), a Wilcoxon Signed-Rank test was conducted based on r values. Cross-Correlation Functions (CCF) were evaluated to assess lags and leads (-lag) in the peak correlations ($\mathrm{CCF}_{\mathrm{max}}$) of (i) and (ii).

Table 5.1 - *Monitoring site characteristics and missing data.*

	Name	Predominant Source	Distance from source (m)	Altitude (m.a.s.l.)	Missing data	Cause
S1	Ödenwinklkees Snout	Melt	5	2194	All	Loss of loggers- not re-installed
S2	Rifflkees Stream	Melt	1280[b] (100[a])	2184		
S3	Eisboden (Site A)	Melt	1030	2135	155-181, 2009	Marmot chewed through logger cable
S4	Hillslope 1	Groundwater	80[b]	2127	242, 2008 -183, 2009	Flow below logger level/ no flow
S5	Eisboden	Mixed	1090	2124		
S6	Eisboden	Mixed	1080	2125	198-220, 2008; 218-246, 2009	No flow in channel (change to flow routing)
S7	Eisboden	Mixed	1080	2125		
S8	Eisboden	Mixed	1080	2125	206-246, 2008	Logger out of stream/ change to flow routing
S9	Eisboden	Mixed	1080	2125	183-185, 214-239, 2008; 184-212, 2009	No flow in channel (change to flow routing)
S10	Hillslope 2	Groundwater	0	2125	242-319, 2008	Flow below logger level; extremely low/ no flow
S11	Weiβsee Tributary	Groundwater / Weiβsee	20[b]/400	2136	183, 2008-181, 2009	Not yet installed
S12	Site C	Mixed	1340	2120		
S13	Braidplain Spring	Alluvial Groundwater / Mixed	0/1330	2119		
S14	Site F	Groundwater	70	2120		
S15	Eisboden	Mixed	1450	2118	199-209, 2009	Logger out of stream/ change to flow routing
S16	Site D	Mixed	1440	2117		
S17	Braidplain Stream	Alluvial Groundwater / Mixed	50 [b] /1380	2117		
S18	Eisboden	Melt	1400	2117	263-354, 2008; 80-82, 136-141, 219-246, 2009	Logger out of stream/ change to flow routing
S19	Braidplain Stream (Site E)	Alluvial Groundwater / Mixed	110 [b] /1430	2116		
S20	Eisboden (Site B)	Melt	1500	2110	179-182, 2008	Loss of power
S21	EisbodenlacK Inflow	Groundwater	30 [b]	2124	183, 2008-181, 2009	Not yet installed
S22	Hillslope 3	Groundwater	90	2100		
S23	Eisboden	Melt	1820	2099	203-221, 289-319, 2008; 183-201, 2009	Logger out of stream/ change to flow routing

[a] *Denotes distance from nearest upwelling where main source stream had a subterranean section.*

[b] *Denotes approximate mean as streams were sourced from multiple springs. Where the flow source intermittently switched, distances to both sources are given.*

The thermal implications of late-summer overspill from the Weiβsee on the main Eisboden channel have been the subject of a previous investigation (Dickson et al., 2010). The present study expands this work by considering the nature of thermal effects induced by the Weiβsee overspill for a range of stream types. To allow the analysis of equivalent calendar periods in 2008 and 2009, the first and final 64 days of the total 429 day observation period were defined as 'summer' seasons. Therefore, summer seasons discussed herein refer to day's 183 - 247 in 2008 and days 182 - 246 in 2009 (NB. 2008 was a leap year). To assess the significance of late-summer reservoir overflows on the thermal regime of sites across the braidplain, the summer season for each year was split into two periods: (i) an unregulated period when the Weiβsee overspill channel was inactive, and (ii) an overspill period during which the Eisboden experienced flow from the Weiβsee reservoir (Figure 5.2). Thermal regimes of sites were compared for the defined summer seasons between unregulated and overspill periods. Due to the non-parametric nature of the daily mean data sets (water temperature, incoming radiation, air temperature and precipitation), Mann-Whitney U tests were used to test for significance differences between unregulated and overspill periods. Results were considered significant for $p < 0.05$.

To examine high resolution diurnal synchronicities of flow permanency and water temperature dynamics across the 23 sites, water temperatures were examined in detail for five contrasting extreme hydrometeorological events. The selection criteria and event days were as follows; (Event 1) a late autumn Weiβsee drawdown release where flows from the Weiβsee inundated the west-side of the Central Eisboden Braidplain and maximum mean daily flow was recorded at S20 (day 346, 2008), (Event 2) a summer cooling event during the unregulated flow period, 2009, where the largest drop in air temperature during a 24hr period occurred (10:00 GMT day 198 to 10:00 GMT day 199 in 2009), (Event 3) a clear-sky hot summer day (day 208 in 2009) during the unregulated flow period characterised by high daily incoming radiation and daily mean air temperature in upper 25th percentile of summer 2009 values (i.e. > 13.5 ^{o}C), (Event 4) a clear-sky hot summer day (day 236 in 2009) during the overspill period characterised by high incoming daily radiation and daily mean air temperature > 13.5 ^{o}C. Events 2 - 4 were selected from 2009 data sets to incorporate loggers at S11 and S22 (which were not installed in 2008). Thermal maxima and minima and corresponding times were plotted at each site during each event and compared with local climate data to examine lags between changes in climatic conditions and water temperature response.

Finally, temperature records for S3, S12, S14, S16, S19 and S20 on days 344 in 2008 and 65 in 2009 were compared with direct field observations of snow depth and flow permanency to critically evaluate the utility of temperature records for determining flow permanency during winter (Constantz et al., 2001; Brown et al., 2006b).

5.4 RESULTS

5.4.1 Hydroclimatological conditions in the Eisboden catchment

Incoming shortwave radiation, air temperature, and precipitation followed distinct seasonal cycles through the monitoring period (Figure 5.2; Table 5.2). Both summers were characterised by large daily fluctuations in shortwave incoming solar radiations (max. = 28.5 MJ $m^{-2}d^{-1}$ [day 198 in 2008]; min. = 1.5 MJ $m^{-2}d^{-1}$ [day 216 in 2009]; Figure 5.2a). During the two summer melt seasons, periods with high day-time and above freezing night-time temperatures (max. daily mean = 16.3 ^{o}C; day 232 in 2009) were interspersed with shorter colder periods where night-time temperatures dipped below freezing and day-time temperatures remained subdued (min. daily mean and max. daily mean = -0.3 ^{o}C on day 199 in 2009; Figure 5.2b). Overall, the 2008 summer was wetter than 2009 (daily mean 10.3 *vs* 8.1 mm, respectively). Precipitation events were particularly prolific in July and became less frequent into August and September during 2008 (Figure 5.2c). In contrast, precipitation fell more uniformly through summer 2009 although drier periods were generally longer (e.g. days 217 – 219, 235 – 239) and storms more intense later in the summer.

The summer of 2008 experienced three snowfall events (days 204, 229 and 236) compared with four in 2009 (days 188, 189, 191 and 199). A distinct drop in mean daily air temperature occurred on day 258, 2008 (Figure 5.2c) during a cold period. Mean daily air temperatures recovered slightly for short lengths of time over the subsequent 48 days but never exceeded the temperatures prior to the cold event. From day 316 in 2008 mean daily air temperature remained below freezing until day 93 in 2009 when it rose gradually into late spring. Daily incoming shortwave radiation also declined into the winter and was extremely subdued during December. Incoming shortwave radiation began to increase in January and although daily incoming radiation during late-winter/early-spring did not reach the maximum daily values observed during summer, the minimum daily values observed during late winter/early spring were markedly greater than some of those observed during the summers (Figure 5.2a).

Mean daily discharge from the catchment (monitored at S20) was greater during the unregulated period of 2009 than 2008 (2.55 *vs.* 1.93 m^3s^{-1}; Figure 5.2d see also Chapter 4). Overspill from the Weiβsee started on day 230 in 2008 compared to day 218 in 2009. Discharge was markedly higher during the overspill period of 2009 cf. 2008 (mean daily 3.21 *vs*. 2.66 m^3s^{-1}). Overspill from the Weiβsee continued from late summer throughout the autumn of 2008 until day 312, although the frequency of dam overflow declined after day 262. A series of much larger drawdown releases occurred from day 332 in 2008 through to day 44 in 2009. This discharge release inundated the NW part of the Central Eisboden Braidplain and led to dramatic step fluctuations in discharge (Figure 5.2d). From day 44 in 2009 discharge at S20 remained low (0.2 m^{3}s^{-1}) until day 128 when a gradual increase marked the start of the melt season.

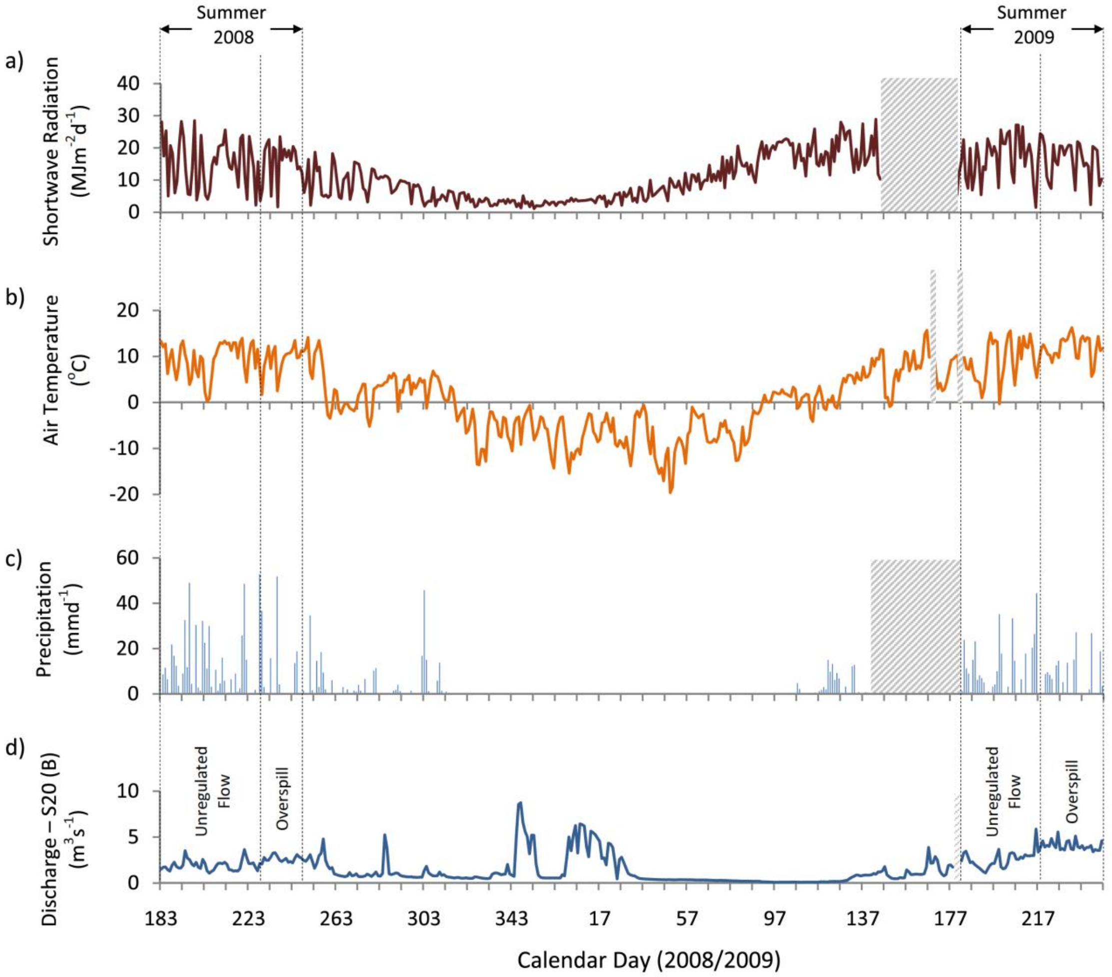

Figure 5.2 - *a) Daily incoming shortwave radiation; b) mean daily air temperature; c) total daily precipitation, and; d) Mean daily discharge [Nb. shaded areas of plots indicate missing data].*

Table 5.2 - *Summary statistics for hydroclimatological data.*

	T_{air} (^{o}C)	*Ppn* (mm)*	*Incoming shortwave ($MJ\ m^2\ d^{-1}$)*	*$Q_{(S20)}$ (m^3s^{-1})*
SUMMER SEASON 2008 (day 183-247)				
Mean (sum*)	9.4	10.3	15.4	2.13
Max	20.7	54.2	28.5	8.21
Min	-0.6	0.0	1.6	0.98
Range	21.3	54.2	26.8	7.23
St. Dev.	4.6	14.2	7.3	0.82
SUMMER SEASON 2009 (day 182-246)				
Mean (sum*)	10.3	8.1	16.7	3.21
Max	25.4	44.4	27.1	9.07
Min	-2.6	0.0	1.5	1.03
Range	28.0	44.4	25.6	8.04
St. Dev.	5.2	1.5	6.3	1.21
UNREGULATED PERIOD 2008 (day 182-229)				
Mean (sum*)	9.5	10.5	14.9	1.93
Max	20.7	49.2	28.5	8.21
Min	-0.6	0.0	2.2	0.98
Range	21.3	49.2	26.3	7.23
St. Dev.	4.7	12.8	7.7	0.76
OVERSPILL PERIOD 2008 (231-247)				
Mean (sum*)	9.8	6.2	16.5	2.66
Max	20.0	51.8	23.5	6.35
Min	-0.3	0.0	1.6	1.42
Range	20.3	51.8	21.9	4.94
St. Dev.	4.4	13.3	5.9	0.69
UNREGULATED PERIOD 2009 (182-217)				
Mean (sum*)	9.1	9.7	17.1	2.55
Max	25.4	44.4	27.1	8.77
Min	-2.6	0	1.5	1.03
Range	28.0	44.4	25.6	7.74
St. Dev.	5.6	11.7	6.8	1.07
OVERSPILL PERIOD 2009 (219-246)				
Mean (sum*)	11.9	6.3	16.0	4.04
Max	22.8	27.2	21.9	9.07
Min	0.2	0	2.3	2.80
Range	22.6	27.2	19.6	6.28
St. Dev.	4.1	8.4	5.5	0.81

** Precipitation statistics are based upon daily totals.*

5.4.2 Stream thermal dynamics during summer

A clear longitudinal thermal gradient was evident along the Eisboden main river channel during the unregulated periods of both summers based upon the temperature records of S3, S20 and S23 (Figure 5.3). Thermal heterogeneity during unregulated summer flow periods plotted for the main stem (Figure 5.4) indicated that longitudinal thermal gradients in the main Eisboden river were relatively stable in comparison with thermal heterogeneity amongst other site groupings. The mean thermal increase over the 0.8 km distance from S3 to S23 during the unregulated summer flow periods was 1.2 °C. Although water temperature was not recorded continuously at the Ödenwinklkees snout, spot measurements were in the range of 0.8 - 1.1 °C and indicated the water temperature was relatively stable throughout the summer. In contrast, S2 (Rifflkees stream) monitored at a similar altitude to S1 generally had the highest summer water temperature and the greatest inter-daily thermal heterogeneity.

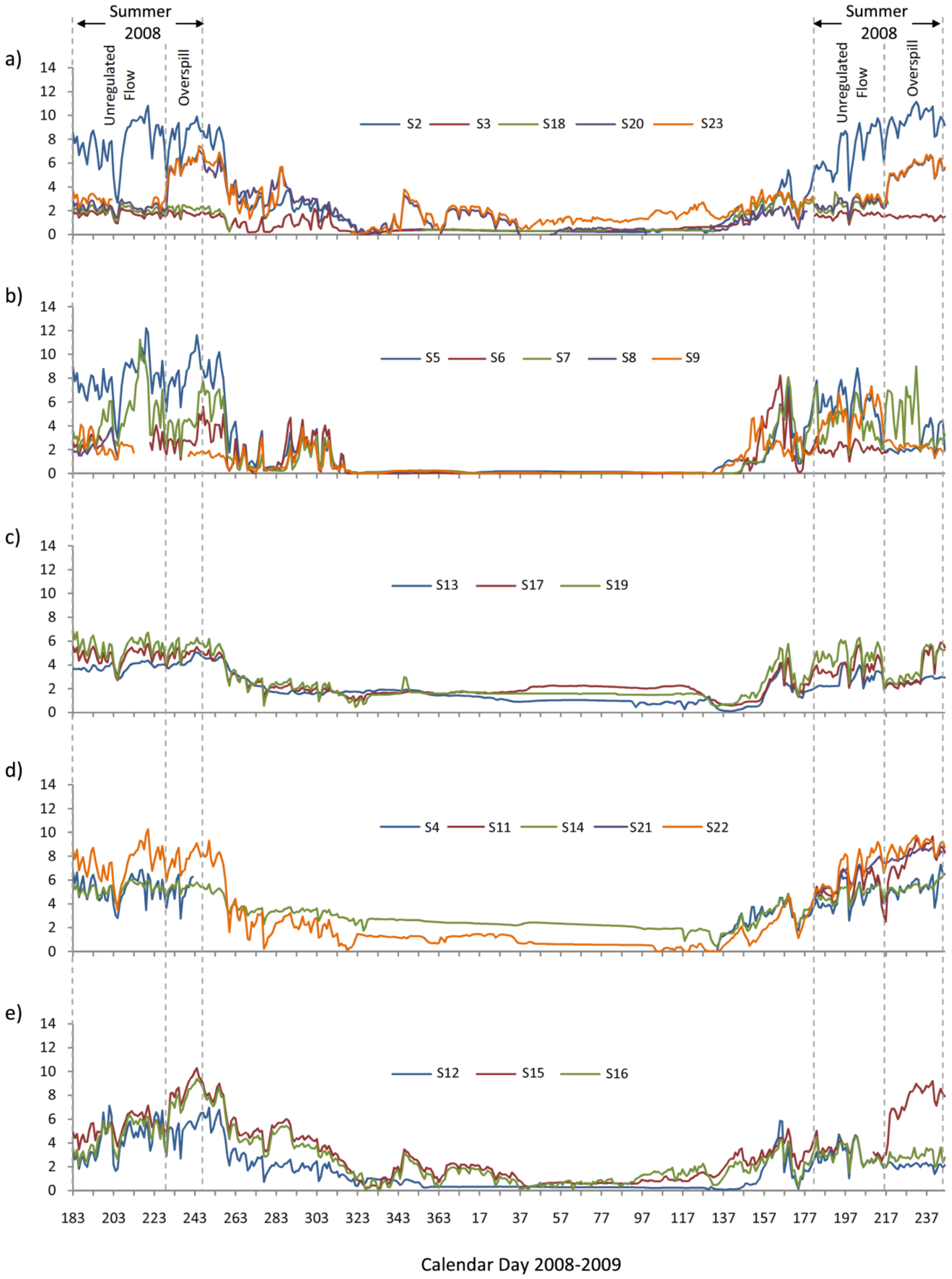

Figure 5.3 - *Daily mean water temperature for (a) Eisboden and Rifflkees main stem sites, (b) Eisboden braidplain central transect, (c) alluvial groundwater sites, (d) hill slope groundwater sites, and (e) mixed sites.*

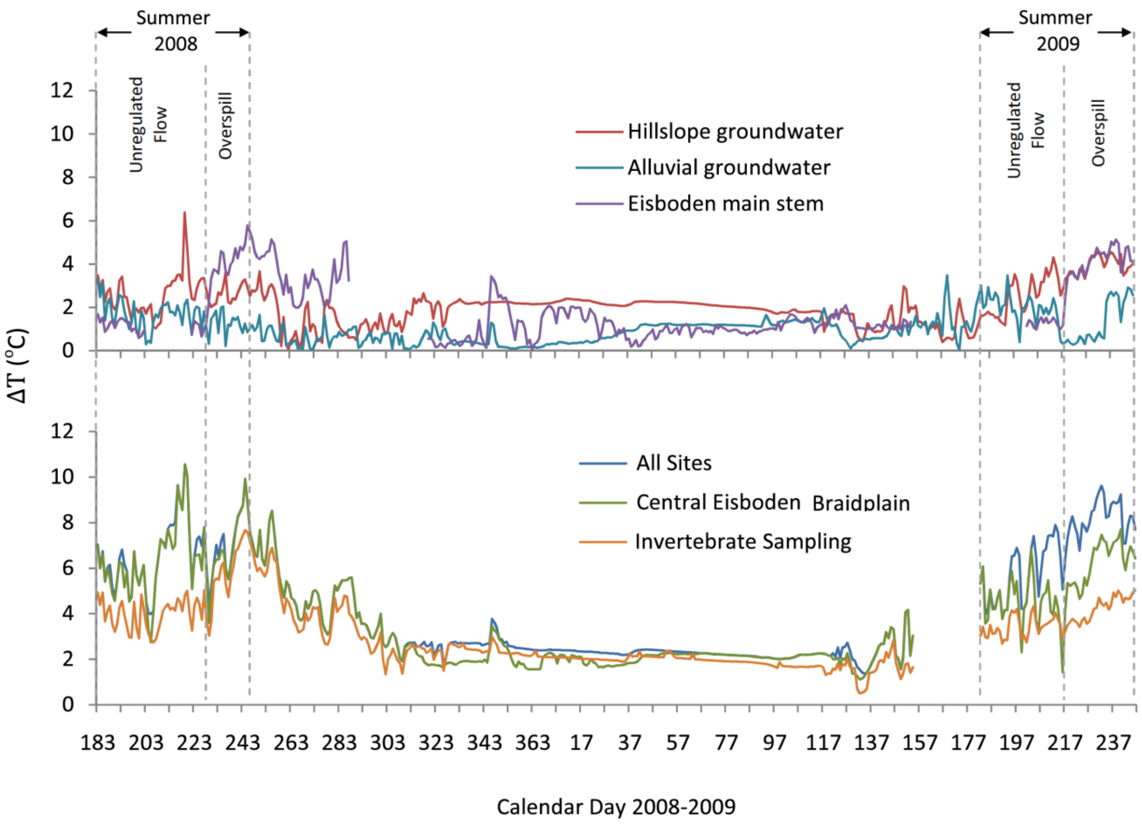

Figure 5.4 - *Water temperature heterogeneity for site groupings: hillslope groundwater (S4, S10, S14, S22); alluvial groundwater (S13, S17,S19); Eisboden main stem (S3, S20, S23); all sites (ex. S1, S11, S21); Central Eisboden Braidplain (S3, S5-9, S12, S13, S15-20), and; invertebrate sampling sites (S3, S12, S14, S16, S19,S20).*

The lateral transect of loggers dissecting the Central Eisboden Braidplain indicated that there was no consistent lateral thermal pattern, although heterogeneity was evidently high compared to other site groupings (Figure 5.4). Water temperature in mixed channels also exhibited no consistent spatial pattern although during unregulated summer flow periods mean water temperatures were respectively 1.3, 1.9 and 1.6 ^{o}C cooler in 2009 than in 2008. A clear longitudinal thermal gradient was observed in the alluvial groundwater stream located in the centre of the main Eisboden braidplain. Water temperature increased on average by 3.7 ^{o}C over the 0.1 km from S13 to S19. During summer 2008, water temperature at the alluvial upwelling spring (S13) lagged air temperature by over 24 hrs (CCF_{max} = 0.523, lag = 32h) in contrast to: (i) 2009 when lag times at S13 were much shorter (CCF_{max} = 0.664, lag = 0.25 h), and; (ii) other groundwater sites during both 2008 and 2009 (see Appendix A).

During the unregulated flow periods of summer 2008 and 2009, mean air temperature and incoming shortwave radiation correlated strongly with water temperature ($r > 0.4$, $CCF_{max} > 0.5$) at all sites with the exception of S13 in 2008, S21 and S23 in 2009, and S10 in both summers. There were no significance differences between r-values of water temperature-incoming radiation and air-water temperature correlations during the unregulated flow periods (WSR test: 2008 $p = 0.748$, or 2009 $p = 0.211$). However, differences at specific sites were evident, for example at S13 during the unregulated period of 2008 water temperature correlated extremely weakly with radiation ($r=0.02$) whilst correlation with air temperature was stronger ($r = 0.33$). Mean daily water temperature at sites upstream of the Weiβsee tributaries (S2, S21) and those on the east side of the Eisboden main stem (S3, S4, S10, S14 and S22) were not significantly different between unregulated and overspill periods in 2008 ($p > 0.05$; Figure 5.5). In 2009, air temperature increased significantly ($p = 0.007$) by 2.8 ^{o}C after the overspill started cf. a statistically insignificant ($p = 0.461$) 0.5 ^{o}C increase 2008. The air temperature increase was paralleled by a significant increase in water temperature ($p < 0.05$) at groundwater fed sites (S2, S4, S10, S14, S21 and S22), but a statistically significant decrease in the Eisboden main stem at S3 (Figure 5.5). In contrast, water temperature increased significantly in the Eisboden main stem below the confluences of the Weiβsee overspill tributaries during overflow periods of both 2008; 3.7 ^{o}C at S20 and 3.2 ^{o}C at S23, and 2009; 3.0 ^{o}C at S20 and 2.7 ^{o}C at S23.

No significant increases in daily mean water temperatures were evident across the upper transect during the overspill period except at S8, 2008. In contrast, significant increases in daily mean temperature occurred in 2008 at sites situated on the central braidplain proximal to the Weiβsee tributaries (S12 = 1.1^{o}C; S13 = 0.6^{o}C; S15 = 3.4^{o}C; S16 = 3.6^{o}C; S19 = 0.2 ^{o}C). A small yet statistically significant temperature increase (0.2 ^{o}C) also occurred at S18. During the 2009 overspill period, daily mean water temperature only increased significantly at S11 (2.7 ^{o}C) and S15 (4.3^{o}C).

5.4.3 Year-round thermal dynamics

Daily mean water temperatures generally declined into the autumn at all sites, although this decline was punctuated by periodic fluctuations associated with meteorological variations (Figure 5.3). Daily mean water temperatures at S20 and S23 continued to be greatly elevated relative to S3 during the autumn due to overspill from the Weiβsee (Figure 5.3a). Over winter, water temperatures at S2, S5, S6, S7 and S9 stabilised close to freezing beginning around day 323 in 2008 (Figures 5.3a, b). Daily mean water temperature at alluvial groundwater sites; S13, S17 and S19 stabilised around day 330 in 2008 at ~ 1.8, 1.6 and 1.5 ^{o}C, respectively, although a spike in the temperature record at S19 occurred on day 346 corresponding to a major drawdown release from the Weiβsee (Figure 5.3c). Hillslope groundwater sites; S14 and S22 (S4 ran dry on day 242) stabilised around day 330, 2008 at ~2.6 and 1.5 °C, respectively (Figure 5.3d).

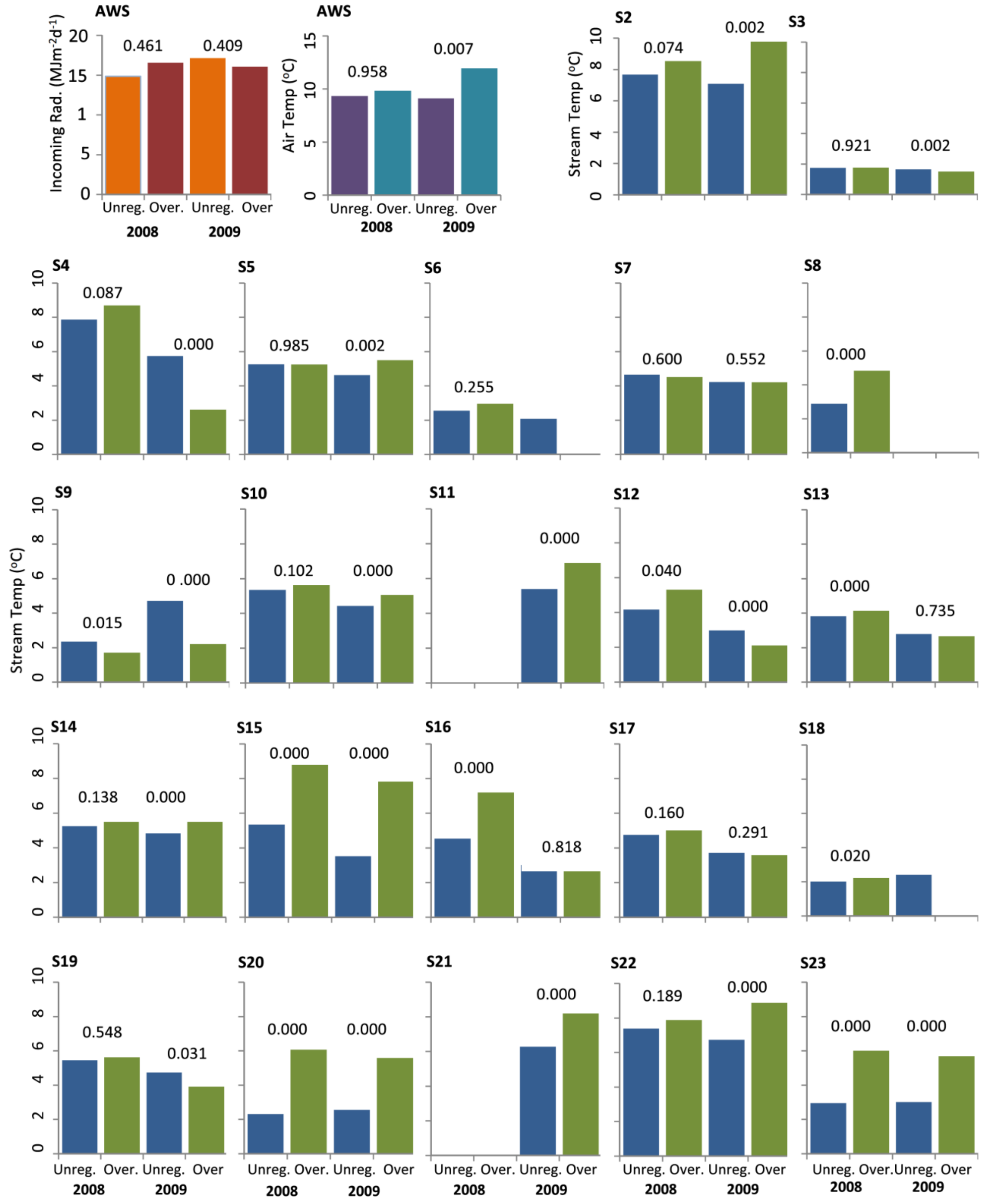

Figure 5.5 - *Comparisons of mean incoming solar radiation, air temperature and water water temperature between unregulated and overspill periods in 2008 and 2009. P-values from Mann-Whitney U tests of unregulated vs. overspill within years are noted above charts.*

A series of extreme drawdown releases from day 332 in 2008 through to day 44 in 2009 caused dramatic stepped increases in mean daily water temperature at S15, S16, S20 and S23.

The maximum daily mean water temperature in the main Eisboden stem during this period was 3.3 °C on day 346. Temperature fluctuations at S13 and S22 were evident during drawdown events in contrast with stable temperatures recorded at S14 (Figure 5.7b cf. 5.6a). From day 44 - 100 in 2009 water temperature at S16 and S23 fluctuated in the range of 0 - 2.6 °C and 0.5 -1.7 °C, respectively. From day 100 in 2009 water temperature began to rise across the catchment but the nature and timing of temperature increases differed between stream types and location. For example, water temperatures at S15, S16 and S23 began to rise gradually from day 100 in 2009 with pronounced diurnal fluctuations evident (Figures 5.3a,e). In contrast, water temperature rose gradually at S3 from day 100 in 2009 but diurnal variations were not evident until day 147. Water temperatures remain relatively stable at the alluvial ground water sites until ~day 125 when a marked drop in temperatures occurred during a period of sustained subzero air temperature. Water temperature recorded at sites located on the central braidplain transect increased dramatically and began to experience diurnal variations, starting on days 131 (S5), 136 (S9), 143 (S7) and 146 (S9) (Figure 5.5b).

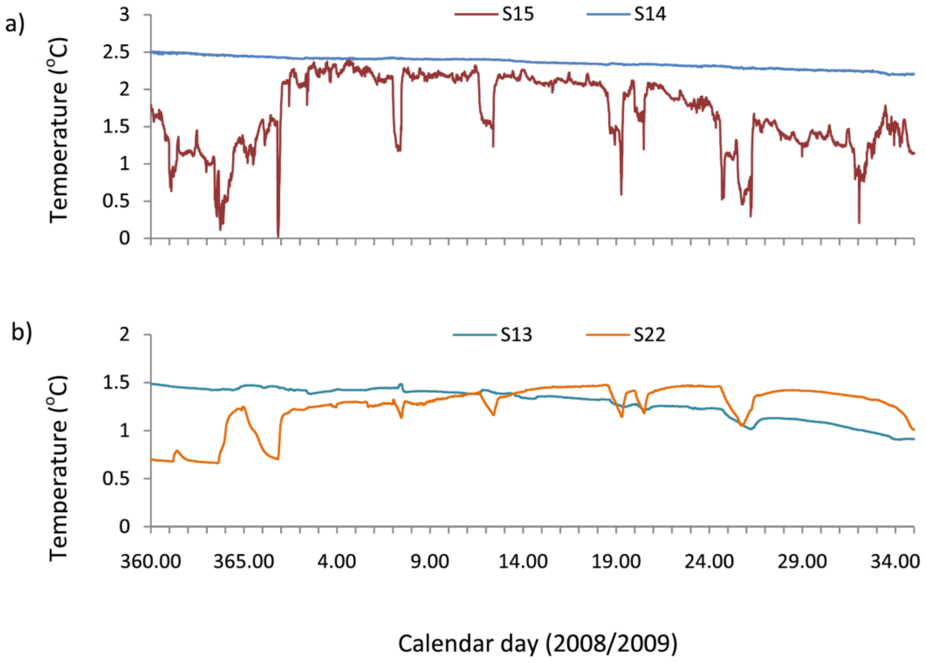

Figure 5.6 - *Water temperature dynamics during Weißsee drawdown events (day 360, 2008 – day 35, 2009) at, a) a thermally stable groundwater stream (S14), and an inundated mixed side channel close to the Weißsee tributaries (S15), and b) groundwater streams S13 and S22, exhibiting thermal responses associated with drawdown events.*

5.4.4 Event scale thermal dynamics

5.4.4.1 Event 1 (day 346 in 2008: Weißsee drawdown)

During Event 1, discharge at S20 was extremely high at between 8 – 9 m^3s^{-1} ($\overline{Q}$ = 8.55 m^3s^{-1}) and elevated flows inundated channels on the NW side of the central braidplain. Air temperature experienced a general decline through the day (0.5 to -8.5 °C) whilst incoming radiation was suppressed by cloud cover (max. 147 Wm^{-2}; Figure 5.6a). Water temperature range at all sites was very low (< 0.5 °C), but particularly at S2 - S7, S9, S10, S13, S14 and S10 (< 0.1 °C; Figure 5.7a). Water temperatures recorded at S2 - S7, S9 and S10 were < 0.5 °C, while water temperatures at S13 - S17, S19, S20, S22 and S23 remained > 1 °C. The recorded maximum temperature was 3.6 °C at S15. Thermal maxima and minima were largely asynchronous (Figure 5.7b) and no strong diurnal variations were evident (Figure 5.7c).

5.4.4.2 Event 2 (day 198 10:00 GMT- day 199 10:00 GMT in 2009: Rapid cooling event)

Event 2 was defined by a dramatic fall in air temperature occurring across the 24hr period from 10:00 GMT, day 198, 2009 (Figure 5.7d) and precipitation/snow events. Large temperature declines were evident across all sites following stream thermal maxima between 10:00 and 13:30, day 198 in 2009. Water temperature maxima lagged air temperature maxima (10:15, day 198 in 2009) at all sites except S6 and S14 and occurred close to peak incoming shortwave radiation (11.30, day 198 in 2009) (Figure 5.7e). The time of water temperature minima occurred between 06:00 and 09:45, day 199. Diurnal temperature range amongst sites varied markedly; particularly amongst groundwater streams (i.e. max. = 10.6 °C [S4]; min. = 1.4 °C [S10]; Figure 5.7f).

5.4.4.3 Event 3 (day 208 in 2009: Clear-sky, hot summer day)

High air temperatures (daily mean = 14.1 °C) and the daily incoming radiation maxima during summer 2009 (27.1 MJ $m^{-2}d^{-1}$) were recorded during Event 3. The timing of water temperature minima varied markedly between sites, with most occurring early in the morning but during the evening at S13, S17 and S19 (Figure 5.8b). Water temperature maxima occurred after the air temperature maxima (11:00 GMT) at all sites, and occurred later than during Event 2. Water temperature maxima were not synchronised with peak incoming solar radiation (12:00), occurring shortly before at S6, S12-14, S16 - S20 and S23 and sometime after at S2 (+2.5 hrs) and S9 (+3.25 hrs). However, water temperature ranges were generally lower on day 208, 2009 (Figure 5.8a) relative to those observed during Event 2 (Figure 5.8c cf. 5.6f).

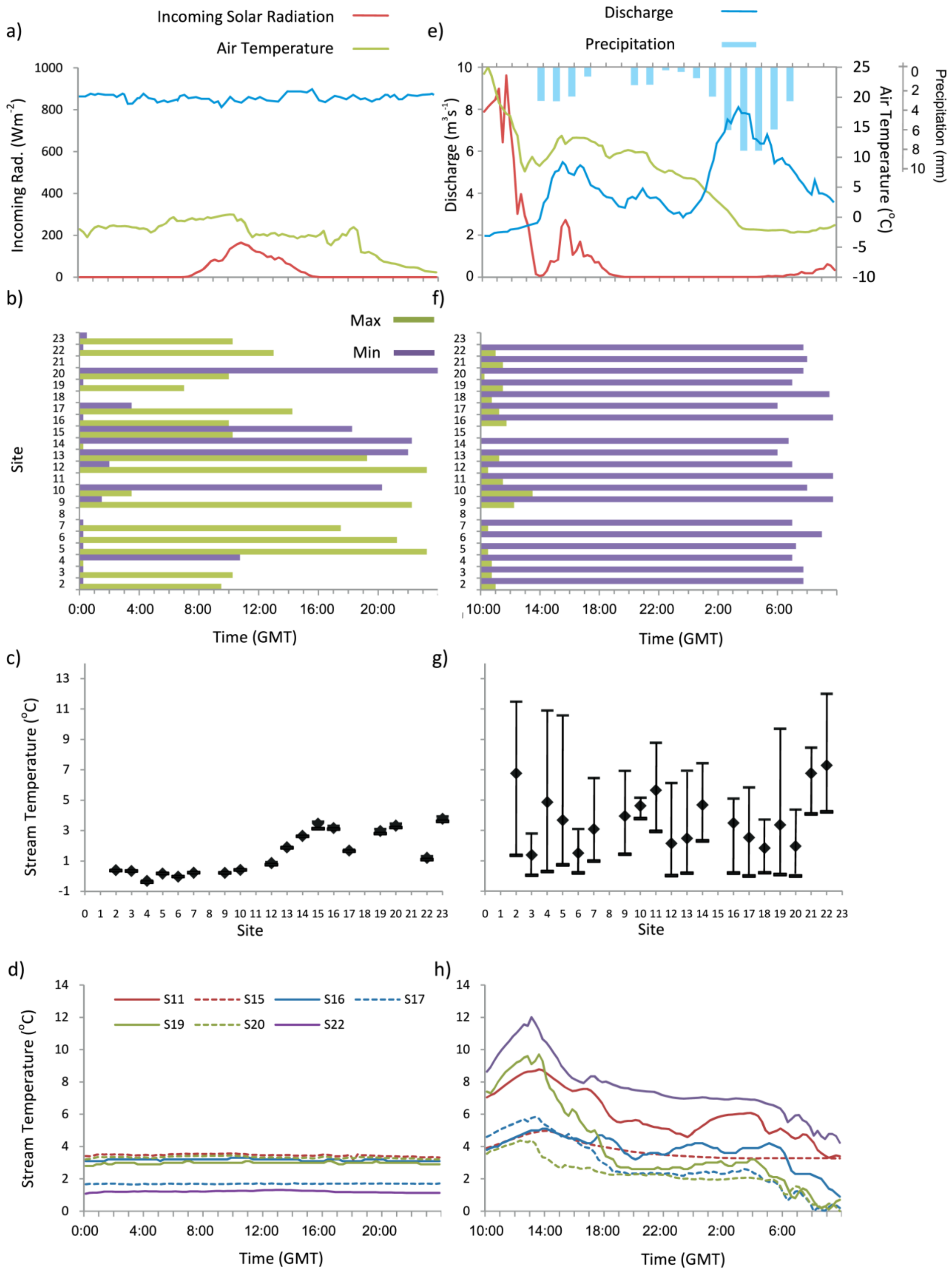

Figure 5.7 - *(a) Air temperature and incoming shortwave radiation; (b) times of water temperature maxima and minima; (c) mean daily water temperature, with errors bars showing maxima and minima, for Event 1: day 346, 2008. [Nb. no precipitation was recorded during Event 1]. Figures (d), (e), and (f) show the same data for Event 2: the 24 hour periods form 10:00, day 198 – 10:00, day 199; 2009, additionally precipitation during Event 2 is plotted in figure (d).*

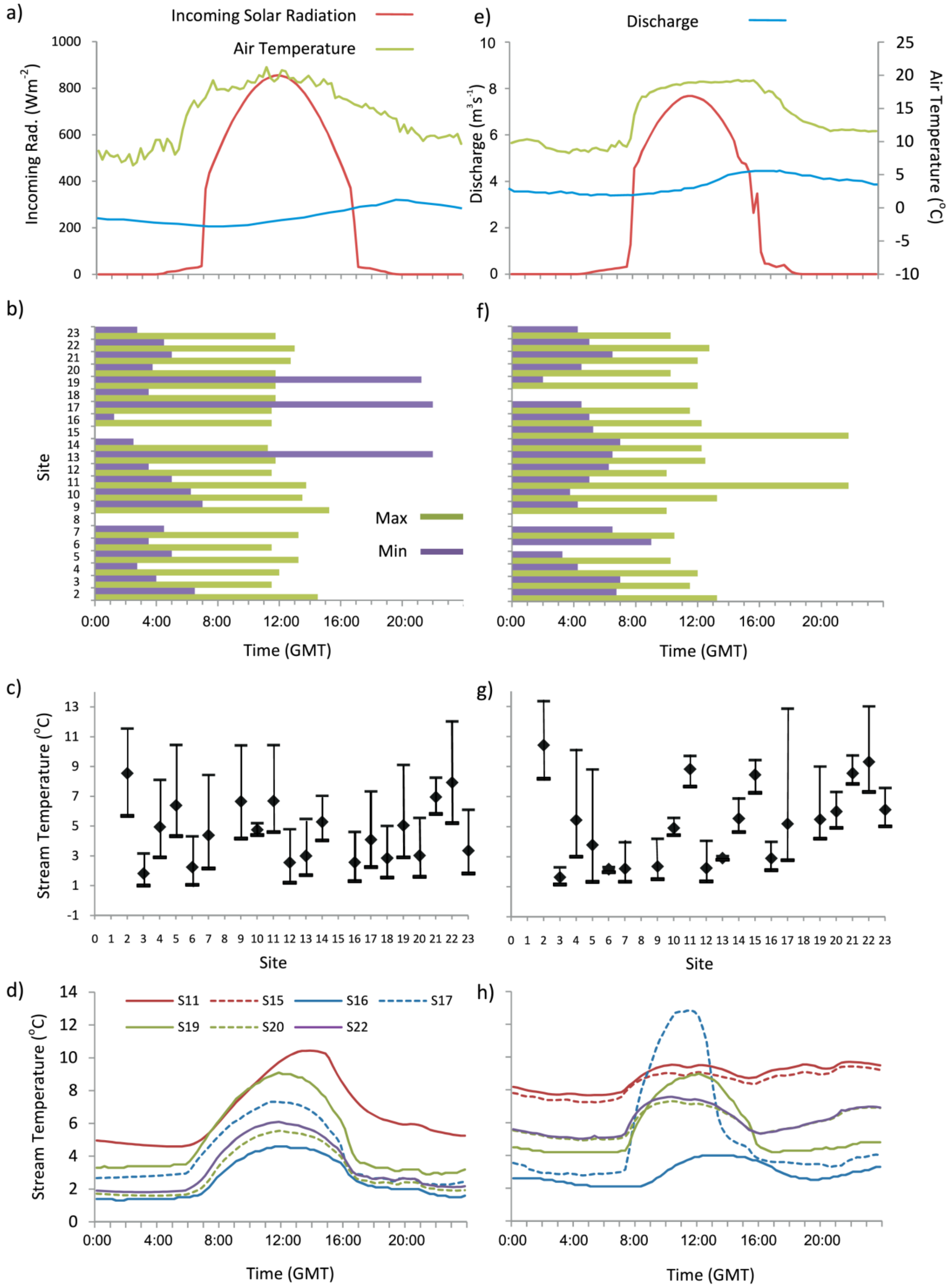

Figure 5.8 - *(a) Air temperature and incoming shortwave radiation; (b) times of water temperature maxima and minima, (c) mean daily water temperature, with errors bars showing maxima and minima, (d) diurnal thermographs for selected sites (sites which exhibited late evening warming during Event 4), plotted for Event 3:day 208; 2009. (e), (f), (g) and (h) show the same data for Event 4: day 236; 2009. Nb. no rainfall was recorded during either event.*

5.4.4.3 Event 4 (day 236 in 2009: Hot summer day with overspill flows from the Weiẞsee)

Event 4 occurred during late summer (day 236 in 2009) when overspill flows from the Weiβsee inundated streams located on the NW side of the Eisboden braidplain. Daily mean air temperature was similar during Event 4 to Event 3 (13.7 *vs.* 14.1 ^{o}C) but despite almost clear-sky conditions daily incoming radiation was lower (21.3 *vs.* 27.1 MJ m^{-2}d^{-1}; Figure 5.8e). Peak water temperature varied by up to an hour at S2-4, S10, S19 - S23 relative to the time of peak incoming solar radiation (Figure 5.8f). At other sites thermal maxima varied markedly, in particular at S11 and S15 where highest water temperatures were recorded at 21:45. Water temperature time series for S5, S7, S11, S15-17, S19 and S20 showed distinct increases in temperature during the evening (Figure 5.8g) as the quantity of relatively warm water overspilling from the Weiβsee increased.

5.4.5 Streamflow and thermal dynamics during winter

Examination of open channels S16 and S20 and excavation of snow covered channel sections hosting S3, S12, S14 and S19 during winter field visits on days 344 in 2008 and day 65 in 2009, revealed a range of stream conditions (Table 5.3). Atmospheric energy inputs were low; mean daily air temperatures and incoming solar radiations were -4.6 ^{o}C and 3.7 MJ m^{-2}day^{-1}, and -6.0 ^{o}C and 10.0 MJ m^{-2}day^{-1} on days 344 in 2008 and day 65 in 2009, respectively, Drawdown flow from the Weiβsee on day 344 in 2008 between 9:45 and 13:00, and after 22:45 clearly warmed S20 and S16 and to a lesser extent S12 and S19 (Figures 5.9 a, c).

On day 344 in 2008 the channel section at S20 was open and continuous flow was observed. Subzero 'water' temperatures were logged at S20 between 0:00 - 9:45 and 14:45 - 22:45, day 344 in 2008 (Figures 5.9a,b) and these correlated with air temperatures ($r = 0.690$, $p < 0.01$) although the amplitude of thermal variations was subdued. S16 also remained open and flowing but water temperature remaining above freezing and were responsive to both atmospheric energy inputs and drawdown flows. Flow was observed under snow covered channels S3, S14 and S19. Logged water temperature at S3 and S14 was stable (0.3 and 2.2 ^{o}C), while temperature at S19 varied minimally $\bar{T}$ = 1.6, T_{range} = 0.2 ^{o}C). No surface flow was observed in the channel at S12 but shallow hyporheic flow was evident when the stream bed was excavated and it is likely that S12 received intermittent flow pulses during drawdown releases. Mean temperature at S12 was 0.5 ^{o}C and temperature range was also low.

On day 65 in 2009, S16 and S20 were only partially open and water temperatures were both lower (mean temperature 0.7 and 0.5 ^{o}C respectively) and more stable (temperature ranges were 0.2 and 0.1 ^{o}C respectively) than on day 344 in 2008. However, water temperatures showed minor responses to atmospheric energy inputs (Figures 5.9c, d). Flow was discovered under a 1.6 m snowpack at S14 and water temperature was relatively warm (mean temperature 1.6 ^{o}C; range 0.1 ^{o}C). No surface flow was discovered at S14 though hyporheic water was present just below the streambed. Mean temperature at S19 was high (2.3 ^{o}C) compared to S3 and S12 (both 0.3 ^{o}C) where no flow was evident and the stream bed was dry when excavated down to ~0.20 m. Temperatures at S3, S12 and S14 were all stable to within 0.1 ^{o}C. The temperature record through the intervening time period between day 344 in 2008 and day 65 in 2009 for S14 indicated a distinct change in thermal characteristics on ~day 37 in 2009 (Figure 5.10); when temperature increased by ~0.2^{o}C and became more stable.

Table 5.3 - *Observed stream conditions and logged water temperature means and ranges on days 344; 2008 and day 65; 2009.*

Site	Snow Depth (m)	Stream flow	Max stream depth (cm)	$\bar{T}$ (^{o}C)	T_{range} (^{o}C)
Day 344, 2008					
S3 (A)	1.0	Flowing	20.0	0.3	0.0
S12 (C)	1.8	Hyporheic	0.0	0.5	0.1
S14 (F)	2.0	Flowing	15.0	2.7	0.0
S16 (D)	Open	Flowing	22.5	1.0	2.7
S19 (E)	0.7	Flowing	9.5	1.6	0.2
S20(B)	Open	Flowing	45.0	-0.7	5.1
Day 65, 2009					
S3 (A)	1.8	Dry	0.0	0.3	0.0
S12 (C)	2.0	Dry	0.0	0.3	0.0
S14 (F)	2.5	Hyporheic	0.0	2.3	0.0
S16 (D)	1.6 -0 (Patchy)	Flowing	25.0	0.7	0.2
S19 (E)	2.7	Flowing	13.0	1.6	0.1
S20(B)	0-1.0 (Patchy)	Flowing	20.0	0.5	0.1

Note: The term hyporheic represents streams where there was no surface flow but water was found close to the surface of streambed sediments.

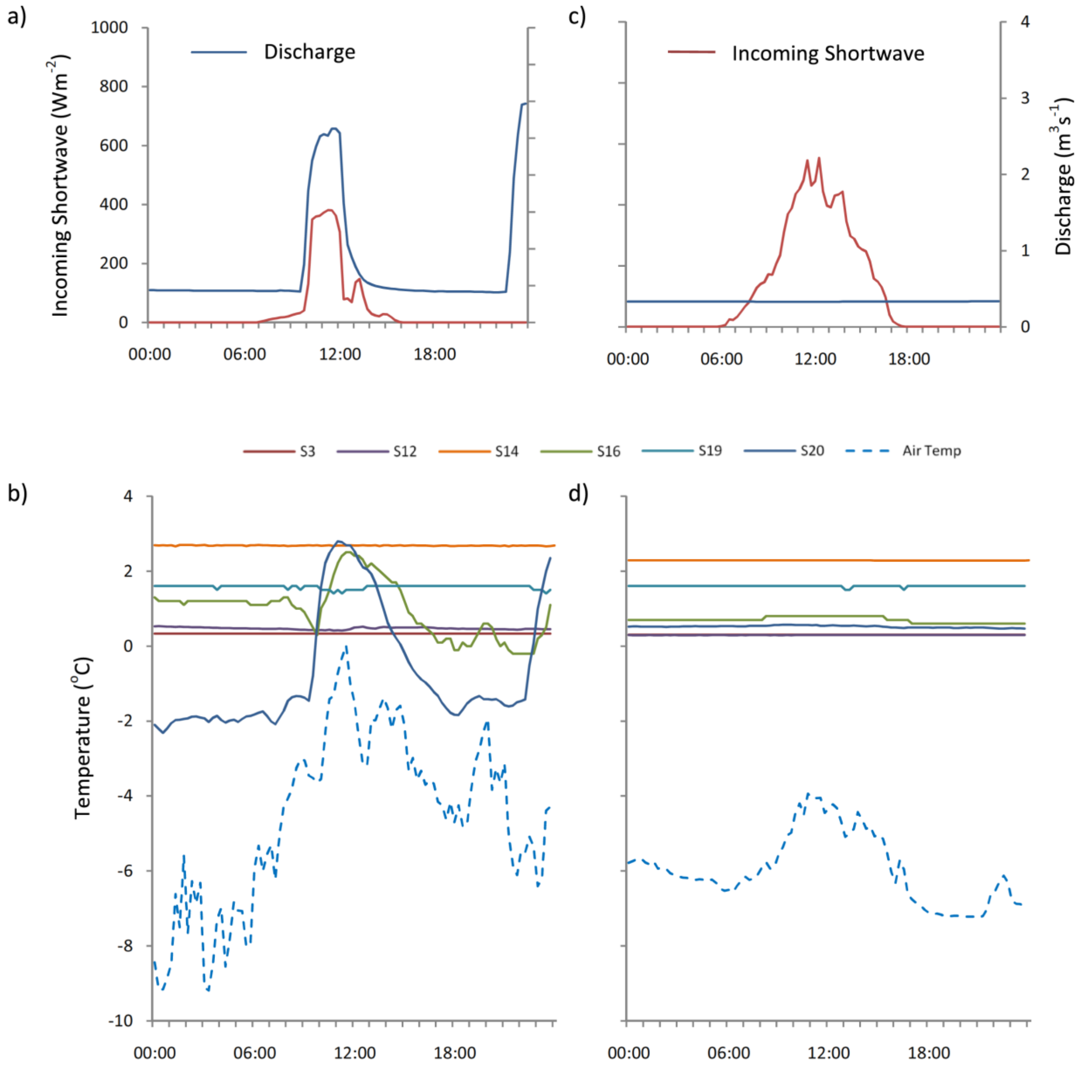

Figure 5.9 - *(a) Incoming shortwave solar radiation, and discharge at S20 for day 344, 2008. (b) Diurnal thermographs of water temperature at macroinvertebrate monitoring sites and air temperature monitored at the AWS. Panels (c) and (d) show data for day 65, 2009.*

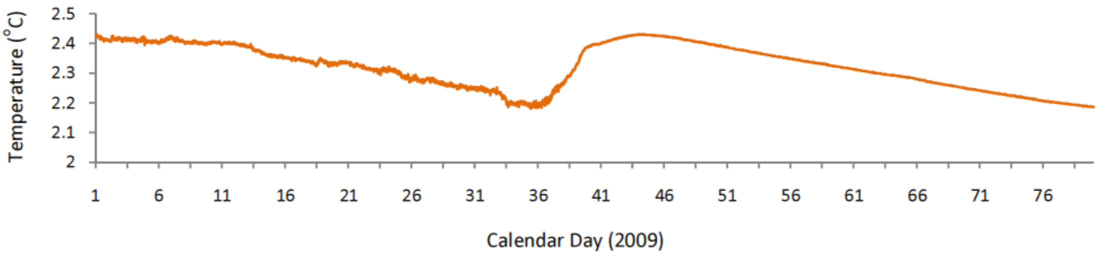

Figure 5.10 – Water temperature at S14, day 1-77, 2009.

5.5 DISCUSSION

This study has expanded on previous alpine water temperature research by analysing *year-round* thermal dynamics spanning two summers and one winter season from a spatially extensive network of streams. Additionally, and in contrast to previous research on near pristine catchments (e.g. Uehlinger et al., 2003b), the type and magnitude of impacts that flows from an alpine reservoir can have on the thermal regime were evaluated by studying an alpine catchment inundated by overspill and drawdown flows from late summer through until late winter. Overall this study has demonstrated (i) the significant interactive influence of climate, water sourcing and flow regulation on year-round spatiotemporal thermal heterogeneity within a relatively small alpine catchment both longitudinally in the main glacial-melt stream and laterally across stream types, and (ii) the utility of high resolution temperature data loggers for assessing year-round flow-permanency and water temperature in alpine environments. These major findings are considered in turn in the subsequent discussion.

5.5.1 Year-round longitudinal thermal heterogeneity of the main Eisboden stem.

A wide range of warming rates have been reported from proglacial alpine streams during summer. Brown and Hannah (2008) observed 7.6 °C km^{-1} increases in the Taillon–Gabiétous basin, French Pyrénées. Uehlinger et al. (2003b) found just 0.3 - 0.6 °C km^{-1} warming along the Roseg River, Switzerland. Cadbury et al. (2008) documented 0.6 °C km^{-1} along the Rob Roy Stream, New Zealand. Brown et al. (2008) suggested that the smaller glacierized area, and consequently lower glacial discharge in the Taillon- Gabiétous catchment, were more conducive to stream warming with distance from the glacier. Indeed, during the unregulated summer monitoring period in the main Eisboden stem (S3 - S20), longitudinal thermal gradients were in the range of 0 - 3.0 °C km^{-1} (i.e. between the extremes reported above). The Eisboden catchment has a moderate glacierized area (23 %) and mean unregulated summer discharge (~2.2 m^{3}s^{-1}) relative to the Roseg river (30 % and 2.8 m^{3}s^{-1}), Rob Roy Stream (30 % and 2.8 m^{3}s^{-1}) and Taillon–Gabiétous catchments (4 % and 0.2 m^{3}s^{-1}).

In alignment with fundamental energy budget analyses (Caissie, 2006; Chikita et al., 2009), warming rates in the Eisboden were found to vary markedly with climatic conditions from event to seasonal scales. For example, during summer periods prior to reservoir overspill, Pearson's product-moment correlations revealed significant associations between longitudinal thermal warming rates and both mean daily incoming radiation and air temperature. Extremely low warming rates were observed (cf. Uehlinger et al., 1998; Brown & Hannah, 2008) during cold summer periods with low incoming shortwave radiation (e.g day 204 in 2008 and day 199 in 2009) compared to warmer periods. Local climatic conditions are clearly a significant factor in addition to glacierized area and discharge when accounting for differences in longitudinal thermal heterogeneity between proglacial streams (Uehlinger et al., 2003b).

In contrast to the valley bottom location of the Ödenwinklkees, the Rifflkees is a hanging glacier. The proglacial stream system of the Rifflkees intermittently flows through sediments before emerging as a continuous small stream (Q = < 0.6m^{3}s^{-1} at S2) close to its confluence with the Eisboden main stem. Assuming melt-waters emerging from the Rifflkees were at 0 ^{o}C, mean August (2008, 2009) daily warming rates were remarkably high (7.1 ^{o}C km^{-1}) and comparable to those observed in the Taillon- Gabiétous catchment by Brown et al. (2008).

Late summer overspill from the Weiβsee differed markedly from flow regime alterations typically associated with hydropower schemes because the periodicity and amplitude of flows are dependent on reservoir inflow and overspill rather than abstraction (cf. Petts & Bickerton, 1994) and resultant hypolimnetic drawdown (cf. Céréghino et al., 2002; Carolli et al., 2008; Zolezzi et al., 2010). Late summer overflow from the Weiβsee had a significant effect on mean daily temperature at main stem sites S20 and S23 (Figure 5.5). For example, mean daily temperatures increased by 3.7 ^{o}C (2008) and 3.0 ^{o}C (2009) at S20 during overflow which contrasts sharply with the significant declines in water temperatures in sub-alpine streams subject to summer hydropeaking from reservoirs (cf. Céréghino et al., 2002; Carolli et al., 2008). Two key factors may have contributed to this novel observation. Firstly, sampling sites were located at much higher altitude (> 2110 m.a.s.l) compared to previous studies (912 m.a.s.l; Céréghino et al., 2002; 1265m.a.s.l; Carolli et al., 2008; 217m.a.s.l; Zolezzi et al., 2010). The high altitude location meant streams were close to snowpack and glacial melt sources resulting in very cold water temperatures. Secondly, it is the surface waters of the Weiβsee that overtop into the Eisboden during the summer period rather than the cooler waters from the hypolimnetic zone that are more commonly discharged into catchments during hydropower regulation (Webb & Nobilis, 1995; Céréghino et al., 2002; Maiolini et al., 2003; Carolli et al., 2008; Toffolon et al., 2010; Zolezzi et al., 2010). Comparable discontinuities in temperature caused by natural lentic inputs from a proglacial stream have been reported during summer months in the Val Roseg Basin, Switzerland, by Uehlinger et al. (2003b) who repoted a 1.9 ^{o}C mean difference betweenthe Roseg proglacial lake stem and downstream of the Tschierva proglacial stem confluence. Significant thermal discontinuities have also been reported in proglacial streams at large groundwater tributaries (e.g. ~1°C; Knispel & Castella, 2003).Temporally, the spatial discontinuity in the Roseg River also manifested rapidly (over just a few days) but during May/June *vs.* August in the Eisboden.

In comparison to summer overspill flows, the winter drawdown releases caused an even greater shift from unregulated stream conditions at S20. Flow from alpine streams would naturally be at a minimum during the winter months (Röthlisberger & Lang, 1987; Jansson et al., 2003) with water temperatures at a minimum and some streams becoming 'dormant' (as observed at S3 cf. Malard et al., 2006)). Uncharacteristically warm water temperatures were recorded at S20 and S23 from December, 2008 until mid-February, 2009. Temperatures were elevated above 3 °C for prolonged periods with little diurnal variation (cf. thermopeaking from hydropower reflux flows; Céréghino et al., 2002; Maiolini et al., 2003; Carolli et al., 2008; Zolezzi et al., 2010) and mean daily water temperatures reached 3.3 °C during December. These water temperatures contrast with near freezing temperatures observed at S3 on day 343 in 2008 when stream flows were receding, and during its dormant state as observed on day 65 in 2009. The water temperatures are also high if compared with minimum mean monthly temperatures of 0 - 1.3 °C as observed along the Roseg River by Uehlinger et al. (2003b) at lower altitudes (2122 - 1766 m.a.s.l). The finding that discharges from reservoir regulation during winter significantly increased water temperatures above natural levels is consistent with other studies examining sub-alpine stream systems in winter (cf. Céréghino et al., 2002; Carolli et al., 2008; Zolezzi et al., 2010). Indeed, regulation caused winter water temperature increases that were comparable in amplitude to those observed by observed by Zolezzi et al. (2010) in the Noce River, Italy at 217 m.a.s.l (~3 °C). However, in contrast increases were sustained for several weeks in the Eisboden (cf. <day; Zolezzi et al., 2010) and increases were above a lower base temperature of ~0 °C (cf. ~3°C; Zolezzi et al., 2010).

5.5.2 Year-round spatial thermal heterogeneity in the Eisboden basin

Absolute discharge and the ratio of melt water to ground water from hyporheic upwelling/tributary inputs in alpine basins are thought to be major controls on water temperature (Malard et al., 1999, 2000; Brown et al., 2005, 2006a). Thus wide spatial fluctuations in thermal profile across the Eisboden central braidplain were not unexpected given (i) large variations in braiding and flow routing through different size channels observed through diurnal to inter-annual scales, and (ii) spatial discontinuities in water sourcing, arising from upwelling and hillslope flow inputs at the lateral extremes. During unregulated summer flow periods the lateral transect of S5 - S9 across the Eisboden central braidplain, and mixed side channels S12, S15 and S16, indicated that there was no temporally consistent lateral thermal profile across the braidplain which is supported by previous studies of lateral thermal dynamics across river braidplains (cf. Arscott et al., 2001; Uehlinger et al., 2003b). Water temperature in braided and mixed channels was also consistently greater than main stem sites (S3, S18 and S20) which is a finding supported by several previous studies (e.g. Arscott et al., 2001; Uehlinger et al., 2003b; Brown & Hannah, 2008; Tonolla et al., 2010). Thermal heterogeneity across the central braidplain (mean daily water temperature range during unregulated summer flow periods = 5.5 ^{o}C) was comparable to heterogeneity observed across the Val Roseg floodplain, Swiss Alps (> 1766 m.a.s.l) during August by Uehlinger et al. (2003b). Mean daily temperatures ranges reported by Arscott et al. (2001) in the Tagliamento, northeast Italy at geomorphic reaches ~700 m.a.s.l and 1000 m.a.s.l were however low (1 ^{o}C and 1.7 ^{o}C, respectively) if compared to the lateral heterogeneity they observed in lower reaches (9.7 ^{o}C at 10 m.a.s.l). Arscott et al. (2001) attributed this increase in thermal heterogeneity to the development of floodplain form with decreasing altitude as the lowland, lower-gradient flood plains in the Tagliomento were more conducive to supporting lentic water bodies with high water temperatures relative to water temperature in the main channel. Overall, the findings herein and by Uehlinger et al. (2003b) and Brown & Hannah (2008) indicate that thermal heterogeneity may be greater at high altitudes (> 1750 m.a.s.l) than previously suggested at > 700 m.a.s.l (Arscott et al., 2001).

Water sourcing is considered to have a strong influence on thermal heterogeneity across alpine catchments, influencing both floodplain rivers and hillslope tributaries. The results from this study are supported by findings from other published studies (Robinson & Matthaei, 2007; Brown & Hannah, 2008). During unregulated summer periods, hillslope and alluvial groundwater streams were generally warmer than the Eisboden main-stem, with the highest mean daily water temperatures (12.2 ^{o}C) observed at S5 when this stream was disconnected from the main-stem upstream. The sudden exposure of upwelling groundwater to warm atmospheric conditions can lead to rapid temperature changes in the headwaters of small streams due to shortwave solar radiation energy inputs and equilibration (Danehy et al., 2005). Indeed, longitudinal analysis of an alluvial ground water stream (S13, S17, S19) indicated warming of 3.5 ^{o}C on average in an alluvial spring stream over just 110m distance (S13 - S19). CCF analysis of water temperature data with incoming radiation and air temperature from the unregulated period of summer 2008 enabled some inference of distinct differences in thermal drivers. Water temperature at the spring (S13) was very poorly correlated to incoming solar radiation and lagged air temperature by over 24 hrs, reflecting a subterranean provenance. In contrast, S19 temperatures were strongly correlated and synchronous with incoming solar radiation ($r = 0.884$). This large heterogeneity along just a short length of a single stream highlights a potential limitation of conclusions drawn from studies with discrete spatial sampling strategies at relatively coarse resolution (Uehlinger et al., 2003b; Tonolla et al., 2010).

During summer 2008, relatively similar hydroclimatological conditions across the Eisboden catchment between unregulated and overspill periods provided an opportunity to assess the spatial extent of altered stream thermal regimes induced by water from the Weiβsee, compared with previous 1-dimensional (upstream-downstream) studies of anthropogenic flow alteration (cf. Céréghino et al., 2002; Carolli et al., 2008; Zolezzi et al., 2010) . As expected, a large and statistically significant difference in mean daily temperature was evident in all sites directly inundated by flows from the Weiβsee during 2008 (i.e. S5, S12, S15, S16, S20 and S23) in contrast to sites upstream and to the east of the main Eisboden stem (S2, S3, S4, S10 and S14). Interestingly, there was also a significant increase in temperature at S13 (0.6 ^{o}C) despite the lack of any surface connection to the Weiβsee overspill stream. This suggests that flow from the Weiβsee either warmed the groundwater system underlying the NW central Eisboden braidplain by conduction, or more likely that there was a significant quantity of overspill water advected into the alluvium underlying the lower part of the Eisboden, from which S13 appeared to be sourced. Comparison of water temperature time-series during winter revealed that the thermal influence of Weiβsee overspill on alluvial groundwater systems is extensive, extending to the most easterly lateral extreme of the Lower Eisboden Braidplain, S22 which is fed predominantly by a hillslope tributary during summer. The thermal signal of Weiβsee overspill was clearly evident at alluvial groundwater sites during the winter as unregulated thermographs at snow covered sites were otherwise relatively stable (e.g. S13 and S22 *vs.* S15; Figure 5.10). Similar hyporheic connections have been inferred in floodplain rivers based on synchronous changes in river stage and water-table level up to 2km from the mainstem (Stanford & Ward, 1988).

Hydroclimatological conditions were less similar between unregulated and overspill periods during 2009, and consequently the impact of Weiβsee flows on water temperatures was less clear at inter-daily scales (except S15, S20 and S23). In addition, S5, S12, S13, S15-S17, S19, S20 and S23 were inundated by cold melt-waters during late summer following bifurcation of the main Eisboden stem and major re-routing of flows (see Chapter 4). The mixing of cold melt waters acted to offset warming from Weiβsee flows and largely negated differences in mean daily temperatures between unregulated and overspill periods. Event scale analysis of day 236, 2008 revealed the inundation of flows from the Weiβsee raised stream temperature during late afternoon/evening at S5, S7, S11, S12, S15- S17, S19, S20, S22 and S23. This finding suggests that while anthropogenic flow regulation can clearly effect thermal regime laterally as well as longitudinally, to assess the wider ecological impacts of these effects they need to be quantified relative to the potentially large thermal dynamism of unregulated parts of braided river systems (Uehlinger et al., 2003b; Brown & Hannah, 2008).

5.5.3 Assessing year-round flow permanency

Previous studies have hypothesised that flow permanency may be inferred from water temperature records based on the following assumptions; (i) close association with > air temperatures in the absence of an insulating snowpack is indicative of dewatering around the probe, (ii) temporary stability of water temperatures ~ 0 °C when air temperature is below freezing, but increased variability when air temperatures rise > 0 °C, is indicative of intermittent water column freezing, and (iii) stable water temperatures at ~ 0 °C when air temperature fluctuates above and below 0 °C is indicative that a stream is flowing but insulated from atmospheric energy fluxes by a snowpack (see Constantz et al., 2001; Brown et al., 2006b). However, the utility of temperature datasets for assessing year-round alpine stream flow permanency has not been validated by field observations. Detailed comparisons of field observations and water temperature logger records allowed hypotheses (i) and (iii) to be tested. Temporary surface freezing was not directly observed in the field so hypothesis (ii) could not be tested.

During the summer monitoring periods, field observations confirmed that in the groundwater streams (where sensors could be carefully installed on the stream bed to remain within the flow even during very low-flow conditions), close association with air temperature corresponded with extremely low, or no flow conditions. However, in the Eisboden main stem, it was not always possible to install a temperature logger that would remain submerged during extremely low flow conditions. Thus, at S20 and S23 although there was evidence of sensor exposure to air on several occasions, it is extremely likely that flow persisted below the level of, or laterally aside the water temperature logger (cf. Constantz et al., 2001). Indeed, discharge records indicate that flow at S20 was perennial. Therefore, close association of stream and air temperatures might imply exposure of the sensor but this may not always equate to a cessation of streamflow; flow observations are necessary to validate inferences from thermal records.

Dewatering was evident in the main Eisboden channel around the probes at S3 and S20 on day 344 in 2008, although the exact thermal response to this dewatering differed between sites. Temperature at S23 dropped below freezing and correlated more strongly with air temperature when dewatering occurred, although there was typically a large difference between temperatures at S20 and air temperature which was probably due to an insulating effects of snow and ice around the radiation shield (cf. Brown et al., 2006b). In contrast, the temperature recorded at S3 was relatively stable throughout the winter (~ 0.3 °C). An examination of S3 on day 344 in 2008 revealed significant pooling in the channel beneath a 1m snowpack. However, dewatering had occurred around the temperature probe which was actually buried in the snowpack. This finding further highlights a need for direct observations before assuming that stable temperatures close to 0 ^{o}C reflect the presence of melt-waters flowing through a channel insulated from the atmosphere by snowpacks (Kobayashi et al., 1999; Brown et al., 2005, 2006b). Examination of the temperature time series leading up to day 344, 2008 revealed that temperature at S3 fell below freezing between days 327 - 329 before slowly building to ~ 0.3 ^{o}C and remaining stable throughout the winter. It is therefore probable that dewatering occurred around the temperature probe between days 327 - 329 in 2008 when the channel was openly exposed to air and then it became insulated by snow. However, if dewatering had occurred after the build-up of a snowpack, the logger temperature record alone may have proved insufficient to deduce with confidence if dewatering around the probe had occurred.

The temperature records and field observations suggested that surface flow generally ceased in the channel at S14 after ~day 37 in 2009, yet stagnant surface waters remained in the pool in which the logger was located. A possible explanation for the marked increase in logged temperature and increased stability of the temperature time series around day 37, 2009 is that surface freezing of the pool gave additional insulation from the atmosphere and snowpack whilst heat transfer from the bed continued. This theory is supported by the increased stability of temperatures at S14 after day 42 in 2009, associated with surface freezing (Kobayashi et al., 1999; Brown et al., 2006b). The evidence for pooling at S14 despite the lack of observed surface flow at close proximity may reflect the high spatial variability of surface/hyporheic flows in small streams during low flow conditions (Boulton et al., 1998).

A key barrier to determining flow permanency from water temperature records from the Eisboden main stem was the impracticality of installing temperature loggers in the stream thalweg. Instead, some loggers were located at the stream edge close to an anchoring point on the bank. Thus, from logged temperature alone it was only possible to conclude that stage had dropped below the temperature sensor rather than if stream flow had stopped altogether in the channel. Due to the typical instability of the stream bed in main glacial channels, and the inaccessibility for most of the year for maintenance due to fast, deep flows, the issue of dewatering around loggers before the discontinuation of stream flow is likely to be restrictive to flow permanency analysis in most monitoring situations of large proglacial streams. In addition, where dewatering does not occur, near 0^{o}C stable water temperature profiles in melt streams insulated from the atmosphere by a snowpack (Kobayashi et al., 1999; Brown et al., 2006b) will be difficult to separate with confidence from snow temperature profiles. In more stable groundwater streams, dataloggers can be more carefully sited. However evidence from S14 suggests that if placed in a pool to ensure that the sensor remains underwater even in low flow conditions, relatively high logged temperatures in winter will not always be associated with spatially continuous surface stream flow as pools may be interconnected by interstitial flow (Boulton et al., 1998). In order to improve the reliability of flow permanency predictions from water temperature records, the following recommendations are suggested when designing a monitoring network; (i) Install primary water temperature sensors as close as possible to the stream thalweg, in a pool or river gauging structure if possible to remain in the stream at extremely low flow conditions, (ii) Install a secondary sensor at each site in a riffle to give a broader indication of reach-scale differences in surface flow, and (iii) Install additional sensors out of the stream on the stream bank to record air temperature/snow temperature to provide an accurate terrestrial reference temperature with which to compare against water temperature (see Reusser & Zehe, 2011).

5.6 CONCLUSIONS

This study has illustrated how flow from hydropower storage reservoirs can have a dramatic and dynamic influence on the thermal dynamics of stream systems in alpine basins. In particular, previously observed hydropeaking patterns of reduced summer mean stream temperatures may not apply to streams that experience periodic flow from high-alpine reservoirs, particularly overspilling flows. This finding suggests that conclusions from previous studies examining the thermal response of sub-alpine rivers to flow regulation and the consequences of flow regulation for ecosystems (see Céréghino et al., 2002; Bruno et al., 2009b) are not necessarily applicable to stream systems at higher altitudes where (i) antecedent water temperatures may be cooler due to greater meltwater influence, and (ii) the timing and durations of flows discharged to regulate reservoir levels may vary from hydropeaking flows associated with peak power production which typically impact sub-alpine reaches (see Webb & Nobilis, 1995; Céréghino et al., 2002; Maiolini et al., 2003; Carolli et al., 2008; Toffolon et al., 2010; Zolezzi et al., 2010). Additionally, this study suggests that the effects of flow regulation on water temperatures can extend laterally across floodplains into mixed and groundwater streams reducing thermal heterogeneity even where there is no direct surface connectivity.

More research is needed to quantify the extent to which high alpine catchments are affected by hydropower reservoirs and to establish the significance of alternations to thermal habitat on river ecosystems. Milner's and Petts's (2001a) model of alpine community distribution suggests that water temperature is a key factor driving the distribution of benthic macroinvertebrates. Natural 'discontinuities' such as inputs from lakes or tributaries (Saltveit et al., 2001; Knispel & Castella, 2003; Uehlinger et al., 2003b; Brown et al., 2007a) are known to cause sustained or dramatic changes in water temperature (and other physicochemical variables) that impact upon aquatic ecosystems. In a similar manner, the releases from hydropower lakes as exemplified herein can be expected to alter stream community structure and function markedly. Indeed anthropogenic regulated flows may excert a particularly large influence within alpine basins (cf. natural discontinuities) because they are active outside of the summer melt season when naturally-occurring meltwater discharge, water temperature fluctuations and disturbance events are at a minimum (Anselmetti et al., 2007) and 'windows of opportunity' arise for ecosystems (Schütz et al., 2001; Malard et al., 2006; Tockner et al., 2010). More *year-round* research is required to establish the natural functioning of alpine ecosystems and to develop a holistic understanding of how flow regulation may impact upon alpine stream habitats. Pressures on alpine environments are likely to grow in the future due to further anthropogenic influence as well as climate change (Fette et al., 2007; Brown et al., 2009b). In the face of such pressures, it is vital that the full ecosystem effects of hydropower activities are better understood to inform management and the conservation of biodiversity.

CHAPTER 6: SPATIOTEMPORAL DYNAMICS OF STREAM MACROINVERTEBRATE COMMUNITIES

6.1 INTRODUCTION

The alpine zone hosts a unique array of benthic stream habitats, with spatial and temporal variations in glacier melt, snowmelt, and groundwater contributions to stream flow resulting in considerable spatiotemporal heterogeneity of physicochemical habitat conditions (Milner & Petts, 1994; Füreder, 1999; Brittain & Milner, 2001; Brown et al., 2003; Hieber et al., 2005; Brown et al., 2006d). However, the strong links between water source and physicochemical habitat conditions (Smith et al., 2001; Hannah et al., 2007a; Brown et al., 2009b) mean that that stream habitats are likely to be highly sensitive to anthropogenic pressures, particularly (i) climate change, and (ii) flow regulation which is widespread across the European Alps for hydropower, water supply and irrigation (Füreder et al., 2002; Wehren et al., 2010b). Therefore, a better understanding of alpine stream ecosystem response to anthropogenic pressures, is necessary to inform management and conservation practices (McGregor et al., 1995; Hannah et al., 2007a).

The major focus of ecological research on alpine stream systems over the last two decades has been to examine changes in macroinvertebrate community distributions longitudinally with respect to distance from the glacial margin, during the summer melt season (e.g. Burgherr & Ward, 2001; Gíslason et al., 2001; Lods-Crozet et al., 2001; Malard et al., 2001; Milner et al., 2001b; Snook & Milner, 2001; Ilg & Castella, 2006; Brown et al., 2007c; Jacobsen et al., 2010). Braided proglacial river reaches can however exhibit considerable physicochemical habitat diversity laterally which has largely been overlooked (Malard et al., 1999, 2000; Burgherr & Ward, 2001; Malard et al., 2006). During late-spring/early-summer, increased meltwater discharge leads to the lateral expansion of channel networks across floodplains, and melt water mixes with alluvial and hill-slope groundwater in varying proportions generating habitat heterogeneity (Malard et al., 1999; Malard et al., 2006). A number of studies (e.g. Tockner et al., 1999; Karaus, 2004; Arscott et al., 2005; Paillex et al., 2007) have noted the high beta diversity (between habitat; see Ward et al., 1999b) of biota colonising different habitats across *sub-alpine* floodplain reaches. Primarily the focus of these studies was to examine trends between channel connectivity and biota distributions. Tockner et al. (1999) found that a series of overlapping species richness maxima for macrophyte, mollusc, odonate and amphibian groups existed along a connectivity gradient across the floodplain of the Danube River, Austria. Conversely, Karaus (2004), Arscott (2005) and Paillex et al. (2007) examined macroinvertebrate distributions and found no clear relationships between macroinvertebrate community composition and connectivity. Arscott (2005) and Karaus (2004) did however observe strong taxa-to-environment concordance laterally. No studies to the authors knowledge have examined macroinvertebrate distributions across a truly alpine floodplain although Burgherr et al. (2002) found that high habitat heterogeneity existed across the Val Roseg floodplain, (situated close to the tree-line in the Swiss Alps) and that high beta diversity of macroinvertebrates occurred during the summer melt-season as a result of the spatial heterogeneity of physicochemical habitats. Collectively these studies suggested that relationships between macroinvertebrate community compositions and connectivity cannot be reduced to simple gradients and that there is a need to consider in more detail the complex patchwork of physicochemical habitats that arise as a consequence of spatiotemporal connectivity dynamics and to explicitly examine relationships between physicochemical habitat variables and macroinvertebrate community distributions at the floodplain scale.

In addition to the lateral dimension, the temporal dimension (see Ward, 1989), of alpine ecosystem dynamics, particularly year-round, has also been largely neglected. The alpine-zone remains snow covered for 6-9 months of the year which makes year-round access to sampling sites challenging and so most sampling programmes have been constrained to the summer months (Schütz et al., 2001). During spring and autumn, physicochemical conditions in proglacial channels are less harsh as melt contributions to stream flow are drastically reduced (Robinson et al., 2001; Saltveit et al., 2001; Schütz et al., 2001; Burgherr et al., 2002; Malard et al., 2006). The limited number of studies that have been conducted during these periods suggest that community structure in cold proglacial streams may diversify during spring and autumn (Saltveit et al., 2001; Burgherr et al., 2002), and that this diversification is associated with increases in benthic organic matter and growth of the golden alga *Hydrurus foetidus* (Robinson et al., 2001; Schütz et al., 2001; Malard et al., 2006). For example, Burgherr et al. (2002) and Salveit et al. (2001) found Ephemeroptera and Plecoptera close to the glacial margin during Spring and Autumn despite maximum temperatures not exceeding 4^{o}C (cf. Milner et al., 2001a). Ecological surveys have rarely been conducted during mid-winter owing to thick snowpack cover (but see Lavandier & Décamps, 1985; Schütz et al., 2001). Schütz et al. (2001) provided a novel insight into mid-winter macroinvertebrate distributions along the partially snow covered proglacial Rotmoosache stream, Austria. Schütz et al. (2001) found elevated abundances (during winter cf. summer) of several taxonomic groups including Ephemeroptera and Plectoptera, and 4 % of all taxa recorded were found only during winter. The finding of *Capnia vidua* (Plecoptera) was particularly significant as they had not been previously described in glacial streams above 2000m, probably because only early instars are present during summer and emergence occurs early in spring (Schütz et al., 2001). More research is needed to corroborate the findings of Schütz et al. (2001) and to further explore the drivers of year-round community composition.

Many alpine stream habitats are potentially compromised by anthropogenic regulation particularly as a consequence of storage and re-routing of water for hydropower generation (Füreder et al., 2002; Wehren et al., 2010b; see also Chapter 2). However, little is known about the effects of flow regulation on alpine stream macroinvertebrate communities as most studies have focussed on subalpine reaches below the reflux point of hydropower storage plants (e.g. Brunke, 2002; Céréghino et al., 2002; Bruno et al., 2009b). In contrast, Petts and Bickerton (1994) showed flow abstraction close to the glacial margin in the Borgne d'Arolla, Switzerland, significantly altered the longitudinal distribution of macroinvertebrate communities. Immediately downstream of abstraction points, streams were devoid of fauna due the intermittency of streamflow and frequent highly turbid purging flows. Conversely, further downstream the reduction of glacial melt water as a proportion of streamflow (cf. groundwater) ameliorated the physicochemical habitat of streams allowing a broader range of macroinvertebrates to colonise closer to the glacial margin than expected. Chapters 4 and 5 of this thesis have shown that re-routeing of flow from high altitude reservoirs can have large effects on river discharge (cf. Anselmetti et al., 2007; Wüest, 2010) and stream temperature of alpine stream systems, but no studies have examined the impacts of high altitude reservoirs on alpine benthic macroinvertebrate communities. It was hypothesised that macroinvertebrate community assemblages in the Eisboden would be sensitive to changes in physicochemical habitat conditions resulting from flow regulation.

This study examined year-round macroinvertebrate community distributions across the Central Eisboden Braidplain, which is impacted by water discharged from the Weiβsee reservoir (see chapters 4, 5). The aims were to: (i) examine spatiotemporal variability of benthic macroinvertebrate communities with respect to physicochemical habitat dynamics, across an alpine floodplain through two consecutive summer seasons; (ii) investigate year-round dynamics of macroinvertebrate distributions with respect to physicochemical habitat dynamics and snow cover, and; (iii) assess the impacts of flow regulation from a storage reservoir on alpine macroinvertebrate communities.

6.2 METHODS

Physicochemical variable and benthic macroinvertebrate sampling were conducted at six sites (A-E) across the Central Eisboden Braidplain (Figure 3.1). Details of the study area and sampling site locations are provided in Chapter 3. Sites were sampled three times during the summers of 2008 and 2009 at approximately monthly intervals (see Table 6.1), and additionally during December, 2008 (day 344) and March, 2009 (day 66). Throughout this chapter samples are referred to with a site code (A-F), season code (S = summer, W = winter), a period code (1-3) and the year as defined in Table 6.1. For example, sample C-S2-2009 refers to the sample collected at Site C during the second sampling period in Summer 2009.

During winter a snowpack up to 2.7 m depth covered Sites A, C, E and F. A dual phase Leica GPS500 differential GPS (±5 cm horizontal, ±10 cm vertical accuracy) was used to locate these snow covered sampling sites and a short length of channel (~2 m) was excavated carefully to allow access to the stream for sampling. To mitigate for any disturbance to benthic fauna during excavation, channel sections were covered with a black tarpaulin and left undisturbed for 24hrs prior to sampling (as per Schütz et al., 2001 (pers. comm.)).

6.2.1 Stream environmental variables

Electrical Conductivity (EC) and pH were measured at each site using a Hach HQ 40d meter. Stream water samples (~500 ml) were collected and Suspended Sediment Concentration (SSC) later determined in the laboratory by filtering (using Whatman 0.45 µm cellulose nitrate filter papers), drying and weighing (see Jones et al., 1999). Channel stability was assessed using the bottom component of the Pfankuch (PFAN) index (Pfankuch, 1975). Snow depth was measured at each snow covered site during winter sampling.

Stream discharge and water temperature records (see Chapters 4.2 & 5.2) were used to derive the following three indices based on continuous 15 min resolution data over the 7 days prior to 0:00GMT of sampling dates: (i) $\bar{Q}$, mean discharge; (ii) $\bar{T}$, mean water temperature and; (iii) T_{max}, maximum water temperature. Continuous discharge and water temperature data were not available for Site A for the week prior to sampling period 6 (30/06/09) due to a marmot severing the logger cable. A linear regression model constructed from 15 min data at Sites A and B during the following week was used to approximate discharge ($r^2 = 0.94$, $p < 0.01$) and water temperature ($r^2 = 0.97$, $p < 0.01$) at Site A to enable the calculation of indices (i-iii) for sampling period 6 (30/6/09).

6.2.2 Benthic Sampling

Five replicate Surber samples (0.05 m^2, 250 µm mesh net) were collected randomly from different sub-habitats (riffles, glides) at each site except A-W1-2008. Here, due to extremely low water and air temperatures, the Surber sampling net became clogged with ice and only three samples were collected. Samples were collected during the morning to avoid sampling patches only wetted during peak diurnal flow occurring late afternoon/evening. Benthos samples were preserved in the field in 70 % ethanol prior to sorting. Macroinvertebrates were sorted from samples and retained. Ash-Free Dry Mass (AFDM) of Particulate Organic Matter

(POM) in the remaining material (including algae which was not separated from samples) was determined by determining loss on ignition (see Steinman et al., 2006). Macroinvertebrates were initially sorted and counted under a light microscope (x10 magnification). Chironomidae were sub-sampled (n_s = 50), cleared by soaking in 10 % solution of KOH for ~12 hrs, mounted ventral side up on slides using Euporal and examined at x200-1000 magnification (see Epler, 2001). Taxa were identified to the lowest possible taxonomic level using current keys (see Appendix B). Most Ephemeroptera and Trichoptera to species level, Chironomidae to species, sub-genus or genus level, most non-chironomid Diptera to family and Plecoptera generally to genus level (except *Nemurella pictetii*). Where taxa could not be confidently identified to species level but were clearly distinguishable based on gross morphological features, these were separated into morpho-groups. Oligochaeta were not counted.

Table 6.1 - *Physicochemical variable and benthic sampling dates, with calendar days given in parentheses.*

Period code-year	Site A	Site B	Site C	Site D	Site E	Site F
S1-2008	01/07 (183)	01/07 (183)	01/07 (183)	01/07 (183)	01/07 (183)	01/07 (183)
S2-2008	31/07 (213)	31/07 (213)	31/07 (213)	31/07 (213)	01/08 (214)	01/08 (214)
S3-2008	28/08 (241)	28/08 (241)	28/08 (241)	28/08 (241)	28/08 (241)	28/08 (241)
W1-2008	09/12 (344)	09/12 (344)		09/12 (344)	09/12 (344)	09/12 (344)
W2-2009		07/03 (66)		07/03 (66)	07/03 (66)	
S1-2009	30/06 (181)	30/06 (181)	30/06 (181)	30/06 (181)	30/06 (181)	30/06 (181)
S2-2009	27/07 (208)	27/07 (208)	27/07 (208)	27/07 (208)	27/07 (208)	27/07 (208)
S3-2009	27/08 (239)	27/08 (239)	27/08 (239)	27/08 (239)	27/08 (239)	27/08 (239)

6.2.3 Statistical Analysis

The five replicate samples collected at each site/date were pooled prior to reach scale analysis to prevent patch-scale variability impeding the elucidation of reach scale trends (e.g. Woodward & Hildrew, 2002; Brown et al., 2006c). Macroinvertebrate spatiotemporal distribution data was summarised for each site on each sampling date by calculating; (i) total abundance, (ii) taxonomic richness (number of taxa) and; (iii) percentage composition of six taxonomic groups (Ephemeroptera, Plecoptera, Trichoptera, Orthocladiinae, Diamesinae and other taxa). Abundance data were $\log_{10}(x+1)$ transformed prior to statistical analysis to improve the normality of distributions.

To assess variance of abundance and richness between streams during the summer melt season, a repeated measures analysis of variance (ANOVA) was used with sites as the categorical factor and sampling date as the repeated measures factor, followed by Tukey's HSD tests (see Burgherr et al., 2002). To identify environmental variables associated with changes in stream macroinvertebrate analysis, multivariate ordination analysis was undertaken in the program CANOCO (Lepš & Šmilauer, 2003). The analysis was conducted using monthly samples (S1,2,3-2008 and, S1,2,3-2009). A preliminary Detrended Correspondence Analysis (DCA) was conducted to test the linearity of response of predictor variables and determine the appropriate ordination method. Responses were relatively linear (gradients <2.5) thus a direct gradient Redundancy Analysis (RDA) was conducted using a stepwise forward selection procedure with Monte-Carlo Permutation tests to assess the significance of associations between taxa and physicochemical predictor variables (see McGarigal et al., 2000; Lepš & Šmilauer, 2003). Variables were considered as significant predictors where $p < 0.05$, and probabilities for simultaneous tests were corrected with a sequential Bonferroni technique. To explore the relationship between upstream connectivity with the main glacial channel and macroinvertebrate communities at mixed sites; C and D during the summer melt season, linear regressions were conducted between: $\overline{Q}$, and abundance and taxonomic richness. $\overline{Q}$ was deemed a suitable indicator of connectivity, as discharge at Sites C and D was primarily driven by upstream surface connectivity with the main glacial channel. Data from D-S3-2008 and D-S3-2009 were excluded from these regression analyses because overtopping from the Weiβsee and may have confounded connectivity relationships.

To assess the impacts of overtopping from the Weiβsee on the macroinvertebrate community in the main glacial channel, a before-after-control-impact (BACI) design was used. Individual sampling replicates (five per site) collected on S2-2008 and S2-2009 were used as before measures and S3-2008 and S3-2009 as after measures. Site A was used as the control and Site B as the impacted site. Two ANOVA's with repeated measures were conducted using abundance and taxonomic richness values calculated for each of the sampling replicates. Time (before/after impact), and year were used as repeated measures. ANOSIM analysis (Warwick et al., 1990; Clarke, 1993) was conducted to test for differences in community composition amongst BACI samples for each year based on the Bray-Curtis dissimilarity matrix computed between all BACI replicates. ANOVA and ANOSIM analysis were both conducted using the programme PAST.

6.3 RESULTS

6.3.1 Summer melt season

6.3.1.1 Stream physicochemical habitat variables

Clear spatiotemporal differences in physicochemical habitat variables were evident between sites (Table 6.2). In general main stem sites (A and B) had the harshest physicochemical habitat (i.e. low $\overline{T}$, T_{max}, PFAN, and POM concentrations, but high $\bar{Q}$ and SSC). Sites C and D had intermediate habitat conditions and, Sites E and F the least harsh conditions. Spatiotemporal trends in stream discharge and water temperature amongst sites have been discussed in detail in Chapter 4 and 5. Sites B and D, and to a lesser extent Site E were affected by overspill from the Weiβsee prior to the sampling period S3 in 2008 and 2009 which elevated stream temperatures and discharge. During summer 2009, a greater proportion of flow from the main channel was routed across to the west side of the braidplain resulting in higher discharges and lower stream temperatures (Figures 4.6, 5.3). The stream in which Site E was situated also became connected with the mixed side channels feeding down the west side of the braidplain which caused a reduction in channel stability and had a large effect on $\bar{Q}$ (Figure 4.6).

Table 6.2 - *Mean physicochemical habitat variables at each site during the summers of 2008 and 2009. Standard deviations are given below in parentheses.*

	A		**B**		**C**		**D**		**E**		**F**	
	2008	**2009**	**2008**	**2009**	**2008**	**2009**	**2008**	**2009**	**2008**	**2009**	**2008**	**2009**
PH	7.36	7.57	7.59	7.57	7.37	7.67	7.52	7.60	7.60	7.75	7.81	7.96
	[0.44]	[0.07]	[0.19]	[0.24]	[0.40]	[0.06]	[0.32]	[0.09]	[0.08]	[0.08]	[0.19]	[0.09]
EC (µScm^{-1})	33.3	29.3	31.9	27.9	30.0	30.2	43.8	25.0	44.7	45.7	68.2	59.1
	[10.6]	[2.1]	[3.8]	[8.4]	[7.1]	[1.6]	[6.7]	[4.3]	[23.4]	[5.9]	[8.2]	[2.6]
PFAN	52	52	49	49	34	34	34	34	19	24	20	20
	[0]	[0]	[0]	[0]	[0]	[0]	[0]	[0]	[1]	[7]	[0]	[0]
SSC (mgL^{-1})	301	42	279	632	151	54	132	53	4	1	1	4
	[202]	[23]	[191]	[104]	[172]	[29]	[104]	[28]	[2]	[2]	[1]	[7]
POM (gm^{-2})	1.33	3.16	1.74	1.46	1.16	1.89	0.95	1.76	3.44	2.74	2.52	19.05
	[0.29]	[2.81]	[1.15]	[0.56]	[0.59]	[0.57]	[0.59]	[0.28]	[1.90]	[2.64]	[1.38]	[21.64]
$\bar{Q}$ (m^{3}s^{-1})	1.1	1.15	1.50	2.06	0.11	0.24	0.29	0.76	0.012	0.026	0.013	0.009
	[0.43]	[0.60]	[0.56]	[1.74]	[0.15]	[0.12]	[0.22]	[0.59]	[0.002]	[0.015]	[0.004]	[0.004]
$\overline{T}$ (°C)	1.88	1.49	3.66	3.43	4.24	2.29	4.59	2.68	5.72	4.04	5.43	4.55
	[0.13]	[0.41]	[1.94]	[2.38]	[1.00]	[1.04]	[3.41]	[0.84]	[0.55]	[1.30]	[0.10]	[1.23]
T_{max} (°C)	3.72	2.80	6.06	5.75	10.74	6.00	7.40	6.37	10.49	8.57	7.83	6.57
	[0.50]	[0.74]	[1.39]	[1.94]	[2.97]	[3.26]	[4.08]	[2.89]	[0.64]	[1.62]	[0.22]	[1.08]

6.3.1.2 Macroinvertebrate communities

Sixty-six taxa of the total 71 observed in the study were found during the summer observation periods (see Appendix C for taxa list). ANOVA revealed that significant differences in taxonomic richness and, to a lesser extent, abundance occurred between sites during summer (Table 6.3, 6.4). Taxonomic richness in predominantly groundwater fed sites (E and F) was significantly higher than richness at all other sites ($p < 0.0005$), abundance and taxonomic richness were distinctly lower in the main glacial channel at Site A compared to other sites, except the lower glacial-channel site (B). Abundance and taxonomic richness (Figure 6.1) increased with decreasing habitat harshness from glacial through to groundwater dominated streams.

Table 6.3 - *Results of ANOVA comparing macroinvertebrate log (abundance+1) and taxonomic richness recorded at each site (DOF = degrees of freedom).*

		DOF	F-value	p-value
Log (abundance +1)	Between Groups	5	9.302	<0.001
	Within Groups	30		
Taxonomic Richness	Between Groups	5	38.919	<0.001
	Within Groups	30		

Macroinvertebrate assemblages exhibited considerable temporal variation in terms of abundance both within and between summers 2008 and 2009. For example, abundances recorded at mixed stream sites (C and D) were markedly greater during the summer 2008 than 2009, although richness and community composition remained similar (Figures 6.2, 6.3). Particularly high total abundance was observed at B-S3-2009 (6300 ind.m^{-2}) and E-S1-2009 (11124 ind.m^{-2}; Figure 6.2). These abundance peaks were not associated with a major dominance of one species, instead being composed predominantly of *Diamesa bertrami* (636 ind.m^{-2}), *Diamesa cinerella/zernyi gr.* (1516 ind.m^{-2}) and *Diamesa latitarsis gr.* (3720 ind.m^{-2}) at B-S3-2009, and; *D.cinerella/zernyi gr. gr.* (3108 ind.m^{-2})*, Orthocladius rivicola gr.gr*. (3092 ind.m^{-2}), and *Parorthocladius nudipennis* (2080 ind.m^{-2}) at E-S1-2009. Figure 6.2 shows that in the predominantly groundwater fed streams (Sites E and F), and the main-glacial stream at Site A, the highest total abundance typically occurred during late June/ early July, reached a low in late July /early August and then a secondary smaller peak in abundance in late August. This bi-seasonal peak in abundances at Sites A, E and F was much stronger in 2009 than 2008; indeed in 2009 the same trend was also observed at Sites C and D. However, these bi-seasonal temporal patterns in abundance were not considered significant as monthly abundance peaks were not consistently associated with any specific taxa in both 2008 and 2009 and samples were not considered to be spatially independent.

Table 6.4 - *Significance values from Tukey's HSD Post Hoc analysis of ANOVA comparing macroinvertebrate log (abundance+1) and taxonomic richness recorded at each site.*

		Site A	Site B	Site C	Site D	Site E
Abundance	Site A					
	Site B	0.091				
	Site C	0.043	0.999			
	Site D	0.002	0.686	0.865		
	Site E	0.000	0.107	0.206	0.823	
	Site F	0.000	0.036	0.077	0.533	0.996

		Site A	Site B	Site C	Site D	Site E
Taxonomic Richness	Site A					
	Site B	0.130				
	Site C	0.052	0.998			
	Site D	0.028	0.982	1.000		
	Site E	0.000	0.000	0.000	0.000	
	Site F	0.000	0.000	0.000	0.000	0.995

In terms of community composition Chironomidae, particularly the sub-family Diamesinae, were by far the most dominant taxa at Sites A-D (Figure 6.3), with the exception of A-S3-2008 when *Cheilotrichia sp.* (Limoniidae) dominated the relatively small assemblage (abudance= 40 ind.m^{-2} vs. total abundance = 56 ind.m^{-2}). Although Sites E and F had on average significantly higher taxonomic richness than any other sites ($p < 0.0005$, Tukey's HSD Post Hoc analysis of ANOVA), community composition exhibited considerable temporal variation. For example, Diamesinae dominated at E- and F-S1-2008 accounting for 69.3 % and 83.4 % of individuals respectively, compared to E- and F-S3-2008 when Diamesinae accounted for only 6.9 % and 0.5 % of individuals respectively. For the latter, Orthocladinae were the dominant taxa (accounting for 79.4 % and 82.8 % of individuals respectively). In addition to Orthocladiinae, other Diptera, particularly *Clinocera sp., Cheilotrichia sp., Dicranota sp.,* and *Prosimulium sp.*, the Ephemeroptera *Baetis alpinus*, and Trichoptera (particularly *Drusus monticola*) were also prevalent in ground water streams (Sites E and F).

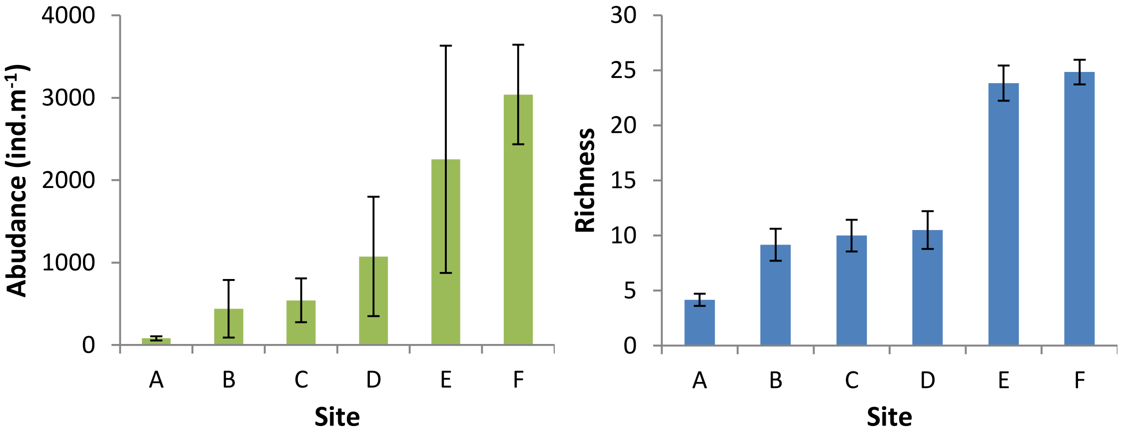

Figure 6.1 - *Bar charts showing mean; a) abundance (back transformed from log (abundance +1) means) and; b) taxonomic richness, observed at each site during summer 2008 and 2009. Error bars indicate SE.*

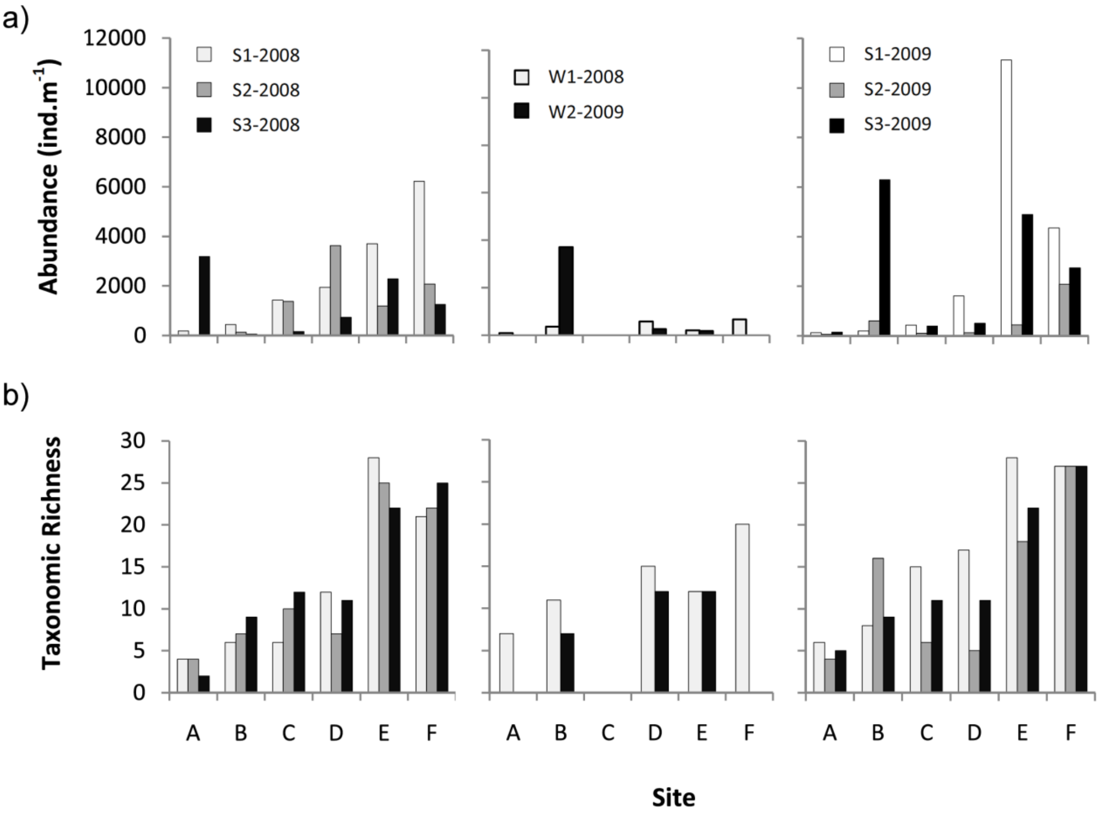

Figure 6.2 - *Bar charts showing; (a) total abundance and; b) taxonomic richness, observed at each site during summer 2008, Winter 2008/2009 and summer 2009.*

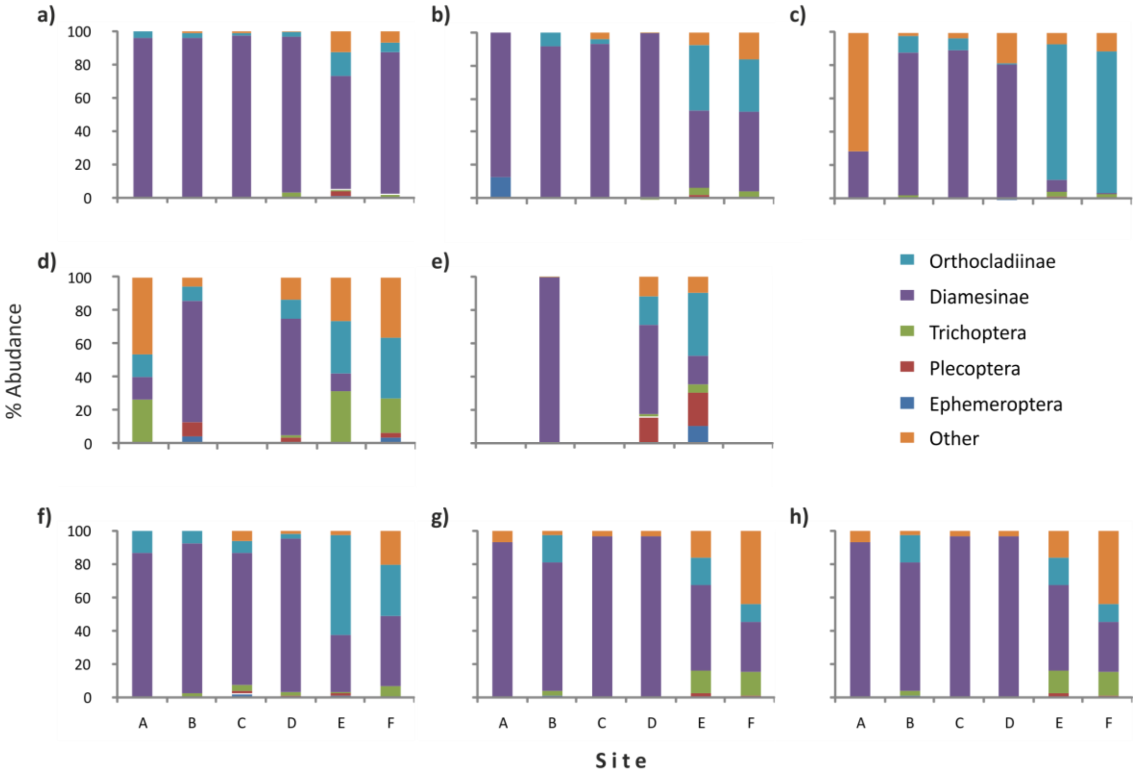

Figure 6.3 - *Relative abundance of selected macroinvertebrate Orders and Chironomidae sub-families at a) S1-2008, b) S2-2008, c) S3-2008, d) W1-2009, e) W2-2009, f) S1-2009, g) S2-2009 and h) S3-2009.*

6.3.1.3 Physicochemical habitat and macroinvertebrate community relationships

Axis 1 and 2 of the RDA (summer data set) respectively accounted for 37.4 and 8.7 % of species variation and 62.4 and 14.6 % of species-environment variation (Table 6.4). Species-environment correlations for axis 1 and 2 were 0.978 and 0.799, respectively. Forward selection reduced the environmental variables dataset to PFAN, $T_{max,}$ conductivity and $\bar{Q}$. These variables respectively explained 49.0, 12.2, 8.2 and 8.2 % of variance in the macroinvertebrate data (Table 6.6). The first RDA axis was strongly correlated with conductivity (r = 0.82), and inversely correlated with PFAN (r = -0.92) and $\bar{Q}$ (r = -0.65). The second RDA axis was strongly correlated with T_{max} (r = 0.82) (Figure 6.4).

Most taxa exhibited strong associations with conductivity, channel stability and low discharge, although differences between taxonomic groups were evident from the RDA analysis (Figure 6.3). For example, Trichoptera (with the exception of Psychomyiidae, the only non-case bearing Trichoptera recorded) had negative scores on the 2nd RDA axis in contrast to Plecoptera and Ephemeroptera which had positive scores. The majority of Orthocladiinae species had weak negative or neutral scores on the 2nd RDA axis (except *O.rivicola*, *Corynoneura sp., Orthocladius frigidus* and *Orthocladius s.str*), *Diamesa* species on the other hand had relatively strong positive scores on the 2nd RDA axis. Spatial heterogeneity was evident from the separation of sites along the 1st RDA axis. Main glacial stem sites (A and B) generally had the most negative scores on the 1st RDA axis, mixed sites (C and D) had slightly negative or neutral scores whilst predominantly groundwater fed sites (E and F) had positive scores. Regression analysis revealed no significant relationship between $\bar{Q}$ and abundance or taxonomic richness ($p=0.731$, $r^2=0.02$ for both tests) at mixed sites (C and D).

Table 6.5 - *Summary of results for RDA axis 1, 2 and 3 for the summer analysis*

	Axis 1	**Axis 2**	**Axis 3**	**All**
Summer analysis (S1,2,3-2008 & S1,2,3-2009)				
% variance explained of species variation	37.4	8.7	4.5	-
% variance explained of species-environment variation	62.4	14.6	7.4	-
Eigenvalue	0.304	0.071	0.036	1
p-value	0.001	0.003	0.293	0.001
Species-environment correlation co-efficient	0.978	0.799	0.878	

Table 6.6 - *Selected variables based on step-wise forward selection*

	% Variance explained	**p-value**	**f-value**
Summer analysis (S1,2,3-2008 & S1,2,3-2009)			
PFAN	49.0 %	0.001	12.47
$\boldsymbol{T_{max}}$	12.2 %	0.001	2.79
EC	8.2 %	0.007	2.50
$\boldsymbol{\bar{Q}}$	8.2 %	0.008	1.61

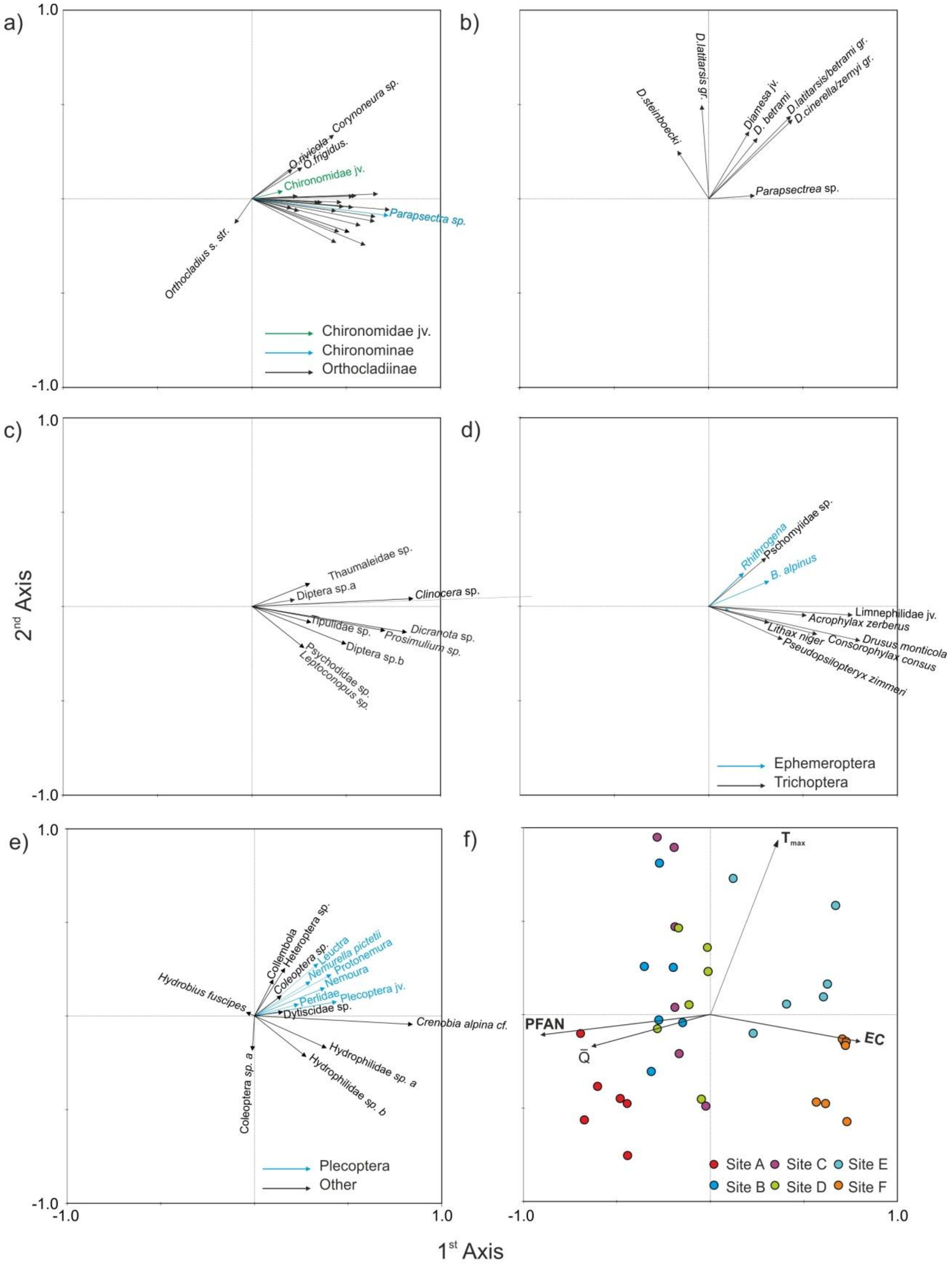

Figure 6.4 - *RDA analysis output for summer data. Individual panels show; (a) Chironomidae jv., Chironominae and Orthocladiinae; (b) Diamesinae; (c) non-chironomidae Diptera larvae; (d) Ephemeroptera and Trichoptera; (e) Plecoptera and other taxa, and; (f) sites.*

6.3.2 Winter

6.3.1.1 Stream physicochemical habitat variables

During winter sites, unaffected by drawdown from the Weiβsee; A, C and F, were covered by a thick snowpack on W1-2008 (1-2 m thick) and an even thicker snowpack on W2-2009 (1.8-2.5 m) (Table 6.4). Site C was not flowing on W1-2008 and no stream flow was observed at Sites A, C or F on W2-2009. Continuous time-series stream temperature and discharge data sets showed that where streams were flowing, diurnal variability in discharge and water temperature underneath snowpacks was greatly suppressed during the winter months, (see Chapters 4 and 5). Indeed; $\bar{Q}$, $\bar{T}$, and T_{max} were all markedly reduced at Sites A and F for W1-2008 and, POM and SSC were also reduced here compared to observations during summer.

Table 6.7 - *Physicochemical habitat variables during winter (W1-2008 and W1-2008). [Nb. where no data except snow depth is given, no stream flow was present and sites could not be sampled]*

	A		B		C		D		E		F	
	W1-2008	W2-2009	W1-2008	W2-2009	W1-2008	W2-2009	W1-2008	W2-2009	W1-2008	W2-2009	W1-2008	W2-2009
pH	7.32	-	7.52	6.58	-	-	7.19	6.56	7.32	6.58	6.85	-
EC (µScm^{-1})	24.6	-	45.7	32.5	-	-	37.5	27.1	54.2	68.3	65.2	-
PFAN	52	-	49	49	-	-	34	34	20	20	20	-
SSC (mgl^{-1})	0	-	60	0	-	-	20	0	2	0	0	-
POM (gm^{-2})	0.04	-	0.31	1.23	-	-	1.63	4.64	1.58	1.56	1.81	-
$\bar{Q}$ (m^{3}s^{-1})	<0.01	-	1.28	0.34	-	-	0.35	0.01	<0.01	0.01	<0.01	-
$\bar{T}$ (^{o}C)	0.20	-	0.81	0.47	-	-	0.87	0.62	1.54	1.60	2.68	-
T_{max} (^{o}C)	0.3	-	2.9	0.7	-	-	2.70	1.20	1.6	1.6	2.7	-
Snow Cover	1.0	1.8	0.0	Patchy	1.4	2.0	0.0	Patchy	0.7	2.67	2.0	2.5

6.3.1.2 Macroinvertebrate communities

Forty-two taxa of the total 71 observed were found during winter and five of these were found only during winter (D*iamesa permacer/dampfyi gr.*, *Brillia modesta*, *Smittia sp.*, Nemouridae jv. and Brachyptera sp.). Of these, *B.modesta* and *Smittia sp.* were only observed at sites under snow cover. A large diversification of the macroinvertebrate assemblage occurred in the snow covered main glacial river was observed at Site A in December (Figures 6.2b, 6.3). The number of taxa collected at Site A increased to seven, compared with 2-6 taxa observed during summer. The total abundance of Diamesa fell drastically and *D.latitarsis* were the only species of this genus observed (8 ind.m-1). In contrast to summer, *Acrophylax zebrus*, *Parapsectra sp.*, *Heleniella serratosioi*, *Clinocera sp.* and *Dicranota sp.* were present in the assemblage. Overall, abundance and richness observed in the snow covered groundwater stream (Site F) were lower during winter compared to summer (Figure 6.2). However, the relative abundance of non-chironomidae taxa increased during winter at Sites F (Figure 6.3) as there was a particularly large decrease in Chironomidae abundance.

6.3.2 Effects of Weißsee overspill and drawdown on macroinvertebrate communities

6.3.2.1 - Summer overspill

Water temperature and discharge increased significantly at Site B (see chapters 4 and 5) during periods of overspill while physicochemical conditions at Site A were relatively similar in the periods prior to sampling at S2-2008 and S2-2009, and S3-2008 and S3-2009. ANOVA with repeated measures indicated that there was no significant change in taxonomic richness or abundance with time (i.e. before and after overspill; Table 6.8).

Table 6.8 - *Result of repeated measures ANOVA to assess the effect of Weißsee overspill on* log_{10}*(abundance +1) and taxonomic richness at Site B compared to the control Site A.*

	Log_{10}(Abundance +1)		**Taxonomic Richness**	
	F	**Sig.**	**F**	**Sig.**
Time (before-after)	2.443	.193	.784	.426
Site	15.534	.017	59.796	.002
Year	17.511	.014	13.037	.023
Time * Site	.088	.782	.930	.389
Time * Year	7.263	.054	1.739	.258
Site * Year	6.017	.070	47.515	.002
Time * Site * Year	3.282	.144	6.291	.066

** shows significance of interactions between variables.*

ANOSIM result suggests that there was no significant difference in community composition between any of the BACI samples (before overspilling - after overspilling - Site A- Site B); see Table 6.9. In 2009 the results are less clear; un-corrected p-values indicate that significant differences in community composition existed between; (i) Sites A and B before regulation, (ii) Site A before and Site B after regulation, (iii) Site B before and Site B after regulation, and (iv) Site A after regulation and Site B after regulation. However, in all cases Bonferroni corrected values indicated no significant differences between samples.

Table 6.9 - *ANOSIM Results, significant values are highlighted in bold italics; Bonferroni corrected values are in round parentheses, R values are in square parentheses below. Overall test statistics; R = 0.169, mean rank within groups = 331.5, mean rank between groups = 397.2, and p = 0.0009*

2008			
	Site A- Before	**Site B - Before**	**Site A - After**
Site B - Before	0.740 (1) [-0.084]		
Site A - After	0.167 (1) [0.13]	0.050 (1) [0.324]	
Site B - After	0.9102 (1) [-0.142]	0.6324 (1) [-0.048]	0.1432 (1) [0.162]
2009			
Site B - Before	***0.024*** (0.658) [0.384]		
Site A - After	0.442 (1) [-0.002]	***0.020*** (0.563) [0.22]	
Site B - After	***0.008*** (0.227) [0.376]	***0.007*** (0.199) [0.588]	***0.008*** (0.235) [0.340]

6.3.2.1 - Winter drawdown

Drawdown releases from day 332, 2008, through to day 44, 2009, affected the stream physicochemical conditions at Sites B and D, and to a lesser Site E during winter (See Chapter 5). Site B and D were subject to large drawdown flows from the Weiβsee in the week preceding the sampling day W1-2008. $\bar{Q}$, $\bar{T}$, and T_{max} were all markedly elevated at Sites B and D, by relatively warm waters discharged from the Weiβsee. SSC values > 20 mgl^{-1} were also observed on W1-2008 at Sites B and D in contrast to values < 2 mgl^{-1} recorded elsewhere during winter on W1-2008, and at flowing sites; B, D and E on W1-2009. Sites B and D were free of snow cover on W1-2008. Drawdown stopped 22 days prior to the sampling period W2-2009 and patchy snow cover had accumulated at Sites B and D by W2-2009. $\bar{Q}$ and T_{max} were markedly lower on W2-2009 by 0.9 m^{3}s^{-1} and 2.2 ^{o}C, and 0.3 m^{3}s^{-1} and 1.5 ^{o}C respectively at Sites B and D, relative to W1-2008. $\bar{T}$ was slightly lower (by 0.3 ^{o}C at both Site B and D). Large blooms of the golden alga *Hydrurus foetidus* were observed on W2-2009 at Sites B and D, and POM observed increased by a factor of 4 and 3 at Sites B and D respectively from observations on W1-2008.

In common with observations at un-impacted sites (A and F), generally numbers of chironomidae taxa and particularly Diamesa taxa which dominated summer assemblages decreased markedly at sites inundated by reservoir drawdown waters (B and D), indeed *D.latitarsis/bertrami* and *Diamesa steinboecki* disappeared from the assemblage altogether during winter. However, *D.cinerella/zernyi gr.* proved a notable exception which was prolific at sites inundated by reservoir drawdown waters (Site B; 264 and D; 320 ind.m^{-2}) during winter, in contrast it was absent at non-inundated sites (A and F) and only 4 ind.m^{-2} were observed at Site E. Although *D.cinerella/zernyi gr.* was common at all sites during summer, maximum abundance of *D.cinerella/zernyi gr. was* observed in winter (3624 ind.m^{-2}) at B-W2-2009. *D.dampfyi/*permacer gr. was another exception that was observed exclusively at Site D and only on winter sampling dates. In contrast to all other flowing snow covered sites, Trichoptera taxa were not common at Site D (<8 ind. m^{-1}) and were absent from Site B.

Site E was snow covered on both W1-2008 and W2-2009 but under the snowpack flow persisted throughout the winter. With the exception of day 346, 2008, no surface connection was present between Site E and upstream flows from the Weiβsee. However, temperature time series (see chapter 5) showed that water from the Weiβsee influenced water temperature slightly at Site E when drawdown occurred. Both $\bar{Q}$ and T_{max} were ~ 1 ^{o}C cooler at E-W1-2008 in comparison to conditions at groundwater Site F (Table 6.7). Abundance and taxonomic richness were respectively 70 % and 40 % lower at Site E than Site F on W1-2009. In terms of community composition, in contrast to Site F, Site E contained *Diamesa* taxa, but no *Baetis* or Plecoptera. Whilst on W2-2008, Site F was not sampled as the stream bed was dry, Site E was flowing and abundance and taxonomic richness remained almost unchanged from W1-2009.

6.4 DISCUSSION

This study has investigated the spatiotemporal dynamics of macroinvertebrate assemblages across the Eisboden braidplain through two summer melt seasons and the intervening winter period. There are there key novel aspects to the data set collected and analysed: (i) no studies to my knowledge have previously examined macroinvertebrate assemblages amongst different stream types across a truly alpine floodplain (but see 2002 who examined macroinvertebrate assemblages across the Val Roseg floodplain, which is situated close to the tree-line in the Swiss Alps), (ii) very few studies have sampled alpine streams year-round due to logistical difficulties during winter (but see Lavandier & Décamps, 1985; Schütz et al., 2001; Burgherr et al., 2002; Robinson et al., 2002), and (iii) no studies to my knowledge have examined the effects of reservoir over-spilling, or drawdown on habitat and macroinvertebrate assemblages in an alpine catchment. The proceeding discussion focuses on each of these novel aspects of the study in turn.

6.4.1 Summer macroinvertebrate assemblages

This study generally supported the view that during the summer melt-season, distinct floodplain habitats support distinct macroinvertebrate assemblages (see Arscott et al., 2000; Burgherr et al., 2002). Channel stability and T_{max} are considered to be key physicochemical drivers influencing longitudinal trends in macroinvertebrate assemblages along proglacial streams (Burgherr & Ward, 2001; Gíslason et al., 2001; Lods-Crozet et al., 2001; Malard et al., 2001; Milner et al., 2001a; Milner et al., 2001b; Snook & Milner, 2001; Ilg & Castella, 2006), and accordingly in this study, they were also found to explain the greatest proportion of variance in macroinvertebrate gradients. Conductivity and $\bar{Q}$ were also found to explain a significant but smaller proportion of variance (8.2 % each) in macroinvertebrate distributions (see Steffan, 1971; Brown et al., 2007b)

The lowest total abundance (max 184 ind.m^{-1}) and taxonomic richness (6 taxa) were observed at Site A, which was characterised by harsh physicochemical conditions including low channel stability, conductivity < 45 µScm^{-1} and T_{max} < 3.7 ^{o}C. The assemblage here during summer was typical of a European glacial stream reach close to the glacial margin (Füreder et al., 2001; Milner et al., 2001a; Snook & Milner, 2001), predominantly consisting of *Diamesa* with the occasional *Eukiefferiella claripennis* and *Cheilotrichia sp*. In glacial streams not impacted by flow regulation, macroinvertebrate communities are generally expected to diversify downstream primarily due to increasing stream temperatures and channel stability (Burgherr & Ward, 2001; Gíslason et al., 2001; Lods-Crozet et al., 2001; Malard et al., 2001; Milner et al., 2001b; Snook & Milner, 2001; Ilg & Castella, 2006). Indeed in the Eisboden, in June and July, when the Weiβsee was not overtopping, *Pseudokiefferiella sp.,* Orthocladiinae taxa, Prosimulium sp. Thaumaleidae, *Rhithrogena sp.* and Limnephilidae jv., also appeared in the community assemblage, less than 500m further downstream at Site B. Given the increase in T_{max} to 5.6^{o}C and increased channel stability, with the exception of Heptageniidae and Limnephildae *jv.* these observations support the conceptual model of Milner and Petts (2001a). Several studies have reported exceptions to Milner et al.'s (2001a) model, for example Lods-Crozet et al., (2001) and Füreder et al. (2001) reported EPT (Ephemeroptera, Plecoptera and/or Trichoptera) taxa where T_{max} < 4 °C suggesting that the model may provide only a general approximation. However, Heptageniidae and Limnephildae *jv.* appeared in the assemblage only in summer 2009 when a large volume of flow was routed down the west side of the braidplain into previously unconnected groundwater streams (e.g Site E; see chapter 4). Enrichment from more benign tributaries has previously been suggested as a mechanism to explain the presence of EPT taxa in habitats where they would not be expected due to the harshness of the immediate environment (Saltveit et al., 2001; Knispel & Castella, 2003). It is possible that the presence of Heptageniidae and Limnephildae *jv.* at Site B was due to enrichment from groundwater streams that became connected as the braidplain became more active during Summer 2009. That fact that the Limnephildae observed were juveniles may also be significant, because Lavandier and Décamps (1985) suggested that although young larvae may be fairly ubiquitous, their development will be restricted in overly harsh habitats.

In predominately groundwater fed Sites E and F, total abundance was significantly higher than in the main glacial stream and macroinvertebrate assemblages were considerably more diverse. This finding is supported by several studies that have observed greater abundances and richness in alpine streams predominantly sourced from groundwater rather than streams at similar altitudes sourced from glacial melt (e.g. Füreder, 1998; Füreder, 1999; Ward et al., 1999b; Burgherr et al., 2002; Brown et al., 2007b). However, this community level finding may not hold for individual taxa. In a study in the French Pyrénées, Brown et al. (2007b) found lower Trichoptera abundance in streams with large groundwater components. However, in contrast, across the Eisboden braidplain, RDA analysis revealed that abundances of Trichoptera taxa (with the exception of Psychomyiidae, the only caseless Trichoptera observed) were heavily correlated with conductivity which is typically associated with increasing groundwater contributions (Ward et al., 1999a; Smith et al., 2001; Brown et al., 2006c; Malard et al., 2006; Brown et al., 2007b). A possible explanation for this discrepancy is that whilst Trichoptera may be associated with decreasing groundwater influence (see Brown et al., 2007b), ultimately there exists a threshold below which physicochemical are too harsh for habitation by Trichoptera (Milner et al., 2001a) and habitat conditions are evidently below that threshold at Sites A-D during the summer melt season. This finding highlights the need for caution in assuming the generality of taxa-environment gradients across habitats (see Guisan & Zimmermann, 2000; Vaughan & Ormerod, 2003).

6.4.2 Winter macroinvertebrate assemblages

Proglacial floodplains typically contract during winter as melt driven inputs are drastically reduced and discharge becomes insufficient to maintain lateral surface connectivity or sustain subsurface pathways feeding groundwater upwellings (Malard et al., 1999; Arscott et al., 2002; Malard et al., 2006). In some basins, surface flow may be curtailed even in a main glacial channel during winter; for example, Malard et al. (1999) found that water source contributions declined to such an extent that no surface flow was present in the main glacial channel along the length of the upper Val Roseg floodplain during winter. At sites on the Eisboden floodplain unaffected by flow-release from the Weiβsee (Sites A, C and F) discharge declined drastically during autumn/winter to such an extent that no surface water was observed during December at Site C, and by March there was also no surface flow present in the main channel at Sites A or in the groundwater stream hosting Site F. Sites B, D and E were perennial and possessed similar stream characterisitics to those observed in previous studies during winter once drawdown from the Weiβsee had ceased (Malard et al., 2000; Füreder et al., 2001; Robinson et al., 2001; Schütz et al., 2001; Burgherr et al., 2002). In summary, discharge, stream temperature and SSC were relatively low and diurnally stable compared with the summer observations made at these sites.

In the main glacial channel at Site A, a distinct shift in the macroinvertebrate community composition was observed in December, and several taxa not present in the assemblage during summer were observed, including members of the Trichoptera, Plecoptera, Empididae, Pediciidae and Chironomidae families. Because Site A was only sampled once during winter and only three sub-samples were collected due to the Surber sampler freezing, the relatively modest increase in taxonomic richness from summer to winter (from between two and six taxa in summer, to seven in December) may actually be a conservative representation of the community diversification that occurred. The tendency for community composition to diversify in main glacial channels during winter when habitat conditions become more benign has been observed previously (see Burgherr & Ward, 2001; Füreder et al., 2001; Robinson et al., 2001; Schütz et al., 2001). It has been suggested that some taxa in cold environments actively migrate from freezing/drying streams into flowing waters to avoid desiccation (Irons et al., 1993). As alpine floodplains become less active in winter (Malard et al., 2006), the main glacial channel may act consequently as a refuge to a diverse range of taxa (Lavandier & Décamps, 1985; Lencioni, 2004).

The absence of permanent surface flow at some alpine stream sites during winter has been suggested as a key antecedent factor that lowers macroinvertebrate abundance and subsequently restricts the presence of many taxa in upstream reaches during the spring and summer (see Kownacka & Kownacki, 1972; Snook & Milner, 2001; Lencioni, 2004). Certainly there was a large change in community composition above and below the longitudinal threshold of year-round flow permanency between Sites A and B. However the diversification that occurred at Site A during winter, prior to flow cessation suggests that that taxa are able to colonise within a few months when conditions ameliorate. Robinson et al. (2001) observed, very restricted macroinvertebrate assemblages during summer in perennial Swiss proglacial streams, yet during winter when conditions ameliorated significant diversification occurred. It seems therefore that it is mainly the harshness of physicochemical conditions during summer that restrict the presence of taxa from the summer community composition in upstream reaches of proglacial streams rather than the lack of year-round flow. It is however likely that survival rates of taxa that attempt to over-winter in-situ by diapausing rather than emigrating

(Danks, 1971b; Lavandier & Décamps, 1985; Irons et al., 1993; Lencioni, 2004), will be reduced during winter if the stream bed freezes due to increased mortality rates associated with desiccation and freezing (Irons et al., 1993). Abundance of some non-migrating taxa such as some chironomids and empidids may therefore be reduced subsequently during the summer at sites where the streambed freezes in winter.

Chironomidae abundance fell dramatically during winter at sites under snow cover (A, E and F), a finding which is supported by the results of Schütz et al. (2001) from the proglacial Rotmoosache stream, Austria, and by those of Lavandier & Décamps (1985) in the Estaragne, an alpine non-glacially fed Pyrénéan stream. A possible explanation for these consistent findings is that most Chironomidae, and particularly Orthocaldiinae larvae (see Lavandier & Décamps, 1985), do not overwinter in the upper layer of the benthos. Instead they seek refuge deeper in the hyporheic zone (Schütz et al., 2001) perhaps because here the sediments can remain unfrozen even when the upper streambed is (Irons et al., 1993), or because they seek refuge from predators prior to diapause (Lencioni, 2004). However, not all chironomidae taxa exhibit reduced abundance under snow cover and relatively large abundances of *Parapsectra sp.* were observed under snow cover at Sites A, E and F in a manner similar to findings by Lavandier & Décamps (1985) for other Tanytarsini.

6.4.3 Effects of alpine flow regulation on macroinvertebrate communities

Very few studies have investigated the effects of flow regulation on macroinvertebrate communities in alpine streams (but see Petts & Bickerton, 1994; Maiolini et al., 2003). As described in Chapters 3, 4 and 5, the Weiβsee affects the flow regime of the Eisboden in two ways: (i) in late summer/ early autumn as over spill occurs, and; (ii) during winter as a series of planned drawdown events transfer water via the Eisboden to the Tauernmoossee. To my knowledge, no published studies have investigated the effect of reservoir overtopping on an alpine river system and the effects of drawdown discharges have only been assessed in sub-alpine systems (see Céréghino et al., 2002; Robinson et al., 2004; Bruno et al., 2009a) and so the results of this study represent a significant advance in understanding of anthropogenic modification of alpine river systems.

6.4.3.1 Late summer overtopping

Overtopping had a clear effect on the physicochemical habitat at Site B, increasing $\overline{Q}$ by ~ 25 %, $\overline{T}$ by ~ 3.2 ^{o}C and T_{max} by ~ 2.2 ^{o}C from values observed at the end of July (see also chapters 3 and 4). However, no clear impacts on the macroinvertebrate community were identified. ANOVA analysis revealed no statistically significant change in total abundance or taxonomic richness at Site B as a result of overtopping. Bonferroni corrected ANOSIM results also showed that there was no significant difference in community composition at Site B as a result of overtopping. However this result requires the proviso that the un-corrected ANOSIM results suggested that the data in 2009 was inconclusive because although a significant change occurred at Site B, Site A did not provide an adequate control with which to compare the change. Direct examination of the macroinvertebrate data revealed that there was an anomalous explosion in overall abundances of *D.bertrami* (636 ind.m^{-2}), *D.cinerella/zernyi gr.* (1516 ind.m^{-2}) and *D.latitarsis* (3720 ind.m^{-2}) at B-S3-2009 and overall abundance increased over 10-fold from the previous month (B-S2-2009). Such a peak may however be expected as a part of natural temporal variation (cf. Lavandier & Décamps, 1985; Robinson et al., 2001; Schütz et al., 2001); explosions in populations of taxa with annual life-cycles can arise in natural alpine streams where habitat conditions are particularly favourable to development, due to the rapid biological cycles and high reproductive ability many alpine taxa, particularly Chironomidae (Lavandier & Décamps, 1985; Brown et al., 2006d). It is not possible to say to what degree the abundance peak at B-S3-2009 was as a consequence of specific physicochemical conditions arising due to flow contributions from the Weiβsee but the fact that a similar abundance peak did not occur in late summer, 2008, suggests that it is not an annual re-occurring phenomena arising consistently as a result of overtopping. Céréghino et al. (2002) studied the effects of hypolimnetic water re-flux into the River Oriège which was similar to the situation at the Eisboden in that water from a reservoir was discharged into a river with an otherwise natural flow regime (i.e. the base flow is not regulated, see for example; Robinson et al., 2004; Bruno et al., 2009a). Céréghino et al. (2002) found that decreases in the benthic abundance of most species occurred downstream of the point of re-flux and some species disappeared from the assemblage altogether (e.g. B.muticus, see; Céréghino & Lavandier, 1998b). A key difference between the Eisboden and sites studied in the River Oriège by Céréghino et al. (2002) is that the Eisboden is situated at much higher altitude (2100 m.a.s.l vs. 912 m.a.s.l) and is much closer to the glacial margin than the reach studied in the River Oriège. As such the macroinvertebrate community in the Eisboden likely consist of taxa better adapted to the extreme levels of disturbance and harsh physicochemical conditions associated with near-glacial reaches (Milner & Petts, 1994). The macroinvertebrate community in the Eisboden were therefore potentially less sensitive to changes in flow conditions, indeed Céréghino et al. (2002) found that taxa with flattened (*Rhithrogena, Ecdyonurus*) or cylindrical bodies (*Esolus, Limnius, Limoniidae*, Empididae, Chironomidae), or crawlers and clingers (e.g. some Trichoptera), were more tolerant of hydropeaking flows, or able to move towards refugia (see Bruno et al., 2009b). It is also the case that water temperature decreased due to hypolimnetic reflux in the River Oriège, which may have placed a greater physicochemical constraint on the development and survival of taxa than thermal increases observed in the Eisboden as a result of overtopping.

6.4.3.1 Winter drawdown

Year-round flow was only sustained at sites that were impacted by drawdown from the Weiβsee reservoir. This was the most apparent physicochemical difference between impacted sites (B, D and E) and non-impacted sites (A, C and D). The antecedent implications of a lack of flow permanency at sites have been discussed (see section 6.3.2) but it is not possible to say with certainty whether Sites B, D and E would have ceased to flow in winter without flow contributions from the Weiβsee. At the Val Roseg floodplain, Switzerland, Malard et al. (1999) found that although surface flow ceased at the upper part of the floodplain, upwelling occurred and flow was sustained year-round in the lower half. It is possible that flow may have been sustained at impacted sites (B and D) without the influence of the Weiβsee. Certainly though, the Weiβsee did increase discharge significantly at Sites B and D, and also prevented the formation of snowpacks across the channels. Only after drawdown stopped did snowpacks start to accumulate over directly inundated steams.

In contrast to unregulated sites where a snow pack formed, Chironomidae abundances at sites inundated by drawdown waters (B and D) remained relatively high during winter and this has been observed previously at sites in winter at streams with a natural flow regime but free from snow cover (see Robinson et al., 2001; Burgherr et al., 2002). However, there was a large difference observed between abundances of specific Chironomidae taxa during the winter in the Eisboden. For example, abundances of most Chironomidae taxa declined markedly during winter at all sites and some taxa prolific in summer, such as *D.latitarsis/bertrami gr.,* disappeared from the assemblage altogether but at sites kept free from snow cover by regulation (Sites B and D), exceptionally high abundances of *D.cinerella/zernyi gr.* taxa were recorded. Indeed abundances of *D.cinerella/zernyi gr.* were mainly responsible for maintaining high abundances of Chironomidae during winter at sites free from snow cover. This may have also been the case in the studies by Robinson (2001) and Burgherr and Ward (2001) however it is not possible to verify this as taxa were not generally identified beyond family or sub-family level. If *D.cinerella/zernyi gr.* do migrating deeper into the benthos as an overwintering strategy then it seems that the development of a snowpack and exclusion of light may act as photoperiod stimulus for migration and potentially diapause (see Danks, 1971b; Irons et al., 1993; Armitage et al., 1995; Lencioni, 2004).

Several studies have noted the increased presence of Plecoptera and Ephemeroptera in proglacial rivers during winter (Robinson et al., 2001; Schütz et al., 2001; Burgherr et al., 2002) and it has been hypothesised that they are able to colonise during winter as conditions ameliorate when melt inputs decline (Schütz et al., 2001), providing a 'window of opportunity'(Tockner et al., 2010). Interestingly, Plecoptera (*Leuctra sp.*, *Nemoura sp.*, and *N. pictetii*) and Ephemeroptera (*B.alpinus* and *Rhithrogena sp.)* were found at Sites B and D during winter despite sustained riverbed disturbances from high discharge drawdown resulting in extremely high discharges which are associated with high bed shear stress and bed disturbance (Céréghino et al., 2002; Mürle et al., 2003; Gibbins et al., 2007a). Although drawdown flows increased temperature significantly in the Eisboden, T_{max} still did not exceed 3.5°C during winter. This temperature is below the threshold for the appearance of Plecoptera and Ephemeroptera as predicted by Milner et al. (2001a), but Plecoptera and Ephemeroptera have also been observed at temperatures close to freezing during winter elsewhere (see Robinson et al., 2001; Schütz et al., 2001; Burgherr et al., 2002). It can be deduced from these findings that during the melt-season in alpine proglacial streams, if the presence of Plecoptera and Ephemeroptera is directly constrained by a physicochemical factor, then it is not low temperatures, or bed disturbance created by discharge pulses. Potentially high suspended sediment concentration pulses which are common in proglacial rivers during the summer (Warburton, 1990; Orwin & Smart, 2004) and were observed regularly during July and August in the Eisboden could be an alternative restricting factor or biotic constraints such as food.

6.5. CONCLUSIONS

The heterogeneity of stream habitats and the diversity of the ecosystems that can be found in a relatively small floodplain suggests that a consideration of the lateral dimension is essential to appreciating the complexity of alpine river systems, particularly if conservation and management priorities are high (Arscott et al., 2002). Alpine macroinvertebrate communities also exhibit considerable temporal variation; macroinvertebrate assemblages in this study varied markedly at sub-seasonal (cf. Lavandier & Décamps, 1985; Füreder et al., 2001), intra-annual (cf. Robinson et al., 2001; Schütz et al., 2001; Burgherr et al., 2002) and inter-annual (cf. Milner, 1994; Lods-Crozet et al., 2001; Brown et al., 2006d) time scales. Quantifying these multi-scale variations in macroinvertebrate dynamics is an essential step to understanding consequences of climate change and flow regulation for lotic ecosystems because without a holistic understanding of the current dynamics of unregulated alpine stream ecosystems it is not possible to predict a future response to change (Milner et al., 2009).

This study has provided novel insights into the effects of reservoir overtopping and drawdown on stream habitats and macroinvertebrate communities because it is the first study to assess reservoir regulation effects on a high alpine glacier-fed river system. Although both overtopping and drawdown had a relatively large effect on the physicochemical conditions in the Eisboden, in general the macroinvertebrate community appeared to be relatively resilient to these disturbances in comparison with the largely reduced abundance and richness of macroinvertebrate assemblages that have been reported from sub-alpine rivers (e.g. Céréghino et al., 2002; Cortes et al., 2002). It is acknowledged that the utility of the data from this study to investigate the effects of flow inundation from a storage reservoir on benthic ecology is limited as the study was restricted to a sampling program in a single basin and so spatial sampling replicates were essentially only pseudoreplicates (Hurlbert, 1984) rather than true replicates of the experimental unit (i.e. a river subject to regulation). It is therefore essential that the impacts of different forms of anthropogenic flow regulation be assessed more widely and over longer time scales to provide a fuller picture of anthropogenic impacts to alpine river ecosystems.

CHAPTER 7: BIOLOGICAL AND FUNCTIONAL TRAIT DIVERSITY OF BENTHIC MACROINVERTEBRATE COMMUNITIES

7.1 INTRODUCTION

In an attempt to develop a mechanistic understanding of the relationship between organisms and stream ecosystems, trait-based (or functional) approaches have been increasingly embraced in recent years (e.g. Charvet et al., 2000; Statzner et al., 2004; Paillex et al., 2007; Gaudes et al., 2010; Sokol et al., 2011; Walters, 2011). The key difference between a functional and more traditional taxonomical approach (cf. Chapter 6) is that the former focuses on the relationships between the functional attributes or traits of taxa (for example feeding habit, life-cycle characteristic, or size) and environmental gradients, whereas the latter typically looks directly for correlations between abundance and environmental gradients. As such, the major advantage of using trait-based approaches is that they may tell us more about the mechanisms that control community assemblages along environmental gradients (Poff, 1997; Westoby & Wright, 2006; Green et al., 2008) and facilitate an examination of the role of stochastic versus deterministic processes in governing community assemblages (Chase, 2007; Ellis & Ellis, 2010). Because of their more mechanistic basis, predictive distribution models derived from functional trait-environmental relationships are likely to be more robust and generalizable than those derived from taxonomic-environmental correlations (Poff, 1997; Usseglio-Polatera et al., 2000; Poff et al., 2010). In contrast taxonomical predictive models often fail to account for the predictive uncertainty associated with stochastic colonisation events (Finn & Poff, 2006) and are limited to the taxonomic pool for which they were defined. For example, the widely cited predicative model of Milner and Petts (1994) was originally synthesised from studies of predominantly European alpine rivers but has subsequently had to be substantially modified (see Milner et al., 2001a) based on findings from North American, South American and New Zealand studies in an attempt to generalize its spatial applicability.

Extending the concept of analyzing biotic assemblages from a functional perspective further, a suite of functional diversity indices have been developed (Petchey & Gaston, 2006; Thompson & Townsend, 2006; Mouchet et al., 2010; Schleuter et al., 2010). These compliment taxonomically based biodiversity indices such as the Simpson’s or Shannon’s index. Functional diversity which can be defined as “the value and range of those species and organismal traits that influence ecosystem functioning” (Tilman, 2001 p.109) can offer fresh insights into the structure and functioning of ecosystems. In contrast to taxonomically defined biodiversity, trait-based indices also reflect the complementarity and/or redundancy of co-existing species

(Petchey & Gaston, 2006; Schleuter et al., 2010) and are therefore considered to reflect more accurately the attributes of ecosystems (Loreau et al., 2001; Schleuter et al., 2010).

Understanding the governing role of habitat conditions on alpine stream communities is crucial to relate how changes to alpine stream habitats, either through natural dynamics (Burgherr & Ward, 2001; Malard et al., 2006), climate change (McGregor et al., 1995; Brown et al., 2007a), or as a result of anthropogenic pressures (Füreder et al., 2002; Wehren et al., 2010b), will affect alpine stream ecosystems. A diverse range of stream habitats hosting a variety of macroinvertebrate assemblages can be found in alpine catchments. The dynamic nature of water source contributions to stream flow drives considerable spatiotemporal heterogeneity amongst habitats (Malard et al., 1999; Brown et al., 2006c; Robinson & Matthaei, 2007). A distinct longitudinal habitat gradient exists, particular in glacier-fed rivers which are characterised by extremely harsh habitat conditions until the increasing influence of groundwater on stream flow ameliorates stream conditions (Malard et al., 1999; Brown et al., 2006c; Brown et al., 2009b). Strong lateral variations exist within alpine catchments; for example between the main glacial stem, snow melt channels and ground water tributaries (Ward, 1994). As such the dynamic mixing of various water source contributions can result in a particularly rich patchwork of habitats across alpine floodplains at the same longitudinal position from a glacier terminus (Malard et al., 2006; Brown et al., 2009b). Temporally, stream habitats fed by meltwater are subject to strong annual cycles (Robinson et al., 2001; Schütz et al., 2001; Burgherr et al., 2002). Many studies have shown that macroinvertebrate assemblages in alpine streams are sensitive to the influence of water source contributions and that specific habitats arising from water source contributions tend to host a predictable array of macroinvertebrates (Milner et al., 2010). However, the underpinning links between the functional characteristics (traits) of taxa and stream ecosystems in which they are found are poorly understood.

Following the theoretical work of Poff (1997), Hieber et al. (2005) proposed that the potential for benthic macroinvertebrates to colonise and persist within different alpine stream habitats can be conceptualised within a framework of nested environmental filters that act to screen the regional species pool according to the functional traits of taxa. Close to the glacial snout of a proglacial river, where glacial influence is strongest, physicochemical conditions place severe constraints on the ability of taxa to colonise and persist (Füreder et al., 2001). Here, in addition to meeting the requirements of regional dispersal filters taxa must also tolerate maximum stream temperatures of < 2 ^{o}C (Uehlinger et al., 2003b; Brown & Hannah, 2008), low channel stability (Nicholas & Sambrook-Smith, 1998), limited food resources (Zah & Uehlinger, 2001; Battin et al., 2004), pulses of high concentration suspended sediment (Orwin & Smart, 2004), high amplitude diurnal discharge fluctuations (Swift et al., 2005) and snow cover for the majority of the year (Schütz et al., 2001). Invertebrates must also have strategies to survive or escape freezing and desiccation should stream-flow cease during winter (Lencioni, 2004; Brown et al., 2006b). Functional diversity is expected to be very low where glacial influence is strong because in order to survive the extremely harsh habitat conditions taxa must be highly adapted to their environment and so the species pool is tightly restricted. It is hypothesised that where glacial influence is strong, assemblages are characterised by taxa with scraper feeding habits, uni or even semi-voltine life-cycles, small streamline bodies and diapause strategies (cf. Snook & Milner, 2002; Finn & Poff, 2006; Ilg and Castella, 2006; Füreder, 2007). As the influence of glacial meltwater diminishes and groundwater sources contribute more significantly to stream flow, habitat conditions become less restrictive. Therefore, in line with Hieber et al. (2005), it is hypothesised that taxa with a greater range of functional characteristics will colonise and biotic interactions will play an increasing significant role in structuring assemblages (Poff, 1997). To date very few studies have adopted a functional approach to analysing alpine stream ecosystems (but see Snook & Milner, 2002; Finn & Poff, 2006; Ilg & Castella, 2006; Füreder, 2007), and so there is only minimal support for the use of this functional trait framework in these systems. Trait based studies by Snook and Milner (2002), Finn and Poff (2006) and Ilg and Castella (2006) focused on analysing longitudinal trends in macroinvertebrate communities with respect to habitat harshness. These studies proposed that adopting trait-based approaches could provide valuable insight into alpine stream ecosystem structure and functioning, but examinations of lateral and temporal dimensions remain to be undertaken.

This study examined the year-round biological and functional trait characteristics of macroinvertebrate assemblages at six sites across the Central Eisboden Braidplain. The aims were to: (i) examine spatial dynamics in the functional trait characteristics of benthic macroinvertebrate communities with respect to habitat harshness through two consecutive summer seasons; (ii) identify key functional adaptations that allow taxa to persist in the most deterministically controlled (harshest) habitats, and; (iii) investigate the year-round functional dynamics of macroinvertebrate assemblages with respect to changes in stream habitat conditions.

7.2 METHODS

Full details of physicochemical variable and benthic macroinvertebrate sampling at the Eisboden braidplain between June 2008 and August 2009 are given in Chapter 6.2. For a detailed description of the study area refer to Chapter 3. Throughout this chapter samples are referred to with a site code (A-F), season code (S = summer, W = winter), a period code (1-3) and the year as defined in Chapter 6.2. Samples collected during the summer (S1, S2 and, S3-2008 and S1, S2 and, S3-2009) were included in an initial analysis to examine spatiotemporal patterns during the summer melt season. A second set of analyses were conducted on quarterly data including samples collected on S3-2009, W1-2008, W2-2009 and S1-2009.

7.2.1 Data Analysis

Ilg & Castella's (2006) Glaciality Index (GI) was used to derive a single quantitative measure of habitat harshness by synthesising four physicochemical variables that are associated with the influence of glacial runoff; maximum water temperature (T_{max}), electrical conductivity *(*EC), channel stability (PFAN) and suspended sediment concentration (SSC) (see also Townsend et al., 1997; Burgherr et al., 2002). The reciprocal of PFAN and SSC+1 was calculated so that all indices were associated negatively with glacial influence. SSC+1 were used rather than SSC to accommodate the processing of negligible values of SSC observed in groundwater streams (cf. Ilg & Castella, 2006). T_{max}, EC , 1/PFAN, and 1/(SSC+1) were standardised from 0 to 1 and processed using a non-centred Principal Component Analysis (PCA) to reduce the data set to a single axis of variation. Ordination scores along PC axis 1 were used as an index of glaciality (GI) which is inversely proportional to glacial influence.

The biological traits of the 71 taxa collected were characterised primarily using the database of Tachet et al. (2000). Taxa were classified according to 11 traits: maximum potential size, potential number of life-cycles per year, aquatic life stages, reproduction, dispersal, resistance forms, respiration, locomotion and substrate relation, food and feeding habits, defined using a total of 61 trait modalities (see Appendix D). These traits were selected as they surmise a broad range of biological and behavioural characteristics that were each hypothesised to play a significant role in mechanistically underpinning taxa-environment gradients in alpine lotic ecosystems (see Snook & Milner, 2002; Ilg & Castella, 2006; Füreder, 2007). The affinity of each taxa was defined using a fuzzy coding approach where zero indicated 'no affinity', and either three or five represented 'high affinity' (see Usseglio-Polatera, 1991; Chevene et al., 1994). Where taxa had been identified to Order or Family level, fuzzy codes for all underlying genera were averaged (Ilg & Castella, 2006). Juvenile taxa that could only be reliably identified to Family level were coded by calculating the average of all taxa that were recorded within that Family at the given site (see Ilg & Castella, 2006). Trait coding of the Chironomidae sub-families Diamesinae and Orthocladiinae were refined from the database of Tachet et al. (2000) based on the work of Ilg & Castella (2006). Overall, the trait modality coding was assigned to 30 taxa. Trait modalities were standardised from 0 to 1, and then a abundance weighted trait score by sample array was calculated subsequently by multiplying the relative abundance of taxa for each sample by standardised trait modalities (Bonada et al., 2007).

To assess spatiotemporal patterns in trait characteristics, weighted trait modalities were ordinated by sampling site using Non Metric Multidimensional Scaling (NMDS) in PAST v1.95 (Hammer et al., 2001). Separate analyses were undertaken using the summer samples data set and the quarterly data set. Prior to each analysis the weighted trait modalities were arcsin transformed. Each NMDS was constrained to two-dimensions, with Bray-Curtis scores used as the dissimilarity measures. The similarity of percentages routine (SIMPER; see Clarke & Chorley, 2006) was used to identify the top five traits which accounted for the greatest dissimilarity spatially between: (i) all sites during summer; (ii) predominantly glacial fed sites (A and B), and predominantly groundwater fed streams (Sites E and F) during summer, and; (iii) snow covered (A,E,F-W1-2008, and E-W2-2009) and non-snow covered (B,D-W1-2008 and B,D-W2-2009) sites during winter.

To characterise the functional diversity of each sample, the weighted trait modality by sample array was used to calculate two functional diversity components following Mouchet et al. (2010) and using FDiversity (Casanoves et al., 2010):

(i) Rao’s Quadratic Entropy (QE), which summarises both functional richness and functional divergence (Mouchet et al., 2010), was calculated as the sum of pairwise Euclidean distances between species in trait space weighted by relative abundance (Rao, 1982);

$$\mathrm{QE} = \sum_{i=1}^{S-1} \sum_{j=i+1}^{S-1} d_{ij} p_i \, p_j$$

where *S* is the total species richness, d_{ij} the dissimilarity between taxa *i* and *j*, and p_i is the relative abundance of species *i*;

(ii) Dendrogram based Functional Diversity (FD), a measure of functional richness (Petchey & Gaston, 2006; Schleuter et al., 2010) primarily driven by species richness (Mouchet et al., 2010) was calculated. First, a distance matrix was derived from the standardised trait modality array, based on Euclidean pair-wise distances between species in trait space. Subsequently a hierarchal cluster analysis utilising the pair-group clustering method using arithmetic averages (UPGMA) was used to derive a dendrogram based on the entire community observed (i.e. commmunity based, see Petchey & Gaston, 2002). The branch length of this dendrogram was taken as the FD of the entire Eisboden community. Thereafter, The branch lengths of taxa present in individual samples, excluding the branch length needed to connect to the root (see

Petchey & Gaston, 2006) were determined and standardised by FD for the entire assemblage. Accordingly, zero values represented communities consisting of single taxa, or a group of taxa with identical functional traits (Petchey & Gaston, 2006).

Ordinary Least Square (OLS) regression was used to asses how trait characteristics and functional diversity varied with habitat harshness associated with the influence of glacial runoff. GI values were used in regression analyses against: (i) abundance weighted arcsine transformed trait modalities values for each site (only the five trait modalities found to explain the most of variance in the summer set based on SIMPER analysis were used in regression analysis); (ii) QE and; (iii) FD. Both linear and quadratic regression forms were calculated and relationships were considered significant for $p<0.05$. Statistical analyses were carried out in SPSS v.17.

7.3 RESULTS

7.3.1 Summer melt season

The PCA to calculate GI values produced factor loading scores of 0.60 (T_{max}), 0.77 (EC), 0.94 (1/PFAN), and 0.66 (1/[SSC+1]). The first PC explained 56.7 % of variance. GI values suggested that; (i) predominately glacial fed sites (A and B) were the harshest with the highest glacial influence (lowest GI), (ii) predominantly groundwater fed sites (E and F) were the most benign and, (iii) mixed water source sites (C and D) in between these extremes (see Table 7.1). There were only small differences in the range and standard deviation of GI between Sites A-D. Conversely, GI at Site E was more variable, whilst Site F was the most stable of all sites in terms of GI.

Table 7.1 - *Mean, range and standard deviation of Glaciality Index (GI) for each site.*

Site	Mean	Range	σ
A	-1.12	0.97	0.34
B	-0.88	1.02	0.36
C	-0.21	0.82	0.33
D	-0.24	0.95	0.38
E	1.11	1.39	0.54
F	1.34	0.56	0.21

The traits based NMDS analysis of summer samples produced a 2-dimensional solution with a stress of 0.05. Samples from Sites A, B, C and D were clustered relatively tightly on both axes 1 and 2 (Figure 7.1). A notable exception to this was the sample A-S3-2008 which was distinctly separated from other samples from Sites A, B, C and D on axis 1 and all samples on axis 2. This sample was removed from subsequent SIMPER and regression analysis as it was not considered to reflect a true streambed community (see 7.4.1 for further explanation). Samples from predominantly groundwater fed sites (E and F) tended to have higher values on both axes but were also more dispersed along both axis than Sites A, B, C and D (Figure 7.1).

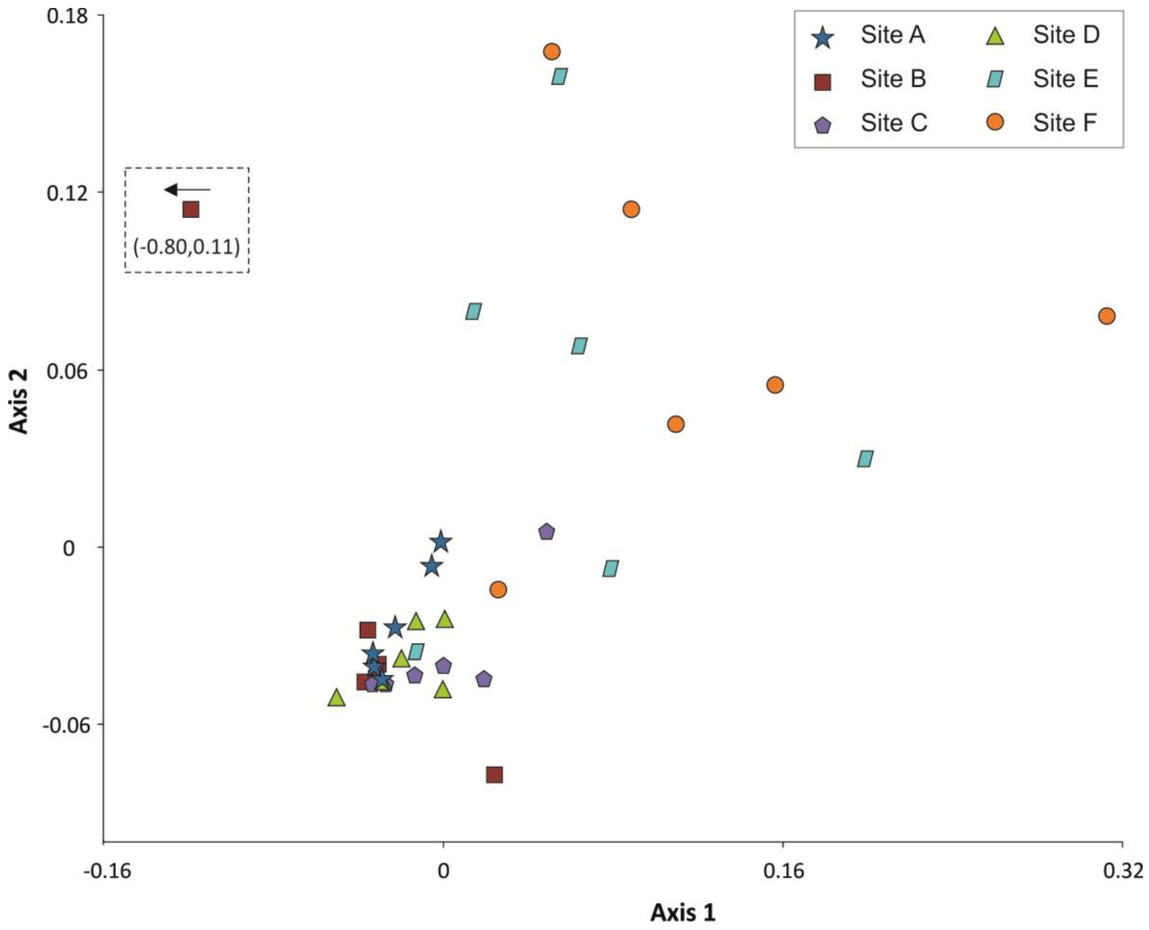

Figure 7.1 - *Non Metric multi-Dimensional Scaling plot for the summer data set.*

The SIMPER analysis indicated that the five trait modalities that explained the greatest amount of variance in macroinvertebrate communities spatially between all sites during summer were: (i) ‘No Resistance Form’ (NRF; 13.1% of variance); (ii) ‘Scraper Feeding Habit’ (SFH; 5.6 %); (iii) ‘Deposit Feeder’ (DF; 4.0 %); (iv) ‘Semi-Voltine (SV; 3.8 %), and; (v) ‘Food; Living Microphytes’ (FLM; 3.4 %). The relationship between four of these traits and the GI was relatively strong and best modelled by a quadratic regression (Table 7.2, Figure 7.2); NRF, SFH, SV and FLM were significantly inversely related to GI. However, the scatter plots in Figure 7.2 suggest that the relationship between GI and SFH, SV and FLM was weak amongst predominantly glacial fed and mixed sites (A and B, and C and D) but that there was a clear difference between these sites and predominantly groundwater fed sites (E and F). A second SIMPER analysis comparing the functional trait characteristics of communities at predominantly glacial fed sites (A and B), and groundwater fed sites (E and F) showed that the same five trait characteristics (in the same order) explained the greatest amount of variance between predominantly glacial fed and groundwater stream-types (Table 7.2).

Table 7.2 - *Results of SIMPER analysis between all sites*$^{(1)}$ *and predominantly glacial-fed (A and B) and groundwater fed (E and F) sites*$^{(2)}$*, showing the percentage variance explained by each of the top five trait modalities, and results of linear and polynomial regressions between glacial index (GI) values and standardised trait modalities.*

Trait - modality	**% var** $^{(1)}$	**% var** $^{(2)}$	**Linear regression**		**Quadratic regression**	
			r^2	**p**	**r^2**	**p**
Resistance forms - none	13.1	6.1	0.460	<0.001	0.459	<0.001
Feeding habits - scraper	5.6	3.9	0.489	<0.001	0.497	<0.001
Feeding habits - deposit feeder	4.0	3.6	0.191	0.264	0.043	0.486
Life cycle duration - semi-voltine	3.8	3.6	0.480	0.001	0.513	0.001
Food - living microphytes	3.4	3.4	0.491	<0.001	0.505	<0.001

Functional diversity measures Q and FD were both significantly positively correlated with GI, (i.e. community at sites with harshest physicochemical habits where the influence of glacial melt is greatest tended to have the lowest functional diversity functional diversity). Polynomial regression models were significant between both Q ($r^2 = 0.40$, $p < 0.001$) and FD ($r^2 = 0.69$, $p < 0.001$), and GI (Figure 7.3).

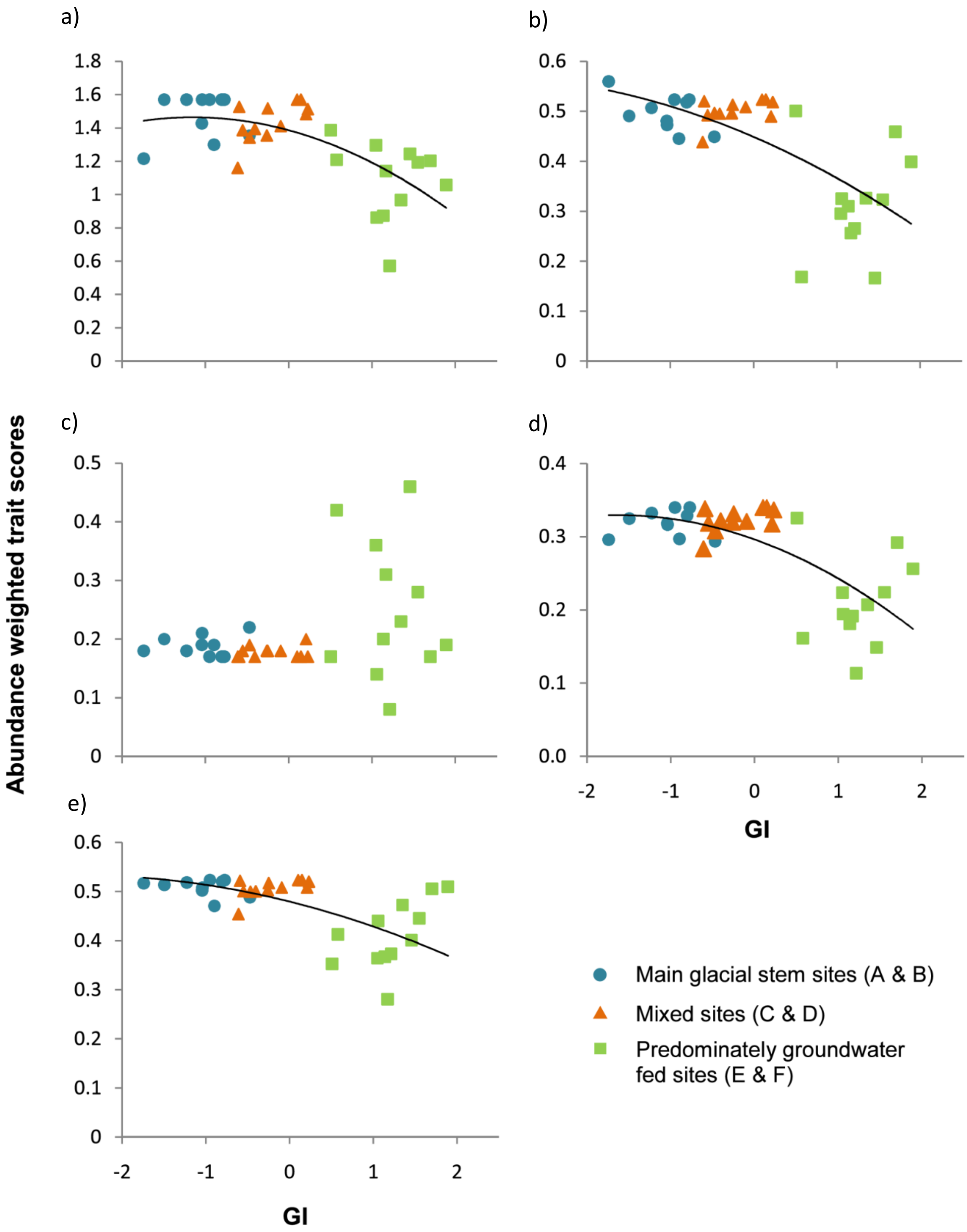

Figure 7.2 - *Regression of macroinvertebrate community abundance weighted trait score; a) No Resistance Form (NRF); b) Scraper Feeding Habit (SFH); c) Deposit Feeder (DF); d) Semi-Voltine (SV), and; e) Food: Living Microphytes (FLM), against Glaciality Index (GI).*

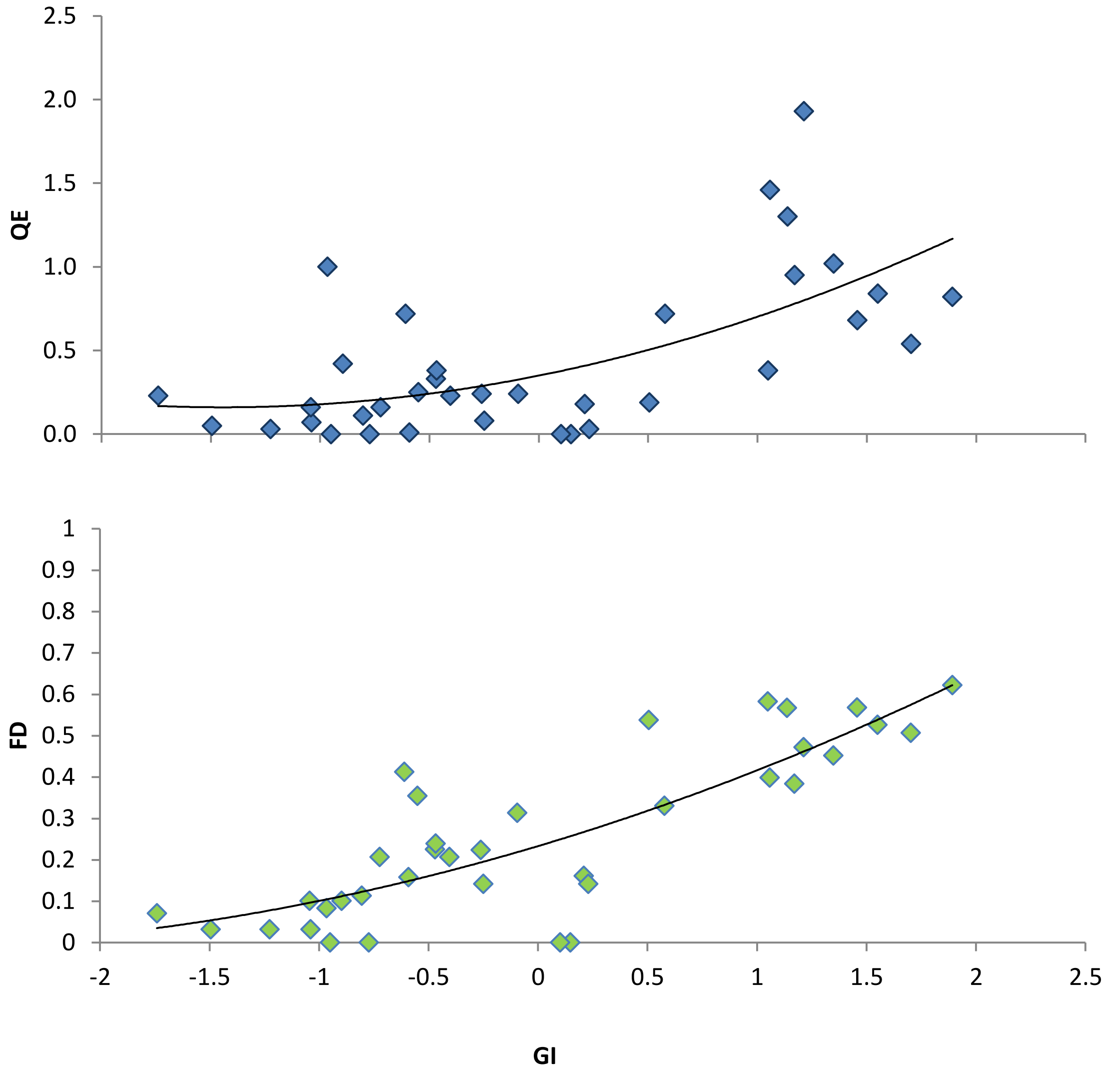

Figure 7.3 - *Relationships between against Glaciality Index (GI) and: (a) Rao's Quadratic Entropy (QE), and; (b) dendrogram based Functional Diversity (FD).*

7.3.2 Quarterly data

The trait based NMDS analysis of quarterly samples produced a 2-dimensional solution with a stress of 0.05 (Figure 7.4). Along the first axis, the quarterly NMDS clustered samples from snow covered sites in December with low negative scores, and sample E-W2-2009 (the only snow-covered sample from March 2009) was placed in isolation with a more positive score. Samples from all non-snow covered sites collected in summer or winter (with the exception of sample A-S3-2008 which was also an anomaly in the NMDS analysis of samples) were clustered with positive scores on axis 1. Sites predominantly influenced by groundwater (E and F) separated from Sites A, B, C and D along the second NMDS axis.

SIMPER analysis indicated that the five functional trait characteristics explaining the greatest amount of variance in macroinvertebrate communities during winter between snow covered and non-snow covered sites were; (i) ‘No Resistance Form’ (NRF; 7.6%); (ii) ‘Shredder Feeding Habit ‘(ShFH; 8.5% of variance); (iii) Crawler Locomotion and Substrate Relation (CLSR; 5.7%).; (iv) Univoltine (UV; 6.4%), and; (v) Scraper Feeding Habit (SFH; 4.9%). Of these trait modalities, NRF and SFH were associated with open sites, and ShFH, CLSR and UV were associated with snow covered channels (Table 7.3). QE during winter was markedly higher at all sites compared to summer (Figure 7.5a), but increases in FD were only seen at predominantly glacial fed sites (A and B; Figure 7.5b)

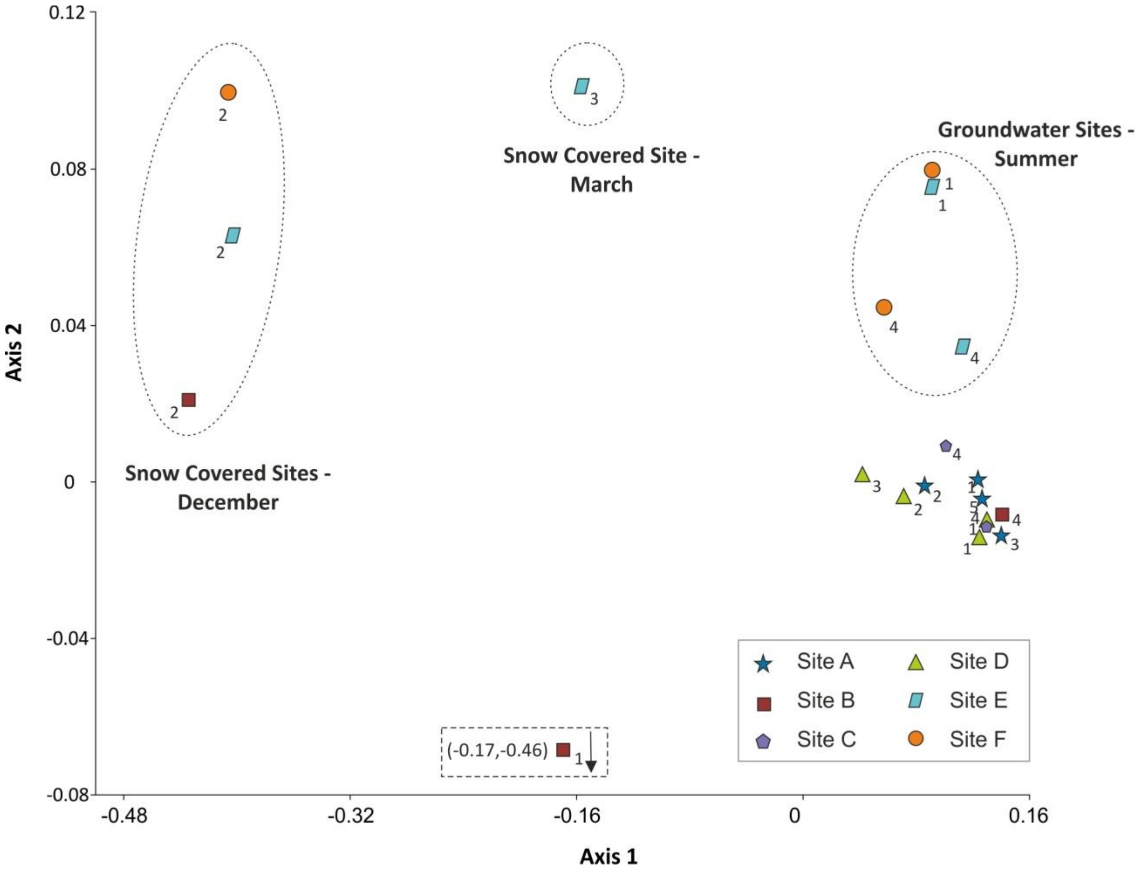

Figure 7.4 - *Non Metric Multi Dimensional Scaling (NMDS) plot of quarterly data set. Labels 1-4 refer to the following quarterly sampling codes and dates; 1= S3-2008, 2=W1-2008, 3=W2-2009, 4=S1-2009.*

Table 7.3 - *Results of SIMPER analysis comparing winter samples from sites with and without snow cover.*

Trait - modality	***% var.***	***Mean Affinity***	
		snow covered	**no snow covering**
Resistance form - none	8.3	0.81	1.31
Feeding habits - shredder	7.2	0.52	0.082
Locomotion and substrate relation - crawler	5.7	0.79	0.45
Life cycle duration - uni-voltine	4.9	0.86	0.57
Feeding habits - scraper	4.4	0.16	0.42

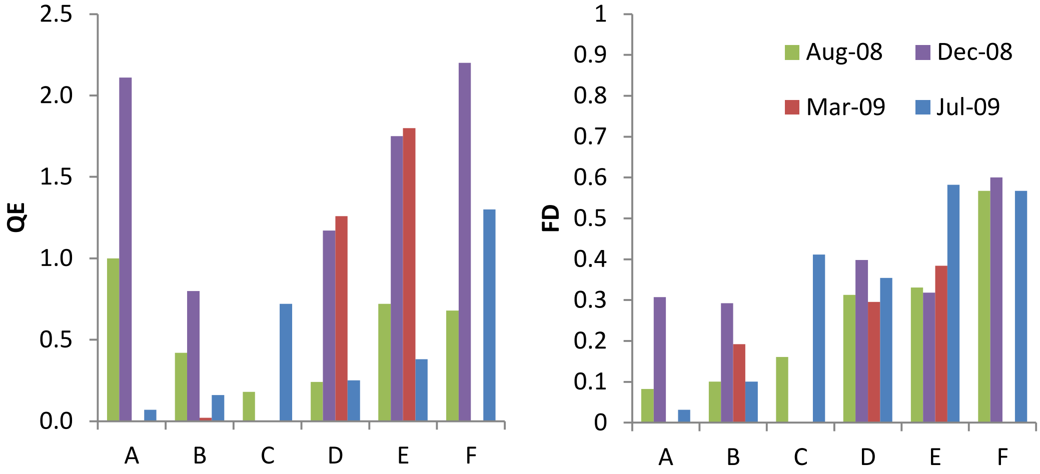

Figure 7.5 - *Functional diversity indices calculated for quarterly samples (a) Rao's Quadratic Entropy (QE), and; (b) dendrogram based Functional Diversity (FD). Missing data represent seasons when steams were not flowing.*

7.4 DISCUSSION

This study has investigated for the first time how the functional trait characteristics of macroinvertebrate assemblages respond to spatiotemporal habitat heterogeneity across an alpine floodplain. The subsequent discussion explores (i) trends in functional trait characteristics during the summer melt season by considering spatiotemporal patterns in functional characteristics, the role of specific trait characteristics underlying these patterns, and relationship between functional diversity and environment harshness and, (ii) how spatial patterns in the functional characteristics and functional diversity can change temporally at the seasonal scale, with particular reference to the harsh-benign concept of alpine stream habitats (Peckarsky, 1983; Uehlinger et al., 2002; Brown et al., 2007c)

7.4.1 Summer Melt Season

The few studies that have investigated macroinvertebrate assemblages across headwater floodplains of proglacial rivers have quantified diversity from a taxonomical perspective (see Arscott et al., 2000; Burgherr et al., 2002, Chapter 6 herein). These studies indicated that high diversity amongst sites (β-diversity) can exist and that distinct floodplain habitats support distinct arrays of macroinvertebrate taxa. The trait based NMDS ordination of summer samples in this study suggested that communities occupying distinct floodplain habitats are also divergent in terms of their functional trait characteristics. Sites predominantly fed by groundwater were shown to be particularly distinct from glacial fed sites in terms of functional trait characteristics. Similarly, studies by Brown (2007b), Burgherr et al. (2002), Ward et al. (1999a) and Füreder (1998, 1999), and Chapter 6 in this thesis have demonstrated that groundwater streams are ‘hotspots’ for taxonomical diversity along proglacial river corridors, and support assemblages of species that are somewhat distinct from proglacial streams. Indeed groundwater streams close to the glacial margin can support rich communities of taxa that would be expected in proglacial streams only much further downstream (see Milner & Petts, 1994; Milner et al., 2001a). The NMDS ordination in this study suggested that differences in assemblages occupying groundwater streams compared to glacial fed and mixed streams are underpinned by substantial differences in functional trait characteristics. Another striking feature of the NMDS ordination was that samples from sites predominantly influenced by groundwater were much more dispersed in trait space than glacial and mixed sites. There are two potential explanations for this trend. The first is that spatiotemporal variation in trait characteristics amongst groundwater streams were driven by spatiotemporal dynamism in physicochemical conditions in the groundwater streams. There is however little evidence to support this explanation. Site E did experience flooding from adjacent mixed channels late in summer 2009 (See Chapters 4 and 5) which led a large decrease in GI for S3-2009. However, GI was otherwise relatively stable in groundwater sites, in fact Site F had the most stable GI of all sites, indeed groundwater streams are generally considered to provide more stable habitat conditions than glacial fed or mixed sites (Brown et al., 2006d; Brown et al., 2007b). A second more likely explanation is that stochastic colonisation and redistribution processes are more influential in governing the assembly of macroinvertebrate communities of groundwater sites, because the available niche space is less deterministic than under harsher stream conditions where glacial influence is greater (Chase, 2007; Ellis & Ellis, 2010). An anomaly to the clustering of samples from mixed and glacial-fed sites was the sample A-S3-2008. As noted in Chapter

6.3, the community in sample A-S3-2008 had very low abundance (56 ind.m^{-1}) and consisted primarily of *Cheilotrichia sp.* (71% of community) which were otherwise very rare at main glacial stem sites (A and B). The trait characteristics of this sample were therefore dominated by *Cheilotrichia sp.* and rather distinct from other samples. A likely explanation for the relatively high abundance of *Cheilotrichia sp.* in sample A-S3-2008 is that geomorphic change at Site A (which was observed regularly throughout both melt seasons) led to flow inundating what was previously a transitional aquatic-terrestrial zone at the stream margin. If such an change occurred shortly prior to sampling and some replicates were collected in these areas, then this could explain the occurrence of *Cheilotrichia sp.* and absence of *Diamesa* in some of the A-S3-2008 replicates as Limoniidae are generally found in transition zone between aquatic and terrestrial habitats (Staudacher & Fuereder, 2007). Indeed, T_{max} for A-S3-2008 was <4°C and so Limoniidae would not be expected to tolerate the thermal conditions in the main glacial channel but it is possible that Limoniidae can survive in the transitional zone where it is potentially warmer due to the mixing of upwelling alluvial groundwater (Milner et al., 2001a). This sample was not included in the regression or SIMPER analysis as it was not considered to be representative of a streambed community which was the focus of this study.

SIMPER and regression analysis highlighted that stream assemblages in glacial and mixed streams were comparatively more dominated by taxa with no resistance forms, scraper feeders, semi-voltine taxa and taxa feeding on living microphytes. To the author's knowledge no previous studies have investigated the trends in functional traits amongst alpine floodplain habitats. However a handful of studies have examined longitudinal gradients in functional trait characteristics associated with physicochemical habitat gradients (Snook & Milner, 2002; Finn & Poff, 2006; Ilg & Castella, 2006) and these studies provide a basis for comparison in terms of trait characteristics versus habitat harshness/glacial influence (GI). Whilst Finn and Poff (2006) and, Snook and Milner (2002) did not define different resistance forms as traits, the work of Ilg and Castella (2006) supports the finding that the trait modality 'no resistance form' correlated positively with GI. This implies that taxa occupying harsher physicochemical habitats with greater glacial influence are more likely to have no specific resistance strategies for coping with periods of extreme physicochemical conditions (Lencioni, 2004), for example stream bed freezing or desiccation (Irons et al., 1993), or extremely low light levels and food supply under snow cover during winter (Schütz et al., 2001). However, it should be noted that this correlation, is very sensitive to the coding of 'resistance form traits' for Chironomidae sub-families; Diamesa and Orthocladiinae as these taxa tend to dominate streams with high glacial influence (see Milner & Petts, 1994; and Chapter 6 herein; Milner et al., 2001a; Ilg & Castella, 2006). For consistency with other European studies investigating trends in trait characteristics including the alpine study of Ilg and Castella (2006), the codings of Tachet et al. (2000) were used in the present study. However, there is evidence to suggest that many Chironomidae do indeed adopt resistance forms such as diapause and cocoon building (e.g. Armitage et al., 1995; Lencioni, 2004). The conclusion that stream habitats heavily influenced by glacial melt support a greater number of taxa possessing no resistance forms than more benign habitats is therefore questionable and there is a need for more research to clearly define the resistance forms of the Chironomidae family to substantiate the relationships between GI and resistance forms.

The association of scraper feeding habits, and taxa living on mainly microphytes with harsher habitats where glacial influence is strong was also observed by Ilg and Castella (2006) and Snook and Milner (2002). Food supply in glacial fed channels is greatly restricted by (i) a lack of riparian vegetation which limits allocthonous resource supply, and (ii) fast flowing currents which limit channel retention of organic matter. The available food resources are therefore predominantly epliithic diatoms and algae which evidently favour taxa with the capability to adopt a scraping feeding habit (Zah & Uehlinger, 2001). By analysing multiple isotope signatures Zah et al. (2001) found that allochthonous sources only contribute significantly to food supply in groundwater streams where riparian vegetation and slower currents provide a supply and enable retention. This suggests that a lack of suitable food supply (i.e. coarse plant material) may be principal factor restricting principally shredding taxa such as Plecoptera to groundwater streams during the summer melt season in floodplains close to the glacial margin. The availability of food supply may also be a principal factor in restricting filter feeders, namely the black fly *Prosimulium* sp. from sites with high glacial influence as ‘seston’ concentration close to the glacial margin is generally dominated by inorganic matter which has the potential to damage filtering appendages (see Hieber et al., 2003; Hieber et al., 2005; Brown et al., 2007b).

The trend for harsh, proglacial habitats to contain more taxa with the potential to complete semi-voltine life cycles is supported by the findings of Ilg and Castella (2006). They suggested that along the longitudinal gradient of harshness in a glacial stream, semi-voltinism tends to be associated with the harshest habitats (proximal to the glaciers) and bi/multi-voltinism with more benign habitats (further downstream). It has been demonstrated that some lotic macroinvertebrates exhibit trends in life-cycle duration along a longitudinal gradient of harshness i.e. where conditions are not conducive to development due to low temperatures and/or poor food supply, life-cycles may be extended. For example, Brittain (1978) found that the Plecoptera *Nemurella pictetii* exhibited semi-voltinism in mountainous habitats rather than univoltinism in low land areas. Mutch and Prichard (1982) observed a similar trend for *Zapada* *columbiana* and Lavandier and Décamps (1985) found that *Pachyleuctra benlocchi* could take as long as 4 years to complete their life-cycles in mountain streams of the Pyrénées. The findings in this study and those of Ilg and Castella (2006), suggest that a gradient also exists at the community level, with taxa capable of semi-voltinism being more prolific in harsher habitats where glacial influence is greater. In contrast, studies by Snook and Milner (2002) and Finn and Poff (2006) suggested that semi-voltinism was a trait primarily associated with benign habitats, and that long-life cycles may be a disadvantage in harsh environments. However, this difference is likely to be predominately down to a discrepancy in the coding of the life-cycle trait for Chironomidae taxa between studies. In this study the fuzzy coding of Ilg and Castella (2006) was used which accounts for the fact that Diamesa and Orthocladiinae can extend their life-cycles in adverse conditions (Saether, 1968; Fureder et al., 2005).

Rao's quadratic entropy (QE) and Functional Diversity (FD) both correlated positively with GI which suggests that as glacial influence decreases, macroinvertebrate assemblages became more functionally diverse. These results support the hypothesis that with increased habitat harshness, habitat filters become more restrictive and the pool of traits that enable successful habitation becomes smaller (Statzner et al., 2001; Statzner et al., 2004; Hieber et al., 2005). The relationship between QE, which takes into account the abundance of taxa (Petchey & Gaston, 2006; Mouchet et al., 2010) was poorly defined below GI values of ~0.5. This concurs with the NMDS analysis (also abundance weighted) and suggests that in abundance terms, sites with intermediate GI values (i.e. mixed sites; C and D) are dominated by taxa with the same trait characteristics as predominately glacial fed sites. Conversely, the quadratic regression model between FD, which does not account for abundance, and GI was stronger and more linear in nature. This suggest a low functional evenness (Petchey & Gaston, 2006; Mouchet et al., 2010) within macroinvertebrate communities in streams with intermediate glacial influence and that the array of taxa with different functional attributes is larger than in harsher sites but the community is still dominated by taxa with the same trait characteristics as those found in harsher sites. Ilg and Castella (2006) found that in concordance with declining harshness, a strong upstream-downstream trait diversity gradient existed in three glacial-fed streams in the Swiss and French Alps. Füreder (2007) proposed that in alpine streams, functional diversity generally increases with declining harshness (i.e. decreasing glacial and increasing groundwater influence). The findings herein generally concur with this proposal but demonstrate that the exact form of the relationship between functional diversity and habitat harshness depends on how diversity is defined. Additionally, the results of this study show that a strong gradient between functional diversity and habitat harshness can exist even within a narrow longitudinal (<0.5km), and altitudinal band (<25m) (cf. Finn & Poff, 2006).

7.4.2 Quarterly

In common with the analysis of summer samples, the NMDS for quarterly samples distinguished the trait characteristics of groundwater samples from mixed and glacial fed samples. However, a second, orthogonal distinction between samples was also evident in the quarterly data set. The presence/ absence of snow cover clearly distinguished the two main clusters of sites along the 1st NMDS factors. A limited number of studies have examined the effects of snow cover on macroinvertebrate communities in alpine streams (see Lavandier & Décamps, 1985; Schütz et al., 2001) though none to the author's knowledge have analysed functional traits. Schütz (2001)and Lavandier & Décamps (1985) found that Chironomidae abundances dropped dramatically under snow, a finding which was also evident in the Eisboden (see Chapter 6). Given the dominant presence of Chironomidae taxa at open sites (see chapter 6), the shift in the functional trait characteristics of the community when the abundances of Chironomidae dropped dramatically under snow cover was unsurprising since traits were weighted by abundance. SIMPER analysis suggested that scrapers and no resistance form were key distinguishing trait modalities associated with open sites whilst shredders, crawlers and uni-voltinism were associated with snow covered sites. However, these trait distinctions largely reflect the abundance/scarcity of Chironomidae taxa within samples and, although absent from samples, Chironomidae likely persisted deeper within the benthos under snow cover (see Danks, 1971b; Irons et al., 1993; Armitage et al., 1995; Lencioni, 2004). Therefore, it is unlikely that the traits identified represent specific survival adaptations to snow cover. It should also be noted that open sites (B and D) were affected by overspill and drawdown from the Weiβsee prior to S2-2008 through to day 44, 2009, 22 days prior to sampling day S2-2009 (see Chapters 4, 5, and 6). Thus, flow regulation was also a potentially important factor in structuring the macroinvertebrate community during winter at Sites B and D (see Chapter 6) and snow-cover cannot be said with certainty to be the definitive driver defining the community of snow-covered compared to open sites.

Several previous studies have found that the abundance and taxonomic diversity of alpine stream communities can exhibit considerable seasonal-scale fluctuations (Lavandier & Décamps, 1985; Füreder et al., 2001; Milner et al., 2001a; Robinson et al., 2001; Schütz et al., 2001; Burgherr et al., 2002; Robinson et al., 2002) but none to my knowledge have examined trends in functional diversity. Based on the harsh- benign concept of Peckarsky (1983), Brown et al. (2007c) proposed a conceptual model that envisaged: (i) seasonal variations in biotic abundance and diversity to be driven by changes in physicochemical habitat conditions and follow a distinct annual pattern, and; (ii) the amplitude of seasonal variations in alpine stream habitats and benthic macroinvertebrate communities depend upon water source contributions (see Figure 7.6). In general agreement, this study found clear seasonal variations in functional diversity which were associated with water source. However, QE was greatest at all sites during the winter (except B-S2-2009), whereas a clear increase in FD was only evident at glacial fed sites (A and B). As explained for summer trends (see 7.4.1), QE considers abundance (Petchey & Gaston, 2006; Mouchet et al., 2010) and as the abundance of most Chironomidae taxa fell under snow cover during winter (see chapter 6), in abundance terms Chironomidae became less dominant in the community resulting in higher QE. FD on the other hand reflects more closely the absolute number of species/ taxa present (Petchey & Gaston, 2006; Mouchet et al., 2010; Schleuter et al., 2010) which changed little in groundwater streams but markedly in glacial fed sites (A and B) during winter. It was not possible to compare the exact form of the seasonal benign-harsh-benign progression from Autumn-Winter-Spring (Brown et al., 2007c) with the pattern observed in this study due to the lack of temporal resolution in winter samples (see also Robinson et al., 2001; Burgherr et al., 2002) but it seems probable from comparing the results of Burgherr et al. (2002), Robinson et al. (2001), Schütz et al. (2001) and this study that in-fact a simpler summer-harsh, winter-benign pattern is typical, at least at sites free from snow cover (see Uehlinger et al., 2002). Very few studies have examined the effect of snow cover on seasonal diversity trends in alpine streams. In the Eisboden QE increased at all snow covered sites and FD and species diversity (see chapter 6) also increased in the main glacial stem whilst remaining relatively stable elsewhere. However, Schütz (2001) found that species diversity was erratic under snow cover, at times high but at other times diversity was no higher than in summer. The driver behind the fluctuations observed by Schütz (2001) was not evident, more studies examining snow covered alpine streams in winter at high resolution are therefore required to corroborate the summer-harsh, winter-benign pattern observed in this study. It should be noted that no studies to my knowledge have attempted to quantify alpine seasonal trends in abundance and diversity at the floodplain or river scale, instead studies have focussed on the reach scale. It is therefore unknown to what extent changes in diversity and population densities during winter in perennial channel sections are a consequence of taxa migrating to escape desiccating/freezing channels/ channel sections (Lavandier & Décamps, 1985; Malard et al., 2006). Seasonal trends at the river or floodplain scale may differ markedly from those observed in perennial channel sections.

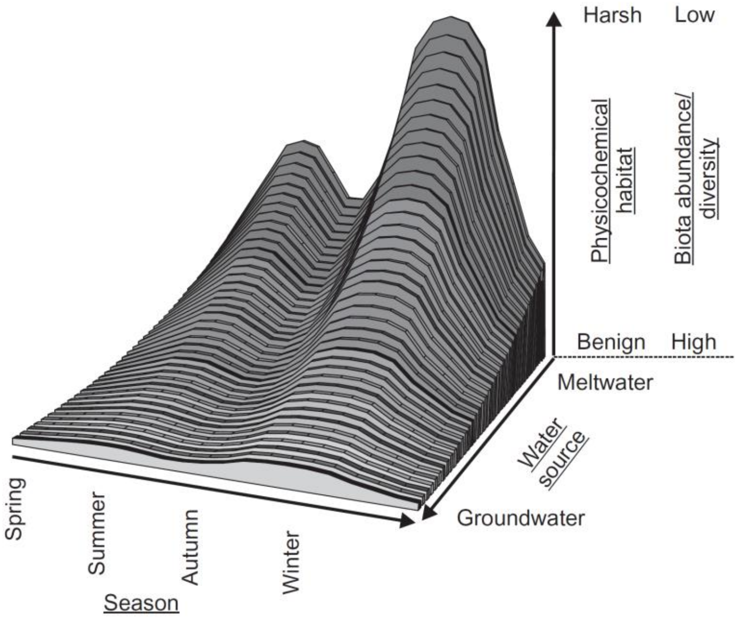

Figure 7.6 - *Conceptual diagram illustrating stream biotic diversity and abundance along a harsh–benign physicochemical habitat gradient, as a function of time (season) and water source contribution (Brown et al., 2007c).*

7.5 CONCLUSIONS

Understanding the functional links between habitat conditions and biotic assemblages is a key step in the development of mechanistic assemblage-environment models which will likely be more generalizable and robust than correlative approaches to predicting community function (Poff, 1997). This study has provided novel insights into the spatiotemporal structure of macroinvertebrate assemblages across and an alpine braidplain with respect to the functional characteristics of taxa and habitat harshness. In the harshest environments where glacial influence was high, macroinvertebrate assemblages were extremely constrained with low functional diversity which suggested that deterministic assembly processes were dominant. Therefore, a very specific array of functional traits such as a scraping feeding habit and the ability to adopt semi-voltinism were required for taxa to colonise. Where and when glacial influence declined, environmental conditions were less restrictive and as a result a more stochastic assemblage, with a greater range of functional traits, was present.

The findings of this study coupled with previous work of Füreder (2007), Ilg and Castella (2006), Finn and Poff (2006) and Snook and Milner (2002), together show that functional trait-based approaches can offer new and valuable insights into the structure and functioning of ecosystems. However, this study also highlighted that there have been inconsistencies between these studies with regard to the coding of functional traits used (see also Ilg & Castella, 2006), and potentially these differences in coding could have a large bearing on aspects of the conclusions drawn. Clearly more research is required to clarify the functional characteristics of taxa and to refine functional databases. In particular there is a need to focus on the characteristics of taxa in more extreme environments where functional trait characteristics of taxa may be exhibit considerable plasticity, for example in feeding habits (Zah et al., 2001; Füreder, 2007) or life-cycles (Saether, 1968; Fureder et al., 2005). This study took a fuzzy approach to coding the functional trait characteristics (cf. Ilg & Castella, 2006) which has the advantage over a binary approach of increased sensitivity and having the capacity to account for the plasticity of functional trait characteristics. However, there is a trade-off associated with using a fuzzy-coding approach over a binary base which is that a richer trait database is required. As such, the traits of many taxa have yet to be ‘fuzzy-coded’ beyond family or sub-family level. More research to establish the differences in functional trait characteristics of taxa (particularly Chironomidae because of their proliferation amongst alpine stream communities) at the genus/species level would enable a greater depth of analysis of alpine functional assemblages potentially revealing a great deal more about community structure and function in alpine ecosystems.

CHAPTER 8: A SYNTHESIS OF EISBODEN RIVER ECOSYSTEM DYNAMICS AND PROPOSED FUTURE RESEARCH DIRECTIONS

8.1. INTRODUCTION

This chapter synthesis the key findings of this thesis, considers the implications of these novel findings for rethinking existing conceptual models, and suggests future directions for alpine stream research. Section 8.2 provides a synopsis of key findings from each of the analytical chapters (4-7) in this thesis. Section 8.3 considers the implications of these findings for current conceptual understanding of alpine catchment runoff and stream ecosystems (reviewed in Chapter 2). A review of the constraints of this study, alongside suggestions for future research on alpine stream systems, is provided in Section 8.4. The final section (8.5) concludes by summarising the key contributions of this thesis to knowledge of alpine stream systems and freshwater ecosystems research more generally.

8.2. RESEARCH SYNOPSIS

This thesis has investigated the year-round dynamics of an alpine proglacial stream ecosystem that is impacted by anthropogenic flow regulation. An interdisciplinary approach was taken to examine the cascade of processes that ultimately determine the structure and functioning of ecological communities and alpine streams (Figure 2.3). Chapters 4 and 5 examined the links between climate, water source dynamics, and hydrological functioning (Chapter 3), and water temperature dynamics (Chapter 4). Chapters 6 and 7 investigated the implications of the findings of Chapters 3 and 4 by examining the relationships between physicochemical habitat characteristics and macroinvertebrate community structure (Chapter 6) and their biological and functional trait characteristics (Chapter 7). A synopsis of findings from each of these chapters is provided herein.

8.2.1 Spatial and temporal dynamics of stream flow

This study advanced the application of a statistical diurnal hydrograph classification technique to explore the hydrological functioning of multiple stream types with distinct water source characteristics, through two consecutive melt seasons. Analysis of the Central Eisboden Braidplain’s outflow hydrograph (Site B) from the start of melt season demonstrated that a clear seasonal progression was evident in both hydrograph shape and magnitude (see Paterson, 1994; Hannah et al., 2000; Swift et al., 2005). During the transition from winter through the early part of the melt-season, base-flow increased significantly which reflected a transition from low hydrological activity due to freezing conditions in the winter, through to snowmelt in the spring in response to increased atmospheric energy inputs and a recharging of the catchment groundwater system. During this spring period, hydrograph shape evolved resulting in increasing diurnal amplitude and a shortening of lag-time between peak energy inputs to the catchment and peak flow. However, despite this clear seasonal progression, the diurnal melt signal remained relatively weak (cf. Gurnell et al., 1992; Hannah et al., 2000; Swift et al., 2005), and precipitation events caused a great deal of 'interference' in diurnal meltwater runoff signals (see Hannah et al., 1999; Hannah et al., 2000) and were associated with all major flow-events.

The flow regime of the Eisboden is impacted episodically by overspill and drawdown from a hydropower storage reservoir (the Weiβsee). Inter-catchment transfer flow the Weiβsee to the Eisboden resulted in three of the four forms of anthropogenic flow regulation reviewed in Chapter 2.4; (i) hydropeaking and short-term flow pulses, (ii) reduced amplitude of seasonal flow cycles, and (iii) mean flow increase. The analysis of the hydrological and ecological implications of the Weiβsee provided a novel aspect of this research because no studies have examined the impacts of inter-catchment flow transfer on a recipient catchment in an alpine setting and indeed very few studies have examined the effects of inter-catchment in other environments (see Golladay & Hax, 1995; Matthews et al., 1996; Hax & Golladay, 1998; Gibbins et al., 2000). Overtopping flows from the Weiβsee during late summer drastically increased the mean daily discharge at the outflow of the Central Eisboden Braidplain (~63 - 72% increase). On predominately melt-driven days, peak flow from the Weiβsee catchment lagged that of the Eisboden resulting in a prolonged period of peak flow or, on some days, a distinct double flow peak (Dickson et al., 2010). Discharge receded markedly during autumn but from mid-November through until mid-February, a series of drawdown events led to extreme step-fluctuations in flow elevating base flow by ~10-fold.

Hydrograph analysis of mixed-source floodplain streams across two consecutive melts seasons and during winter revealed four key scales of flow routing dynamism across the Central Eisboden Braidplain; (i) at the annual to inter-annual scale, erosive flooding led to geomorphic change and the restructuring of channel networks (see Kollmann et al., 1999; Tockner et al., 2000; Ward et al., 2002); (ii) at the seasonal scale, the extent and pattern of flow routing was driven by seasonal melt cycles (see Malard et al., 1999; Arscott et al., 2002); (iii) at the sub-seasonal scale during the summer melt season, discharge in specific braid channels varied independently of catchment discharge, which implied that relatively stochastic geomorphic processes exerted a dominant influence on flow routing at sub-seasonal scales (see Murray & Paola, 1994), and; (iv) at the event scale, river channel network expansion was driven by high discharges from peak diurnal melt or storm events (see Tockner et al., 2000; Ward et al., 2002). Hydrograph analysis of groundwater streams revealed that there was only minimal data ‘structure’; however a weak diurnal pulse, lagging behind glacial stem and mixed sites, suggested that a weak glacial melt signal influences the alluvial ground water system of the Eisboden.

8.2.2 Spatiotemporal dynamics of water temperature

An examination of the *year-round* spatiotemporal dynamics of water temperature and flow permanency in the Eisboden catchment across a spatially extensive network of streams advanced previous alpine water temperature research which has predominantly focused on melt season thermal dynamics (but see Uehlinger et al., 2003b; Brown et al., 2006b). Additionally, and in contrast to previous research on near pristine catchments (e.g. Uehlinger et al., 2003b), the type and magnitude of impacts that overspill and drawdown flows from a high alpine reservoir had on the thermal regime were evaluated for the first time.

The interactive influences of climate and water sourcing were found to control year-round spatiotemporal thermal and flow variability. During the summer melt season, thermal heterogeneity across the catchment was high as a result of two key factors: (i) variations in the thermal characteristics of water source contributions to sites (i.e. groundwater vs. glacial melt), and; (ii) longitudinal warming. In addition to these natural drivers of thermal variation, flow regulation from the Weiβsee hydropower reservoir had a significant impact on the thermal regime of the Eisboden. This resulted in a large thermal discontinuity in the main glacial stem during two distinct periods: (i) late summer, when dam overspill occurred (mean daily increase 3.0-3.7^{o}C), and; (ii) early winter, when reservoir drawdown caused abrupt and sustained increases in stream temperature (up to 3.3^{o}C mean daily increase). Stream thermal responses to flow regulation extended laterally across the Eisboden floodplain even where there was no direct surface connectivity, suggesting hyporheic flow and/or conductance of heat through the coarse alluvium.

During winter, thermal heterogeneity was reduced markedly (relative to summer) amongst flowing sites not affected by drawdown flows. However, water temperature at flowing groundwater streams were still markedly warmer (up to 2.5^{o}C) than in the main glacial stem which was close to freezing. The evaluation of temperature time-series alongside winter field observations indicated that dewatering occurred in many of the streams during winter. However, surface flow was sustained into spring at sites affected by the Weiβsee, which suggested that recharging of the alluvial groundwater system in the lower portion of the Central Eisboden Braidplain may have a significant antecedent effect in sustaining flow downstream.

8.2.3 Spatiotemporal dynamics of stream macroinvertebrate communities.

This study investigated the year-round spatiotemporal dynamics of macroinvertebrate assemblages across the Eisboden. There were there key novel aspects to the physiochemical habitat and macroinvertebrate samples collected and analysed in this study: (i) No studies have examined previously macroinvertebrate assemblages amongst different stream types across a truly alpine floodplain (but see Burgherr et al. (2002) who examined macroinvertebrate assemblages across the Val Roseg floodplain, which is situated close to the tree-line in the Swiss Alps; (ii) Very few studies have collected macroinvertebrate samples during the winter in alpine catchments (but see; Lavandier & Décamps, 1985; Robinson et al., 2001; Schütz et al., 2001; Burgherr et al., 2002), and; (iii) no studies have examined the effects of reservoir over-spilling or drawdown on habitat and macroinvertebrate assemblages in an alpine catchment.

This study generally supported the view that distinct floodplain habitats support divergent macroinvertebrate assemblages during the summer melt-season (see Arscott et al., 2000; Burgherr et al., 2002). Stream temperature and channel stability were found to explain the greatest proportion of variance amongst communities and, with respect to these variables, spatial distribution patterns in the main glacial channel were found to broadly conform to the model of Milner et al. (2001a). Some notable differences were however evident in floodplain channels, for example Leuctridae, Nemouridae, Limnephilidae and Baetidae were found in less stable and colder habitats than expected (cf. Milner et al., 2001a). Macroinvertebrates in groundwater streams were found to be considerably more abundant and diverse than at other habitats suggesting that floodplain groundwater streams act as important ‘hot-spots’ of biodiversity along proglacial river corridors. A distinct shift in macroinvertebrate communities occurred during winter, in mixed and main glacial stem sites a more diverse range of taxa were able to colonise as physicochemical habitat conditions become more benign. In contrast, abundance and diversity were reduced in groundwater fed streams as physicochemical habitat conditions became harsher. Although reservoir overspill and drawdown both had a relatively large effect on the physicochemical conditions in the Eisboden, in general the macroinvertebrate community appeared to be relatively resistant to these disturbances.

8.3.4 Biological and functional trait diversity of benthic macroinvertebrate communities

This study investigated how the functional trait characteristics of macroinvertebrate assemblages respond to spatiotemporal habitat heterogeneity across an alpine floodplain. Macroinvertebrate assemblage traits were found to be extremely constrained, with low functional diversity in the harsh main glacial stem sites. This novel finding suggested that deterministic assembly processes were dominant. Communities were dominated by taxa with a very specific array of functional traits such as a scraping feeding habit and the ability to adopt semi-voltinism. In more benign habitats, where environmental conditions were less restrictive, a more stochastic assemblage with a greater range of functional traits was present. Traits analysis suggested that streams with intermediate glacial influence had a low functional evenness and that the array of taxa with different functional attributes was larger than in harsher sites but the community was still dominated by taxa with the same trait characteristics as those found in harsher sites. Seasonal fluctuations were evident in community functional diversity and these were greatest in sites where glacial influence was dominant during the summer. In contrast, groundwater streams exhibited no clear seasonal fluctuations in functional diversity.

8.3. RESEARCH IMPLICATIONS

This section considers the implications of the findings from this thesis with respect to three themes which are closely aligned with the central aims of this thesis (see Chapter 1.2): (i) understanding hydrological functioning, water source dynamics and physicochemical habitat conditions in alpine catchments; (ii) understanding alpine stream ecosystem structure, and; (iii) evaluating anthropogenic impacts on alpine stream ecosystems.

8.3.1 Hydrological functioning, water source dynamics and physicochemical habitat conditions in alpine catchments.

Understanding the hydrological functioning of alpine catchments is of critical importance for: (i) managing the future water supply of surrounding regions (Barnett et al., 2005; Viviroli et al., 2007; Wehren et al., 2010b), and; (ii) predicting and developing appropriate conservation strategies for aquatic ecosystems in the face of anthropogenic pressures and climate change (Hannah et al., 2007a; see also figure 2.3). Melt ablation is a major hydrological driver in alpine catchments and predictable diurnal and seasonal variations in thermal energy inputs, and snow and ice mass balance result in broadly predictable discharge trends (Gurnell et al., 1992; Smith et al., 2001; Swift et al., 2005). It is likely that projected increases in global temperature (IPCC, 2007) will significantly affect the timing and magnitude of runoff from snowmelt and glacier melt dominated catchments. For example, at the inter-annual time scale it is expected that in alpine catchments experiencing glacial shrinkage (which is the vast majority, see Dyurgerov & Meier, 2005; Kaser et al., 2006), net runoff from ablation will initially increase in response to increased energy inputs and then in the longer term decrease in response to the exhaustion of long term snow and ice water stores (Jansson et al., 2003; Barnett et al., 2005; Stahl et al., 2008; Milner et al., 2009). Accordingly, a shift in seasonal discharge timing can also be anticipated; in the long term it is expected that the bulk of annual flow will be discharged earlier in the year due to a reduction in supply from glacial sources later in the season. The degree to which *ablation* responses to climate will affect the overall hydrological characteristics of a catchment will depend on the proportion of catchment outflow that is sourced from long-term (seasonal to inter-annual) glacial or snowpack stores rather than precipitation (Braun et al., 2000; Collins, 2006). However, as this study has demonstrated (see also Collins, 1998; Hannah et al., 1999; Hannah et al., 2000; Wehren et al., 2010a) rainfall can have a large effect on the discharge characteristics of a glacierized alpine catchment. Indeed, if glacial influence decreases in response to climate change, hydrological functioning will become increasingly sensitive to, and dependant on precipitation regimes (Collins, 1998, 2006; Milner et al., 2009). To predict catchment runoff response to climate change it is therefore necessary to consider the effect of climate change on both rainfall and snow/ice mass balance {Barnett, 2005 #319;McGregor, 1995 #217}.

The effects of variations in alpine precipitation, ablation and groundwater discharge at event/diurnal to intra-annual scales are conceptualised in Figure 8.1. At the event scale major flows can arise from precipitation. The amplitude of these events is likely to be greatest when heavy rainfall occurs late in the melt season when glacial flow pathways are well developed and most efficient (Röthlisberger & Lang, 1987; Paterson, 1994; Fountain & Walder, 1998), and in glacierized catchments when precipitation events coincide with a period of high runoff from melt (Collins, 1998, 2006). At sub-seasonal time scales fluctuations in precipitation and atmospheric thermal energy inputs, associated with regional weather patterns contribute to variations in base flow as observed in this study (Figure 8.1b). Precipitation also compounds ablation driven seasonal fluctuations in runoff (e.g. Swift et al., 2005) as rainfall events occur typically from mid-spring to mid-autumn when ablation is also occurring (Figure 8.1c). During the winter precipitation falls as snow and therefore has no immediate effect on runoff (Wehren et al., 2010a). In contrast to predictions of future air temperature change, there is less certainty regarding the influence of climate change on precipitation in alpine catchments (Barnett et al., 2005). Indeed there is little agreement of the magnitude or even the direction of regional precipitation changes (Giorgi et al., 2001; Giorgi & Bi, 2005; Dai, 2006). Given the large potential impact of precipitation on the hydrological functioning in alpine catchments, greater certainty in predictions of regional precipitation are required to strengthen current predictions of hydrological response to climate change (McGregor et al., 1995; Barnett et al., 2005).

Shifts in water source dynamics in response to climate change or anthropogenic flow regulation have large potential impacts for the physicochemical conditions in alpine streams due to the strong coupling that exists between water source and habitat conditions (Smith et al., 2001; Hannah et al., 2007a; Brown et al., 2009b). As Chapter 6 of this thesis has demonstrated, water temperature is strongly associated with macroinvertebrate assemblages in alpine streams. This study has shown how water source contributions mixing over space and time, combined with variations in atmospheric thermal inputs, lead to a high degree of spatiotemporal heterogeneity at a variety of time scales across an alpine catchment. In glacierized basins, water flowing from the glacial snout is close to freezing and a strong longitudinal thermal gradient results as waters are heated downstream from: (i) atmospheric thermal inputs, and; (ii) mixing with warmer alluvial and hillslope groundwater contributions (cf. Füreder et al., 2001). This study has revealed cold glacial waters also drive lateral thermal heterogeneity across floodplains resulting in a particular diverse mix of thermal habitat. A reduction in glacial melt inputs would have large implications for lateral and longitudinal thermal profiles of alpine stream systems, resulting in less thermal heterogeneity amongst habitats which might also lead to lower β-diversity (see also Füreder et al., 2001). Whilst it was beyond the scope of this study to conduct detailed heat energy budgets for steams, temperature time series of floodplain streams disconnected from the main glacial channel suggested that the hydrological and thermal signature of water charging the alluvial groundwater system can be observed in floodplain streams disconnected from the main glacial channel. This suggests that heat transfer due to advection or conduction can occur through the alluvium (see also Stanford & Ward, 1988), and as such thermal changes in main glacial channels arising as a result of climate change or flow regulation may impact upon the thermal regime of alluvial groundwater streams that otherwise have no direct surface connection.

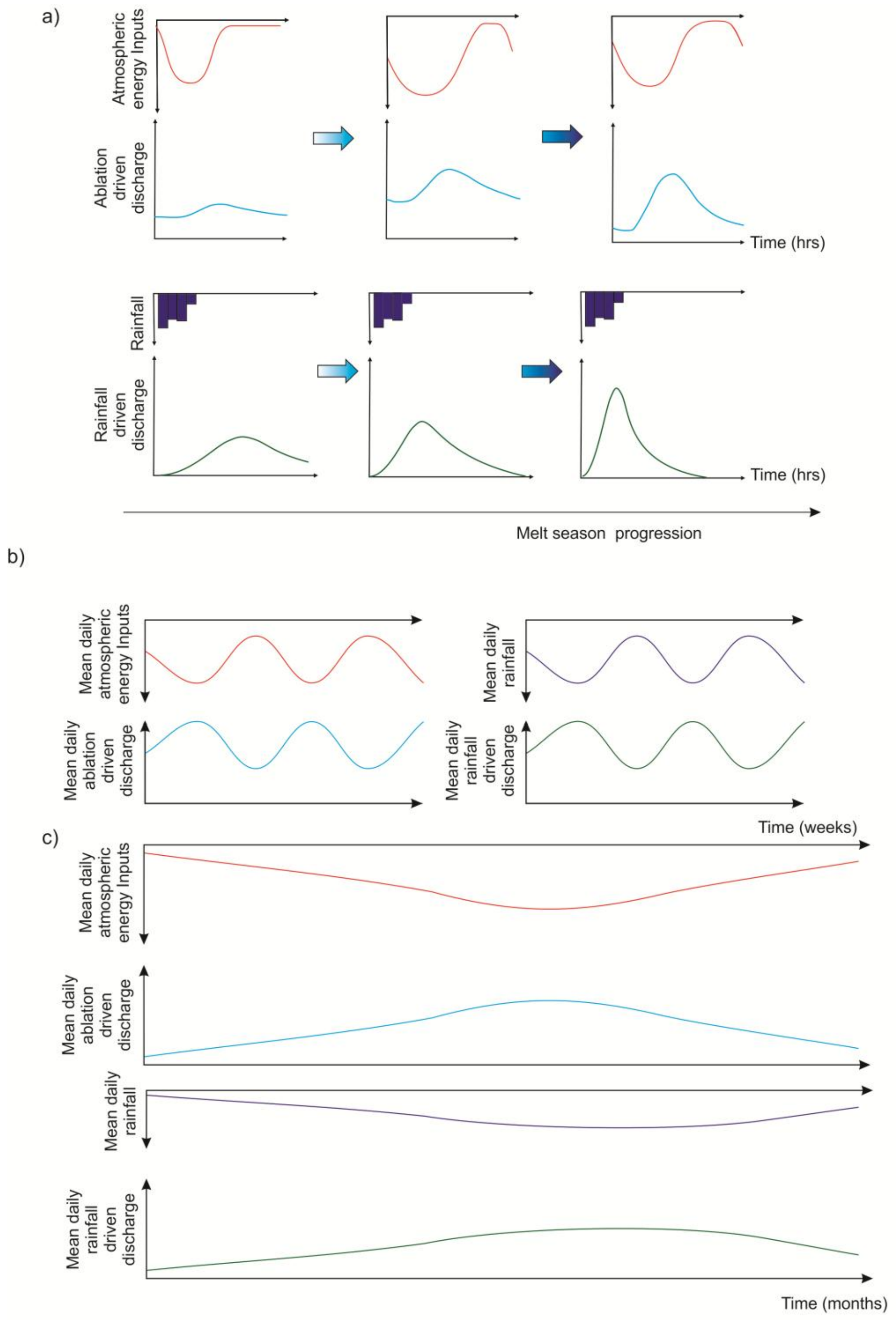

Figure 8.1 - *Conceptual relationships between precipitation and thermal energy inputs, and catchment discharge components during the summer melt season; (a) at the diurnal/event scale arising from diurnal variations in thermal energy inputs and specific rainfall events; (b) sub-seasonal scale due to local meteorological variation in atmospheric energy inputs and precipitation, and; (c) seasonal-scale due to increased rainfall and increased atmospheric energy inputs during summer compared to winter.*

Observations of flow permanency and stream temperature made during winter have large implications for our understanding of alpine stream ecosystem dynamics. It was evident from the combination of stream temperature records and field observations that although surface flow in many stream reaches ceased at some point during the winter: (i) surface flow could persist well into the winter providing a ‘window of opportunity’ for growth and development of macroinvertebrates before flow cessation occurred; (ii) surface water may exist intermittently along the stream length particularly in pools, and; (iii) the hyporheic zone may not necessarily be desiccated or frozen even when surface flow has ceased. The latter two points suggest that even after the surface flow of a stream has ceased, patches of surface habitat may exist and the hyporheic zone may remain habitable by macroinvertebrates even if they are unable to survive freezing or desiccation (Danks, 1971a,b; Irons et al., 1993; Lencioni, 2004). These findings have large implications for our understanding of how macroinvertebrates may survive the winter in alpine streams without migrating away from the freezing front or without adaptations to survive desiccation or freezing.

8.3.2 New understanding of alpine stream ecosystem structure

The conceptual model of Milner et al. (2001) has been used widely as a reference with which to compare the observations of benthic macroinvertebrate surveys of alpine rivers. A substantial number of studies investigating longitudinal ecological gradients along alpine streams have generally corroborated this model (e.g. Burgherr & Ward, 2001; Gíslason et al., 2001; Lods-Crozet et al., 2001; Malard et al., 2001; Snook & Milner, 2001; Ilg & Castella, 2006). Based on observations made at the Val Roseg floodplain, Switzerland, Milner et al. (2001a) were open in suggesting that the model may not be valid for predicting assemblages across floodplains, because it does not take account of vertical thermal gradients arising between the hyporheic zone and the water column due to upwelling alluvial groundwater contrasting with cold glacial flows. Milner et al. (2001a) suggested that some Ephemeroptera and Plecoptera may be able to persist in the streams with colder water columns where there are more equable conditions in the hyporheic zone. However, to my knowledge no studies have since tested the applicability of the model to an alpine floodplain. Another limitation of the Milner et al. (2001a) model is that it only conceptualises distributions during the summer melt season and very few studies have considered how findings in winter may alter this conceptual understanding (but see Robinson et al., 2001; Schütz et al., 2001; Burgherr et al., 2002). The data set from this study presented a unique opportunity to examine the relevance of the model of Milner et al (2001a) to lateral and temporal dimension of alpine floodplain ecosystems.

The ecological data collected in summer samples in this study are presented in Figure 8.2a in a similar format as the conceptual model of Milner et al. (2001a; Figure 8.2b). The first appearance of families of macroinvertebrates are plotted with respect to stream temperature and channel stability. In Figure 8.3 the abundances of families of macroinvertebrates collected during the summer melt seasons (indicated by bubble size) are plotted with respect to stream temperature and channel stability to provide a more in-depth representation of the relationship between community assemblages and habitat conditions. Three key differences can be observed between observations made across sites of the Eisboden floodplain and the model of Milner et al. (2001a).

(i) Tipulidae appeared in the assemblage only at a site where water temperature and channel stability was greater than predicted by the model.

(ii) Nemouridae, Baetidae, Limnephilidae, Leuctridae and Heptageniidae were all found at mixed floodplain sites, with uncharacteristically low channel stability and water temperature when compared with the model.

(iii) As predicted by the model, Chironominae taxa were only present at very stable sites (i.e. groundwater streams); however, T_{max} of groundwater sites where they were found was considerably lower than expected, (see also Figure 8.3).

The first of the discrepancies is unlikely to be significant. Tipulidae were present in only one sample and their absence from lower temperature and stability sites cannot be assumed to because of physicochemical constraints since they were so rare within the catchment. To evaluate the implications of the second of the discrepancies stated above it is first necessary to highlight a key difference between how T_{max} was defined in the model of Milner et al. (2001) and in this study. A limitation of the Milner et al. (2001) model is that it essentially assumes that macroinvertebrate assemblages do not exhibit temporal variation (i.e. no time frame is specified for which T_{max} was calculated). This limitation is particularly salient to its application to floodplain ecosystems where habitats are highly dynamic and stream temperatures may exhibit considerable variation at sub-seasonal time scales. It is thus necessary to define a relevant time period over which to calculate T_{max} because, for example, the physicochemical habitat conditions of a floodplain site may exhibit a wholesale transformation preceding a change in flow routing of the main glacial channel. The antecedent T_{max} may then be redundant and a poor predictor of the new community assemblage. In this study, T_{max} was defined as the maximum water temperature measured (15 min res.) in the week prior to sampling. This was based on the judgement that one week would occlude short term (sub-weekly) cold periods where stream temperatures could be uncharacteristically low in otherwise relatively benign habitats (i.e. groundwater streams; see Chapter 5), but still reflect sub-seasonal changes in water temperature arising from variations in water source dynamics. Clearly this judgement is somewhat subjective and there is a need for more research to determine how best to define T_{max} given the inherent temporal variability of water temperatures across alpine floodplains. If T_{max} was re-defined for the dataset in this study to reflect the maximum temperature monitored at each site through the whole study period, then the assemblages observed would more closely map onto the model of Milner et al. (2001); however, this representation would underrepresent the temporal dynamics of both physicochemical habitats and macroinvertebrate communities during the summer melt season across alpine floodplains (see chapters 6 and 7).

The third discrepancy stated above suggests that the model of Milner et al. (2001a) does not reliably predict the presence of Ephemeroptera, Plecoptera and Trichoptera (EPT) taxa across floodplain habitats. This limitation was acknowledged by Milner et al. (2001a) but they hypothesised that assemblages may deviate from the model at floodplains due to the influence of upwelling alluvial groundwater causing a disparity between thermal conditions measured in the water column and the typically warmer thermal conditions of the hyporheic zone that taxa may use as a refuge. However, the results from this study suggest that EPT taxa may also be found in streams with lower channel stability than expected in floodplain channels, which suggests that their presence cannot be solely attributed to warmer hyporheic temperatures. Additional or alternative factors may be that: (i) floodplains provide a highly dynamic heterogeneous range of habitats in close proximity, so when stream physicochemical conditions ameliorate in specific floodplain channels, EPT taxa are able to colonise rapidly from more equable habitats, or; (ii) taxa are able to tolerate harsh conditions, for example by using the hyporheic zone as a refuge, for short periods of time but rely on a return to more benign conditions for example for further feeding, growth and development. It is important to note that although mixed streams may be more diverse in terms of taxonomic richness, functional analysis of macroinvertebrate communities in mixed floodplain streams with intermittent glacial influence suggested that the array of taxa with different functional attributes was larger than in harsher sites but the community was still dominated by taxa with the same trait characteristics as those found in harsher sites. This suggests that although mixed floodplain channels with intermittent glacial influence may be habitable by EPT taxa, there is still some constraint on abundance at least for periods of the summer melt-season.

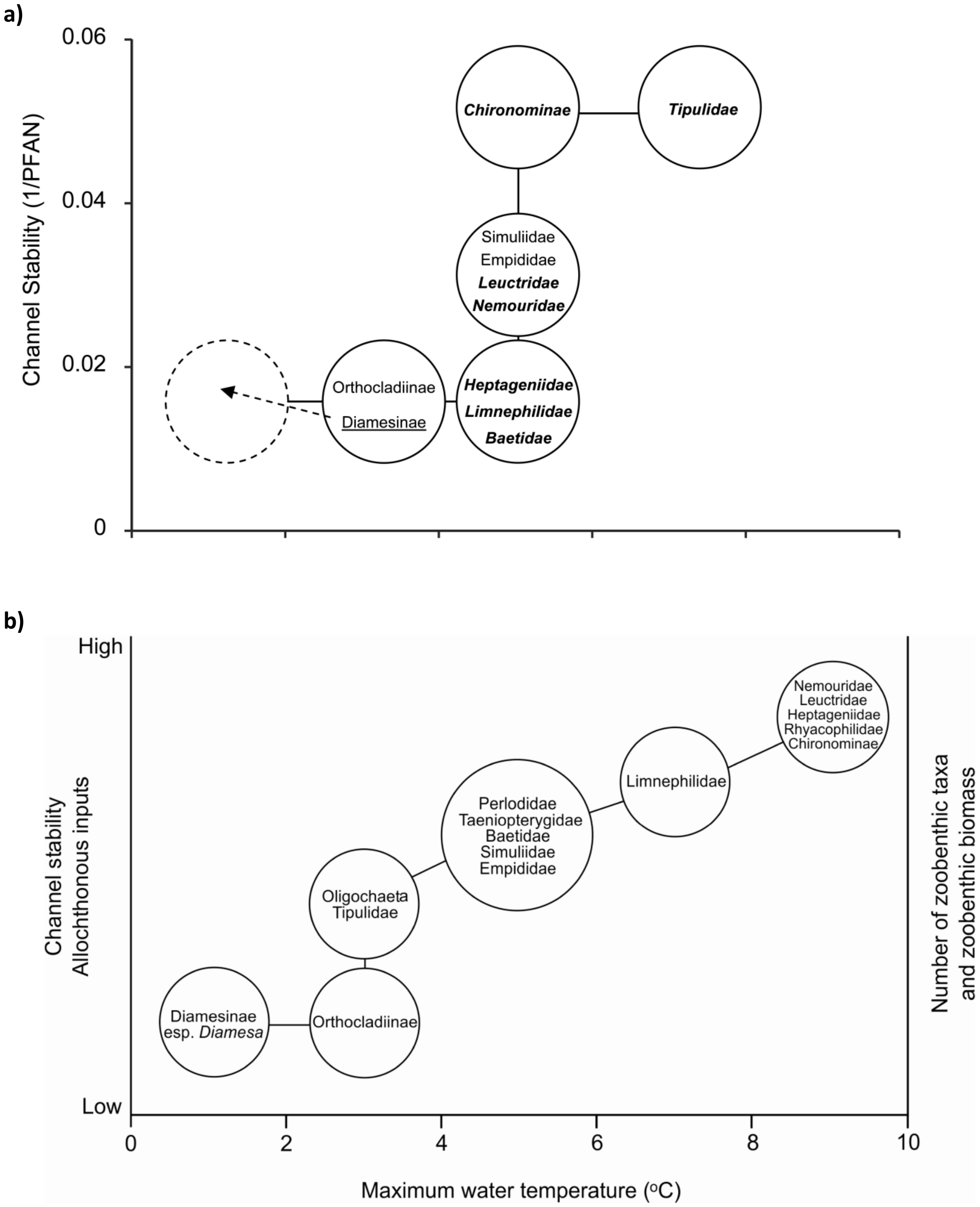

Figure 8.2 - *(a) First appearances of macroinvertebrate taxa along a gradient of increasing water temperature and channel stability found during the melt season at sites across the Eisboden central braidplain; (b) Conceptual model reproduced from Milner et al. (2001) describing the likely first appearance of macroinvertebrate taxa along an upstream-downstream continuum from the glacier margin with increasing water temperature and channel stability during the melt season for European glacier-fed rivers.*

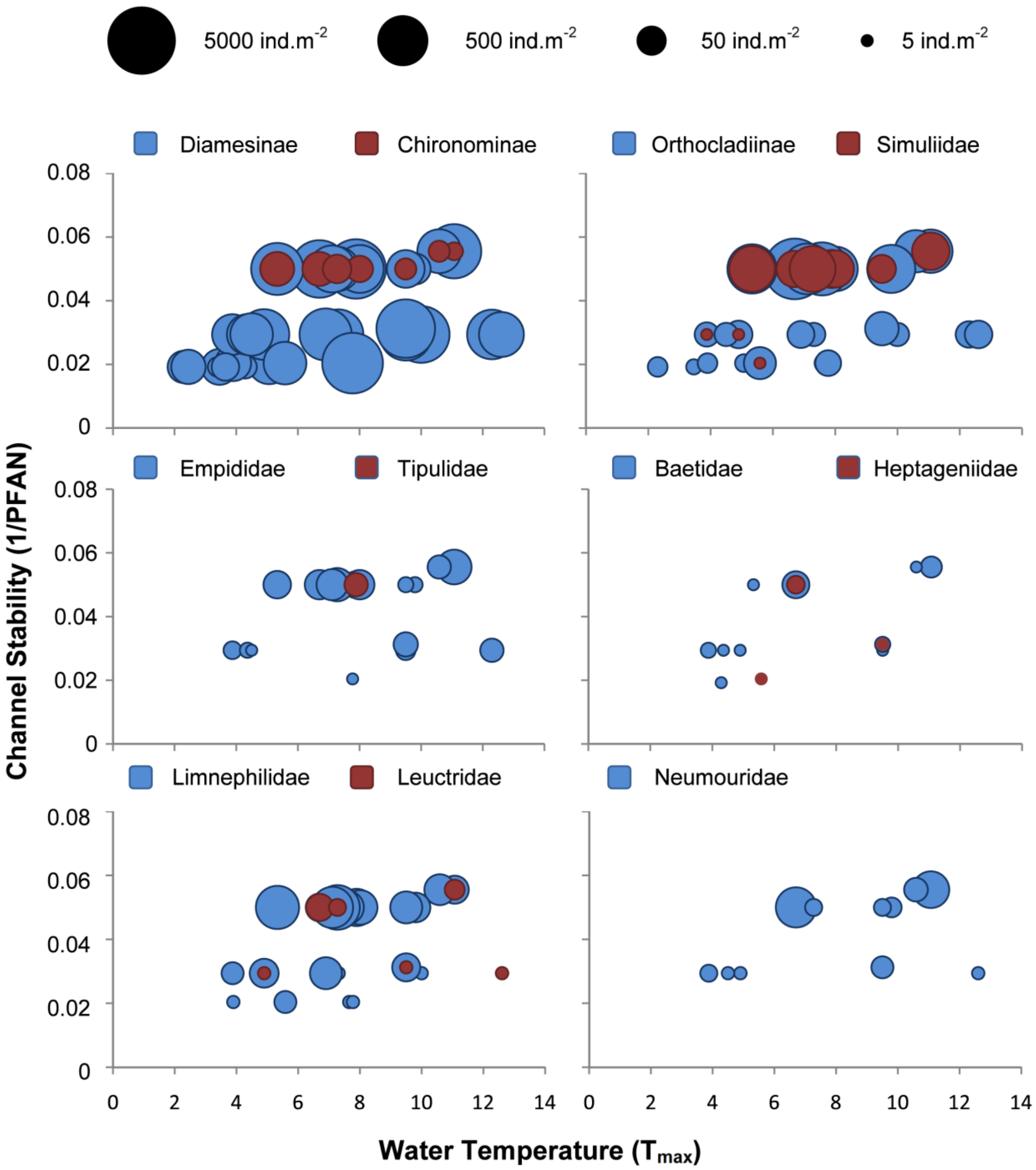

Figure 8.3 - *Bubble plots showing the number of individuals of families as included in the conceptual model of Milner et al. (2001) and observed at sites in this study as a function of water temperature and channel stability.*

Overall this study has shown how macroinvertebrate communities inhabiting floodplain habitats can vary considerably from those expected in a glacial river close to the glacial margin (cf. Milner, 1994). The model of Milner et al. (2001) does not adequately reflect the spatiotemporal dynamism that occurs across a floodplain ecosystem. These findings suggest that floodplains require specific consideration when assessing the ecological status of alpine rivers and this concurs with studies that have identified sub-alpine and low land floodplains as areas of high conservational importance due to their unique ecosystems (e.g. Junk et al., 1989;

Tockner et al., 1999; Ward et al., 1999b; Arscott et al., 2000; Brunke, 2002; Tockner et al., 2010).

This study revealed that macroinvertebrate assemblages across the Central Eisboden Floodplain exhibit strong seasonal variations, and so an obvious implication of this observation is that if floodplain ecosystems are only studied during summer then this will lead to a rather incomplete and unbalanced view of ecosystem structure and functioning. This study generally supports the view that sites influenced by glacial melt-water exhibit summer-harsh, winter-benign physicochemical habitat characteristics (Lavandier & Décamps, 1985; Uehlinger et al., 2002; Brown et al., 2007c; Tockner et al., 2010) and that an associated shift towards a more diverse macroinvertebrate assemblage occurs in channels that remain flowing during winter. However, although a ‘summer-harsh, winter-benign’ trend was evident in specific channels whilst they remained flowing, at the floodplain scale the area of flowing habitat is greatly reduced due to floodplain contraction and it is not clear to what extent any increases in diversity and abundance in flowing channels are a function of the macroinvertebrate communities becoming concentrated in much smaller flowing areas. As Tockner (2010) pointed out, benign periods may be viewed as ‘windows of opportunity’ for floodplain habitats and therefore maintaining the integrity of natural flow conditions during these periods may be of particular importance for annual biological productivity. More *year-round* research is necessary to elucidate how floodplain ecosystems function during winter and to determine how sensitive floodplains may be to for example climate change or anthropogenic flow regulation.

8.3.3 Anthropogenic impacts on alpine stream ecosystems

This study has provided novel insights into the effects of reservoir overspill and drawdown on stream habitats and macroinvertebrate communities because it is the first study to assess reservoir regulation effects on a high alpine glacier-fed river system. Reservoir hydrology had a relatively large effect on the physicochemical conditions in the Eisboden, for example by increasing stream temperature both in winter and summer (cf. Zolezzi et al., 2010)), increasing mean daily discharge, causing large step fluctuations in discharge during winter, and preventing the formation of a snow pack over parts of the stream (see Plate 8.1). However, in general the macroinvertebrate community appeared to be relatively resistant to these disturbances in comparison with the largely reduced abundance and richness of macroinvertebrate assemblages that have been reported from sub-alpine rivers (e.g. Céréghino et al., 2002; Cortes et al., 2002). A potential explanation for this is that close to the glacial margin the macroinvertebrate community are better adapted to disturbance due to the natural instability and harshness of stream habitats (Ward, 1994; Brown et al., 2007c). This study has investigated the effects of flow inundation from a storage reservoir on benthic ecology on one floodplain which is subject to a specific set of reservoir overspill and drawdown events with specific timing and magnitude. It is essential that the impacts of different forms and magnitudes of anthropogenic flow regulation be assessed more widely and over longer time scales to provide a fuller picture of anthropogenic impacts to alpine river ecosystems.

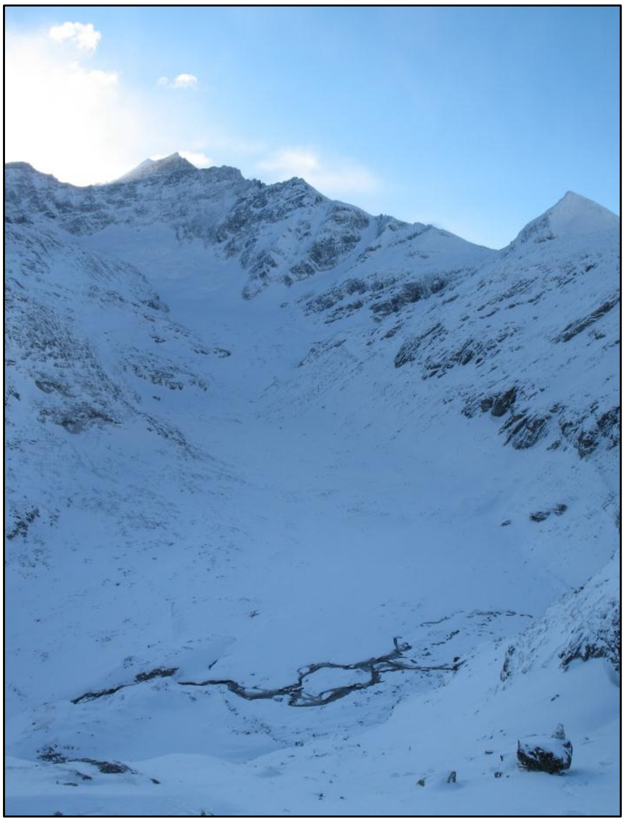

Plate 8.1 - *Photograph taken in December, 2008 showing the contrast between channels that are kept free from snow-cover by drawdown flows from the Weißsee (obvious channels at the bottom of the photograph) and channels which are not regulated and are indistinguishable from the snowpack (cf. Plate 3.1)*

8.4. STUDY LIMITATIONS AND SUGGESTED DIRECTIONS FOR FUTURE RESEARCH

This section considers the limitations of this research and suggests future directions for further research with respect to the same themes discussed in the previous section (8.3).

8.4.1 Researching hydrological functioning, water source dynamics and physicochemical habitat conditions in alpine catchments.

This study adopted an interdisciplinary approach and a large volume of meteorological, hydrological, geomorphologic and ecological field data were collected to provide complimentary data sets. This thesis focused on the concurrent analysis of meteorological, discharge, water temperature, reach scale variables measured to characterise physicochemical habitat and benthic macroinvertebrate data to meet its central aims (see Chapter 1.2).

However, the analysis of additional field data collected concurrently will undoubtedly provide further insight into catchment hydrological functioning, water source dynamics and physicochemical habitat conditions. Additional data that has been collected but requires further analysis is outlined briefly:

(i) Turbidity was measured during the summer melt-seasons at Sites A and B and suspended sediment – turbidity rating curves were constructed based on water samples collected using a pump sampler at Site B through a range of turbidity values. These data could be used to analyse spatiotemporal sediment transfer patterns with respect to hydrological and metrological conditions (e.g. Orwin & Smart, 2004; Crosa et al., 2010).

(ii) Time-lapse photography was used to monitor braiding dynamics across the Central Eisboden braidplain during the summer monitoring periods. It is anticipated that these photographs will be orthorectified and used to calculate braiding and connectivity indices that could be analysed alongside discharge and suspended sediment data sets to yield a greater understanding of braiding dynamics (e.g. Luchi et al., 2007).

(iii) Snow pack and water chemistry sampling was conducted concurrently with ecological sampling during the melt-season of 2009 and samples were analysed for major anions, major cations, Silica and Bicarbonate concentrations in the laboratory. This data set provides an opportunity to test the applicability of ARISE (A Classification Tool for Alpine River and Stream Ecosystems developed by Brown et al., 2009b) to an alpine floodplain ecosystem.

This study was the first to assess the validity of using water temperature data alongside stage measurements to analyse year-round flow-permanency in an alpine catchment. Stream temperature records were compared with direct field observations made during winter by excavating snowpacks to reveal channel sections. Three recommendations were made in Chapter 5.5 of how to best use temperature sensors to assess year-round flow permanency. Further work to assess the utility of the recommendations suggested would be valuable as flow permanency has large implications for ecosystem structure (see Chapters 6 and 7, Burgherr et al., 2002) and is likely to be highly sensitive to climate change and anthropogenic flow regulation due to its dependence on discharge.

8.4.2 Researching alpine stream ecosystem structure

Four key improvements are suggested herein to expand the work of this study and further develop knowledge of year-round structure of alpine benthic ecosystems.

i - This study was restricted to streambed sampling; however, it was hypothesised from the absence of taxa, particularly Chironomidae taxa in snow covered channels, that the hyporheic zone may be used as a refuge during periods of adversity. Sampling of the hyporheic zone, for example by using coring techniques (Fraser & Williams, 1997) would provide fascinating insights into how fauna vary through the vertical dimension (Ward, 1989; Milner et al., 2001a) and if, and to what extent, the hyporheic zone provides a refuge from stream bed freezing and/or desiccation (Lavandier & Décamps, 1985; Lencioni, 2004).

ii - Most year-round alpine studies including this study have sampled relatively infrequently during winter. Only Schütz et al. (2001) have sampled at a monthly resolution (although observations were limited to one snow-covered, and one open site) and they found that under snow cover macroinvertebrate abundances varied erratically. In order to ascertain with greater certainty how macroinvertebrate assemblages change at the seasonal scale, more studies with greater sampling resolution need to be conducted during winter, particularly at sites under snow cover.

iii - Macroinvertebrates have been the major focus of benthic alpine studies. However, meiofauna samples which were collected concurrently with macroinvertebrate samples in the Eisboden during the summer melt season, 2009, are currently being analysed. This data will provide a more holistic picture of benthic faunal community structure in the Eisboden and provide additional insights into distributions of the macroinvertebrate communities. particulary because some provide a valuable food supply for macroinvertebrates (Suren, 1992; Hakenkamp & Morin, 2000).

iv - The trait-based approach adopted in Chapter 7 provided valuable insights into macroinvertebrate functional diversity in the Eisboden. However, this approach is currently limited by a lack of trait information at species/genus levels for many of the taxa found in the Eisboden, and discrepancies between trait databases (e.g. database used by Finn & Poff, 2006; Ilg & Castella, 2006) regarding the coding of several key trait characteristics of Chironomidae taxa. Further work is required to refine trait databases for alpine taxa.

8.4.3 Researching anthropogenic impacts on alpine stream ecosystems

The utility of the data to investigate the effects of flow inundation from a storage reservoir on benthic ecology was limited in the sense that sampling was restricted to a single basin, and so spatial sampling replicates were essentially only pseudoreplicates (Hurlbert, 1984) rather than true replicates of the experimental unit (i.e. a river subject to regulation). It is therefore essential that anthropogenic flow regulation is investigated more widely (i.e. in different catchments and over longer time scales) to provide a fuller picture of flow regulation to alpine river ecosystems. In addition, the focus of this study was on inter-catchment transfer from a reservoir by overspill and drawdown that led to an increase flow in the Eisboden. Flow regulation in other catchments may differ significantly from the particular regulation regime observed in this study (see Chapter 2.4) and more studies are therefore required to ascertain how different forms and severities of flow regulation effect alpine stream communities. Indeed, there is also need for more research into how other human activities impact upon alpine stream ecosystems such as artificial snow compaction (Schiermeier, 2004; Wemple et al., 2007; Pintar et al., 2009; Wehren et al., 2010b), ice/snowpack contamination from persistent organic pollutants (Blais et al., 2001; Caruso, 2002; Bogdal et al., 2009) and groundwater contamination from grazing livestock and pollution from mountain huts (Kralik, 2001; Reischer et al., 2008).

8.5. SUMMARY

The central aim of this thesis, 'to examine the spatiotemporal dynamics of an alpine proglacial floodplain ecosystem that is impacted by anthropogenic flow regulation' has been met by achieving the four central objectives defined in Chapter 1.

(i) An objective hydrograph classification technique was used to analyse the hydrological functioning of an alpine floodplain stream system in Chapter 4.
(ii) Year-round flow permanency and thermal dynamics of streams across the floodplain and more widely across the basin were investigated in Chapter 5.
(iii) Chapter 6 examined the spatiotemporal dynamics of a macroinvertebrate floodplain community with respect to physicochemical habitat conditions.
(iv) The biological and functional trait characteristics of floodplain macroinvertebrate assemblages were examined in Chapter 7.

This chapter has demonstrated how the resultant findings have contributed to knowledge of hydrological functioning, ecosystem structure and the implications of flow regulation for alpine stream ecosystems.

In summary, the findings of this thesis suggest that the spatiotemporal dynamics of alpine floodplain ecosystems are highly complex due to the interactive role of hydrological, geomorphological and meteorological drivers which can vary markedly at event/diurnal to inter-annual timescales. This complexity results in a dynamic patchwork of habitats that support a diverse and unique ecosystem. This study has shown that alpine stream ecosystems are resistant, to an extent, to flow regulation, perhaps because they are naturally well adapted to disturbance regimes typical of proglacial systems. A major future challenge will be to further refine our understanding of alpine stream (and indeed other river systems) ecosystem structure and functioning to quantify tolerance thresholds and impact gradients to anthropogenic pressures such as flow regulation and climate change.

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APPENDIX A: AIR- WATER TEMPERATURE CORRELATIONS

Air- water temperature and Incoming shortwave radiation-water temperature correlation coefficients for 15 min data expressed in the form: Pearson's r, CCF$_{max}$, [lag (hrs to nearest 0.25 h)]. All correlations significant (P < 0.01) unless marked: * (significant at P < 0.05), or ** (not significant).

Site	**Unregulated Period 2008**		**Overspill Period 2008**		**Unregulated Period 2009**		**Overspill Period 2009**	
	Air Temp.	Short wave.	Air Temp.	Short wave.	Air Temp.	Short wave.	Air Temp.	Short wave.
S2	0.906,0.915 [0.75]	0.524,0.623 [2.00]	0.931,0.937 [0.50]	0.617,0.727 [1.75]	0.815,0.894 [2.00]	0.553,0.632 [1.75]	0.883,0.894 [0.50]	0.686, 0.769 [1.75]
S3	0.604,0.618 [-0.50]	0.821,0.821 [0.25]	0.638,0.659 [-0.75]	0.859, 0.863 [0.25]	0.729, 0.783 [1.25]	0.841,0.845 [0.25]	0.774,0.774 [0.00]	0.853,0.879 [0.5]
S4	0.815,0.815 [0.00]	0.817, 0.832 [0.25]	0.856,0.862 [-0.25]	0.867,0.887 [0.50]	0.781,0.820 [1.25]	0.790,0.797 [0.75]	0.794,0.794 [0.00]	0.851,0.859 [1.00]
S5	0.847,0.847 [0.00]	0.681,0.705 [1.00]	0.839,0.839 [0.00]	0.732, 0.754 [0.75]	0.663, 0.688 [0.75]	0.772,0.775 [0.25]	0.437,0.492 [-1.50]	0.514,0.526 [-0.25]
S6	0.596,0.610 [-0.75]	0.807,0.811 [0.25]	0.704,0.730 [-1.00]	0.943, 0.943 [0.00]	0.736, 0.736 [0.00]	0.806 0.822 [-0.50]	0.698, 0.712 [0.25]	0.776 776 [0.00]
S7	0.587,0.596 [-0.75]	0.544,0.544 [0.00]	0.700,0.735 [-1.00]	0.934, 0.934 [0.00]	0.545, 0.566 [1.00]	0.675,0.682 [0.50]	0.516,0.530 [-1.00]	0.613,0.623 [0.25]
S9	0.630,0.653 [-1.25]	0.753,0.753 [0.00]	0.721,0.765 [-0.75]	0.921, 0.922 [-0.25]	0.859,0.860 [0.25]	0.907,0.914 [0.25]	0.675,0.711 [-1.00]	0.905,0.918 [-0.25]
S10	0.459,0.459 [0.00]	0.320,0.350 [1.50]	0.809, 0.809 [0.00]	0.537,0.605 [1.25]	0.749,0.809 [1.75]	0.469,0.502 [1.25]	0.581,0.585 [0.25]	0.513,0.552 [1.00]
S11	-	-	-	-	0.747,0.787 [1.50]	0.665,0.706 [1.00]	0.490,0.491 [0.25]	0.155,0.160 [0.75]
S12	0.628,0.644 [-0.75]	0.710,0.770 [0.00]	0.733,0.763 [-1.00]	0.902,0.902 [0.00]	0.617,0.641 [1.00]	0.799,0.801 [-0.25]	0.696,0.738 [-1.00]	0.906,0.924 [-0.25]
S13	0.330,0.523 [32.00]	0.020*,0.132 [36.00]	0.286,0.341 [23.50]	0.018**, 0.062*[25.75]	0.662,0.664 [0.25]	0.566,0.569 [-0.25]	0.289,0.291	0.229,0.238 [0.75]
S14	0.817,0.825 [-0.25]	0.807, 0.807 [0.00]	0.824, 0.843 [-0.50]	0.910,0.912 [0.25]	0.831,0.831 [0.00]	0.742,0.769 [-0.75]	0.395,0.395 [0.00]	0.509,0.512 [0.25]
S15	0.580,0.612 [0.50]	0.548,649 [1.5]	0.728,0.729 [1.00]	0.342,0.379 [1.5]	0.456,0.515 [1.50]	0.535,0.558 [0.75]	0.418,0.420 [0.25]	0.083,0.087 [0.75]
S16	0.680,0.682 [0.25]	0.575,0.676 [1.50]	0.705,0.706 [0.25]	0.377,0.410 [1.00]	0.549,0.617 [1.75]	0.669,0.704 [0.75]	0.614,0.614 [0.00]	0.558,0.570 [0.50]
S17	0.828,0.842 [-0.50]	0.837,0.841 [- 0.25]	0.818,0.831 [-0.50]	0.914,0.914, [0.00]	0.729,0.744 [0.75]	0.754,0.754 [0.00]	0.481,0.507 [-1.00]	0.598,0.603 [-0.25]
18	0.696,0.696 [0.00]	0.791,0.791 [0.00]	0.648,0.699 [-1.00]	0.911,0.912 [-0.25]	0.556, 0.590 [1.00]	0.690,0.960 [0.00]	0.558,0.589 [1.00]	0.691,0.691 [0.00]
S19	0.817,0.829 [-0.50]	0.884,0.884 [0.00]	0.828,0.834 [-0.25]	0.930,0.932 [0.25]	0.754,0.785 [1.00]	0.859,0.859 [0.00]	0.503,0.520 [-0.75]	0.632,0.632 [0.00]
S20	0.647,0.655 [-0.50]	0.877,0.891 [0.25]	0.487,0.510 [-1.00]	0.443, 0.443 [0.00]	0.729, 0.775 [1.25]	0.878,0.885 [0.25]	0.578,0.596 [-1.00]	0.471,0.474 [-0.25]
S21	-	-	-	-	0.551,0.602 [1.50]	0.459,0.474 [0.75]	0.680, 0.682 [-0.25]	0.719,0.719 [0.00]
S22	0.842,0.842 [0.00]	0.659,0.707 [1.25]	0.857,0.862 [0.25]	0.738,0.841 [1.25]	0.758,0.820 [1.50]	0.634,0.664 [1.00]	0.828,0.840 [0.50]	0.764,0.848 [1.25]
S23	0.535,0.548 [- 0.75]	0.849,0.849 [0.00]	0.545,0.552 [-0.50]	0.533, 0.539 [0.25]	0.335, 0.383 [1.50]	0.591,0.613 [0.75]	0.409,0.422, [-1.00]	0.380,0.384 [-0.25]

APPENDIX B: MACROINVERTEBRATE IDENTIFICATION KEYS

Keys used for the identification of benthic macroinvertebrates;

Elliott, J.M., Humpesch, U.H. & Macan, T.T. (Eds.) (1988) *Larvae of the British Ephemeroptera:A Key with Ecological Notes* Cumbria, Freshwater Biological Association.

Klausnitzer, B. (1984) *Käfer Im Und Am Wasser* Wittenberg Lutherstadt : Ziemsen.

Rivosecchi, L. (Ed.) (1984) *Ditteri (Diptera)*, Consigli Nazionale Delle Ricerche.

Schmid, P.E. (Ed.) (1993) *A Key to the Larval Chironomidae and Their Instars from Austrian Danube Region Streams and Rivers: Part 1, Diamesinae, Prodiamesinae and Orthocladiinae*, Federal Institute of Water Quality, Ministry of Agriculture and Forestry.

Seitz, G. (Ed.) (1998) *Bestimmungsschlüssel Für Die Präimaginalstadien Der Kriebelmücken Deutschlands*.

Smith, K.G.V. (1989) *An Introduction to the Immature Stages of British Flies: Diptera Larvae, with Notes on Eggs, Puparia and Pupae,* London, Royal Entomological Society.

Waringer, J. & Graf, W. (1997) *Atlas Der Österreichischen Köcherfliegenlarven; Unter Eienschluß Der Angrenzenden Gebiete,* Wien, Facultas-Universitätsverlag.

Wiederholm, T. (1983) Chironomidae of the Holarctic Region. Keys and Diagnoses. Part 1. Larvae. *Scandinavian Entomology,* 19**,** 449.

Zwick, P. (2004) Key to the West Palaearctic Genera of Stoneflies (Plecoptera) in the Larval Stage. *Limnologica - Ecology and Management of Inland Waters,* 34**,** 315-348.

APPENDIX C: LIST OF IDENTIFIED TAXA

Taxonomic classifications of all taxa observed at in the Eisboden and in included in Chapters 6 and 7. Sub-classifications are given in parenthesis.

Name	**Order**	**Family**	**Genus**	**Species**
Dytiscidae sp.	Coleoptera	Dytiscidae		
Hydrophilidae *sp a.*	Coleoptera	Hydrophilidae		*sp. a*
H.fuscipes	Coleoptera	Hydrophilidae	*Hydrobius*	*fuscipes*
Hydrophilidae *sp b.*	Coleoptera	Hydrophilidae		*sp.b*
Coleoptera *sp.*	Coleoptera			
Collembola	Collembola			
Leptoconopus sp.	Diptera	Ceratopogonidae	*Leptoconopus*	
Parapsectra sp.	Diptera	Chironomidae (Chironominae)	*Parapsectra*	
D.bertrami	Diptera	Chironomidae (Diamesinae)	*Diamesa*	*bertrami*
D.cinerella/zernyi gr.	Diptera	Chironomidae (Diamesinae)	*Diamesa*	*cinerella/zernyi gr.*
D.latitarsis gr.	Diptera	Chironomidae (Diamesinae)	*Diamesa*	*latitarsis gr.*
D.latitarsis/bertrami gr.	Diptera	Chironomidae (Diamesinae)	*Diamesa*	*latitarsis/bertrami gr.*
D.permacer/dampfi gr.	Diptera	Chironomidae (Diamesinae)	*Diamesa*	*permacer/dampfi gr.*
D.steinboecki	Diptera	Chironomidae (Diamesinae)	*Diamesa*	*steinboecki*
Diamesa jv.	Diptera	Chironomidae (Diamesinae)	*Diamesa*	
Pseudokiefferiella sp.	Diptera	Chironomidae (Diamesinae)	*Pseudokiefferiella*	

Chironomidae *jv.*	Diptera	Chironomidae (Diamesinae)		
B.modesta	Diptera	Chironomidae (Orthocladiinae)	*Brillia*	*modesta*
C.vitellinus gr.	Diptera	Chironomidae (Orthocladiinae)	*Chaetocladius*	*vitellinus*
Corynoneura sp.	Diptera	Chironomidae (Orthocladiinae)	*Corynoneura*	
COP *sp.a*	Diptera	Chironomidae (Orthocladiinae)	*Cricotopus-Orthocladius-Paratrichocladius gr.*	*sp. a*
COP *sp.b*	Diptera	Chironomidae (Orthocladiinae)	*Cricotopus-Orthocladius-Paratrichocladius gr.*	*sp. b*
E.claripennis cf.	Diptera	Chironomidae (Orthocladiinae)	*Eukiefferiella*	*claripennis cf.*
E.coerulescens cf.	Diptera	Chironomidae (Orthocladiinae)	*Eukiefferiella*	*coerulescens cf.*
E.cyanea cf.	Diptera	Chironomidae (Orthocladiinae)	*Eukiefferiella*	*cyanea cf.*
Eukiefferiella	Diptera	Chironomidae (Orthocladiinae)	*Eukiefferiella*	
H.serratosioi	Diptera	Chironomidae (Orthocladiinae)	*Heleniella*	*serratosioi*
O.frigidus	Diptera	Chironomidae (Orthocladiinae)	*Orthocladius*	*frigidus*
O.sp.a	Diptera	Chironomidae (Orthocladiinae)	*Orthocladius*	sp.a
O.sp.b	Diptera	Chironomidae (Orthocladiinae)	*Orthocladius*	sp.b
O.sp.c	Diptera	Chironomidae (Orthocladiinae)	*Orthocladius*	sp.c
O.rivicola gr.	Diptera	Chironomidae (Orthocladiinae)	*Orthocladius*	*rivicola gr.*
Orthocladius s.str	Diptera	Chironomidae (Orthocladiinae)	*Orthocladius*	*s.str*
O. (Euorthocladius) sp.	Diptera	Chironomidae (Orthocladiinae)	*Orthocladius (Euorthocladius)*	
Paratrichocladius sp.	Diptera	Chironomidae (Orthocladiinae)	*Paratrichocladius*	
P.nudipennis	Diptera	Chironomidae (Orthocladiinae)	*Parorthocladius*	*nudipennis*
P.(Pachydiamesa) sp.	Diptera	Chironomidae (Orthocladiinae)	*Pseudodiamesa (Pachydiamesa)*	

Smitta sp.	Diptera	Chironomidae (Orthocladiinae)	*Smittia*	
Thienemanniella sp.	Diptera	Chironomidae (Orthocladiinae)	*Thienemanniella*	
Tventia sp.	Diptera	Chironomidae (Orthocladiinae)	*Tvetenia*	
Orthocladiinae jv.	Diptera	Chironomidae (Orthocladiinae)		
Podonominae *sp.a*	Diptera	Chironomidae (Orthocladiinae)		*sp.a*
Podonominae *sp.b*	Diptera	Chironomidae (Orthocladiinae)		*sp.b*
Clinocera sp.	Diptera	Empididae	*Clinocera*	
Cheilotrichia sp.	Diptera	Limoniidae (Chioneinae)	*Cheilotrichia*	
Dicranota sp.	Diptera	Pediciidae (Pediciinae)	*Dicranota*	
Psychodidae	Diptera	Psychodidae		
Prosimulium	Diptera	Simuliidae	*Prosimulium*	
Thaumaleidae	Diptera	Thaumaleidae		
Tipulidae	Diptera	Tipulidae		
Diptera sp.a	Diptera			*sp.a*
Diptera sp.b	Diptera			*sp.b*
B.alpinus	Ephemeroptera	Baetidae	*Baetis*	*alpinus*
Rhithrogena	Ephemeroptera	Heptageniidae	*Rhithrogena*	
Heteroptera sp.	Hemiptera (Heteroptera)			
Leuctra	Plecoptera	Leuctridae	*Leuctra*	
Nemoura	Plecoptera	Nemouridae	*Nemoura*	
N pictetii	Plecoptera	Nemouridae	*Nemurella*	*pictetii*

Protonemura	Plecoptera	Nemouridae	*Protonemura*	
Nemouridae jv.	Plecoptera	Nemouridae		
Perlidae	Plecoptera	Perlidae		
Brachyptera sp.	Plecoptera	Taeniopterygidae	*Brachyptera*	
Plecoptera jv.	Plecoptera			
L.niger	Trichoptera	Goeridae	*Lithax*	*niger*
A.zerberus	Trichoptera	Limnephilidae	*Acrophylax*	*zerberus*
C.consors	Trichoptera	Limnephilidae	*Consorophylax*	*consors*
D.monticola	Trichoptera	Limnephilidae	*Drusus*	*monticola*
P.zimmeri	Trichoptera	Limnephilidae	*Pseudopsilopteryx*	*zimmeri*
Limnephilidae jv.	Trichoptera	Limnephilidae		
Psychomyiidae	Trichoptera	Psychomyiidae		
C.alpina cf.	Turbellaria	Planariidae	*Crenobia*	*alpina cf.*

APPENDIX D: TRAIT MODALITY AFFINITIES OF TAXA

Functional Trait	**Maximal potential size**							**Potential number of cycles per year**			**Aquatic stages**			
Trait Modality	≤ 0.25 cm	> 0.25-0.5 cm	> 0.5-1 cm	> 1-2 cm	> 2-4 cm	> 4-8 cm	> 8 cm	semivoltine	univoltine	bi/multi-voltine	egg	larva	nymph	adult
B.alpinus	0.00	0.00	3.00	1.00	0.00	0.00	0.00	0.00	2.00	3.00	3.00	3.00	0.00	0.00
Brachyptera sp.	0.00	0.00	1.00	3.00	0.00	0.00	0.00	0.00	3.00	0.00	3.00	3.00	0.00	0.00
C.alpina cf.	0.00	0.00	0.00	2.00	3.00	0.00	0.00	0.00	3.00	0.00	3.00	3.00	0.00	3.00
Cheilotrichia sp.	0.00	1.00	3.00	0.00	0.00	0.00	0.00	0.00	3.00	1.00	2.00	2.00	0.00	0.00
Clinocera sp.	0.00	0.00	3.00	0.00	0.00	0.00	0.00	0.00	3.00	1.00	0.00	3.00	3.00	0.00
D.monticola	0.00	0.00	0.00	3.00	0.00	0.00	0.00	1.00	3.00	0.00	3.00	3.00	3.00	0.00
Diamesinae	0.00	1.00	3.00	1.00	0.00	0.00	0.00	0.00	1.00	3.00	1.00	2.00	3.00	0.00
Dicranota sp.	0.00	0.00	0.00	1.00	3.00	2.00	0.00	0.00	3.00	1.00	2.00	2.00	0.00	0.00
Diptera	0.00	0.40	1.98	1.07	0.40	0.12	0.00	0.19	2.43	1.24	1.02	2.45	1.88	0.00
Dytiscidae sp.	0.00	1.65	0.59	0.76	0.26	0.03	0.00	0.00	1.94	1.79	3.00	3.00	0.00	2.03
Hydrophilidae	0.00	1.86	1.00	0.29	0.14	0.21	0.00	0.00	3.00	1.00	3.00	3.00	0.00	2.00
L.niger	0.00	0.00	3.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00	3.00	3.00	0.00
Leptoconopus sp.	0.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00	2.00	1.00	0.00	3.00	2.00	0.00
Leuctra	0.00	0.00	3.00	1.00	0.00	0.00	0.00	1.00	3.00	0.00	3.00	3.00	0.00	0.00
Limnephilidae	0.00	0.00	0.00	3.00	2.00	0.00	0.00	0.00	3.00	0.00	3.00	3.00	3.00	0.00
Nemouridae	0.00	0.50	3.00	0.25	0.00	0.00	0.00	0.75	2.75	0.00	3.00	3.00	0.00	0.00
N.pictetii	0.00	0.00	3.00	0.00	0.00	0.00	0.00	1.00	3.00	0.00	3.00	3.00	0.00	0.00
Neumora	0.00	1.00	3.00	0.00	0.00	0.00	0.00	2.00	2.00	0.00	3.00	3.00	0.00	0.00
Orthocladiinae	0.00	1.00	3.00	2.00	0.00	0.00	0.00	1.00	3.00	2.00	0.00	2.00	3.00	0.00
Parapsectra sp.	0.00	2.00	3.00	0.00	0.00	0.00	0.00	0.00	3.00	3.00	0.00	3.00	3.00	0.00
Perlidae	0.00	0.17	3.00	0.42	0.00	0.00	0.00	0.58	2.92	0.00	3.00	3.00	0.00	0.00
Plecoptera jv.	0.00	0.19	2.67	0.90	0.00	0.00	0.00	0.76	2.82	0.00	3.00	3.00	0.00	0.00
Podonominae	0.00	0.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00	3.00	0.00
Prosimulium	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	2.00	3.00	2.00	3.00	3.00	0.00
Protonemura	0.00	0.00	3.00	1.00	0.00	0.00	0.00	0.00	3.00	0.00	3.00	3.00	0.00	0.00
Psychodidae	0.00	0.00	3.00	0.00	0.00	0.00	0.00	0.00	1.00	3.00	2.00	2.00	2.00	0.00
Psychomyiidae	0.00	0.40	3.00	0.40	0.00	0.00	0.00	0.00	0.60	2.80	3.00	3.00	3.00	0.00
Rhithrogena	0.00	0.00	1.00	3.00	0.00	0.00	0.00	1.00	3.00	0.00	3.00	3.00	0.00	0.00
Thaumaleidae	0.00	0.00	0.00	3.00	0.00	0.00	0.00	0.00	3.00	0.00	1.00	2.00	2.00	0.00
Tipulidae	0.00	0.00	0.00	0.00	3.00	2.00	0.00	1.00	3.00	1.00	2.00	2.00	2.00	0.00

	Reproduction								Dispersal					Resistance forms				
	ovoviviparity	aquatic passive	aquatic active	aerial passive	aerial active	eggs, statoblasts	isolated eggs, free	aquatic passive	aquatic active	aerial passive	aerial active	eggs, statoblasts	asexual reproduction	eggs, statoblasts	cocoons	housings against desiccation	diapause or dormancy	none
B.alpinus	0.00	3.00	2.00	1.00	3.00	2.00	0.00	3.00	2.00	1.00	3.00	2.00	0.00	2.00	0.00	0.00	0.00	2.00
Brachyptera sp.	0.00	2.00	2.00	0.00	1.00	1.00	0.00	2.00	2.00	0.00	1.00	1.00	0.00	1.00	0.00	0.00	2.00	0.00
C.alpina cf.	0.00	1.00	2.00	0.00	0.00	3.00	0.00	1.00	2.00	0.00	0.00	3.00	1.00	3.00	0.00	0.00	0.00	0.00
Cheilotrichia sp.	0.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00
Clinocera sp.	0.00	1.00	1.00	0.00	3.00	0.00	0.00	1.00	1.00	0.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
D.monticola	0.00	3.00	2.00	0.00	2.00	0.00	0.00	3.00	2.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
Diamesinae	0.00	2.00	1.00	1.00	1.00	0.00	0.00	2.00	1.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00
Dicranota sp.	0.00	2.00	1.00	0.00	1.00	0.00	1.00	2.00	1.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	2.00
Diptera	0.10	1.19	0.88	0.71	1.24	0.36	0.50	1.19	0.88	0.71	1.24	0.36	0.00	0.36	0.05	0.00	0.86	1.60
Dytiscidae sp.	0.00	0.44	1.00	0.00	2.91	0.00	0.00	0.44	1.00	0.00	2.91	0.00	0.00	0.00	0.00	0.00	0.00	3.00
Hydrophilidae	0.00	0.07	1.00	0.00	3.00	0.00	0.00	0.07	1.00	0.00	3.00	0.00	0.00	0.00	0.00	0.21	0.00	2.79
L.niger	0.00	1.00	1.00	1.00	2.00	0.00	0.00	1.00	1.00	1.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Leptoconopus sp.	0.00	0.00	0.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00
Leuctra	0.00	2.00	2.00	0.00	1.00	1.00	0.00	2.00	2.00	0.00	1.00	1.00	0.00	1.00	0.00	0.00	0.00	3.00
Limnephilidae	0.00	0.00	1.00	0.00	2.00	2.00	0.00	0.00	1.00	0.00	2.00	2.00	0.00	2.00	0.00	0.00	0.00	2.00
Nemouridae	0.00	2.25	2.00	0.00	1.25	0.50	0.00	2.25	2.00	0.00	1.25	0.50	0.00	0.50	0.00	0.00	1.25	2.50
N.pictetii	0.00	3.00	2.00	0.00	1.00	0.00	0.00	3.00	2.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	2.00
Neumora	0.00	2.00	2.00	0.00	2.00	0.00	0.00	2.00	2.00	0.00	2.00	0.00	0.00	0.00	0.00	0.00	1.00	3.00
Orthocladiinae	0.00	2.00	1.00	1.00	1.00	0.00	0.00	2.00	1.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00
Parapsectra sp.	1.00	1.00	1.00	3.00	1.00	0.00	0.00	1.00	1.00	3.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	3.00
Perlidae	0.00	2.42	2.00	0.00	1.08	0.50	0.00	2.42	2.00	0.00	1.08	0.50	0.00	0.50	0.00	0.00	1.08	2.50
Plecoptera jv.	0.00	2.24	2.00	0.00	1.18	0.58	0.00	2.24	2.00	0.00	1.18	0.58	0.00	0.58	0.00	0.00	1.01	2.25
Podonominae	0.00	2.00	1.00	1.00	1.00	0.00	0.00	2.00	1.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00
Prosimulium	0.00	2.00	1.00	3.00	1.00	1.00	1.00	2.00	1.00	3.00	1.00	1.00	0.00	1.00	0.00	0.00	1.00	0.00
Protonemura	0.00	2.00	2.00	0.00	1.00	1.00	0.00	2.00	2.00	0.00	1.00	1.00	0.00	1.00	0.00	0.00	1.00	3.00
Psychodidae	1.00	3.00	1.00	0.00	1.00	0.00	0.00	3.00	1.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00
Psychomyiidae	0.00	1.20	1.00	1.00	1.00	0.00	0.00	1.20	1.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00
Rhithrogena	0.00	3.00	2.00	1.00	3.00	2.00	1.00	3.00	2.00	1.00	3.00	2.00	0.00	2.00	0.00	0.00	0.00	2.00
Thaumaleidae	0.00	2.00	1.00	0.00	1.00	0.00	0.00	2.00	1.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00
Tipulidae	0.00	0.00	1.00	0.00	1.00	0.00	3.00	0.00	1.00	0.00	1.00	0.00	0.00	0.00	2.00	0.00	0.00	2.00

	Respiration						**Locomotion and substrate relation**						
	tegument	gill	plastron	spiracle	hydrostatic vesicle	flier	surface swimmer	full water swimmer	crawler	burrower	interstitial	temporarily attached	permanently attached
B.alpinus	1.00	2.00	0.00	0.00	0.00	0.00	0.00	3.00	4.00	0.00	1.00	0.00	0.00
Brachyptera sp.	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.00	1.00	1.00	0.00	0.00
C.alpina cf.	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.00	0.00	1.00	0.00	0.00
Cheilotrichia sp.	0.00	0.00	0.00	3.00	0.00	0.00	0.00	0.00	1.00	5.00	0.00	0.00	0.00
Clinocera sp.	1.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	2.00	1.00	1.00	0.00	0.00
D.monticola	3.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00
Diamesinae	3.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	3.00	1.00	2.00	1.00	0.00
Dicranota sp.	0.00	0.00	0.00	3.00	0.00	0.00	0.00	0.00	2.00	2.00	0.00	0.00	0.00
Diptera	1.05	0.88	0.00	1.43	0.05	0.00	0.62	0.69	2.40	1.07	0.33	0.60	0.05
Dytiscidae sp.	1.00	0.00	0.00	3.00	0.00	0.97	0.00	2.91	2.97	0.00	0.15	0.00	0.00
Hydrophilidae	1.14	0.21	1.14	3.00	0.00	1.00	0.00	3.00	3.00	0.00	0.00	0.00	0.00
L.niger	2.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00
Leptoconopus sp.	0.00	3.00	0.00	0.00	0.00	0.00	1.00	0.00	3.00	1.00	0.00	0.00	0.00
Leuctra	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.00	2.00	1.00	0.00	0.00
Limnephilidae	2.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00
Nemouridae	3.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00
N.pictetii	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00
Neumora	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00
Orthocladiinae	3.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	3.00	1.00	1.00	1.00	0.00
Parapsectra sp.	3.00	1.00	0.00	0.00	0.00	0.00	0.00	2.00	3.00	0.00	1.00	2.00	0.00
Perlidae	3.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00
Plecoptera jv.	3.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	5.00	0.50	0.33	0.00	0.00
Podonominae	3.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	2.00	3.00	0.00	0.00	0.00
Prosimulium	3.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00	1.00	4.00	0.00
Protonemura	3.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00
Psychodidae	0.00	0.00	0.00	3.00	0.00	0.00	1.00	0.00	2.00	0.00	0.00	0.00	0.00
Psychomyiidae	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00	3.00	0.60
Rhithrogena	1.00	3.00	0.00	0.00	0.00	0.00	0.00	1.00	5.00	0.00	1.00	0.00	0.00
Thaumaleidae	0.00	0.00	0.00	3.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00
Tipulidae	2.00	1.00	0.00	3.00	0.00	0.00	0.00	0.00	1.00	4.00	0.00	0.00	0.00

	Food									**Feeding habits**							
	microorganisms	detritus (< 1mm)	dead plant (>= 1mm)	living microphytes	living macrophytes	dead animal (>= 1mm)	living microinvertebrates	living macroinvertebrates	vertebrates	absorber	deposit feeder	shredder	scraper	filter-feeder	piercer	predator	parasite
B.alpinus	0.00	2.00	2.00	5.00	1.00	1.00	0.00	0.00	0.00	0.00	1.00	0.00	3.00	0.00	0.00	0.00	0.00
Brachyptera sp.	0.00	2.00	0.00	3.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	3.00	0.00	0.00	0.00	0.00
C.alpina cf.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00	0.00
Cheilotrichia sp.	1.00	0.00	3.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00	0.00	2.00	0.00	0.00	0.00	0.00
Clinocera sp.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00	0.00
D.monticola	1.00	0.00	1.00	3.00	2.00	0.00	0.00	2.00	0.00	0.00	0.00	2.00	3.00	0.00	0.00	0.00	0.00
Diamesinae	0.00	2.00	0.00	4.00	1.00	0.00	1.00	0.00	0.00	0.00	1.00	0.00	3.00	1.00	0.00	0.00	1.00
Dicranota sp.	0.00	0.00	1.00	0.00	0.00	0.00	0.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00	0.00
Diptera	0.07	1.14	0.81	2.00	0.31	0.19	0.86	1.67	0.00	0.00	1.00	0.62	0.90	0.57	0.40	1.07	0.19
Dytiscidae sp.	0.00	0.00	0.00	0.00	0.00	0.00	1.56	3.00	0.50	0.00	0.00	3.00	0.00	0.00	2.91	0.06	0.00
Hydrophilidae	0.00	0.00	0.00	2.57	0.14	0.00	2.71	1.29	0.00	0.00	0.00	3.00	0.00	0.00	0.00	1.14	0.00
L.niger	0.00	1.00	2.00	4.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	2.00	3.00	0.00	0.00	0.00	0.00
Leptoconopus sp.	0.00	0.00	1.00	3.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	1.00	0.00	0.00	0.00	0.00
Leuctra	0.00	1.00	1.00	2.00	2.00	1.00	0.00	0.00	0.00	0.00	1.00	3.00	1.00	0.00	0.00	0.00	0.00
Limnephilidae	0.00	1.00	5.00	0.00	2.00	1.00	0.00	0.00	0.00	0.00	0.00	3.00	0.00	0.00	0.00	0.00	0.00
Nemouridae	0.00	1.00	2.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.25	3.00	0.00	0.00	0.00	0.00	0.00
N.pictetii	0.00	1.00	2.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00	0.00	0.00	0.00	0.00	0.00
Neumora	0.00	1.00	2.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00	0.00	0.00	0.00	0.00	0.00
Orthocladiinae	0.00	2.00	0.00	2.00	0.00	0.00	1.00	0.00	0.00	0.00	3.00	0.00	1.00	1.00	0.00	0.00	1.00
Parapsectra sp.	1.00	4.00	1.00	2.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00	2.00	2.00	1.00	0.00	0.00	0.00
Perlidae	0.00	1.00	2.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	3.00	0.00	0.00	0.00	0.00	0.00
Plecoptera jv.	0.00	1.17	1.50	1.50	0.67	0.17	0.00	0.00	0.00	0.00	0.18	2.67	0.67	0.00	0.00	0.00	0.00
Podonominae	0.00	1.00	0.00	1.00	0.00	0.00	3.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00	3.00	0.00
Prosimulium	0.00	2.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	3.00	0.00	0.00	0.00
Protonemura	0.00	1.00	2.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	3.00	0.00	0.00	0.00	0.00	0.00
Psychodidae	0.00	2.00	4.00	2.00	1.00	2.00	0.00	0.00	0.00	0.00	2.00	3.00	1.00	0.00	0.00	0.00	0.00
Psychomyiidae	0.00	1.80	0.60	3.00	0.40	0.00	0.80	0.20	0.00	0.00	0.40	0.00	3.00	1.40	0.00	0.20	0.00
Rhithrogena	0.00	1.00	0.00	3.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	3.00	0.00	0.00	0.00	0.00
Thaumaleidae	0.00	2.00	2.00	4.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	3.00	0.00	0.00	0.00	0.00
Tipulidae	0.00	2.00	4.00	2.00	2.00	0.00	1.00	2.00	0.00	0.00	2.00	3.00	0.00	0.00	0.00	2.00	0.00