Spatio-temporal community patterns of lotic zoobenthos across habitat gradients in an alpine glacial stream ecosystem

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The research conducted for this thesis investigated the zoobenthos in a stream ecosystem of an alpine glacial flood plain. The major part of this work was dedicated to the examination of spatio-temporal patterns in macroinvertebrate distributions, and to the identification of relationships between faunal and environmental gradients. The final chapter aimed to test specific hypotheses generated from these descriptive gradient analyses.

The first study compared the benthic macroinvertebrate assemblages between a kryal stream and an adjacent proglacial lake outlet. Non-metric multidimensional scaling in combination with analysis of similarity and a similarity percentages procedure was used to examine differences between sites. Community structure and total densities were less variable in the lake outlet than in the kryal channel. Furthermore, the kryal stream zoobenthos was clearly dominated by Chironomidae (i.e., > 95% Diamesa spp.), whereas Ephemeroptera, Plecoptera and Trichoptera, as well as Chironomidae, contributed substantially to the zoobenthic community in the lake outlet. In contrast to the predominance of filter-feeding organisms reported for low-elevation lake outlets, a scraper predominance was found in the proglacial lake outlet. Temperature, substrate stability, turbidity, and flow regime constituted major environmental factors responsible for the observed differences in zoobenthic assemblage structure between the kryal and proglacial lake outlet stream.

The second study addressed the temporal variability in longitudinal patterns of macroinvertebrate distributions in relation to environmental gradients along the 11.3 km long Roseg River. Co-inertia analysis clearly revealed a strong relationship between environmental conditions and benthic community structure. In contrast to Milner & Petts’ conceptual model from 1994, macroinvertebrate communities followed predicted zonation patterns for alpine glacial streams only in summer. In addition to this temporal variability in longitudinal response patterns, a similarity in temporal patterns among individual sites along the longitudinal gradient was found. In summary, the results suggest that longitudinal zoobenthic gradients were not solely related to temperature and channel stability. Seasonal shifts in sources and pathways of water (i.e., extent of glacial influence), and periods of favourable environmental conditions (in spring and late autumn/early winter) also had a strong influence on zoobenthic distributions.

Glacier-fed streams are thought to provide a poor habitat for Simuliidae, yet these animals are often the first non-chironomid taxa occurring in glacier-fed streams. These 2 contradictory statements were the motivation for the simuliid study presented in chapter 4. In a first step, an assessment of the species present in the main glacial channel was conducted. Samples were collected along the longitudinal gradient from sites near the glacier terminus down to the river mouth. Different channel types in the glacial flood plain also were surveyed for additional species. In a second
Summary

step, longitudinal patterns in simulid associations during different seasons were investigated. Last, relationships between simulid distribution patterns and environmental factors were examined using partial least squares regression. About 20% of all Simuliidae species currently known in Switzerland were recorded in the Val Roseg flood plain, indicating glacial streams provide more adequate habitats for these insects than generally perceived. Temperature and channel stability constrained Simuliidae colonization close to the glacier. Although suspended particular organic matter represent the most important food source for Simuliidae, results suggest that feeding plasticity may be a key factor for persistence in this harsh environment.

In contrast to temperate and tropical river-flood plain systems, glacial flood plains and their ecological dynamics have received little attention, although they comprise predominant landscape features in recent and former proglacial areas. Therefore, the primary goal of the fourth study was to gain insight into how habitat heterogeneity in the glacial flood plain of Val Roseg affects the structure and composition of benthic macroinvertebrate communities. For this purpose a study design combining the longitudinal perspective with a lateral habitat gradient covering 3 distinct habitat types was applied. These investigations demonstrated that connectivity and spatio-temporal heterogeneity were linked to variations in ecosystem size (i.e., seasonal changes in the length of floodplain channels). Connectivity and spatio-temporal heterogeneity appear to be the primary structuring agents that set the habitat template for the community structure in each habitat (channel) type in the glacial flood plain of Val Roseg.

The fifth study was initiated to explore how the complex mosaic of different stream types constrains dispersal and influences other life history traits of an aquatic macroinvertebrate species commonly found in alpine glacial flood plains. The genetic structure, energy flow and food preferences of a limnephilid caddisfly (Acrophyllax zerberus Brauer) in 3 spatially distinct stream types was analyzed. Little migration between habitats was found within a single generation. Furthermore, results of allozyme electrophoresis suggested that dispersal most likely occurs through flying adults in this glacial flood plain. Carbon and nitrogen stable isotope analyses and food preference experiments were indicative of a generalist feeding strategy by A. zerberus, suggesting feeding plasticity may be a key factor for the successful dispersal and persistence of this patchily distributed species.

In conclusion, alpine glacial flood plains are highly dynamic systems with respect to both their environmental conditions and zoobenthic communities. Seasonal changes in the balance between glacial meltwater and groundwater contributions result in shifting patterns of spatial heterogeneity. Spatial heterogeneity reduces the negative effects of summer high flows (e.g., high turbidity, unstable substrates) by providing numerous refugia for the biota, thus enhancing overall ecosystem stability and biodiversity. From an organismic view, plasticity in life history traits (e.g., feeding behavior) may play an important role in sustaining aquatic insect populations in alpine glacial streams.
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In der fünften Studie wurde am konkreten Beispiel einer in alpinen glazialen Schwemmebenen häufig gefundenen aquatischen Makroinvertebraten-Art die Einfluss des komplexen Mosaiks verschiedener Fließgewässertypen auf die Verbreitung und das Ernährungsverhalten untersucht. Die genetische Struktur, der Energiefluss, sowie die Ernährungspräferenzen einer Köcherfliege der Familie Limnephilidae (Acrophyllax zerberus Brauer) wurde in 3 räumlich deutlich verschiedenen Fließgewässertypen untersucht. Innerhalb einer Generation wurde nur ein geringer Austausch zwischen den Populationen in den 3 verschiedenen Habitaten gefunden. Darüberhinaus deuten die Resultate der Allozym-Elektrophorese darauf hin, dass die Ausbreitung in dieser glazialen Schwemmebene sehr wahrscheinlich durch geprü-

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Chapter 1

Introduction

Give me space and motion, and I will give you a world.
Descartes (1596 – 1650)

1.1 The alpine environment

Areas covered by alpine and arctic vegetation, ranging from 80° N to 67° S and reaching elevations of more than 6000 m a.s.l. in the sub-tropics, amount to roughly 11 million km² or 8% (5% arctic, 3% alpine) of the terrestrial surface of the earth (Chapin III & Körner, 1995). Another 15.9 million km² worldwide are covered by ice; 2909 km² of which form the 4500 glaciers in the Alps (Maisch, 1992). Streams and rivers are integral features of alpine landscapes (Füreder, 1999). For example, 31% of the discharge of the Rhine River originates from the Alps, and make up 11% of its catchment. Alpine stream ecosystems have recently received increased attention, as it has become widely recognized that these high elevation headwater streams play an important role in the dynamics of major river systems throughout the world (Füreder, 1999).

Although high mountain regions have long been developed and cultivated by man (Franz, 1979), today’s human activities are influencing and altering the functioning of ecosystems at a rate and magnitude much faster than „normal evolution“ (Chapin III & Körner, 1994). Alpine stream ecosystems have been proposed to be particularly sensitive to climate change and human impacts (i.e., water resource developments, tourism) (McGregor et al., 1995), yet relatively little is known of their ecology (Ward, 1994). Whether global warming would lead to the recession of glaciers through increased ablation or their expansion through increased precipitation is still under debate. Irrespective of which scenario takes place, changes in hydrology, temperature, and channel stability should cause predictable changes in the structure of zoobenthic communities in alpine stream systems (Milner & Petts, 1994; McGregor et al., 1995). However, such predictions require a much more comprehensive understanding of the interplay between abiotic factors and biotic communities.
1.2 Alpine stream types

Based on their local water sources and temperature regimes, Ward (1994) distinguished 3 major types of alpine streams: (1) kryal stream segments fed by glacial meltwater, (2) krenal segments fed by ground water, and (3) rhithral segments dominated by snowmelt/rainfall. Harsh environmental conditions (i.e., cold temperatures and low food resources) are a general feature of alpine streams. Alpine stream networks often form a complex mosaic of kryal, krenal and rhithral segments because of differences in climate, geomorphology and hydrology of alpine environments (Ward, 1994; McGregor et al., 1995).

Kryal stream segments are characterized by (1) year-round low temperatures, (2) large diel flow fluctuations in summer with peaks in late afternoon from glacial melting, (3) high loads of suspended sediments ("glacial flour") from glacial scouring, and (4) a gradient of channel stability with sites close to the glacier being highly unstable and stability increasing downstream (Milner & Petts, 1994; Ward, 1994). The kryal can be further subdivided into eukryal, the temporary aquatic habitat on or within the glacier, metakryal adjacent to the glacier ($T_{\text{max}} < 2^\circ \text{C}$), and hypokryal where diel and seasonal variability in temperature is greater, but maximum temperature does not exceed $4^\circ \text{C}$ (Ward, 1992; Füreder, 1999). Downstream of the kryal segment, a glacio-rhithral zone fed by a mixture of water sources can extend for a considerable distance, with temporal changes in discharge and temperature reflecting the relative proportion of glacial influence (Füreder, 1999). In contrast, groundwater-fed streams or krenal biotopes typically exhibit (1) constant flow regimes, (2) low temperature amplitudes close to the source that can increase considerably downstream, (3) physico-chemical constancy, and (4) high water clarity (Ward, 1994). Temperatures of non-thermal springs are close to the mean annual air temperature at their sources, and exhibit a summer-cool/winter-warm pattern (Ward, 1985).

1.3 Overview on research in alpine streams

Investigations on the fauna of glacier-fed streams started over 100 years ago (Nordenskjöld, 1870 in Franz, 1979). At the beginning of the 20th century the works of Steinmann (1907), Thienemann (1912), Steinböck (1934), Dorier (1937) and Léger (1937) established the ecological study of high mountain streams in Europe. Later studies of alpine streams have dealt mostly with hydrology, glaciology, geomorphology and physico-chemical attributes (Gurnell & Fenn, 1985; Röthlisberger & Lang, 1987; Prowse, 1994; Gurnell et al., 1999). In contrast, comprehensive studies examining longitudinal distribution patterns of alpine benthic macroinvertebrate communities (e.g., Elgmork & Saether, 1970; Kownacka & Kownacki, 1972; Kownacki & Kownacka, 1973; Allan, 1975; Kownacki, 1991) or the autecology of individual species or higher taxonomic groups (e.g., Saether, 1968;
Steffan, 1971; Irons III et al., 1993) are rather scarce, and often of limited duration and intensity. Comparative studies of biota in different alpine stream types have received little attention (e.g., Kownacki, 1991; Fürer et al., 1998), and virtually nothing is known regarding the aquatic biota of glacial flood plains.

1.4 Thesis goals

The present thesis aimed to enhance our limited knowledge of alpine glacial streams in general and to contribute to the understanding of the ecology of glacial floodplain systems in particular; systems that constitute predominant landscape elements in recent and former proglacial areas. The overall objective was to determine how spatio-temporal habitat heterogeneity contributes to distribution patterns of lotic zoobenthos. For this purpose, investigations were conducted in the glacial floodplain stream ecosystem of Val Roseg in the Swiss Alps.

In a synthesis of Alaskan and European literature reporting on the ecology of glacial-fed streams, Milner & Petts (1994) proposed a qualitative model relating gradients of zoobenthic communities to temperature and channel stability; both being a function of distance from the glacier terminus and time since deglaciation. They suggest that close to the glacier, where summer temperatures typically do not exceed 2°C, chironomids of the genus Diamesa are generally the dominant, if not the only, animals. Where maximum temperatures are between 2 and 4°C, other Diamesinae, Orthocladiinae and Simuliidae may be present. Further downstream where water temperatures exceed 4°C, Baetidae, Nemouridae and Chloroperlidae typically colonize glacial streams. Additional families of Ephemeroptera, Plecoptera and Diptera, as well as Trichoptera, appear with increasing distance downstream. The same authors also suggested that these distinctive downstream patterns can be disrupted by tributaries, proglacial lakes or changes in valley confinement.

In chapter 2 a kryal channel and an outlet stream of a proglacial lake were compared. In contrast to kryal habitats, higher water temperatures, and relatively stable, single-thread outlet channels are found below proglacial lakes (Milner & Petts, 1994). The primary objective of this chapter was to assess how different environmental conditions in these 2 habitat types affected benthic macroinvertebrate community structure.

Our present knowledge about longitudinal changes in community structure of alpine benthic macroinvertebrates, as conceptualized in the model of Milner & Petts (1994), is largely based on studies that did not consider seasonal dynamics. As a consequence, year-round studies, such as conducted by Lavandier & Décomps (1984) in the Estaragne River in the French Pyrenees, are sorely needed. The main objective of the study in chapter 3 was to examine longitudinal and seasonal patterns in macroinvertebrate distributions and environmental conditions in a glacier-fed stream. Specifically, 3 questions were addressed: (1) Do environmental conditions exhibit distinct patterns with increasing distance from the glacier terminus and across sea-
sons? (2) Are there predictable spatio-temporal patterns reflected in the benthic community structure? (3) Is there concordance among environmental and biotic gradients?

Simuliidae are often the first non-chironomid taxon to appear where water temperatures in a glacial stream exceed 2°C (Milner & Petts, 1994; Ward, 1994). However, most studies of glacial stream fauna generally focused on the Chironomidae, Ephemeroptera and Plecoptera, whereas Simuliidae have received little detailed study. Therefore, the goal of chapter 4 was to investigate diversity, distribution patterns and seasonal changes of the Simuliidae fauna in a glacial stream system with emphasis on their longitudinal distribution.

As mentioned above, the ecology and dynamics of glacial flood plains have received little attention, although river-floodplain systems in temperate and tropical biomes have been shown to be a key factor determining ecosystem processes and the community structure of biota (Junk et al., 1989). Therefore, the objective of chapter 5 was to determine how spatio-temporal habitat heterogeneity and connectivity gradients influence distribution patterns of lotic zoobenthos among various habitat (channel) types in a glacial flood plain.

Many aquatic macroinvertebrates have not adapted to the extreme environmental conditions in alpine streams (Füreder, 1999). Therefore, the occurrence of a particular species is a direct expression of its ability to tolerate or adapt to the thermal regime and other population constraints (Ward, 1992; Füreder, 1999). In contrast to the preceding chapters, the focus in chapter 6 was not at the community level but rather at the level of the individual species by addressing how a particular species can successfully disperse and persist in a fragmented and harsh environment. For this purpose, the genetic structure and feeding behavior of an aquatic insect that inhabits specific stream types in an alpine glacial flood plain were examined.

1.5 References


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Chapter 2

Zoobenthos of kryal and lake outlet biotopes in a glacial flood plain

Abstract

Although alpine streams are considered harsh environments, a diversity of stream types was found in a glacial flood plain in the Swiss Alps. Here we compare macroinvertebrate communities between a kryal stream and a glacial lake outlet. Benthic communities displayed similar abundances over time, but differed substantially in taxonomic composition. Chironomidae dominated the kryal stream, whereas Ephemeroptera, Plecoptera and Trichoptera were abundant in the lake outlet. Assemblage differences were attributable to differences in temperature, substrate stability, turbidity, and flow regime.

2.1 Introduction

Although alpine stream systems are considered harsh environments, they consist of a complex mosaic of kryal, krenal and rhithral segments (Ward, 1994; McGregor et al., 1995). Kryal habitats, restricted to the uppermost reaches of glacial-fed streams, are characterized by temperatures below 4°C and large diel flow fluctuations in summer (Ward, 1994). In contrast, proglacial lakes lead to relatively stable outlet channels with higher temperatures (Milner & Petts, 1994). Here, we report on benthic macroinvertebrate assemblages in a kryal stream and an adjacent glacial lake outlet in Val Roseg, Swiss Alps. Our primary objective was to compare community structure between these two markedly different habitat types.

2.2 Study area

Val Roseg is situated in the Bernina Massif (granite/diorite) of the Swiss Alps. The catchment area is 66.5 km², of which 30% is glaciated and 40% is bare rock or glacial till without vegetation cover. Elevations range from 1760 m a.s.l. (confluence with Bernina River) to 4049 m a.s.l. (Piz Bernina). The outlet stream from Roseg Lake (0.27 km²), situated at the base of the Roseg Glacier, and the kryal stream flowing from the Tschierva Glacier converge in the upper part of the main flood
plain to form the Roseg River. A more detailed description is given in Tockner et al. (1997).

Macroinvertebrates were sampled at 16 sites encompassing both the longitudinal gradient and different habitat types. Here we report on 2 sites: the glacial lake outlet channel and the kryal site (Table 2.1).

**Table 2.1:** Characterisation of sampling sites. Values are means ± 1 SD. Coefficients of variation (CV = SD / mean) in parentheses. Sample size was n = 12 for the lake outlet, and n = 10 for the kryal channel (sampling was not possible in February and March 1997).

<table>
<thead>
<tr>
<th></th>
<th>Lake outlet</th>
<th>Kryal channel</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>General characteristics</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Location</td>
<td>50 m below Roseg Lake</td>
<td>600 m from Tschierva Glacier</td>
</tr>
<tr>
<td>Elevation (m a.s.l.)</td>
<td>2159</td>
<td>2100</td>
</tr>
<tr>
<td>Stream order</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><strong>Physico-chemical variables</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Temperature (°C)</td>
<td>1.5 ± 1.6 (1.09)</td>
<td>0.6 ± 0.4 (0.71)</td>
</tr>
<tr>
<td>Conductivity (µS/cm)</td>
<td>50.6 ± 16.9 (0.33)</td>
<td>62.8 ± 31.8 (0.51)</td>
</tr>
<tr>
<td>Turbidity (NTU)</td>
<td>70.5 ± 52.2 (0.74)</td>
<td>68.9 ± 75.9 (1.10)</td>
</tr>
<tr>
<td>Substrata (cm)</td>
<td>11.3 ± 7.4 (0.66)</td>
<td>10.3 ± 5.3 (0.52)</td>
</tr>
<tr>
<td><strong>Sedimentary organic matter</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coarse BOM (g/m²)</td>
<td>0.97 ± 0.89 (0.92)</td>
<td>0.43 ± 0.41 (0.96)</td>
</tr>
<tr>
<td>Fine BOM (g/m²)</td>
<td>0.66 ± 0.35 (0.53)</td>
<td>0.66 ± 0.32 (0.48)</td>
</tr>
</tbody>
</table>

### 2.3 Methods and data analysis

Three replicate Hess samples (area = 0.043 m², 100 µm mesh size) were collected at monthly intervals from February 1997 to January 1998 (sampling in the kryal channel was not possible in February and March 1997). In the laboratory, macroinvertebrates were sorted and identified to the lowest practical taxonomic level using a dissecting microscope. The remaining material from each sample was dried at 60°C, ashed at 550°C and weighed for determination of benthic organic matter (BOM) as ash-free dry mass (AFDM). Temperature was measured continuously with instream data loggers. Monthly measurements of conductivity and turbidity were taken early in the morning to minimize the effects of daily fluctuations and to make data comparable. Substratum particle size was assessed in the field by measuring the b-axis (width) of 100 stones selected randomly.
Differences in mean total abundances of zoobenthos from each site and sampling date were analysed using two-way analysis of variance (ANOVA). Data were log$_{10}$-transformed to meet the assumptions of ANOVA prior to analysis. Differences in community structure were determined using non-metric multidimensional scaling (NMDS) of 4th root transformed abundance data using the Bray-Curtis similarity measure. Data were transformed to obtain a better representation of the total community structure, not just the dominant taxa. A two-dimensional ordination plot was produced using centroids of the 3 replicates taken from each site on each date. Two-way crossed analysis of similarity (ANOSIM) was used to test for significant differences in community structure. The influence of particular taxa in separating among sites was quantified using the similarity percentage procedure (SIMPER). Statistica (Statsoft, 1995) was used for ANOVA and NMDS, the Primer package (Carr, 1997) for the 2 other analyses. Statistical significance was assessed at a probability level of 0.05.

2.4 Results

Average faunal abundances were between 1023 to 8899 ind./m$^2$ in the lake outlet, whereas abundances in the glacial channel varied between 109 and 25,891 ind./m$^2$ (Fig. 2.1). Ephemeroptera and Plecoptera collectively contributed from 33.5% to 84.6% of total zoobenthos in the lake outlet, and from 0% to 43.3% in the kryal channel. The respective percentages for Chironomidae were 6.8 - 54.5% and 56.7 - 98.2% (Fig. 2.2). Other common taxa included Crenobia alpina, Oligochaeta, Nematoda, Acrophylax zerberus and Limoniidae. The limnephilid caddisfly Acrophylax zerberus was collected only in the lake outlet.

Results of two-way ANOVA indicated significant differences in zoobenthic abundances between sites (p = 0.007), dates (p < 0.0001) and the site x date interaction (p < 0.0001). The stress value of 0.203 for the NMDS ordination indicated a fair representation of the original data in 2 dimensions. The resulting ordination plot clearly delineated the lake outlet and the kryal channel. Community structure in the glacial channel was more variable over time than in the lake outlet, where data points were more tightly clustered (Fig. 2.3). This coincided with mean total abundances (Fig. 2.1). Two-way crossed ANOSIM confirmed that the differences in community structure between the 2 sites were significant (Global R = 0.885, p = 0.01). The 6 taxa that contributed most to the separation between the 2 sites (both averaged across dates) in the SIMPER analysis are listed in Table 2.2.
Fig. 2.1: Average abundances of zoobenthos at the 2 sites during the study period. Error bars represent 1 SD.

Fig. 2.2: Percent composition of zoobenthos in the lake outlet and the kryal channel during the study period.
Fig. 2.3: NMDS ordination plot representing centroids of replicate samples. Numbers represent months: 1 = January, 2 = February, etc.

Table 2.2: Results of SIMPER breakdowns. The 6 taxa contributing most to the average dissimilarity between the 2 sites (both averaged across dates) are listed with their percentage contribution and cumulative contribution to overall dissimilarity.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Individual contribution (%)</th>
<th>Cumulative contribution (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rhithrogena spp.</td>
<td>13.9</td>
<td>13.9</td>
</tr>
<tr>
<td>Chironomidae</td>
<td>11.1</td>
<td>25.0</td>
</tr>
<tr>
<td>Oligochaeta</td>
<td>10.8</td>
<td>35.8</td>
</tr>
<tr>
<td>Crenobia alpina</td>
<td>8.8</td>
<td>44.6</td>
</tr>
<tr>
<td>Protonemura spp.</td>
<td>8.3</td>
<td>52.9</td>
</tr>
<tr>
<td>Leuctra spp.</td>
<td>7.3</td>
<td>60.2</td>
</tr>
</tbody>
</table>
2.5 Conclusions

The benthic community of the lake outlet exhibited less variability in total abundances and community structure than the one in the kryal channel. This is in correspondence with the predictions of the model of Milner & Petts (1994). Chironomidae clearly dominated the kryal stream zoobenthos, whereas Ephemeroptera, Plecoptera and Trichoptera, in addition to Chironomidae, were abundant in the lake outlet. The lake outlet did not show a predominance of filter-feeding organisms as described for lower elevation lake outlet streams (Lillehammer & Brittain, 1978), but rather a scraper predominance as found in the High Tatra (Kownacki et al., 1997). Assemblage differences are likely to be attributable to differences in temperature, substrate stability, turbidity, and flow regime. Although kryal streams have harsh conditions, they are by no means “deserts”, and they sustain a very characteristic benthic fauna.

2.6 References

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Longitudinal and seasonal distribution patterns of the benthic fauna of an alpine glacial stream (Val Roseg, Swiss Alps)

Abstract

Seasonal changes in longitudinal patterns of environmental conditions and macroinvertebrate community distributions were examined in an alpine glacial stream (Roseg River, Switzerland). Physico-chemical parameters reflected seasonal changes in glacial influence via shifts in water sources and flowpaths (glacial meltwater vs. ground water), and were best described by turbidity, particulate phosphorous and specific conductance. High nitrogen concentrations indicated snowmelt was the main water source in June. Macroinvertebrate densities and taxon richness were highest during spring (4526 ind./m$^2$ and 16 taxa, all sites combined) and late autumn/early winter (8676 to 13,398 ind./m$^2$ with 16 to 18 taxa), indicating these periods may be more favorable for these animals than summer when glacial melting is maximal. Diamesa spp. (Chironomidae) dominated the fauna at the upper 3 sites (>95% of zoobenthos) and were abundant at all locations. Other common taxa at lower sites (M4 to M10) included other Chironomidae (Orthocladiinae, Tanytarsini), the mayflies Baetis alpinus and Rhithrogena spp., the stoneflies Leuctra spp. and Protonemura spp., blackflies (Simulium spp., Prosimulium spp.), and Oligochaeta. Co-inertia analysis revealed a strong relationship between environmental conditions and benthic macroinvertebrate assemblages. Furthermore, it elucidated temporal variability in longitudinal response patterns, as well as a similarity in temporal patterns among individual sites. Our results suggest that zoobenthic gradients are not related solely to temperature and channel stability. Seasonal shifts in sources and pathways of water (i.e., extent of glacial influence), and periods of favourable environmental conditions (in spring and late autumn/early winter) also strongly influenced zoobenthic distributions.
3.1 Introduction

Treeline and the permanent snowline comprise 2 important boundaries for life in alpine environments. Above treeline the alpine zone is characterized by sedge-mat vegetation that gradually fades into grass hummocks and cushion plants in the subnival zone (Landolt, 1992). Three principal types of stream ecosystems can be distinguished in areas of high altitude (Ward, 1994): kryal (glacier-melt dominated), krenal (groundwater-fed) and rhithral (seasonal snowmelt dominated). Environmental harshness (cold temperatures and low food resources) is a general feature of alpine streams. Because of heterogeneity in the climate, geomorphology and hydrology of alpine environments, alpine stream networks often form a complex mosaic of kryal, krenal and rhithral segments (Ward, 1994; McGregor et al., 1995).

Kryal stream segments are characterized by (1) year-round low temperatures \( T_{\text{max}} = 4^\circ \text{C} \), (2) large diel flow fluctuations in summer with peaks in late afternoon from glacial melting, (3) highly turbid water from suspended rock flour through glacial scouring, and (4) usually low channel stability close to the glacier, but with increasing stability downstream (Milner & Petts, 1994; Ward, 1994). Furthermore, instream environmental conditions depend on distance from the glacier terminus, season, and the contribution of non-glacial water sources. Downstream of the kryal segment, a glacio-rhithral zone, fed by a mixture of water sources, can extend for a considerable distance, with temporal changes in discharge and temperature reflecting the relative proportion of glacial influence (Füreder, 1999).

Alpine streams play an important role in river systems throughout the world (Füreder, 1999), and may be more affected by global climate change and anthropogenic impacts than mountain streams at lower elevations (Chapin III & Körner, 1994; McGregor et al., 1995). Despite a well documented interest in high mountain streams at the beginning of the 20th century (Steinmann, 1907; Thienemann, 1912; Steinböck, 1934; Dorier, 1937), most later studies have dealt principally with hydrology, glaciology, geomorphology and physico-chemical attributes (e.g., Gurnell & Fenn, 1985; Röthlisberger & Lang, 1987; Prowse, 1994; Gurnell et al., 1999). In contrast, comprehensive studies examining longitudinal distribution patterns of alpine benthic communities are few (e.g., Saether, 1968; Steffan, 1971; Kownacka & Kownacki, 1972; Kownacki, 1991), and typically of limited duration or intensity. Year-round studies, such as conducted by Lavandier & Décamps (1984) in the Estaragne, an alpine headwater stream in the French Pyrenees, are scarce but of major importance.

Synthesizing the available literature on the ecology of glacial-fed streams, Milner & Petts (1994) proposed a qualitative model that relates gradients of zoobenthic communities to temperature and channel stability; both being a function of distance from the glacier terminus and time since deglaciation. Close to the glacier, where summer temperatures typically do not exceed \( 2^\circ \text{C} \), chironomids of the genus *Diamesa* generally dominate, or are the sole animals found. Where maximum temperatures are between 2 and 4°C, other Diamesinae, Orthocladiinae and Simuliidae typically may be present. When water temperatures exceed 4°C, Baetidae, Nemouridae
and Chloroperlidae typically colonize glacial streams. Further downstream other Ephemeroptera, Plecoptera and Diptera, as well as Trichoptera, are predicted to appear. Milner & Petts (1994) also suggested that modifications of downstream patterns may result from tributaries, changes in valley confinement and lakes. For example, Burgherr & Ward (in press) reported distinct differences in the zoobenthic communities of a kryal channel and an adjacent proglacial lake outlet stream.

The study of relationships between faunal assemblages and their environment is a central theme of community ecology. Whenever possible, the inherent spatial and temporal variation of both the environment and the faunal assemblage should be considered (e.g., Borcard et al., 1992; Franquet et al., 1995) to gain a better understanding of the ecological phenomenon under study (Resh & Rosenberg, 1989). Ordination techniques, designed to summarize and simplify complex data sets, provide a powerful tool for analyzing patterns of biotic assemblages, and relating them to measured environmental variables (ter Braak & Verdonschot, 1995). Recently, co-inertia analysis has been proposed as an alternative to canonical correspondence analysis for the study of the co-structure between faunistic data and environmental measurements (Dolédec & Chessel, 1994). This technique is particularly suitable for the simultaneous detection of faunistic and environmental features in studies of ecosystem structure.

The principal objective of this study was to examine longitudinal patterns in macroinvertebrate assemblages and environmental conditions in the glacial-fed Roseg River, Switzerland. Specifically, the following questions were addressed: (1) Do environmental conditions exhibit distinct patterns with increasing distance from the glacier terminus and across seasons? (2) Are there predictable spatio-temporal patterns reflected in zoobenthic assemblages? (3) Is there concordance among environmental and biotic gradients? Because the co-structure between fauna and environment may vary in space and time, we also present an approach to separate the spatial co-structure among dates and the temporal co-variation among sites.

### 3.2 Study area

**General description**

The study was conducted in the Val Roseg located in the Bernina Massif of the Swiss Alps (lat 46°29'28" N, long 9°53'57" E) (Fig. 3.1a). The 11.3 km long Roseg River (Ova da Roseg) drained a catchment area of 66.5 km², of which 30% was covered by glaciers, 40% was bare rock or glacial till without vegetative cover, and 9% was used for pasture. Bedrock consists of granite and diorite of the Bernina-, Corvatsch- and Sella-Nappes, which all belong to the austroalpine nappes. Elevation ranged from 1760 m a.s.l. (confluence with Bernina River) to 4049 m a.s.l. (Piz Bernina). Precipitation averaged 1600 mm/yr, of which 50% is snow (1951 - 1980, Spreafico et al., 1992). Glacial meltwater from the Tschiera and Roseg glaciers was...
the primary water source of the Roseg River. Mean annual discharge of the Roseg River was 2.76 m³/s (1955-1997, Swiss Hydrological and Geological Society). Discharge peaked in late summer when diel flow fluctuations also were highest. In winter the system was fed largely by groundwater pathways.

Treeline was about 2300 m a.s.l. in the Val Roseg, with subalpine coniferous forests restricted to the lower parts of the valley slopes, whereas no trees occurred on the fluvo-glacial gravel of the valley floor. Dominant tree species were larch (*Larix decidua* Mill.), stone pine (*Pinus cembra* L.) and mugo pine (*P. mugo* Turra). Shrubs consisted mainly of green alder (*Alnus viridis* (Chaix) DC) and willow (*Salix* spp.). In the lower alpine zone, mat-grass (*Nardus stricta* L.) vegetation was dominant. Curved sedge (*Carex curvula* All.) characterized the middle and upper alpine zone. In the subnival zone, sparse hummocks of curved sedge polsters occurred, otherwise only lichens and mosses developed.

**Study sites**

Five distinct reaches characterize the Roseg River: an unstable braided proglacial reach (length 900 m) below Tschierova glacier, a lake outlet stream below proglacial Lake Roseg (length 950 m), a single thread channel incised in glacial till (length 600 m), the main glacial flood plain (length 2750 m), and a canyon-constrained reach that extends downstream to the river mouth at Pontresina (length 7050 m) (Figs. 3.1b, 3.2a). In the main flood plain, 6 distinct channel types can be distinguished (Tockner *et al.*, 1997).

Ten sampling sites (Fig. 3.2a) were located along the main channel (thalweg) of the Roseg River from just below terminus of the Tschierova glacier (site M1) down to the river mouth (site M10), covering an altitudinal gradient from 2150 to 1760 m a.s.l. For comparison with previous work on the hydro-ecology of this glacial river system, sites numbered M1 to M10 in this paper corresponded to codes M-20, M-15, M-10, M-1, M10, M12, M20, M30, M32, and M40 used in previous papers (Tockner *et al.*, 1997; Malard *et al.*, 1999, Ward *et al.*, 1999). Some general site characteristics are summarized in Table 3.1. Samples were collected in June (increasing discharge), August (high discharge), October (decreasing discharge), and November 1997 (low and constant discharge) (Fig. 3.2b). For sites M1 and M2, samples were collected only in August and October.
Fig. 3.1: (a) Geographical location of the Val Roseg study area in the Bernina Massif of the Swiss Alps. (b) Catchment area of the Val Roseg and indication of glaciers, lakes and forests. Black circles indicate locations of sampling sites.
Fig. 3.2: (a) Longitudinal and altitudinal location of sampling sites along the Roseg River. Dashed lines indicate reach borders. (b) Annual discharge of the Roseg River in 1997. Arrows indicate sampling dates for environmental variables and macroinvertebrates.
<table>
<thead>
<tr>
<th>Site</th>
<th>Reach</th>
<th>Elevation (m a.s.l.)</th>
<th>Distance from glacier (m)</th>
<th>Near-bed velocity (m/s)</th>
<th>Annual mean temperature (°C)</th>
<th>Annual degree days (CTU)</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1</td>
<td>Proglacial</td>
<td>2137</td>
<td>147</td>
<td>2.45 (0.22 - 0.74)</td>
<td>0.46 (0.01 - 0.92)</td>
<td>365</td>
</tr>
<tr>
<td>M2</td>
<td>Proglacial</td>
<td>2122</td>
<td>414</td>
<td>0.67 (0.39 - 0.96)</td>
<td>1.18 (0.00 - 1.86)</td>
<td>154</td>
</tr>
<tr>
<td>M3</td>
<td>Proglacial</td>
<td>2109</td>
<td>209</td>
<td>0.46 (0.19 - 0.69)</td>
<td>1.18 (0.00 - 3.54)</td>
<td>248</td>
</tr>
<tr>
<td>M4</td>
<td>Incised</td>
<td>2064</td>
<td>2064</td>
<td>0.40 (0.13 - 0.64)</td>
<td>0.68 (0.00 - 1.86)</td>
<td>248</td>
</tr>
<tr>
<td>M5</td>
<td>Proglacial</td>
<td>2041</td>
<td>2013</td>
<td>0.03 (0.00 - 0.06)</td>
<td>0.68 (0.00 - 4.83)</td>
<td>657</td>
</tr>
<tr>
<td>M6</td>
<td>Flood plain</td>
<td>2021</td>
<td>769</td>
<td>0.40 (0.13 - 0.64)</td>
<td>1.18 (0.00 - 1.86)</td>
<td>248</td>
</tr>
<tr>
<td>M7</td>
<td>Flood plain</td>
<td>1981</td>
<td>1981</td>
<td>0.45 (0.29 - 0.62)</td>
<td>1.18 (0.00 - 3.54)</td>
<td>248</td>
</tr>
<tr>
<td>M8</td>
<td>Flood plain</td>
<td>1901</td>
<td>1901</td>
<td>0.40 (0.13 - 0.64)</td>
<td>1.18 (0.00 - 3.54)</td>
<td>248</td>
</tr>
<tr>
<td>M9</td>
<td>Constrained</td>
<td>1981</td>
<td>1981</td>
<td>0.45 (0.29 - 0.62)</td>
<td>1.18 (0.00 - 3.54)</td>
<td>248</td>
</tr>
<tr>
<td>M10</td>
<td>Constrained</td>
<td>1773</td>
<td>1773</td>
<td>2.59 (0.00 - 6.11)</td>
<td>1.18 (0.00 - 3.54)</td>
<td>248</td>
</tr>
</tbody>
</table>

Centigrade temperature units (CTU), given for near-bed velocity and annual mean temperature. Annual degree days are expressed as general characteristics of the sampling sites. Means and ranges in parentheses are.
3.3 Materials and methods

Physico-chemical parameters were collected in the morning at each site and sampling date to minimize the influence of daily discharge fluctuations and ensure data comparability. Turbidity was determined with a portable turbidity meter (Cosmos; Fa. Züllig, Switzerland). Specific conductance and temperature were measured in the field using a pocket conductivity meter (WTW LF323-B; Wissenschaftliche-Technische Werkstätten, Germany). Suspended solids (SS) were estimated according to APHA (1989). Nitrate (\( \text{NO}_3^-\)) was determined according to Downes (1978) and modifications by Stöckli (1985). Soluble reactive phosphorous (SRP) was analyzed according to the molybdenum blue method (Vogler, 1965). Particulate nitrogen (PN) and particulate phosphorous (PP) were quantified as \( \text{NO}_3^-\) and SRP after digestion with \( \text{K}_2\text{S}_2\text{O}_8 \) at 121°C (Ebina et al., 1983). Dissolved organic carbon (DOC) was measured by wet oxidation with subsequent acidification and \( \text{CO}_2 \) IR-detection, whereas total inorganic carbon (TIC) was measured as \( \text{CO}_2 \) with a Horiba IR-detector after samples had been acidified and heated to 860°C. For further details see Tockner et al. (1997). Continuous temperature records (1 hr intervals; StowAway XTI temperature loggers, Onset Corporation, USA) were available for 6 of the 10 sites (U. Uehlinger, unpubl. Data). Near-bed current velocities were measured at the same positions where benthic samples were taken using a flow meter (Mini Air 2; Schiltknecht Messtechnik AG, Switzerland). Substrate size was assessed in the field by measuring 100 randomly selected stones (b-axis, width). Initiation of sediment transport was used as a measure of channel stability because it also was considered a useful disturbance threshold for benthic macroinvertebrates. Estimates of dimensionless critical shear stress (based on channel geometry and grain size distributions; Gessler, 1965) were used to determine the critical discharge at which bed sediments start to move, using the software FLUSSBAU (Laboratory of Hydraulics, Hydrology and Glaciology, Swiss Federal Institute of Technology, Zurich, Switzerland).

Three Hess samples (area 0.043 m\(^2\), 100 µm mesh size) from randomly selected locations in riffle/run habitats were collected at each site and date, and preserved in 4% formalin. In the laboratory, macroinvertebrates were sorted, enumerated and identified to the lowest practical taxonomic level for most groups using a dissecting microscope. However, Chironomidae were only identified to subfamilies and tribes except for Diamesa spp. for which some estimates for species groups were made. Limnephilid caddisflies also were pooled, as identification to the species level is only possible using fifth instar larvae (Waringer & Graf, 1997). Nematoda, Hydrachnellae, Crustacea and Oligochaeta were not identified further. After removal of invertebrates, the remaining material from each sample was split into 2 fractions (>1 mm and <1 mm), dried at 60°C, weighed, ashed at 550°C and reweighed for determination of coarse and fine benthic organic matter (BOM) as ash-free dry mass (AFDM).
Macroinvertebrate community analyses included estimates of mean densities, taxon richness and Simpson's index of concentration (SI) as a measure of diversity. 

\[ SI = \Sigma \left( \frac{n^2 - n}{N^2 - N} \right) \]

where \( n \) is the number of individuals in a species, and \( N = \Sigma n \). As recommended by Rosenzweig (1995), SI values were converted to \(-\ln(SI)\) such that values increase as the number of species does, independently of sample size.

Co-inertia analysis (CIA) was used to simultaneously study the structure in the environmental and faunistic data, and to determine if concordance (i.e., co-structure) between these 2 independent structures existed (Doledec & Chessel, 1994). Environmental data were normalized to ensure equal weights for all variables, whereas the faunistic data were log\(_{10}\)(x+1) transformed and centered to reduce strong inter-taxonomic differences in densities. CIA is a two-table ordination method, as is canonical correspondence analysis (CCA). However, CIA enables the joint analysis of tables having similar (even low) as well as different numbers of environmental variables, species, and/or samples (Dolédec & Chessel, 1994). In contrast, in CCA a small number of environmental variables is required to predict the faunistic structure, otherwise it would be reduced to a simple correspondence analysis of the faunistic table. Last, the temporal co-variation and spatial co-structure of the 2 data sets were examined using within-class co-inertia analysis (Franquet & Chessel, 1994; Franquet et al., 1995). All multivariate analyses were computed using the ADE-4 software (Chessel & Dolédec, 1996).

3.4 Results

Environmental conditions

A detailed description of the physico-chemical templet of the Val Roseg was previously summarized (Tockner et al., 1997; Malard et al., 1999); therefore, only a selection of parameters distinctive for kryal streams will be presented here. Substrata at all sites consisted mainly of cobbles and boulders. Average particle size (b-axis, width) ranged between 9 to 12 cm. Estimates of critical shear stress indicated bed sediments in the main channel of the Roseg River should start to move if discharge exceeds 8 m\(^3\)/s. This threshold was exceeded on 41 days in 1997; 15x in June, 6x in July, and 20x in August. Daily mean water temperature in the main channel ranged from 0.01 to 0.92°C at site M2, 0.39 to 4.83°C at M5, and 0.00 to 6.73°C at M10. Annual degree days increased from 154 CTU (Centigrade Temperature Units) at site M2, to 657 CTU at M5, and 945 CTU at M10 (Table 3.1). Nitrate (NO\(_3\)-N) was the dominant nitrogen species (87%) in surface water of the Roseg River (Malard et al., 1999). The average nitrate concentration was highest in June at 421 ± 17 µg/L (mean ± SD), and between 180 and 266 µg/L on the other sampling dates (Fig. 3.3a). Values of specific conductance (Fig. 3.3b) were lower during the peak of glacier melting (36 ± 5 µS/cm in August, 38 ± 5 µS/cm in October). Specific conduct-
Longitudinal and seasonal distribution patterns

Turbidity and particulate phosphorous (PP) (Fig. 3.3c,d) peaked in August due to glacier melting and associated high loads of glacial flour, with an average of 84 ± 11 NTU (Nephelometric Turbidity Units) for turbidity and 49 ± 16 µg/L for PP. In June and October (when discharge was increasing and decreasing, respectively) intermediate levels were observed (turbidity: 51 ± 13 NTU and 58 ± 18 NTU; PP: 29 ± 7 µg/L and 29 ± 6 µg/L), whereas during low flow in November minimum values were recorded (13 ± 12 NTU for turbidity, 11 ± 5 µg/L for PP). Turbidity and to a lesser extent PP reached substantially higher values in the incised reach compared to the proglacial area, whereas further downstream values were attenuated again. Overall, longitudinal patterns in physico-chemical parameters exhibited pronounced seasonal changes.

Macroinvertebrates

Total densities of macroinvertebrates ranged from 116 ind./m² (M2 in August) to 24,380 ind./m² (M10 in October), varying along both temporal and spatial dimensions. Lowest densities, all sites combined, were found in August (1472 ± 1356 ind./m²), intermediate in June (4526 ± 2723 ind./m²) and November (8676 ± 4434 ind./m²), and highest in October (13,398 ± 6113 ind./m²). Generally, average densities per site increased with increasing distance from the glacier terminus (Table 3.2). CVs were highest in the proglacial reach (M1 to M3), decreased to a minimum at M6, and then increased again downstream to M10.

The number of taxa recorded at a site ranged from 1 to 26. Lowest taxon richness was found within the proglacial reach (M1 to M3), followed by a progressive increase to M6 at the lower end of the flood plain, then similar richness at the 4 lowermost sites (Table 3.2). Overall, Chironomidae, Baetis alpinus Pictet, Rhithrogena spp., Leuctra spp., Protonemura spp., Simuliidae, and Oligochaeta were the predominant taxa (Table 3.3). Other taxa generally made up <1% of the total community, although some exceptions on certain dates and sites occurred (e.g., Rhypholophus sp. comprised 6 to 13% in the proglacial area in August, Crenobia alpina ca. 3% at M3 and M4 in August, and Limnephilidae 7% at M10 in October). The few large individuals of limnephilid Trichoptera were identified as Acrophylax zerberus Brauer and Drusus biguttatus Pictet. Taxa not used in multivariate analyses (<0.05% of the assemblage or semi-aquatic) were not included in Table 3.3. These were Ecdyonurus picteti Meyer-Dür, Dictyogenus spp., Siphonoperla spp., Rhyacophila intermedia McLachlan, Ceratopogonidae, and Collembola.

Diamesa spp. was the only genus of Chironomidae found close to the glacier terminus. Orthocladiinae first appeared at M3, but in low abundance. At M4, relative densities of Diamesa spp. declined by ca. 30%, whereas Orthocladiinae contri-
Fig. 3.3: Longitudinal patterns of (a) nitrate (NO₃-N), (b) specific conductance, (c) turbidity, and (d) particulate phosphorous (PP) on each sampling date. Dashed lines indicate reach borders. Order of sampling sites and names shown in Fig. 3.2a.
buted >1%. Further downstream, the ratio of Diamesa spp. to Orthocladiinae varied between 1 to 4. Tanytarsini always constituted a minor part of total Chironomidae present. Common Diamesa-groups found, were D. steinboecki-gr., D. latitarsis-gr., D. bertrami-gr., D. cinerella-zernyi-gr., and D. cf. incallida. Baetis alpinus was ca. 2.5x more abundant than Rhithrogena spp. Rhithrogena loyolaea Navás and R. nivata Eaton were the 2 predominant Rhithrogena-species at all sites, while R. alpestris Eaton and R. degrangei Sowa were most abundant in the constrained reach. Simpson’s index was low in the proglacial reach, but increased in the incised reach and the flood plain, and reached a maximum at sites in the constrained reach (Table 3.2).

Table 3.2: Means ± 1 SD, and in parentheses coefficients of variation (CV in %) for densities, taxon richness, and Simpson’s index (-ln SI) of the macroinvertebrate communities at the 10 sampling sites.

<table>
<thead>
<tr>
<th>Site</th>
<th>Density (ind./m)</th>
<th>Taxon richness</th>
<th>Simpson’s index (-ln SI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1</td>
<td>2632 ± 3536</td>
<td>5 ± 1</td>
<td>0.27 ± 0.37 (134)</td>
</tr>
<tr>
<td>M2</td>
<td>2469 ± 3327</td>
<td>2 ± 1</td>
<td>0.21 ± 0.29 (141)</td>
</tr>
<tr>
<td>M3</td>
<td>5417 ± 8020</td>
<td>8 ± 1</td>
<td>0.38 ± 0.39 (104)</td>
</tr>
<tr>
<td>M4</td>
<td>5048 ± 4562</td>
<td>11 ± 4</td>
<td>0.71 ± 0.39 (54)</td>
</tr>
<tr>
<td>M5</td>
<td>8438 ± 5237</td>
<td>16 ± 4</td>
<td>1.11 ± 0.41 (37)</td>
</tr>
<tr>
<td>M6</td>
<td>7936 ± 4504</td>
<td>20 ± 5</td>
<td>1.21 ± 0.35 (29)</td>
</tr>
<tr>
<td>M7</td>
<td>8136 ± 5991</td>
<td>20 ± 4</td>
<td>1.42 ± 0.10 (7)</td>
</tr>
<tr>
<td>M8</td>
<td>9138 ± 7074</td>
<td>19 ± 3</td>
<td>1.43 ± 0.27 (19)</td>
</tr>
<tr>
<td>M9</td>
<td>8504 ± 7074</td>
<td>19 ± 2</td>
<td>1.46 ± 0.44 (30)</td>
</tr>
<tr>
<td>M10</td>
<td>8415 ± 10753</td>
<td>18 ± 5</td>
<td>1.34 ± 0.50 (37)</td>
</tr>
</tbody>
</table>

**Multivariate analyses**

The co-structure between the environmental and faunistic data sets revealed by co-inertia analysis (CIA) was highly significant, as confirmed by a Monte-Carlo permutation test (p = 0). The first 2 CIA axes explained 81.1% and 14.5% percent of the total inertia. Turbidity, PP and SS were negatively related to factor 1 of CIA, while TIC and specific conductance showed a positive relationship (Fig. 3.4a). Factor 2 was related to temperature, NO3-N, PN and BOM in the positive region. Axis F1 of the corresponding faunistic structure (Fig. 3.4b) was best explained by Orthocladiinae, Protonemura spp., Prosimulium spp., Tanytarsini, Baetis alpinus, Rhithrogena spp., and Leuctra spp., whereas axis F2 was described by Oligochaeta, Simulium spp., Rhabdiopteryx alpina, and Isoperla spp.
<table>
<thead>
<tr>
<th>Predominant taxa</th>
<th>Sampling sites</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>M1</td>
</tr>
<tr>
<td><strong>Diamesa spp. (Dia)</strong></td>
<td>mean</td>
</tr>
<tr>
<td></td>
<td>SD</td>
</tr>
<tr>
<td>Orthocladiinae (Ort)</td>
<td>0</td>
</tr>
<tr>
<td>Tanytarsini (Tan)</td>
<td>0</td>
</tr>
<tr>
<td><strong>Baetis alpinus Pictet (Bae)</strong></td>
<td>0</td>
</tr>
<tr>
<td><strong>Rhithrogena spp. (Rhi)</strong></td>
<td>4</td>
</tr>
<tr>
<td>Leuctra spp. (Leu)</td>
<td>0</td>
</tr>
<tr>
<td>Protonemura spp. (Pro)</td>
<td>0</td>
</tr>
<tr>
<td>Simulium spp. (Sim)</td>
<td>0</td>
</tr>
<tr>
<td>Prosimulium spp. (Prs)</td>
<td>0</td>
</tr>
<tr>
<td>Oligochaeta (Oli)</td>
<td>8</td>
</tr>
</tbody>
</table>

Table 3. Absolute abundances (ind/m²) for the predominant taxa collected at the sampling sites during the study period. For the other taxa only presence (X) or absence (―) at a site are reported because on average they contributed < 1%. SD = standard deviation. Abbreviations for each taxon used in figures 3.4, 3.5 and 3.6 are in parentheses.
<table>
<thead>
<tr>
<th>Other taxa</th>
<th>M1</th>
<th>M2</th>
<th>M3</th>
<th>M4</th>
<th>M5</th>
<th>M6</th>
<th>M7</th>
<th>M8</th>
<th>M9</th>
<th>M10</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crenobia alpina Dana (Cre)</td>
<td></td>
<td></td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Nematoda (Nmt)</td>
<td></td>
<td></td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
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</tr>
<tr>
<td>Hydrachnellae (Hyd)</td>
<td></td>
<td></td>
<td></td>
<td>-</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Crustacea (Cru)</td>
<td>x</td>
<td>-</td>
<td>x</td>
<td>-</td>
<td>x</td>
<td>x</td>
<td>-</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Rhabdiopteryx alpina Kühtreiber (Rha)</td>
<td></td>
<td></td>
<td></td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Nemoura spp. (Nem)</td>
<td></td>
<td></td>
<td></td>
<td>-</td>
<td>-</td>
<td>x</td>
<td>x</td>
<td>x</td>
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<td>x</td>
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The co-structure between the fauna and the environment is best illustrated by plotting standardized environmental and associated faunistic scores together on the F1xF2 factorial plane and to link the 2 positions by an arrow (Fig. 3.4c). The length of the arrow is then a measure of the strength of the co-structure; the shorter this distance the better the agreement between the 2 structures. In general, all arrows indicated good agreement between the 2 structures. On the F1xF2 factorial map, 4 overlapping groups could be distinguished that corresponded to the 4 sampling dates. However, the dispersion of sampling sites varied from one date to another. The environmental separation of the June samples on axis F2 was caused by high concentrations of NO$_3$-N, whereas the other 3 dates were separated by a gradient of glacial influence along axis F1. High discharge from glacial melting resulted in high levels of particulate variables in August, whereas glacial melting no longer occurred in November and ground water contributed a large proportion to stream water, as reflected by changes in specific conductance and TIC.

The ordination separated samples from June/August and October/November along the positive diagonal (lower left to upper right) (Fig. 3.4c). This is attributable to the lower density and taxon richness of samples from June and August compared to those from October and November. Additionally, there existed a downstream increase in densities and taxon richness within each sampling date. These results demonstrate an important overlap between a temporal effect mainly caused by a changing glacial influence and a different spatial (i.e., longitudinal) response pattern.

A spatial typology was investigated by means of a within-date CIA. The existence of a significant co-structure was confirmed (permutation test, p = 0), with factor 1 explaining most of the observed co-structure (90.6%), and factor 2 contributing only marginally (4.8%). Within-date environmental gradients were related to downstream changes in glacial influence (Fig. 3.5a). Although longitudinal patterns differed among dates, 3 groups of sites were observed (Fig. 3.5c). Sites M1 to M3 in the proglacial reach, and M6 in the lower flood plain together with sites M7 to M10 in the constrained reach formed 2 distinct groups, whereas the group formed by sites M4 and M5 reflected the transition between them. This pattern was most clear in August and October, but less distinct in June, and even weaker in November, indicating conditions were most homogenous on this date. Sites in the constrained reach (M7 to M10) that were fringed by forest exhibited higher BOM concentrations than sites located further upstream (Fig. 3.5a,b). By comparing Fig. 3.5a and 3.5c, the seasonal shifts in taxonomic composition, most evident at sites in the flood plain and in the constrained reach, could be observed.

Last, the temporal stability of macroinvertebrate assemblages at each site assessed using a within-site CIA had a significant co-structure (p = 0): The first 2 axes explained 97.3% of the total inertia (F1 = 80.1%, F2 = 17.2%). The F1xF2 factorial plane showed a distinctive seasonal shift for all sampling sites (counter-clockwise from June to November) that became even more distinct with increasing distance from the glacier terminus (Fig. 3.6c). Positions of June samples on the F1xF2 factorial map (Fig. 3.6c) were related to high concentrations of NO$_3$-N (Fig. 3.6a), while
sample positions in August could be attributed to high levels of turbidity, SS and PP. November samples reflected the substantial contribution of ground water (specific conductance, TIC, and to a lesser extent DOC), whereas October samples showed a transitional shift between the declining glacial influence and the increasing proportion of ground water to stream water. Faunistically, Simuliidae and Oligochaeta contributed highly to the total community at downstream sites in June (Fig. 3.6b,c). In October and November, several taxa of Ephemeroptera, Plecoptera and limoniid Diptera were responsible for site separation (Fig. 3.6b,c).

3.5 Discussion

Environmental conditions

Glacier-fed rivers exhibit distinctive characteristics that distinguish them from other lotic systems (Steffan, 1971). Stability was closely related to the hydrograph of the Roseg River. Moving bed sediments reduced channel stability from June to August. During the remaining time of the year discharge did not exceed the threshold of 8 m³/s, indicating channel stability was higher. Maximum annual temperatures in the proglacial reach (M1 to M3) were below 2°C, and thus are considered metakryal (Ward, 1994). The strong increase in maximum annual temperature at M4 can be attributed to an attenuation of environmental conditions resulting from the influence of the proglacial lake outlet stream. The hypokryal starts downstream of the confluence and extends to the head of the flood plain. Sites M5 to M10 all have maximum temperatures >4°C, being characteristic of a glacio-rhithral zone (Fürderer, 1999). Annual degree days never exceeded 1000 CTU even at the lowermost site. Our data are partially comparable with those of Lavandier (1974) in the River Estaragne (France). He reported 500 CTU at the uppermost site at 2350 m a.s.l. and 1000 CTU at the lowermost site at 1850 m a.s.l. compared to only 154 CTU and 964 CTU, respectively, in this study.

Snowmelt was the main source of water in June as indicated by the high concentration of NO₃-N. As in other mountain areas (Charles, 1991), seasonal patterns in NO₃-N concentrations suggest that atmospheric deposition on snow is the main source of nitrogen in the Val Roseg. The discharge peak in August, due to glacial melting of the Tschierva and Roseg glaciers, was associated with high turbidity and particulate phosphorous values. High concentrations of particulate phosphorous associated with glacial flour have been reported elsewhere (Bretschko, 1966). The peak in turbidity at site M4 is most likely attributable to the proglacial Lake Roseg, because larger sediment particles settle in the lake. Therefore, suspended solids in the lake outlet stream comprise a much higher fraction of smaller particles compared to the kryal stream originating from the Tschierva Glacier, which led to the increase in turbidity below the confluence of the 2 streams. With decreasing discharge in October, specific conductance was still low, indicating that the contri-
Fig. 3.4: Results of the co-inertia analysis (CIA) of 11 environmental variables and 24 taxa from 10 sampling sites and 4 dates. (a) Ordination diagram of the 11 normalized environmental variables in the CIA. Codes are given in material and methods. (b) Position of taxa on the CIA F1xF2 plane. Codes are given in Table 3.3. (c) Standardized co-inertia scores of the environmental and faunistic data sets projected onto the F1xF2 factorial map. Arrows link environmental scores (beginning of an arrow) to faunistic ones (arrowhead). In 3.4a the longer an arrow and the closer to an axis the stronger the relationship to this factor, whereas arrows in 3.4c measure the strength of the co-structure between the fauna and the environment; so the shorter the arrow the better is the agreement between the 2 structures.
Fig. 3.5: Within-date CIA (spatial typology). (a) Co-inertia scores of the environmental parameters, and (b) of the taxa on the F1xF2 factorial plane. (c) Standardized co-inertia scores of sampling sites of the environmental and faunistic data sets onto the F1xF2 factorial maps for each sampling date. In 3.5a the longer an arrow and the closer to an axis the stronger the relationship to this factor, whereas arrows in 3.5c measure the strength of the co-structure between the fauna and the environment; so the shorter the arrow the better the agreement between the 2 structures.
Fig. 3.6: Within-site CIA (temporal typology). (a) Co-inertia scores of the environmental parameters, and (b) of the taxa on the F1xF2 factorial plane. (c) Standardized co-inertia scores of sampling dates of the environmental and faunistic data sets onto the F1xF2 factorial maps for each sampling site. In 3.6a the longer an arrow and the closer to an axis the stronger the relationship to this factor, whereas arrows in 3.6c measure the strength of the co-structure between the fauna and the environment; so the shorter the arrow the better the agreement between the 2 structures.
bution of englacial water had not significantly changed. At low and constant discharge in November, the contribution of ground water had increased markedly, as shown by high values of specific conductance. Seasonal shifts in sources and flow paths of water in the Val Roseg catchment determine the degree of glacial influence (Malard et al., 1999), and have important implications for the biota.

**Benthic macroinvertebrate assemblages**

In general, Chironomidae, especially the genus *Diamesa*, were a predominant constituent of the zoobenthos in the glacial stream of Val Roseg. Larvae of the genus *Diamesa* were the sole inhabitants close to the glacier snout, as reported for many glacier-fed streams in the European Alps (Bretschko, 1969), Tatra Mountains (Kownacka & Kownacki, 1972), Scandinavia (Steffan, 1971), and the Rocky Mountains (Elgmork & Saether, 1970). In contrast, glacial streams influenced by water abstraction were devoid of fauna for 200 to 500 m below the glacier snouts (e.g., Petts & Bickerton, 1994). Although, *Diamesa* chironomids are generally considered cold-stenotherms (Oliver, 1983), some species (e.g., *Diamesa steinböcki*) may occur at warmer temperatures (Rossaro, 1991).

Ephemeroptera, Plecoptera and other taxa, however, also made substantial contributions to benthic assemblages. Within the genus *Baetis*, only *B. alpinus* was found. The absence of *B. melanonyx* Pictet, another common species of this region, is attributed to the high elevation of the Val Roseg and the crystalline substratum (Sartori & Landolt, 1999). These authors report a univoltine life cycle for *B. alpinus* >1500 m a.s.l. with animals overwintering as larvae, which is consistent with our findings. Four *Rhithrogena* species were collected: *R. loyolaea* and *R. nivata* were the 2 most abundant species at most sites, whereas *R. alpestris* and *R. degrangei* were only abundant at the more downstream sites. These distributions correspond to their altitudinal optima, which are between 1000 and 1800 m a.s.l. for *R. alpestris*, and between 700 and 1200 m a.s.l. for *R. degrangei* (Sartori & Landolt, 1999). *Rhithrogena loyolaeae* usually has a univoltine life cycle in the Swiss Alps (Sartori & Landolt, 1999), but Lavandier (1981) showed that larval development requires 3 years above 2100 m in the French Pyrenees. Unfortunately, life cycles of many alpine stream insects are poorly known, although there is a general agreement that the number of generations per year decreases with increasing altitude, and that low temperature at high elevation is likely responsible for later emergence (Ward, 1992).

Total zoobenthic density ranged over 2 orders of magnitude, being lowest in August (116 ind./m²) and highest in October (24,380 ind./m²). Similar values were found by Lavandier & Décumps (1984) in the French Pyrenees although other studies of glacial streams report much lower densities (e.g., Kownacki & Kownacka, 1973; Gislason et al., 1998). However, several factors may be responsible for these differences. Sampling in other studies was typically restricted to the summer period, when sites are easily accessible. Different sampling techniques (qualitative vs. quan-
Longitudinal and seasonal distribution patterns

titative), as well as differences in mesh size, additionally confound comparability of results.

Taxon richness and Simpson’s index of diversity showed similar trends. On all sampling dates, a downstream increase of both measures was observed. In August, taxon richness was markedly lower, most likely due to the extremely harsh environmental conditions. Our results suggest that changes in density and taxon richness are most likely attributable to (1) spatial phenomena (reduced harshness with increasing distance from the glacier), and (2) temporal phenomena (more favourable periods in spring and late autumn/early winter than in summer).

Relationships between fauna and environment

Co-inertia analysis clearly demonstrated that the environmental conditions and benthic community structure were related. Furthermore, it revealed the existence of a strong overlapping spatio-temporal pattern. Within-class analyses eliminate such spatial or temporal effects and enable the examination of changes in the spatial co-structure among sampling dates, and the temporal stability in observed longitudinal patterns. The results of these analyses can be summarized as follows: (1) Seasonal changes in glacial influence (i.e., shifts in sources and flow paths of water) comprised a key factor structuring benthic macroinvertebrate assemblages. (2) Although longitudinal response patterns of zoobenthos varied across seasons, individual sites exhibited similar temporal patterns.

Milner & Petts (1994) proposed a general qualitative model relating zoobenthic gradients to maximum water temperature and channel stability as a function of distance from the glacier margin and time since deglaciation. In general, our results conform quite well with this model; however, some substantial deviations were found. For example, Orthocladiinae were collected at M3, although maximum annual temperatures ($T_{\text{max}}$) were still <2°C. Ephemeroptera and Plecoptera also were found below a $T_{\text{max}}$ of 4°C at sites M3 and M4, especially in October and November, but to a lesser extent at other times. In accordance to our findings, Thomas (1975) reported that B. alpinus can complete its whole life cycle even if water temperature is always between 0 and 3°C. Burgherr & Ward (in press) reported similar findings in another study comparing a kryal stream with a lake outlet channel. Overall, Milner & Petts’ (1994) conceptual model predicted macroinvertebrate distribution patterns accurately during glacial melt in summer, but did not account for seasonal changes in assemblage patterns. However, it is this temporal pattern that is most interesting in these types of systems, but which was not incorporated in their 1994 conceptual model. Consequently, we postulate that, besides temperature and channel stability, a complex interplay of factors determines the distributions of populations in glacial streams. In particular, sources and flowpaths of water, in combination with discharge, reflect changes in glacial influence and strongly modify the habitat templet.
Longitudinal and seasonal distribution patterns

Longitudinal distribution patterns of macroinvertebrates also could be a result of stream age (Milner, 1987; Milner, 1994). However, such a site-specific temporal succession can be constrained by alternating cycles of glacial recession and advance. For example, M3 in the Roseg River has been ice-free since 1955, whereas M2 has been since 1971, and M1 was again covered by the glacier between 1979 and 1991.

Peaks in abundance and taxon richness in spring and late autumn/early winter coincide with accrual of benthic algae, especially the chrysophyte *Hydrurus foetidus* Kirch, enhancing food availability for zoobenthic organisms. During these periods, stream beds are highly stable as shown in this study and reported elsewhere (Fiüeder, 1999), and sediment transport, shear stress and turbidity are minimal (Uehlinger et al., 1998).

Conclusions

In summary, our results show that zoobenthic communities in the Roseg River exhibit a high spatio-temporal variation due to seasonal shifts in glacial influence. During periods of favourable environmental conditions (spring and late autumn/early winter) invertebrate density and taxon richness peak, and cold-adapted taxa other than just *Diamesa* spp. can occur rather close to the glacier terminus. Future modifications and refinements of the conceptual model of Milner & Petts (1994) should account for temporal patterns reported in this study and other investigations (Robinson et al., in press). Other factors to consider include biogeographic patterns (e.g., *Diamesa* is absent in some regions (Willassen & Cranston, 1986)), endemic species that may co-occur with *Diamesa* in metakryal stream segments (Brodsky, 1980), glacial streams that remain clear all year (e.g., in the Colorado Cordillera (Ward, 1994)), and differences in geology, topography and riparian vegetation among river basins within and among geographic regions (e.g., Gislason et al., 1998).

3.6 Acknowledgements

We appreciate the field support by Drs. C.T. Robinson and H. Eisenmann. We are especially grateful to Dr. U. Uehlinger for providing unpublished temperature data, Mr. R. Illi and Mr. B. Ribi for analysing chemical samples, and Dr. B. Janecek for verifying *Diamesa* identifications. We also wish to thank our colleagues from the Val Roseg Project for the excellent collaboration. We are grateful to the villages of Pontresina and Samedan for providing access to the study area, and to Mr. P. Testa and his crew at the Roseg Hotel for their hospitality. Special thanks to Drs. F. Malard and C.T. Robinson, and 2 anonymous reviewers for their valuable critiques that improved the manuscript.
3.7 References


Longitudinal and seasonal distribution patterns


Longitudinal and seasonal distribution patterns


Chapter 4

Diversity, distribution and seasonality of the Simuliidae fauna in a glacial stream system in the Swiss Alps.

Abstract

Spatial and seasonal patterns in the densities and species richness of Simuliidae (blackflies) were examined in the glacier-fed Roseg River, Switzerland. We also investigated how selected environmental factors were related to the observed community structure. Overall, 7 blackfly species were found in streams of this glacial flood plain. Total densities and species richness differed significantly among sampling dates, and densities showed a significant downstream increase. Non-metric multidimensional scaling supported these findings and suggested that seasonal changes were affected strongly by extent of glacial influence. Furthermore, our results were indicative that environmental harshness was ameliorated by increased spatial heterogeneity, resulting in enhanced overall ecosystem stability in this glacier-fed stream. Low temperatures and channel instability limited Simuliidae colonization close to the glacier terminus. Suspended particles represented the most important food source, as expected, for simuliids in the Roseg River. However, our results indicated that feeding plasticity may play an important role in the feeding behavior of Simuliidae in this glacial stream because of the general paucity and high temporal variability of food sources.

4.1 Introduction

Simuliidae larvae often constitute an important zoobenthic component in lotic ecosystems. For this ubiquitous and species-rich dipteran family, 1720 morphospecies are known worldwide (Crosskey & Howard, 1997). In Middle Europe, between 50 and 60 species have been described based on morphological criteria. However, several species have been recognized as complexes of isomorphic sibling species, referred to as cytospecies or cytotypes (Zwick, 1993). Identification of sibling species within previously defined morphological species is possible only by analysis of larval polytene chromosomes (Adler, 1987). The Swiss simuliid fauna has been little studied, except for the comprehensive study by Glatthaar (1978). Currently, 34 species are known for Switzerland (Merz et al., 1998).
Although occurring in almost every lotic habitat type (Burger, 1987; Crosskey, 1990), larvae of Simuliidae often are found in high densities in lake and reservoir outlets (Wotton, 1987; Malmqvist, 1994). As a consequence, Simuliidae can have important functional implications at the ecosystem level. First, they can provide an important trophic link between suspended particles and predators (Malmqvist, 1994). Second, they can alter the size spectrum of fine particulate organic matter, which can affect the retention of organic material because larger fecal material sediments faster than finer particles (Wotton et al., 1998). Ross & Merritt (1987) reviewed the major environmental factors associated with the distribution and population dynamics of larval blackflies. Simuliid associations have been shown to be influenced by a variety of factors such as distance from lake outlets, stream/river size, food supply, substratum, current velocity, depth, light, physico-chemical conditions (e.g., temperature and pH) and pollution (e.g., Glatthaar, 1978; Corkum & Currie, 1987; Malmqvist et al., 1999).

Larval Simuliidae are easily distinguished from most other benthic invertebrates by their labral fans that are used to filter food from the water column. For this reason, they are often regarded as classic examples of filter-feeding organisms. However, filtering is not the only feeding technique. Scraping and collecting-gathering feeding modes have been observed, and filtering is not possible in some genera (e.g., Twinnia, Gymnopais) that lack cephalic fans (Currie & Craig, 1987). Although predation by simuliids is probably an opportunistic behavior, there is evidence that larvae actively capture their prey (Currie & Craig, 1987).

In arctic and alpine tundra streams a depauperate macroinvertebrate fauna, compared to temperate regions and lower elevations, suggests that extreme environmental conditions in these areas may exclude many species (Ward, 1994; Fürereder, 1999). Kryal (glacier-fed) streams represent the most extreme aquatic habitat type in alpine environments; being characterized by year-round low temperatures, high turbidity due to large amounts of pulverized material suspended in the water, and large diel flow fluctuations in summer resulting from glacial melting (Milner & Petts, 1994; Ward, 1994). Although the stream fauna is greatly reduced, downstream faunal changes are distinct and predictable in kryal biotopes (Milner & Petts, 1994; Ward, 1994). Based on the available literature, Milner & Petts (1994) proposed a qualitative model that related zoobenthic gradients in glacial rivers primarily to temperature and channel stability; both a function of distance from the glacier margin and time since deglaciation. However, most studies investigating the macroinvertebrate communities of kryal streams focused on the Chironomidae (especially Diamesa spp.), Ephemeroptera and Plecoptera, devoting less attention to other taxonomic groups (e.g., Steffan, 1971; Kownacka & Kownacki, 1972; Kownacki, 1991). Even though the Simuliidae are among the first non-chironomid taxa to appear in glacial streams (Milner & Petts, 1994), few studies have looked in detail at the diversity and distribution patterns of Simuliidae in alpine and arctic glacier-fed streams (Sommerman et al., 1955; Lavandier, 1979).
The present study examined the diversity and spatio-temporal distribution patterns of the Simuliidae fauna in a glacier-fed stream in the Swiss Alps. Our objective was threefold: (1) identification of the Simuliidae species present in the main glacial channel and to survey distinctively different habitat types for additional species; (2) investigation of longitudinal patterns in blackfly associations during different seasons; and (3) examination of relationships between simuliid distributions and measured environmental factors.

4.2 Materials and methods

Study area

Val Roseg is located in the Bernina Massif of the Swiss Alps (lat 46°29'28" N, long 9°53'57" E) (Fig. 4.1). The 11.3 km long Roseg River drains into the River Inn, a major tributary of the Danube. The primary water source of the Roseg River is meltwater from 2 valley glaciers, namely the Tschierva and Roseg glaciers. Its catchment area is 66.5 km², of which 30% is covered by glaciers, 40% is bare rock or glacial till without vegetative cover, and 9% is used for pasture. Bedrock consists of granite and diorite. Elevations range from 1760 (confluence with Bernina River) to 4049 m a.s.l. (Piz Bernina), with treeline at about 2300 m a.s.l. Subalpine coniferous forests in the Val Roseg are restricted to the lower parts of the valley slopes, whereas on the fluvio-glacial gravel of the valley floor no trees occur. Dominant tree species are larch (Larix decidua Mill.), stone pine (Pinus cembra L.) and mugo pine (P. mugo Turra). Shrubs mainly consist of green alder (Alnus viridis (Chaix) DC) and willow (Salix spp.). A more detailed description is given in Tockner et al. (1997).

Study sites

Five distinct reaches characterize the Roseg River: an unstable braided proglacial reach (length 900 m) below Tschierva glacier, a lake outlet stream below proglacial Lake Roseg (length 950 m), a single thread channel incised in glacial till (length 600 m), the main glacial flood plain (length 2750 m) with 6 distinctive channel types (Tockner et al., 1997), and a canyon-constrained reach that extends downstream to the river mouth at Pontresina (length 7050 m) (Fig. 4.1).

Simuliid assemblages from 16 sampling sites (Fig. 4.1) were investigated at increasing (June), high (August), decreasing (October) and low but constant (November) flow conditions in 1997. Ten sites were located along the main glacial channel of the Roseg River from the snout terminus of the Tschierva glacier down to the river mouth (sites M1 to M10). To check for other species not colonizing the main channel, additional samples were taken from 3 groundwater channels (G1, G2, G3),
2 intermittently-connected channel habitats (I2 and I3), and the outlet stream of Lake Roseg (L1). Groundwater channels are fed by the alluvial aquifer or by a tributary aquifer, and have no upstream surface connection to any other channel. Intermittently-connected channels have a permanent surface connection at their downstream ends, but an intermittent surface connection with the main channel at their upstream ends (Tockner et al., 1997). For comparisons with previous work on the hydro-ecology of this glacial river systems, sites labelled M1 to M10, G1 to G3, I2, I3 and L1 in this paper correspond to codes M-20, M-15, M-10, M-1, M10, M12, M20, M30, M32, M40, G-10, G2, G5, I2, X5 and L-10 used in previous papers (Tockner et al., 1997; Malard et al., 1999; Ward et al., 1999).

Field techniques and laboratory procedures

Physical factors have been shown to strongly effect blackfly distributions, whereas hydrochemical differences show little influence except under extreme conditions (Glatthaar, 1978; Ross & Merritt, 1987). Therefore, apart from specific conductance, only factors describing physical and biotic characteristics were considered. Stream water temperature, turbidity, specific conductance, suspended solids, and the ratio of organic suspended solids (OSS) to inorganic suspended solids (ISS) were measured following the methods outlined in Tockner et al. (1997). Distance from the glacier was calculated using global positioning system data. Water depths and near-bed current velocities (Mini Air 2, Schiltknecht Messtechnik AG, Switzerland) were measured at the same positions where benthic samples were taken.

Three replicate Hess samples (area 0.043 m², 100 µm mesh size) were collected from haphazardly selected locations at each sampling site and date, preserved in 4% formalin and returned to the laboratory, where macroinvertebrates were sorted and identified. Larvae of Simuliidae were separated and subsequently identified to species using the key by Knoz (1965). After removal of invertebrates, the remaining material from each sample was split into 2 fractions (> 1 mm and < 1 mm), dried at 60°C, weighed, ashed at 550°C and reweighed for determination of coarse and fine benthic organic matter (CBOM and FBOM) as ash-free dry mass.

Statistical analyses

Simuliid associations were analyzed for changes in total densities and species richness using two-way analysis of variance (ANOVA), followed by Tukey's Honest Significant Test (HSD) for multiple pairwise comparisons among sampling dates and sites. Prior to analysis, data were log_{10}(x+1) transformed to ensure normality and homogeneity of variances (Zar, 1996).
Fig. 4.1: Location of the Val Roseg catchment in the Bernina Massif of the Swiss Alps. The 5 major reaches and a simplified representation of the channel network of the Roseg River are indicated. Black circles represent sampling sites.
Non-metric multidimensional scaling (NMDS, Primer Software Package, Carr, 1997) was used to classify sites. The raw matrix of average species density per site was initially square-root transformed to downweigh the influence of dominant species but still retain the quantitative information. Then, NMDS was run, based on the Bray-Curtis similarity measure, for all pairs of sites. Last, a two-dimensional ordination plot was produced, where distances from NMDS represented faunal similarity between sites. The adequacy of an NMDS representation can be judged by the stress-value which, for a two-dimensional solution, must be < 0.25 to indicate deviation from random positions.

Partial least-squares regression (PLS) was computed to relate simuliid associations to environmental factors using SIMCA-P V.8 software. This method, rather than multiple linear regression, was used because it has no bias if explanatory variables are strongly correlated, or if the number of explanatory variables is larger than the number of objects. PLS reduces the number of variables to one or several latent components (Martens & Naes, 1989), with the number of components extracted and the statistical significance of the models determined using internal cross-validation (Wold, 1978). The performance of a PLS model can be deduced from the statistics $Q^2$ (predicted Y-variation). The influence of environmental variables on simuliid associations was judged by VIP (variable importance in the projection) values. A VIP $> 1$ indicates a strong influence, whereas a VIP $< 0.8$ indicates a minor influence. Two univariate PLS models (PLS 1) were tested, using either total density (all species combined) or the scores of NMDS axis 1 as the dependent variable versus several environmental variables as explanatory variables. Additionally, a multivariate PLS (PLS 2) model was run with individual densities of simuliid species as dependent variables and the same environmental variables. Environmental variables in all models were those described above. Prior to analysis, variables were log$_{10}$ ($x+1$) transformed to normalize and stabilize the variance (Zar, 1996).

4.3 Results

Diversity and stream type affinities

A total of 1303 Simuliidae larvae were collected from the main channel. The additional sampling in the other habitat types yielded another 311 specimens. Specifically, about 82% of all animals collected came from the main channel, 14.5% from groundwater channels, 3.3% from intermittently-connected channels, and only 0.2% from the proglacial lake outlet stream. Pupae were used only for verification of larval identifications, but not included in data analysis. Overall, 7 species were identified: *Simulium argenteostriatum* Strobl, *Simulium argyreatum* Meigen, *Simulium carthusiense* Grenier & Dorier, *Simulium cryophilum* Rubtsov, *Simulium trifasciatum* Curtis, *Prosimulium latimucro* Enderlein, and *Prosimulium rufipes* Meigen. Most species were found primarily in the main channel, although *P. latimucro* was more
abundant in the intermittently-connected channels than in the main channel and was absent from groundwater channels. The only species not found in the main channel was *S. cryophilum*, which mainly occurred in intermittently-connected channels and sporadically in groundwater channels. The 2 numerically dominant species were *S. argyreatum* (32.3% of the assemblages) and *P. rufipes* (44.9%). *Simulium cryophilum* and *S. trifasciatum*, contributing 9.1% and 7.7%, respectively, were intermediate, whereas *S. carthusiense* (3.3%), *P. latimicro* (2.4%), and *S. argenteostriatum* (0.3%) were least abundant.

**Longitudinal distribution patterns in the main channel**

No Simuliidae were found on any sampling date at the 3 uppermost sites (M1 to M3) in the proglacial reach; therefore, these sites were excluded from subsequent statistical analyses. Total densities (7 main channel sites combined) were lowest in August (30 ± 31 ind./m²) and considerably higher on the other sampling dates (358 ± 305 ind./m² in June, 451 ± 775 ind./m² in October, 605 ± 795 ind./m² in November). Two-way ANOVA indicated significant differences in total simuliid densities among sites ($F_{6,56} = 15.26, p < 0.001$), dates ($F_{3,56} = 16.71, p < 0.001$), and for the interaction term ($F_{12,56} = 3.21, p < 0.001$) (Table 4.1). All pairwise comparisons among dates were significant (Tukey’s HSD, $p < 0.05$), except for June versus November and October versus November. Pairwise comparisons among sites revealed the following patterns: Site M4 in the incised reach and site MS in the upper part of the glacial flood plain were not significantly different from each other (Tukey’s HSD, $p > 0.05$). However, both sites were significantly different from all sites further downstream (Tukey’s HSD, $p < 0.05$). No significant differences were found between sites in the flood plain and the constrained reach (exceptions: M6 versus M9 and M9 versus M10; Tukey’s HSD, $p < 0.05$ for both).

The maximum number of species identified at any site and date never exceeded 4 species (Table 4.1). Two-way ANOVA for species richness also revealed significant differences among sites ($F_{6,56} = 5.48, p < 0.001$) and dates ($F_{3,56} = 8.82, p < 0.001$), but not for the interaction term ($F_{12,56} = 0.64, p > 0.05$). Species richness differed significantly among all dates (Tukey’s HSD, $p < 0.05$), whereas no significant differences were found among sites (excluding M1 to M3, which lacked simulids).

Species response patterns differed among sampling dates (Fig. 4.2). In June and August, *Simulium* spp. contributed 80% of total simuliid densities. In October, this proportion was 72%, but *Prosimulium* spp. abundance had increased greatly at sites M7 to M9. In November, the reverse was observed, with *Prosimulium* spp. (78%) being the dominant genus. In contrast to all other species, *S. argenteostriatum* was found only once, this at site M7 in August. A relatively equal distribution of *S. argyreatum* at sites M6 to M10 was observed in June, whereas the pattern was skewed more downstream in October and November. Neither *S. carthusiense* nor *P. latimicro*...
Simuliidae fauna in a glacial stream system

exhibited distinct longitudinal patterns. Densities of *S. trifasciatum* were higher in the incised reach and the upper part of the flood plain in June, whereas in October and November density maxima had shifted downstream. Last, *P. ruftipes* also showed a quite equal distribution in June, but was more abundant at sites in the constrained reach in October and November.

**Table 4.1**: Summary of Simuliidae densities and species richness at sites M4 to M10. Species richness is expressed as number of species. SD = standard deviation.

<table>
<thead>
<tr>
<th>Site</th>
<th>Densities mean ± SD (ind./m²)</th>
<th>Species richness mean (range)</th>
</tr>
</thead>
<tbody>
<tr>
<td>M4</td>
<td>27 ± 39</td>
<td>1 (0 - 3)</td>
</tr>
<tr>
<td>M5</td>
<td>56 ± 97</td>
<td>1 (0 - 3)</td>
</tr>
<tr>
<td>M6</td>
<td>89 ± 122</td>
<td>2 (1 - 2)</td>
</tr>
<tr>
<td>M7</td>
<td>271 ± 264</td>
<td>2 (2 - 3)</td>
</tr>
<tr>
<td>M8</td>
<td>417 ± 526</td>
<td>2 (1 - 2)</td>
</tr>
<tr>
<td>M9</td>
<td>1231 ± 1060</td>
<td>3 (3 - 4)</td>
</tr>
<tr>
<td>M10</td>
<td>434 ± 412</td>
<td>2 (0 - 4)</td>
</tr>
</tbody>
</table>

A stress value of 0.14 for the NMDS indicated a good representation of the original data in the first 2 dimensions of NMDS space. The resulting ordination plot (Fig. 4.3) mainly separated site M4 in the incised reach and sites M5 and M6 in the floodplain reach from sites M7 to M10 in the constrained reach along NMDS axis 2 (indicated by dashed ellipses in Fig. 4.3). However, 3 sites in each cluster did not follow this pattern (underlined site labels in Fig. 4.3). No clear temporal separation among sampling dates was found, although samples from June and August were primarily positioned towards the positive side of NMDS axis 1, while samples from October and November were on the opposite side. Additionally, sites were most dispersed in two-dimensional space in August and November, whereas sites were more tightly clustered close to the origin in June and October. Sites M4 and M8 in August and site M6 in June were isolated from the other sites, and were the only sites where *P. latimucro* occurred.

The 2 PLS 1 models were not satisfactory, with only 1 significant component for total densities versus environmental variables ($Q^2_1 = 0.408$, $p < 0.05$), and no significant component for scores of NMDS axis 1 versus environmental variables ($Q^2_1 = -0.063$, $p > 0.05$). In contrast, the PLS 2 model with individual species densities as dependent variables yielded 2 significant components ($Q^2_1 = 0.356$, $p < 0.05$; $Q^2_2 = 0.305$, $p < 0.05$). Highest VIP values for suspended solids, distance from glacier, and turbidity indicated these environmental variables were most important in the model, whereas FBOM, current velocity, specific conductance and water depth contributed little (Table 4.2).
Simuliidae fauna in a glacial stream system

Fig. 4.2: Distribution patterns of simuliid species along the main glacial channel on the 4 sampling dates. Only sites M4 to M10 are shown because no Simuliidae were found at M1 to M3. The diameters of circles indicate log10 density classes.

4.4 Discussion

Diversity and stream type affinities

Glacier-fed streams are believed to provide a poor habitat for Simuliidae, and as a consequence, relatively few species colonize them (Burger, 1987; Crosskey, 1990). However, 7 blackfly species were found in the Roseg River, representing 20% of all species currently known for Switzerland. We assume that this number of species provides an accurate representation of simuliid diversity in the glacier-fed Roseg River because sampling was conducted during 4 seasons at 16 sites representing 4
Fig. 4.3: Positions of sampling sites in the first 2 dimensions of non-metric multidimensional scaling (NMDS). Sites with similar blackfly communities are situated close together. Dashed ellipses separate sites from the incised and floodplain reaches from those in the constrained reach. Underlined site labels denote outliers from this pattern. No Simuliidae were found at sites M4 and M5 in October, and site M10 in August.

Table 4.2: Cumulated VIP (Variable importance in the projection, VIP (cum)) values for the first 2 components of partial least squares (PLS) regression reflecting the importance of individual environmental parameters to the model for predicting simuliid associations. A VIP > 1 contributes most, whereas a VIP < 0.8 has little influence.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>VIP (cum)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Suspended solids</td>
<td>1.20</td>
</tr>
<tr>
<td>Distance from glacier</td>
<td>1.19</td>
</tr>
<tr>
<td>Turbidity</td>
<td>1.13</td>
</tr>
<tr>
<td>CBOM</td>
<td>1.12</td>
</tr>
<tr>
<td>Temperature</td>
<td>1.09</td>
</tr>
<tr>
<td>OSS : ISS</td>
<td>0.95</td>
</tr>
<tr>
<td>FBOM</td>
<td>0.82</td>
</tr>
<tr>
<td>Current velocity</td>
<td>0.80</td>
</tr>
<tr>
<td>Specific conductance</td>
<td>0.79</td>
</tr>
<tr>
<td>Water depth</td>
<td>0.75</td>
</tr>
</tbody>
</table>
stream types. However, comparisons are difficult because studies of simuliids in glacier-fed streams are rare, and simuliid larvae often were not identified to species level in other studies of longitudinal distribution patterns. In the River Estaragne in the French Pyrenees, 8 blackfly species occurred (Lavandier, 1979). Ward (1986) reported 7 species in the middle St. Vrain River (USA) fed by the St. Vrain Glaciers. Similar numbers of species also have been found in arctic tundra streams (not glacier-fed) in Alaska by Hershey et al. (1995), if species exclusively found in lake outlets or higher order streams are excluded. Nevertheless, in specific habitat types, e.g., springs in the glacial flood plain of the Val Roseg, some additional species such as *Twinnie hydroides* Novak and *Simulium crenobium* Knoz are likely to occur. Our results suggest that glacier-fed streams, such as the Roseg River, may provide more adequate habitat for Simuliidae than is generally assumed.

Larval simuliids found in the Roseg River belonged to the genera *Simulium* and *Prosimulium*, whereas blackflies reported from high latitudes in Alaska, Canada, and Siberia were mostly *Gymnopaís*, a genus whose larvae have lost their labral fans and become adapted to a scraping feeding mode. Some species of the genera *Prosimulium* and *Simulium* also have been reported in these systems (Burger, 1987; Crosskey, 1990). Another region where blackfly larvae occur in the ice-melt waters of glaciers is in tropical Africa. In glacial streams originating from the summit glaciers of Mount Kenya and other high East African mountains of tropical latitudes, blackflies of the *S. dentulosum* group were found (Crosskey, 1990).

Simuliidae were about 4x more abundant in the main glacial channel than in other stream types; this is not surprising considering the habitat preferences of the individual species (compare Glatthaar, 1978). The 3 species *P. rufipes*, *S. carthusiense*, and *S. argenteostriatum* typically inhabit high altitude streams. Similarly, *S. argyreatum* and *S. trifasciatum* prefer cold, fast flowing streams, although they have their distributional optima at lower elevations. In alpine streams with low gradients, *P. latimucro* also is commonly found. In contrast, *S. cryophilum* only occurred in groundwater and intermittently-connected channels, in accordance with its known preference for spring-fed habitats (Glatthaar, 1978). Whereas lowland lake or reservoir outlet streams often exhibit high densities of simuliid larvae (e.g., Wotton, 1987) and other filter feeding organisms, the outlet stream of Lake Roseg did not follow this pattern (see Burgherr & Ward, in press).

Although the distribution patterns of individual species generally were in good accordance with known habitat affinities (Glatthaar, 1978), temporal responses of larvae to seasonally changing environmental conditions illustrated the variability in distribution patterns through time. This was reflected in changes in density, species richness and assemblage composition among seasons. Therefore, these results emphasize the importance of examining patterns in more than 1 season before drawing general conclusions. This is especially critical for Simuliidae because they are known to exhibit substantial fluctuations in densities within short periods of time (e.g., Kiel, 1996; Matthäi et al., 1996).
**Longitudinal distribution patterns in the main channel**

Along the longitudinal gradient in the main channel, no Simuliidae were found at sites M1 to M3 in the proglacial reach. This is most likely attributable to low temperature ($T_{\text{max}} = 1.86^\circ \text{C}$, 248 annual degree days at M3) and unstable stream beds. Temperature is a key factor determining the distribution, diversity, and abundance patterns of aquatic insects (Vannote & Sweeney, 1980; Ward & Stanford, 1982; Ward, 1992), and unstable stream beds prevent attachment of simuliid larvae even when the temperature regime is suitable (Crosskey, 1990). As annual maximum temperature exceeds $2^\circ \text{C}$ and the channel becomes more stable downstream, Simuliidae are often the first non-Chironomidae taxa to appear (Milner & Petts, 1994; Ward, 1994). Furthermore, our results indicate that the glacial floodplain section exerts a stabilizing effect as inferred by the significantly higher abundances at sites M6 to M10 compared to those upstream. Seasonal patterns of total simuliid densities showed significant differences among sampling dates. Lowest densities were recorded during maximum glacial melting and high discharge in August, whereas densities were 12 to 27x higher on the other dates. These findings support the view of Tockner et al. (1997), who suggested that increased spatio-temporal heterogeneity enhances overall ecosystem stability and may play an important role in sustaining populations under the harsh conditions found in glacial streams.

NMDS confirmed a similar longitudinal trend in assemblage structure as found for total densities. August samples at the periphery of the ordination were clearly separate, whereas the 3 other dates overlapped. However, the more tight clustering of sites in June and October compared to August and November may reflect seasonal changes in discharge. June and October are transition periods between high and low flows, whereas August (high discharge) and November (low but constant discharge) reflect endpoints when environmental conditions are, respectively, more harsh or favourable. This also is in accordance with patterns of total densities that were intermediate in June and October, low in August, and high in November. In conclusion, we postulate that environmental harshness is ameliorated by increased spatio-temporal heterogeneity, resulting in enhanced overall ecosystem stability.

PLS regression revealed that environmental variables describing glacial influence and potential food supply had important implications for simuliid associations. Temperature was a key factor in separating unsuitable habitats for simuliid larvae in the proglacial reach (M1 to M3) from the remaining sites, but was less influential at sites colonized by simuliids, as indicated by PLS regression. Water depth and current velocity contributed little to the PLS regression model, indicating that both parameters were adequate for simuliid associations (Glatthaar, 1978). Suspended solids, distance from the glacier, and turbidity were the 3 most important terms in the PLS regression model, all representing a measure of glacial influence. In addition, distance from the glacier is a function of stream size, which has been shown to be an important variable for simuliid associations (Glatthaar, 1978; Malmqvist et al., 1999), and suspended particles also can play an important role for filter feeding organisms.
Filtering Simuliidae generally ingest organic and inorganic particles < 200 µm, especially between 0.5 - 50 µm (Ross & Merritt, 1987; Crosskey, 1990). However, Wotton (1976) showed experimentally that larvae can filter particles of colloidal size (0.091 µm diameter), and it is likely that even dissolved organic matter (DOM) with diameters < 0.5 µm provide a potential food source (Crosskey, 1990). PLS regression suggested that suspended solids (typically < 0.1 mm in diameter) provide an important food source. Although one would expect the ratio of organic suspended solids (OSS, „seston“) to inorganic suspended sediments (ISS, „clay particles“) to be an important variable for simulids, it had little influence. This may be partially attributable to the negligible quantities of OSS compared to ISS. The ratio of OSS:ISS was low and did not appreciably vary (0.15 ± 0.11). However, the short gut-retention time of simulid larvae, between 20 to 30 min (Ross & Merritt, 1987), allows them to cope with large amounts of non-digestible particles. Benthic organic matter concentrations in the Roseg River are about 1-2 orders of magnitude less than those reported for other lotic systems (see Tockner et al., 1997), suggesting FBOM and CBOM are a less important food source.

High concentrations of suspended solids only occurred during summer high flow, whereas glacial melting is minimal from late autumn to late spring, and as a result, levels of suspended solids are low. Steffan (1971) and Ward (1994) proposed aeolic input of fine organic particles transported by wind (e.g., pollen) as a potential source of organic material for glacial headwaters. Considering the low aerial inputs of organic material in the Val Roseg (Zah et al., in press), this input of organic material seems rather unlikely as a food source for Simuliidae. Similarly, low concentrations of dissolved organic carbon and particulate organic carbon (Tockner et al., 1997) suggest that these 2 carbon sources also are limited.

Late spring and early autumn provide suitable periods for accrual of benthic algae in glacial streams (Uehlinger et al., 1998). Larval simulids are facultative filter feeders, with scraping or grazing as the second most important feeding strategy (Currie & Craig, 1987). Therefore, periphyton offers a potential alternative food source. Furthermore blackflies may ingest algal filaments ≥ 1 mm in length (Ross & Merritt, 1987; Crosskey, 1990), which may be important considering the predominance of the filamentous chrysophyte *Hydrurus foetidus* in this glacier-fed stream (Uehlinger et al., 1998). In addition, simulid larvae also feed on animal matter, including Chironomidae, Ephemeroptera, Plecoptera and most frequently other blackfly larvae (Ross & Merritt, 1987; Crosskey, 1990). Our results suggest that feeding plasticity may play an important role in the feeding behavior of Simuliidae in this glacial stream, as also has been shown for a limnephilid caddisfly in the same system (Burgherr et al., submitted). Flexibility in functional feeding mode has been reported in other studies of blackfly larvae (e.g., Miller et al., 1998), indicating this may in fact be a common phenomenon.
4.5 Acknowledgements

We thank Dr. C.T. Robinson for assistance in the field. Chemical analyses were completed by Mr. R. Illi and Mr. B. Ribi. We are especially indebted to Dr. U. Uehlinger for providing unpublished temperature data. We also wish to thank our colleagues from the Val Roseg Project for the excellent collaboration. We are grateful to the villages of Pontresina and Samedan for providing access to the study area, and to Mr. P. Testa and his crew at the Roseg Hotel for their hospitality. We appreciate the helpful comments of D.B. Arscott and Dr. C.T. Robinson that improved the manuscript.

4.6 References


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Chapter 5

Seasonal variation in zoobenthos across habitat gradients in an alpine glacial flood plain (Val Roseg, Swiss Alps)

Abstract

Flood plains of glacial streams are prominent features of alpine landscapes, yet their ecology has been little studied. The goal of the present study was to assess the effects of habitat stability and heterogeneity of streams in a glacial flood plain in the Swiss Alps on the community structure of benthic macroinvertebrates. Zoobenthic assemblages were investigated during different phases of the annual hydrograph in 3 distinct habitat types (main glacial channel, intermittently-connected channels, and groundwater channels). Communities in the main channel exhibited a high temporal variability in total densities and were dominated by Chironomidae, Ephemeroptera, and Plecoptera (> 95% of total zoobenthos). In contrast, groundwater channels displayed a low temporal variability in community structure, but a high within-channel type variability. Habitat stability, spatio-temporal habitat heterogeneity and connectivity appeared to be key factors in determining the community structure of each channel type as well as individual channels within each type in the glacial flood plain. The complex channel network led to a high spatial heterogeneity, resulting in an enhanced overall ecosystem stability. As a consequence, increased levels of biodiversity at the floodplain scale were possible due to the presence of suitable habitat patches for taxa not able to colonize the main channel, and the provision of numerous refugia for benthic macroinvertebrates during high discharge in summer when environmental conditions in the main channel were unsuitable for most taxa.
5.1 Introduction

Human activities are influencing and altering the functioning of ecosystems at a rate and magnitude much faster than "normal evolution" (Chapin III & Körner, 1994). Although alpine and arctic stream ecosystems have been proposed to be particularly sensitive to climate change and human impacts via water resource developments (McGregor et al., 1995), relatively little is known of their ecology (Ward, 1994). Whether global warming would lead to glacial recession from increased ablation or glacial expansion from increased precipitation is still under debate (Knight, 1992). Nevertheless, changes in hydrology, temperature, and channel stability are likely to cause predictable changes in the structure of zoobenthic communities (Milner & Petts, 1994; McGregor et al., 1995).

Headwater streams and rivers are important features of alpine landscapes. Climate, hydrology, geology, and geomorphology define the local character of running waters. In alpine regions, 3 major types of streams can be distinguished: kryal stream segments fed by glacial meltwater, krenal segments fed by ground water, and rhithral segments dominated by snowmelt (Ward, 1994). Generally, alpine stream networks form a complex mosaic of kryal, krenal and rhithral stream segments (Milner & Petts, 1994; Ward, 1994; McGregor et al., 1995).

Kryal habitats are characterized by low temperatures (T_max < 4°C), large diel flow fluctuations in summer with peaks in late afternoon from glacial melting, high sediment loads and low channel stability (Milner & Petts, 1994; Ward, 1994). However, instream environmental conditions depend on distance from the glacier terminus, season, and the contribution of non-glacial water sources. For example, downstream of kryal segments, a glacio-rhithral zone fed by a mixture of water sources can extend for a considerable distance, with temporal changes in discharge and temperature reflecting the relative proportion of glacial influence (Fürereder, 1999). Few studies have described the longitudinal distribution patterns of benthic macroinvertebrate communities in glacier-fed streams (e.g., Saether, 1968; Steffan, 1971; Kownacka & Kownacki, 1972; Kownacki, 1991), and comprehensive year-round studies such as in the River Estaragne in the French Pyrenees (Lavandier & Décamp, 1984) are rare. Milner & Petts (1994) proposed a qualitative model to predict zoobenthic gradients as a function of water temperature and channel stability.

In contrast to this longitudinal perspective, the spatio-temporal dynamics of streams within glacial flood plains have received little attention (Ward et al., 1998). In river floodplain systems at low elevations, the pulsing of discharge (flood pulse) is a key factor structuring biotic assemblages (Junk et al., 1989). However, the ecological effects of these discharge pulses are potentially reduced in glacial floodplain systems because of low temperatures, diel flow fluctuations in summer, high amounts of suspended materials, and increased bedload transport during summer high flow. Val Roseg, a glacial flood plain in the Swiss Alps, is characterized by a remarkable degree of aquatic habitat heterogeneity attributable to the shifting dominance of
Seasonal variation in zoobenthos across habitat gradients

subcatchment water sources and flow paths (Tockner et al., 1997; Malard et al., 1999; Ward et al., 1999). As a consequence, different floodplain channels show different degrees of permanency and connectivity.

The primary goal of the present study was to assess the effects of habitat heterogeneity among streams in the Val Roseg glacial flood plain on the community structure and composition of benthic macroinvertebrates. Three channel types, based on their hydrological connectivity and their physico-chemical characteristics, were selected that reflected a gradient of increasing habitat (channel) stability: the main glacial channel, intermittently-connected channels, and groundwater channels. The specific hypotheses addressed were: (1) different channel types are inhabited by distinct zoobenthic communities; (2) more stable habitats (i.e., groundwater channels) have the lowest fluctuations in community structure and the highest levels of species diversity; and (3) the mosaic of channel types enhances the biodiversity of glacial flood plains.

5.2 Study area

General description

Val Roseg is situated in the Bernina Massif of the Swiss Alps (lat 46°29'28" N, long 9°53'57" E). Elevation ranges from 1760 m a.s.l. at the lower end of the catchment (confluence with Bernina River) to 4049 m a.s.l. (Piz Bernina). About 30% of the 66.5 km² drainage basin is covered by glaciers, 40% by bare rock or glacial till without vegetative cover, and 9% is used for pasture. Treeline is at about 2300 m a.s.l., with subalpine coniferous forests restricted to the lower parts of the valley side-slopes, whereas no trees occur on the fluvo-glacial gravel of the valley floor. Dominant tree species are larch (*Larix decidua* Mill.), stone pine (*Pinus cembra* L.) and mugo pine (*P. mugo* Turra). Bedrock consists of granite and diorite of the austroalpine nappes. The 11.3 km long Roseg River (Ova da Roseg) is primarily fed by 2 valley glaciers: the Tshierva (6.2 km²) and Roseg (8.5 km²) glaciers. It exhibits a seasonal flow regime (summer peak) and distinct daily discharge fluctuations during maximum glacier melting in summer that is typical of glacial-meltwater dominated rivers (Fig. 5.1). Mean annual discharge of the Roseg River is 2.76 m³/s (1955-1997, Swiss Hydrological and Geological Society). The system is fed largely by ground water in winter (Malard et al., 1999).

Five reaches characterize the Roseg River: an unstable braided reach in the recent proglacial area of the Tshierva glacier (length 900 m), a lake outlet stream below proglacial Lake Roseg (length 950 m), a single thread channel incised in glacial till (length 600 m), the main glacial flood plain (length 2750 m), and a canyon-constrained reach that extends downstream to the river mouth at Pontresina (length 7050 m) (Fig. 5.2). The main flood plain contains a variety of aquatic habitats, domi-
nated by 6 channel types that can be distinguished according to their hydrology and physico-chemical attributes (Tockner et al., 1997).

![Annual discharge pattern of the Roseg River in 1997.](image)

**Fig. 5.1:** Annual discharge pattern of the Roseg River in 1997. The inset represents diel flow fluctuations in summer. Arrows indicate sampling dates.

### Study sites

The study design combined a habitat gradient with longitudinal position. Of the 6 channel types identified in the flood plain, the 3 that were selected are defined as follows (Tockner et al., 1997):

1. **Main channel (M):** The primary channel (thalweg) fed mostly by glacial meltwater.
2. **Intermittently-connected channels (I):** have permanent surface connections at their downstream ends, but an intermittent surface connection with the main channel at their upstream ends.
3. **Groundwater channels (G):** are fed by the alluvial aquifer or by a tributary (hillslope) aquifer, and have no upstream surface connection.

These 3 habitat types cover a gradient of increasing habitat stability from the main channel through intermittently-connected channels to groundwater channels. Habitat (channel) types were selected in the proglacial reach (M1, G1; ca. 2090 m a.s.l.), in the upper part of the flood plain (M2, I2, G2; ca. 2020 m a.s.l.) and in the lower part of the flood plain (M3, I3, G3; ca. 2010 m a.s.l.), thus also incorporating a longitudinal perspective (Fig. 5.2). For comparisons with previous work on the
hydro-ecology of this glacial river system, sites labelled M1, M2, M3, I2, I3, G1, G2 and G3 in this paper correspond to codes M-10, M10, M12, I2, X5, G-10, G2 and G5, respectively, used in previous papers (Tockner et al., 1997; Malard et al., 1999; Ward et al., 1999). Because intermittently-connected channels are restricted to the floodplain section, no site of this habitat type was found in the proglacial reach. These 8 sampling sites were visited at bimonthly intervals from April to December 1997 (arrows in Fig. 5.1) to account for seasonal changes in discharge, water sources and flow paths. In April the system is mostly fed by ground water, although some snowmelt occurs. Snowmelt is the main source of water at increasing discharge in June, whereas glacial meltwater dominates at high discharge in August. In October, discharge is decreasing but the contribution of englacial water to surface flow is not significantly lower (Malard et al., 1999). December corresponds to a phase of constant and low discharge with ground water being the most important source of water. For sites I2 in April and I3 in December, samples could not be taken because surface water was not present. At Site G1 in the proglacial reach, flow in April also was too low to take benthic samples.

5.3 Materials and methods

Total channel length of the channel network in the main flood plain was used as an indicator of spatial heterogeneity at the floodplain scale. A detailed description of the mapping procedure and subsequent calculations are given in Malard et al. (1999). Only selected parameters, from a variety of measured environmental variables, are referred to in this paper to illustrate physico-chemical differences among channel types. Substrate size was assessed in the field by measuring 100 randomly selected stones (b-axis, width). Continuous temperature records (1 hr intervals; StowAway XTI temperature loggers, Onset Corporation, USA) were available for 7 of the 8 sites (U. Uehlinger & F. Malard, unpubl. data). Temperature data from the uppermost site in the constrained reach were used as a substitute for the missing site M3. Specific conductance was determined using a portable conductivity meter (WTW LF323-B, Wissenschaftliche-Technische Werkstätten, Germany). Turbidity (NTUs) was measured with a portable turbidity meter (Cosmos, Fa. Züllig, Switzerland). Specific conductance and turbidity were measured in the morning at each site and sampling date to minimize the effects of daily discharge fluctuations. Near-bed current velocities (Mini Air 2, Schiltknecht Messtechnik AG, Switzerland), water depth and substrate heterogeneity were measured at the same positions where benthic samples were taken. Substrate heterogeneity, used as an indicator of microhabitat structure, was measured with a device modified from Gore (1978), as described in Tockner & Ward (1999). The device was placed within a standard Hess sampler and the coefficient of variation (CV % = SD/mean * 100) of the length of 20 randomly arranged rods above the surface of the plate, indicated the degree of surface heterogeneity. The environmental data collected for each site were initially summarized as
Fig. 5.2: Location of the upper Val Roseg catchment in the Bernina Massif of the Swiss Alps, showing the 5 major reaches. Filled squares represent sampling sites. Inset map shows location of catchment in Switzerland.
Seasonal variation in zoobenthos across habitat gradients

means, standard deviations (SD) and CVs.

Habitat (channel) stability was measured using an approach similar to those described in Death & Winterbourn (1994), and Townsend et al. (1997). A multivariate ordination of 7 variables (substrate size, substrate heterogeneity, range of specific conductance, range of turbidity, range of water depth, maximum near-bed velocity, temperature range) was used to define a single "overall" measure of habitat stability for the 8 sampling sites. Each variable was scaled between 0 and 1 using the equation $x_{ij} = (z_{ij} - \text{min}) / (\text{max} - \text{min})$, where $z_{ij}$ is the value of the $j$th variable for the $i$th site, min and max are the minimum and maximum value of the $j$th variable. The resulting matrix was then analyzed by means of a non-centered principal components analysis. The first component of such an analysis is always unipolar (Noy-Meir, 1973), and can be used as a multivariate instability score.

Three Hess samples (area 0.043 m$^2$, 100 µm mesh size) from randomly selected locations were collected at each site on each date (exceptions mentioned above). Samples were preserved with 4% formalin and returned to the laboratory for processing. In the laboratory, samples were separated into size fractions greater and less than 1 mm. All macroinvertebrates from both fractions were sorted, identified to the lowest taxonomic unit feasible and enumerated. After removal of invertebrates, the remaining material from the coarse (>1 mm) and fine (<1 mm) fraction of each sample was dried at 60°C, weighed, ashed at 550°C and reweighed for determination of coarse and fine benthic organic matter (BOM) as ash-free dry mass (AFDM). Macroinvertebrate data for each site were summarized as means, standard deviations and CVs for total density, taxon richness and Simpson's index. Simpson's index (SI) was expressed as -$\ln$ SI so that values increase as the number of species increases independently of sample size (Rosenzweig, 1995). Data were log_{10}(x+1) transformed to ensure normality and homogeneity of variances (Zar, 1996), and subjected to two-way analysis of variance (ANOVA) to compare differences among sampling sites and dates. Subsequent multiple pairwise comparisons were made using Tukey's Honest Significant Test (HSD). However, the factorial design contained missing treatment combinations, because at sites I2 in April and I3 in December no surface water was present, and flow at site G1 also was too low in April to take benthic samples. In general, there is no one best method to analyze such designs. Furthermore, it is often only possible to estimate main effects (and some interactions) from complete sub-designs (Milliken & Johnson, 1984; Statsoft, 1995; and references therein). Therefore, as a rather conservative approach, a balanced design was achieved by comparing only samples from June, August and October, instead of assigning "zero values" to missing samples.

Finally, the faunistic data set was analyzed by means of centered principal components analysis (PCA) (ADE-4 software, Chessel & Dolédec, 1996). Between-class and within-class PCAs were introduced by Foucart (1978), and Benzécri & Benzécri (1986). Dolédec & Chessel (1989) have demonstrated that these methods are well suited to distinguish between seasonal and spatial effects. First, we focused on the spatial typology of sampling sites using a between-site PCA (Dolédec & Chessel,
The between-site PCA of the initial data table is the PCA of the cumulated (by sites) data table. In order to bring out the variability of each sampling site, the initial data were used in the between-site PCA as supplementary individuals. Second, a within-date PCA (removal of the time effect) was performed to illustrate changes in the spatial distribution of sampling sites among dates. The within-date analysis was an analysis of the residuals.

5.4 Results

Habitat characteristics

On average, the main channel had the lowest mean temperature and also the lowest temperature range, whereas intermittently-connected channels and groundwater channels had higher mean values and encompassed a wider temperature range (Table 5.1). Within each channel type, mean temperature and temperature range increased with increasing distance from the glacier terminus.

Table 5.1: Water temperatures (°C) at sampling sites based on logger data from 1997.

<table>
<thead>
<tr>
<th>Site</th>
<th>Daily mean (range)</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1</td>
<td>0.7 (0.0 - 1.9)</td>
</tr>
<tr>
<td>M2</td>
<td>2.9 (0.4 - 4.8)</td>
</tr>
<tr>
<td>M3</td>
<td>2.6 (0.0 - 6.1)</td>
</tr>
<tr>
<td>I2</td>
<td>4.5 (0.0 - 7.1)</td>
</tr>
<tr>
<td>I3</td>
<td>6.0 (0.2 - 11.0)</td>
</tr>
<tr>
<td>G1</td>
<td>2.9 (0.3 - 6.2)</td>
</tr>
<tr>
<td>G2</td>
<td>4.0 (0.1 - 8.1)</td>
</tr>
<tr>
<td>G3</td>
<td>5.4 (0.5 - 9.4)</td>
</tr>
</tbody>
</table>

Environmental variables of sampling sites are summarized in Table 5.2. Average substrate size was greatest in the main channel (10.3 - 11.7 cm), intermediate in intermittently-connected channels (8.3 - 9.2 cm), and lowest in groundwater channels (5.7 - 7.4 cm). Substrate heterogeneity, water depth, and near-bed velocity generally decreased from the main channel towards ground water channels. Benthic organic matter (CBOM and FBOM) showed the reverse trend. Specific conductance and turbidity were inversely related; whereas specific conductance generally increased from the main channel towards groundwater channels, turbidity showed an opposite pattern. In addition to this spatial variation, these 2 parameters showed temporal differences. Turbidity was highest in August due to maximum glacier melting, whereas
Table 5.2: General characteristics of the sampling sites. Measures expressed as means, stand.-

<table>
<thead>
<tr>
<th>Site</th>
<th>Substrate</th>
<th>Substrate size (cm)</th>
<th>Heterogeneity</th>
<th>Water depth (m)</th>
<th>Near-bed velocity (m/s)</th>
<th>CBOM (g/m²)</th>
<th>FBOM (g/m²)</th>
<th>Specific conductance (µS/cm)</th>
<th>Turbidity (NTU)</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1</td>
<td>Mean</td>
<td>47</td>
<td>53.1</td>
<td>0.01</td>
<td>0.045</td>
<td>0.54</td>
<td>55.8</td>
<td>35.7</td>
<td>101</td>
</tr>
<tr>
<td>M2</td>
<td>Mean</td>
<td>43</td>
<td>51.3</td>
<td>0.01</td>
<td>0.45</td>
<td>0.50</td>
<td>59.2</td>
<td>34.8</td>
<td>101</td>
</tr>
<tr>
<td>M3</td>
<td>Mean</td>
<td>41</td>
<td>51.7</td>
<td>0.01</td>
<td>0.40</td>
<td>0.54</td>
<td>59.0</td>
<td>35.7</td>
<td>101</td>
</tr>
<tr>
<td>M4</td>
<td>Mean</td>
<td>41</td>
<td>51.1</td>
<td>0.01</td>
<td>0.40</td>
<td>0.54</td>
<td>55.8</td>
<td>35.7</td>
<td>101</td>
</tr>
<tr>
<td>M5</td>
<td>Mean</td>
<td>41</td>
<td>51.3</td>
<td>0.01</td>
<td>0.40</td>
<td>0.54</td>
<td>55.8</td>
<td>35.7</td>
<td>101</td>
</tr>
<tr>
<td>M6</td>
<td>Mean</td>
<td>41</td>
<td>51.3</td>
<td>0.01</td>
<td>0.40</td>
<td>0.54</td>
<td>55.8</td>
<td>35.7</td>
<td>101</td>
</tr>
<tr>
<td>M7</td>
<td>Mean</td>
<td>41</td>
<td>51.3</td>
<td>0.01</td>
<td>0.40</td>
<td>0.54</td>
<td>55.8</td>
<td>35.7</td>
<td>101</td>
</tr>
<tr>
<td>M8</td>
<td>Mean</td>
<td>41</td>
<td>51.3</td>
<td>0.01</td>
<td>0.40</td>
<td>0.54</td>
<td>55.8</td>
<td>35.7</td>
<td>101</td>
</tr>
<tr>
<td>M9</td>
<td>Mean</td>
<td>41</td>
<td>51.3</td>
<td>0.01</td>
<td>0.40</td>
<td>0.54</td>
<td>55.8</td>
<td>35.7</td>
<td>101</td>
</tr>
<tr>
<td>M10</td>
<td>Mean</td>
<td>41</td>
<td>51.3</td>
<td>0.01</td>
<td>0.40</td>
<td>0.54</td>
<td>55.8</td>
<td>35.7</td>
<td>101</td>
</tr>
</tbody>
</table>

*Note: except substrate size (n = 100).*

Table 5.2: General characteristics of the sampling sites. Measures expressed as means, stand.-

It was minimal in early spring and winter; in contrast, specific conductance reached.

Seasonal variation in zoobenthos across habitat gradients.
**Habitat heterogeneity and stability**

Total inundated channel length was used as a measure of spatial heterogeneity of channels in the glacial flood plain of Val Roseg. Values increased from April (12.4 km) to June (22.5 km), peaked in August (23.9 km), then decreased in October (20.6 km), and reached a minimum in December (11.1 km). The observed pattern paralleled seasonal variations in discharge and changes in water sources and flow pathways (Malard et al., 1999).

The multivariate instability score revealed that habitat stability increased from the main channel sites towards the groundwater sites (Fig. 5.3). Both main channel and intermittently-connected sites exhibited a lower within channel type variability (ranges 0.55, respectively, 0.46), compared to groundwater sites (range 0.81). Overall, the main channel sites were clearly separated, whereas the 2 other habitat types showed some overlap. Site I3 had a stability comparable to an average groundwater channel, whereas site G2 resembled more an intermittently-connected channel with regard to its stability.

![Multivariate instability score](image)

Fig. 5.3: Multivariate instability scores of sampling sites, based on axis 1 of a non-centered PCA. Higher values indicate a lower overall stability.

**Macroinvertebrates**

Average total densities of macroinvertebrates generally increased from main channel sites towards groundwater sites (Table 5.3). However, similar to the multivariate instability score, total densities at site I3 were closer to the groundwater channel type (i.e., G3), whereas total densities at site I2 were in the range of those found at M1 and M2. Site G3 clearly exhibited the lowest fluctuations (CV = 18%), in accordance with the highest stability reported at this site. Furthermore, total densities were markedly higher at sites in the lower part of the flood plain (M3, I3, and G3), compared to those further upstream. Low coefficients of variation at these 3 sites (18% at G3, 51% at I3, and 58% at M3) were also indicative of more stable communities. Main channel sites had low densities during high discharge in August and high densities in spring and late autumn/winter (Figs. 5.4 and 5.5). In contrast, total densities in groundwater channel sites were not reduced in summer, and intermittently-connected sites also sustained much higher densities at high flow conditions than main channel sites (Figs. 5.4 and 5.5). Two-way ANOVA for all sites and
3 dates (June, August and October) revealed significant differences among sites ($F_{7,48} = 22.9, p < 0.001$), dates ($F_{2,48} = 14.6, p < 0.001$) and the interaction term ($F_{14,48} = 14.7, p < 0.001$), confirming the trends described above when considering all 5 sampling dates. Subsequent pairwise comparisons (Tukey's HSD, $\alpha = 0.05$) can be summarized as follows: Site M1 was significantly different from all other sites; sites M2 and M3 were not different from each other, but were different from intermittently-connected and groundwater channel sites; and sites G3 and I3 showed no significant differences, but site G3 was different from the other groundwater channel sites and site I2.

Taxon richness and Simpson's index exhibited similar patterns to total densities. Both measures increased from the main channel towards groundwater channel sites. Similarly, this pattern also was modified by a within channel type increase of the respective values, indicating that site G3 in the lower part of the flood plain was most stable. Two-way ANOVAS also revealed significant effects for sites ($F_{7,48} = 20.1, p < 0.001$ for taxon richness; $F_{7,48} = 46.0, p < 0.001$ for Simpson's index), dates ($F_{2,48} = 16.7, p < 0.001$ for taxon richness; $F_{2,48} = 49.8, p < 0.001$ for Simpson's index), and for the interaction term ($F_{14,48} = 2.7, p < 0.01$ for taxon richness; $F_{14,48} = 11.2, p < 0.001$ for Simpson's index). Subsequent Tukey's HSD ($\alpha = 0.05$) showed similar, but less distinctive patterns than described for total densities.

Total densities in the main channel showed an inverse relationship to total channel length (Fig. 5.4); i.e., markedly decreased densities during summer high flow conditions when total channel length peaked. In contrast, intermittently-connected and groundwater channels exhibited the reversed pattern. Both channel types sustained much higher densities in August than reported for the main channel. The absolute minimum in total density in the intermittently-connected channels in December was related to the fact that site I3 lacked surface flow, and I2 was almost dry because it became disconnected from the main channel at its upstream end due to low flow conditions.

Temporal faunal changes for individual sites are shown in Fig. 5.5. Ephemeroptera, Plecoptera and Chironomidae dominated the macroinvertebrate assemblages at the main channel sites with combined contributions between 73 to 99% of total zoobenthos. Ephemeroptera and Plecoptera markedly increased in relative abundance at main channel sites in the flood plain (M2 and M3) in October and December, whereas Chironomidae declined. Site M1 showed no such pattern with Chironomidae being the dominant taxon at all sampling dates. At site I2, the relative abundance of Chironomidae also decreased in October and December, but primarily at the expense of non-Insecta. In contrast, Oligochaeta, Nematoda and Crustacea were predominant at site I3, except in December when Ephemeroptera dominated. The faunal composition of site G3 was markedly different than the other groundwater sites. Site G3 was dominated by Oligochaeta, Nematoda and Crustacea, whereas G2 resembled I2, and G1 showed an intermediate pattern between the main channel and intermittently-connected channels.
Table 5.3: Means, standard deviations (SD), and coefficients of variation (CV in %) for macroinvertebrate densities, taxon richness, and Simpson's index.

<table>
<thead>
<tr>
<th>Site</th>
<th>Density (ind./m²)</th>
<th>Taxon richness</th>
<th>Simpson's index</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1</td>
<td>Mean 6966</td>
<td>8</td>
<td>0.33</td>
</tr>
<tr>
<td></td>
<td>SD 7177</td>
<td>2</td>
<td>0.23</td>
</tr>
<tr>
<td></td>
<td>CV (%) 103</td>
<td>26</td>
<td>72</td>
</tr>
<tr>
<td>M2</td>
<td>Mean 6309</td>
<td>14</td>
<td>0.79</td>
</tr>
<tr>
<td></td>
<td>SD 5214</td>
<td>3</td>
<td>0.44</td>
</tr>
<tr>
<td></td>
<td>CV (%) 83</td>
<td>25</td>
<td>55</td>
</tr>
<tr>
<td>M3</td>
<td>Mean 10057</td>
<td>19</td>
<td>0.86</td>
</tr>
<tr>
<td></td>
<td>SD 5785</td>
<td>4</td>
<td>0.52</td>
</tr>
<tr>
<td></td>
<td>CV (%) 58</td>
<td>23</td>
<td>60</td>
</tr>
<tr>
<td>I2</td>
<td>Mean 7227</td>
<td>10</td>
<td>0.55</td>
</tr>
<tr>
<td></td>
<td>SD 7289</td>
<td>5</td>
<td>0.60</td>
</tr>
<tr>
<td></td>
<td>CV (%) 101</td>
<td>49</td>
<td>110</td>
</tr>
<tr>
<td>I3</td>
<td>Mean 16824</td>
<td>21</td>
<td>1.22</td>
</tr>
<tr>
<td></td>
<td>SD 8545</td>
<td>2</td>
<td>0.24</td>
</tr>
<tr>
<td></td>
<td>CV (%) 51</td>
<td>11</td>
<td>19</td>
</tr>
<tr>
<td>G1</td>
<td>Mean 11938</td>
<td>16</td>
<td>0.84</td>
</tr>
<tr>
<td></td>
<td>SD 12788</td>
<td>1</td>
<td>0.62</td>
</tr>
<tr>
<td></td>
<td>CV (%) 107</td>
<td>8</td>
<td>74</td>
</tr>
<tr>
<td>G2</td>
<td>Mean 10214</td>
<td>13</td>
<td>0.56</td>
</tr>
<tr>
<td></td>
<td>SD 10027</td>
<td>2</td>
<td>0.40</td>
</tr>
<tr>
<td></td>
<td>CV (%) 98</td>
<td>16</td>
<td>72</td>
</tr>
<tr>
<td>G3</td>
<td>Mean 21557</td>
<td>20</td>
<td>1.67</td>
</tr>
<tr>
<td></td>
<td>SD 3952</td>
<td>2</td>
<td>0.14</td>
</tr>
<tr>
<td></td>
<td>CV (%) 18</td>
<td>9</td>
<td>9</td>
</tr>
</tbody>
</table>
Seasonal variation in zoobenthos across habitat gradients

Fig. 5.4: Relationship between total length of all channels in the flood plain of Val Roseg and total zoobenthic densities in the 3 channel types. Total densities represent averages per channel type for each sampling date.

Multivariate relationships among channel types

The between-site principal components analysis (PCA) accounted for 58% of the total inertia (Fig. 5.6). Factor F1 was best explained by Ostracoda, Harpacticoida, Nematoda, Oligochaeta and Nemoura spp., whereas factor F2 was primarily related to Rhithrogena spp., Baetis spp. and Protonemura spp. (Fig. 5.6a). Overall, taxa were arranged along a krenal to kryal/glacio-rhithral gradient (arrow in Fig. 5.6a). Sites G3, I3 and G2 were clearly separated, whereas groups formed by M1 and I2, and M2, M3 and G1, respectively, partially overlapped (Fig. 5.6b). Groundwater sites displayed the least differences in community structure over time as suggested by the low dispersion of sampling dates (short bar lengths) around the centroid of each sampling site. In contrast, the other 2 channel types exhibited greater seasonality as indicated by the longer bar lengths.

Furthermore, sites within individual channel types were separated as a function of distance from the glacier terminus. This separation was primarily attributed to factor F1 for intermittently-connected channels and groundwater channels, and to factor F2 for the main channel. These findings indicate that longitudinal changes in community structure of the former 2 channel types were attributable to changes in the ratio of Chironomidae to non-insect taxa, and in the main channel to changes in the ratio of Chironomidae to Ephemeroptera and Plecoptera.
Table 5.5: Temporal changes in percent composition of zoobenthos at individual sampling sites. Bars are averages of 3 replicate samples at a particular site and date. Numbers on top of bars represent average total densities (ind./m²). No sample indicates either that the site lacked surface flow at this date (I2 and I3), or that flow was too low to take benthic samples using a Hess sampler (G1).

The within-date PCA accounted for 85% of the total inertia (Fig. 5.7). Taxa contributing most to factor F1 were Ostracoda, Harpacticoida, Nematoda, Oligochaeta and Nemoura spp., whereas Rhithrogena spp., Baetis spp. Leuctra spp.
and *Protonemura* spp. were most important for factor F2. The arrangement of taxa displayed a similar gradient (arrow in Fig. 5.7a) as in the between-site PCA. Pronounced differences were found among dates (Fig. 5.7b). Sites G3 and I3 formed a group from April to June, whereas I3 was markedly different from G3 in October. The remaining sites formed 2 groups in April and June, merged together in August, and then returned to a more individualistic pattern. Positions of site G3 were most constant on the factorial plane, whereas the other sites moved more, indicating stronger differences in community structure among dates. For example, I3 was no longer similar to G3 in October, which was attributable to a reduction in crustacean densities from about 3800 ind./m² to about 100 ind./m² and an increase of *Ephemeroptera* from about 100 ind./m² to almost 18,000 ind./m². Overall, spatial variability decreased with increasing discharge, and increased again with decreasing discharge.

Fig. 5.6: Ordination plot of the between-site principal components analysis. Factors F1 and F2 explained 66.5%, and 14.7% of the total variance. (a) F1xF2 correlation plot of the 23 macroinvertebrate taxa used in the analysis. The grey arrow indicates a krenal to kryal/glacio-rhithral gradient. (b) F1xF2 factorial map of sites based on their zoobenthic assemblages. Circles represent center of classes for sampling sites. The small black squares indicate the position of sites on each sampling date. Abbreviations of taxa: Cre = *Crenobia alpina*, Nmt = Nematoda, Oli = Oligochaeta, Hyd = Hydrachnellae, Ost = Ostracoda, Har = Harpacticoida, *Ephemeroptera*: Bae = *Baetis* spp., Rhi = *Rhithrogena* spp., Plecoptera: Rha = *Rhabdiopterix alpina*, Nem = *Nerioura* spp., Pro = *Protonemura* spp., Leu = *Leuctra* spp., Cap = *Capnia* spp., Iso = *Isoperla* spp., Per = *Perides intricata*, *Trichoptera*: Lim = Limnephilidae, Diptera: Wied = *Wiedemannia* spp., Dic = *Dicranota* spp., Rhy = *Rhypholophus* spp., Sim = *Simulium* spp., Prs = *Prosimulium* spp., Chi = *Chironomidae*, Cer = *Ceratopogonidae*. 
Fig. 5.7: Ordination plot of the within-date principal components analysis. Factors F1 and F2 explained 46.5%, and 18.7% of the total variance. (a) F1xF2 correlation plot of the 23 macroinvertebrate taxa used in the analysis. The grey arrow indicates a krenal to kryal/glacio-rhithral gradient. (b) F1xF2 factorial maps for the 5 sampling dates based on their zoobenthic assemblages. For abbreviations of taxa see legend of Fig. 5.6.
5.5 Discussion

Downstream faunal changes are expected to be more distinctive in kryal stream segments than in krenal or rhithral biotopes (Ward et al., 1998). However, recent and former glacial activities in glacier-fed stream systems lead to the development of flood plains with different habitat (channel) types with different degrees of permanency and connectivity (Tockner et al., 1997; Ward et al. 1999). As a consequence, longitudinal distribution patterns of lotic zoobenthos are subject to modifications in floodplain sections. However, few data are available about the ecology of glacial flood plains and virtually nothing is known regarding distribution patterns of benthic macroinvertebrates in such systems. Therefore, investigations in the glacial flood plain of Val Roseg were carried out to enhance our fragmentary knowledge. First, it was a necessary prerequisite to assess temporal changes in the spatial habitat heterogeneity and to determine the stability of channel types and individual sampling sites. Then, specific hypotheses about benthic macroinvertebrate community structure in different channel types with regard to habitat stability and spatial heterogeneity were investigated.

Connectivity and water sources

Turbidity and specific conductance were used as indicators of hydrological connectivity and water source (Malard et al., 1999). These 2 parameters showed an inverse relationship with respect to both space and time. Considering the temporal aspect, turbidity peaked during high discharge in summer when glacial meltwater was the main source of water and decreased with receding discharge towards winter. In contrast, specific conductance was highest in winter, indicating ground water was the dominant source of water at this period of the year. Additionally, these 2 parameters also displayed a spatial pattern. Turbidity decreased and specific conductance increased from main channel sites to groundwater sites. Intermittently-connected channels exhibited conditions similar to the main channel at elevated flow conditions, when their upstream ends were connected to the main channel. In contrast, at low flow conditions they were disconnected at their upstream ends and primarily fed by ground water. Groundwater channels never received glacial meltwater, even at high discharge, because they do not have an upstream connection with the main channel. Overall, the glacial flood plain of Val Roseg shifts from a glacial meltwater dominated system in summer to a groundwater controlled system in winter (Tockner et al., 1997; Ward et al., 1999; Malard et al., 1999). As a result, favourable environmental conditions in the main channel only occur in spring and late autumn/early winter. Burgherr & Ward (in press) demonstrated that macroinvertebrate densities and taxon richness also reach their maxima during these periods. In contrast, groundwater channels are not markedly affected by these changes in glacial influence, therefore providing more constant and less harsh environments.
**Spatial habitat heterogeneity and habitat stability**

Seasonal changes in discharge control the expansion and contraction cycle of the channel network in the glacial flood plain of Val Roseg (Malard *et al.*, 1999). This affects the seasonal fragmentation and reconnection of habitats, a poorly studied attribute of stream ecosystems (Stanley *et al.*, 1997). Therefore, total channel length of the channel network in the glacial flood plain was used as an indicator of spatial habitat heterogeneity. Highest spatial heterogeneity was observed during high discharge in summer, whereas it was reduced at low flows. However, spatial heterogeneity also can decrease at extremely high discharge because channels merge and become more similar in their physico-chemical conditions (Tockner *et al.*, 1997). Consequently, spatial habitat heterogeneity is expected to ameliorate the negative effects of diel summer flow fluctuations by providing important refugia for benthic macroinvertebrates (Tockner *et al.*, 1997; Ward *et al.*, 1998). However, the flood plain shifted from a glacial-meltwater dominated system in summer to a groundwater-dominated system in autumn and winter (Malard *et al.*, 1999; Ward *et al.*, 1999). Concomitant with a decrease in total channel length and more homogenous physico-chemical conditions, the main channel progressively disappeared into the alluvium at the upper end of the flood plain and surface flow was almost totally restricted to the downstream end of the flood plain (below site M2) (Ward *et al.*, 1999). The permanency in flow, groundwater-like environmental conditions, and accrual of benthic algae in this section of the main channel during winter provided a potential refugia for species having an univoltine winter life cycle, such as *B. alpinus*. The fact that *B. alpinus* density peaked in late winter (25,790 ind./m² in February 97) supports this notion and is in accordance with the findings in other studies (e.g., Brittain, 1982; Kukula, 1997).

Habitat stability of different channel types and individual channels within a particular type was assessed by means of a multivariate instability score. Generally, a reduction in habitat stability from the main channel towards groundwater channels was observed. Additionally, groundwater channel sites examined in this study were individually stable, but collectively encompassed a greater spatial heterogeneity than the less stable main channel and intermittently-connected channel sites. This is in accordance with Tockner *et al.* (1997) and Ward *et al.* (1998).

**Macroinvertebrate community patterns**

The hypotheses that distinct channel types have distinct zoobenthic communities, and that more stable habitats have the lowest fluctuations in community structure and the highest levels of species diversity (i.e., taxon richness) generally applied, although some site specific deviations were found. On average, total densities, taxon richness, and Simpson’s index increased from main channel through intermittently-connected channels to groundwater channel sites. For example, Craig & McCart
Seasonal variation in zoobenthos across habitat gradients

(1975), Kownacki (1991) and Füreder et al. (1998) reported higher invertebrate densities and species numbers in streams dominated by ground water. Therefore, Craig & McCart (1975) described spring-fed rivers as the „green oasis in the polar environment“. However, among channel patterns in the Val Roseg were modified by temporal aspects and within channel differences.

Lotic zoobenthos of main channel sites was strongly influenced by temporal shifts in glacial influence (i.e., changes in water sources and flow paths), as well as by a decrease in glacial influence with increasing distance from the glacier, which is in accordance with the findings of Burgherr & Ward (in press). For example, total densities were markedly reduced during summer high flows and maximal glacial melting. Furthermore, Chironomidae constituted the dominant faunal group, except in late autumn/early winter and to a lesser extent in spring when Ephemeroptera and Plecoptera also made substantial contributions. In contrast to the conceptual model of Milner & Petts (1994), both groups occurred at lower maximum water temperatures than the 4°C threshold assumed in the model. By moving within the substrate, benthic invertebrates can markedly alter the thermal regime to which they are exposed because of the steep temperature gradient within the alluvium of Val Roseg (Malard et al., in press, a). Therefore, the presence of Ephemeroptera and Plecoptera in the metakryal zone close to the glacier may be linked to the particular thermal regime of the hyporheic water. In summary, the generally low habitat stability of the main channel results in a characteristic array of species and also restricts greater densities with more taxa to limited periods of favourable environmental conditions. Additionally, differences along spatial and temporal gradients were related to habitat stability (i.e., channel stability sensu Milner & Petts (1994)). Stability was closely related to the hydrograph of the Roseg River. Moving bed sediments reduced channel stability from June to August. During the remaining time of the year discharge did not exceed the threshold of 8 m³/s, indicating channel stability was higher (Burgherr & Ward, in press).

The 2 intermittently-connected channels exhibited distinctively different patterns. Site I2 was more similar to the main channel, whereas I3 was more related to G3, as can be seen from biotic metrics such as total densities, taxon richness, and Simpson’s index, as well as from the results of the PCAs. The temporary surface connection (June to October) of site I2 at its upstream end to the main channel clearly affected benthic community structure. Although Chironomidae dominated during high flow conditions, as observed for the main channel, total densities remained much higher than in the main channel (2 to 30x). From October to December total densities showed a drastic decline to less than 200 ind./m², which is most likely attributable to the lost connection to the main channel. As a consequence the channel became partly dry and site I2 was isolated from the remaining channel network. In contrast, site I3 was only marginally influenced by the main channel because of upwelling ground water throughout the year, except in September and October (F. Malard, pers. communication), that was reflected in seasonal changes in macroinvertebrate structure. For example, Crustacea, Oligochaeta and Nematoda
Seasonal variation in zoobenthos across habitat gradients

were important components from April to August as normally expected in groundwater channels. A totally different composition was found in October with Ephemeroptera, and to a lesser extent, Plecoptera and Chironomidae dominating. This change is most likely attributable to the change in the water source. Overall, the degree of connectivity of intermittently-connected channels to the main channel determines the stability of individual channels, hence affecting distribution patterns of macroinvertebrates.

The high within channel type variability in stability observed for groundwater channels also was reflected in benthic community structure. Both, the between-site and the within-date PCA clearly demonstrated that the most stable habitat type also exhibited the lowest fluctuations in community structure. Additionally, average taxon richness combined for all 3 groundwater sites was highest. Furthermore, PCAs and the relative composition of zoobenthos revealed a high within channel type variability as reported above for habitat stability. Site G3 was dominated by permanent aquatic taxa, such as Crustacea, Oligochaeta and Nematoda, that prefer krenal habitats. Glazier (1991) discussed potential reasons (e.g., flow and thermal constancy, absence of thermal cues, etc.) why a non-emergent life style in spring-fed habitats may be advantageous. In contrast, insects were by far the most important constituents of lotic zoobenthos at sites G1 and G2. This discrepancy may be partly attributable to reduced stability and lower temperatures in the proglacial reach, but seems less likely in the upper part of the flood plain. A major reason why permanent aquatic taxa were almost absent in surface zoobenthos at site G2 could be due to the reduced ecological connectivity in the upper part of the flood plain that resulted in a lack of surface water-groundwater interactions, strongly affecting the occurrence of taxa related to the hyporheos (Malard et al., in press, b). Additionally, site G2 changed its nature from a true groundwater channel to an intermittently-connected channel due to a newly established connection to the main channel on 15 August 1997 (F. Malard, pers. communication). In conclusion, the high within channel variability in benthic assemblages was not exclusively attributable to habitat stability.

**Spatial heterogeneity and biodiversity**

The present study yielded some evidence for the hypothesis that the mosaic of channel types enhances biodiversity (i.e., taxon richness) of this glacial flood plain. On average, Simpson's index was higher in intermittently-connected channels and in groundwater channels, suggesting these habitats substantially contribute to an overall increase in biodiversity at the floodplain scale. However, at least 2 key factors are responsible for sustaining a greater taxon richness at the level of the whole flood plain than in particular channel types or individual channels.

First, a variety of taxa had their distributional optima in intermittently-connected and groundwater channels or were totally absent from the main channel. For example, *Baetis rhodani* and *Simulium cryophilum* did not occur in the main chan-
nel. Oligochaeta, as a representative of the permanent aquatic taxa, also showed pronounced differences between the main channel and groundwater channels; not only in densities, but also in species composition, since several species were not found in the main channel, but did occur in groundwater-fed habitats (compare Klein & Tockner, in press; Malard et al., in press, b).

Second, the high spatial habitat heterogeneity provides an increased number of potential refugia for macroinvertebrates (Sedell et al., 1990; Scarsbrook & Townsend, 1993; Townsend & Hildrew, 1994), thus is expected to ameliorate the negative effects of high discharge in summer associated with diel flow fluctuations and increased channel instability in the Val Roseg flood plain. The relationship between total channel length and total macroinvertebrate densities for individual channel types suggested that groundwater channels and intermittently-connected channels may serve as important refugia during high discharge in summer, thus also providing a potential recolonization pathway (besides the hyporheos and ovipositing by winged adults) for the main channel where environmental conditions are too extreme during high discharge in summer. Our results were consistent with the hypothesis that stream invertebrates accumulate in refugia during high flow conditions (e.g., Lancaster, 2000).

Conclusions

In conclusion, habitat stability in concert with spatio-temporal habitat heterogeneity and connectivity appeared to be the primary structuring agents influencing the habitat templet for the benthic communities of different channel types, as well as individual channels, in the glacial flood plain of Val Roseg. Furthermore, alpine stream ecosystems are extreme environments located on the declining limb of a harshness-diversity curve (Tockner et al., 1997). Consequently, habitats with the highest stability (e.g., groundwater channels) exhibited low variability in community structure, and high taxon richness. Finally, our investigations demonstrated that the complex channel network patterns in the Val Roseg flood plain enhance overall ecosystem stability and biodiversity by providing numerous important refugia for benthic macroinvertebrates, which is not the case for glacial streams lacking floodplain sections.
5.6 Acknowledgements

We are especially indebted to Drs. U. Uehlinger and F. Malard for providing unpublished temperature data, and Mr. R. Illi and Mr. B. Ribi for analysing chemical samples. We also wish to thank our colleagues from the Val Roseg Project for the excellent collaboration. We are grateful to the villages of Pontresina and Samedan for providing access to the study area, and to Mr. P. Testa and his crew at the Roseg Hotel for their hospitality. Special thanks to Dr. J. Brittain for his valuable critiques that improved the manuscript.

5.7 References


Chapter 6

Genetic structure and feeding plasticity of
*Acrophy/ax zerberus* (Trichoptera: Limnephilidae)
in a Swiss alpine flood plain

Abstract

Alpine glacial flood plains comprise a variety of stream types that have distinct habitat conditions and food resources. These different stream types form a complex mosaic in a harsh landscape that constrains dispersal and influences other life history traits of aquatic macroinvertebrates. We examined the genetic structure, energy flow, and food preferences of a freshwater caddisfly (*Limnephilidae, Acrophy/ax zerberus* Brauer) from 3 spatially-separated stream types (lake outlet, proglacial spring, and a side-slope springbrook) in a glacial flood plain in the Swiss Alps. Allozyme electrophoresis indicated high levels of heterozygosity for each *A. zerberus* population, conforming with population genetic models for species living in spatio-temporally heterogenous environments. Allozyme results suggest that there was little migration of *A. zerberus* populations among sites in the current generation. Dispersal by flying adults appears to be the most likely mechanism in this glacial flood plain. Signatures from multiple stable isotope analysis (\(^{13}\text{C}, {^{15}\text{N}}\)) indicated animals fed on the predominant food resources at a site. Results of food preference experiments also were indicative of a generalist feeding strategy by *A. zerberus*. Feeding plasticity plays an important role in the successful dispersal and persistence of this patchily distributed species among different stream types in a glacial floodplain mosaic.
6.1 Introduction

Southwood (1977; 1988) posited that habitat provides the template from which evolution forges characteristic life history traits. Based on Southwood’s theoretical work, several templates for running-water habitats have been developed to link organism response to habitat heterogeneity, stability, and productivity (Stanford & Ward, 1983; Hildrew & Townsend, 1987; Poff & Ward, 1990; Townsend & Hildrew, 1994). Multi-scale models that integrate habitat filters and species traits have been proposed to enhance our understanding and predictive power of population distribution and community organisation in freshwater environments (e.g., Tonn et al., 1990; Poff, 1997). Habitat heterogeneity, in concert with connectivity, has been shown to affect a variety of biological attributes of a population, such as population size (Lande & Barrowclough, 1987), migration rates (Stamps et al., 1987), and extinction rates (Gilpin & Hanski, 1991). For example, habitat patchiness via fragmentation often coincides with habitat isolation and loss, and thus could potentially affect the spatial dynamics and persistence of populations (reviewed by Saunders et al., 1991).

Patchiness, at most spatial scales, is a characteristic feature of the distribution of most species (Levin, 1994; Wiens, 1997). Hanski (1999) suggests that spatial patchiness is not synonymous with metapopulation structure because the former refers to patterns rather than processes; e.g., similar spatial patterns can be caused by different processes. Furthermore, the metapopulation approach emphasizes discrete habitat patches that are large enough to support local breeding populations, whereas spatial patchiness also can occur within local populations of a metapopulation (Hanski, 1999). Nevertheless, spatial patchiness and the metapopulation approach complement rather than conflict with each other (Kareiva, 1990).

Streams of alpine glacial flood plains are considered harsh environments; the physical habitat template of which includes extreme thermal conditions, severe habitat expansion/contraction cycles, and sparse food resources (Milner & Petts, 1994; Ward, 1994; Malard et al., 1999). In addition, alpine stream networks are fragmented landscapes because they comprise a complex mosaic of stream types having distinct habitat conditions (Ward, 1994; McGregor et al., 1995; Tockner et al., 1997). The habitat mosaic of alpine floodplain landscapes strongly influences the distribution and dispersal of lotic invertebrates. Stream types with suitable conditions for a particular taxon are often patchily arranged in space or temporally limited in availability (sensu Hanski, 1998). Consequently, macroinvertebrate assemblages within a given stream type usually are quite distinct with populations exhibiting patchy distribution patterns (P. Burgherr, unpublished data).

Even in heterogeneous landscapes, however, few populations are truly isolated. Most species are spatially partitioned as local populations that are connected by dispersal. For many species, populations also are distributed among various habitats of different quality (Pulliam & Dunning, 1997; Diffendorfer, 1998). Although running water invertebrates generally are considered to show a high degree of popu-
cation connectivity (Mackay, 1992), the unidirectional flow of water and the hierarchi-
chal structure of stream channel networks limit within-stream movement (Meffe &
Vrijenhoek, 1988). Further, the presence of natural (e.g., cascades, waterfalls) and
anthropogenic (e.g., weirs, impoundments) barriers effectively reduce dispersal
of many aquatic organisms.

Dispersal also can be restricted by life history attributes, and behavioral or
morphological traits such as through differences in mating strategies, physical habi-
tat preferences, or specificity in diet. Stream insects disperse by adult flight, down-
stream drift, and swimming or crawling of larvae (Mackay, 1992). While swimming
and crawling typically are restricted to small spatial scales for most taxa, adult flight
and larval drift are major mechanisms of dispersal at larger spatial scales (Minshall &
Petersen, 1985; Mackay, 1992). In contrast to terrestrial species, however, the adults
of stream insects are typically short-lived with limited powers of flight (Ward, 1992).

Direct measurements of dispersal distances are often difficult and have been
reported in only a few studies (e.g., Hershey et al., 1993). However, assessing the
level of genetic differentiation among populations provides a powerful alternative
approach for measuring dispersal. For example, population genetic theory predicts
that high dispersal reduces the genetic differentiation among populations (Hartl 1980).
Conversely, natural selection and random genetic drift are the driving forces for
genetic differentiation among populations under limited dispersal or gene flow
(Slatkin, 1985).

In the present study we examined the genetic population structure and feed-
ing behavior of an aquatic insect to gain an understanding of how this species persists
in an otherwise harsh and fragmented alpine glacial flood plain. We used a limnephilid
caddisfly (Acrophylax zerberus Brauer) that inhabits specific stream types in alpine
glacial flood plains. We focused on populations from 3 spatially distinct lotic habi-
tats in the flood plain in which dispersal among habitat patches is only through adult
flight: a glacial lake outlet, a proglacial spring, and a side-slope tributary. A. zerberus
provided an optimal study organism because it is a common, univoltine limnephilid,
but is constrained to specific stream types in alpine floodplain systems. Consequently,
we posited that successful dispersal, colonization, and persistence of A. zerberus among
these different lotic habitats would require some degree of life history plasticity
(Sterns, 1992). Specifically, 3 inter-related topics pertaining to genetic structure
and feeding behavior were investigated. First, we examined whether the populations
at the 3 sites differed in their genetic structure using allozyme electrophoresis. Ge-
netic analysis allowed inference on the extent of dispersal among sites. Second, we
used multiple stable isotope analyses as a tracer to determine potential sources of
energy sustaining A. zerberus at a particular site. Last, we conducted food preference
experiments in the laboratory to reveal if A. zerberus exhibited site specific feeding
behaviors that reflected the predominant food resources at each site.
6.2 Materials and methods

Study organism

The freshwater caddisfly *A. zerberus* is restricted geographically to the Alps, Pyrenees and Carpathians (Botosaneanu & Malicky, 1978). It mostly inhabits running water habitats, but also has been reported from high alpine lakes (Waringer & Graf, 1995). *A. zerberus* primarily feeds by shredding coarse particulate organic matter, and to a lesser extent by grazing on periphyton and associated material, or preying on other invertebrates (Moog, 1995). Most populations are univoltine. Larval development occurs from about July to October (Szczesny, 1986). Overwintering takes place in the pupal stage (Waringer & Graf, 1995; P. Burgherr, personal observation), and adults emerge in March/April (Malicky, 1980). Winged adults typically are active from March to July (Tobias & Tobias, 1981; C.T. Robinson & P. Burgherr, personal observation). Early emerging adults often have been observed running on snow, and brachyptery (reduced wings) is common in certain populations (Waringer & Graf, 1995), especially at higher altitudes.

Study area

The 11.3 km long Roseg River (Ova da Roseg) is situated in the Bernina Massif of the Swiss Alps (lat 46°29'28" N, long 9°53'57" E). The catchment area is 66.5 km², of which 30% is covered by glaciers and 40% is bare rock or glacial till without vegetative cover. Bedrock consists of granite and diorite. Elevations range from 1760 m a.s.l. (confluence with Bernina River) to 4049 m a.s.l. (Piz Bernina), and treeline is at about 2300 m a.s.l. The Roseg River is fed primarily by meltwater from the Tschiera and Roseg glaciers. Discharge peaks in late summer from glacial melting; diel flow fluctuations also are highest in summer. In winter, the system is largely fed by ground water with surface flow ceasing in many channels (Malard et al., 1999). Subalpine coniferous forests are restricted to side-slopes in the lower area of the valley; no trees occur on the fluvio-glacial gravel of the valley floor. Dominant tree species include larch (*Larix decidua* Mill.), stone pine (*Pinus cembra* L.), and mugo pine (*P. mugo* Turra). Shrubs mainly consist of green alder (*Alnus viridis* (Chaix) DC.) and willow (*Salix* sp.). A more detailed description of the flood plain is given in Tockner et al. (1997).
Study sites

This study examined A. zerberus populations from 3 markedly different stream types in the Val Roseg flood plain: a lake outlet stream ~50 m below Lake Roseg (called „Outlet site“), a proglacial spring below Tschierva Glacier at the base of a glacial moraine („Willow site“), and a side-slope springbrook in the main flood plain („Alder site“) (Fig. 6.1). The Outlet and Willow site were separated by a ~100 m high glacial moraine of the Tschierva glacier. Aerial distance between these 2 sites was approximately 0.6 km. The Alder site was about 1.6 km from the Outlet site and 1.0 km from the Willow site. Because of the spatial arrangement of the sites in the floodplain landscape (e.g., no upstream connection among sites), the only means of dispersal among sites was by adult flight. In addition, the Outlet and Alder site had permanent flow, whereas the Willow site lacked surface water by early September in 1998. Although the Outlet site was fed primarily by glacial meltwater, discharge extremes were ameliorated by the lake. The other 2 streams were fed by ground water.

These sites were selected not only because of their spatial arrangement and differences in flow regime, but also because food resources substantially differed. Differences in quality and quantity of food can be an important constraint on the distribution and abundance of populations (e.g., Becker, 1994; Jacobsen & Friberg, 1995). The filamentous algae Hydrurus foetidus (Kirch.) (Chrysophyceae) and, to a lesser extent, epilithic diatoms were dominate food sources at the Outlet site in spring and late summer/fall. Primary production was suppressed in summer because of high turbidity from glacial flour that reduced light and increased scour. Terrestrial inputs of grass and some willow (Salix sp.) made up potential supplementary food resources. Detritus, willow, and the aquatic moss Fontinalis sp. were predominant food resources at the Willow site; periphyton was negligible. Green alder (Alnus viridis), larch (Larix decidua), and stone pine (Pinus cembra) were the main allochthonous inputs at the Alder site, whereas instream food resources consisted of epilithic algae and moss.

Allozyme electrophoresis

Samples of ~50 last instar larvae of A. zerberus were collected from each site and date, quick-frozen in liquid nitrogen (-80°C), and returned to the laboratory. Collections took place on 24 August 1998 at all sites, and at the Outlet and Alder sites on 16 September 1998 (surface flow had ceased at Willow). In the laboratory, allozyme electrophoresis was completed using cellulose acetate gels (Titan III, Morwell Diagnostics GmbH, Switzerland). Seven polymorphic loci were examined: phosphoglucose isomerase (Pgi), phosphoglucomutase (Pgm), glycerol-3-phosphate dehydrogenase (G3pdh), malic enzyme (Me), aldehyde oxidase (Ao), aconitate
Fig. 6.1. Location of the Val Roseg catchment in the Bernina Massif of the Swiss Alps, and indication of sampling sites, glaciers and forests.
Genetic structure and feeding plasticity of A. zerberus

hydrate (Aeon), and malate dehydrogenase (Mdh). Running conditions and staining procedures were adapted from Hebert & Beaton (1989).

Differences in sample sizes are attributable to natural densities of animals in the field, and exclusion of gels that were difficult to read. Allelic frequencies, observed (H\textsubscript{obs}) and expected (H\textsubscript{exp}) heterozygosities, population heterozygosities, deviations from Hardy-Weinberg equilibrium, and F\textsubscript{ST} values were calculated from the scored loci. Average heterozygosities among sites were compared by one-way analysis of variance (ANOVA). If the ANOVA rejected a multi-sample null hypothesis of equal means (p < 0.05), then pairwise comparisons using Tukey’s Honest Significant Test (HSD) were performed (Zar, 1996). Deviations of observed genotypic frequencies from Hardy-Weinberg equilibrium were examined using exact significance probabilities (Weir, 1996). When a heterozygote excess or deficiency was detected, the more powerful tests recommended by Rousset & Raymond (1995) were used to confirm or reject the respective finding. F\textsubscript{ST} values, a measure of the degree of genetic differentiation among populations, were calculated using the method of Weir & Cockerham (1984) and tested for significance following Waples (1987). All statistics were performed with the program packages BIOSYS-2 (Swofford & Selander, 1989), GENEPOP 1.2 (Raymond & Rousset, 1995) and Statistica 5.1 (Statsoft, 1995).

Multiple stable isotopes

For isotope analysis, 10 specimens of last instar A. zerberus larvae per site were collected and transferred alive to the laboratory. These animals were starved for at least 24 h to evacuate gut contents and frozen. Epilithic algae (mostly diatoms) were brushed from single stones and treated with 1N HCl to remove inorganic carbon. Filamentous algae (Hydrurus foetidus), benthic organic matter ("detritus"), senescent biofilm, and Fontinalis sp. were sampled separately and rinsed thoroughly to remove animals prior to analysis. Samples of terrestrial food resources included grass, needles of Pinus cembra and Larix decidua, and leaves of Alnus viridis and Salix sp. Samples of allochthonous and autochthonous materials present at each site were frozen in the field for transport to the laboratory.

All samples for isotope analysis were dried at 60°C and ground. Subsamples of 0.5 to 1.5 mg (from individual A. zerberus larvae, or 2 to 6 of the other materials) were analyzed for stable isotopes of organic carbon (\(1^{3}\text{C}\)) and nitrogen (\(1^{5}\text{N}\)) using a mass spectrometer coupled in continuous flow with a CE-Instruments NCS2500 following standard methods (Peterson & Fry, 1987). Results are reported in the conventional delta (\(\delta\)) notation as per mil (‰) deviation from isotope standards (Peedee Belemnite limestone (PDB) for \(1^{3}\text{C}/1^{2}\text{C}\) and atmospheric nitrogen for \(1^{5}\text{N}/1^{4}\text{N}\) using the equation:

\[
\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} (\text{‰}) = \left( \frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000
\]

where \(R = 1^{3}\text{C}/1^{2}\text{C}\) or \(1^{5}\text{N}/1^{4}\text{N}\).
The carbon isotope $^{13}$C was used to identify the source of energy. The $\delta^{13}$C of animals directly reflects their diets, with only slight enrichment (ca. 1%o) during the feeding process (DeNiro & Epstein, 1978; Rau et al., 1983). The nitrogen isotope $^{15}$N provides information about feeding and other trophic relationships among animals and plants. $\delta^{15}$N increases 3.4 ± 1.1%o between trophic levels (DeNiro & Epstein, 1981; Minagawa & Wada, 1984). Mean isotopic ratios of A. zerberus were compared among sites by one-way ANOVA, and multiple pairwise comparisons among group means were made using Tukey’s Honest Significant Test (HSD). Prior to analysis, data were log$_{10}$($x+1$) transformed to normalize and stabilize the variance (Zar, 1996).

Food preference experiments

Food preference of A. zerberus larvae was examined by conducting laboratory experiments in August 1998 and September 1998. Between 25 and 30 last instar larvae were collected at each site and transferred alive to the laboratory. Animals from each sampling site were used in the 1st experiment, whereas no specimens from the Willow site were available for the 2nd experiment because it had gone dry. The experiments were performed in an environmental chamber at a constant temperature of 4°C using 5 open transparent PVC cylinders ($d = 19$ cm) as replicate aquaria for each site. Each aquarium contained autoclaved fine gravel and coarse sand as substrata, and were filled with aerated tap water to a depth of 5 cm. Coarse sand was added to provide material for larval case-building. Four plastic petri dishes ($d = 5$ cm), each with a different food type, were evenly distributed in each aquarium.

In the 1st experiment, food types consisted of filaments of Hydrurus foetidus (amount per dish: 3 ml), abscissed needles of larch ($0.26 \pm 0.04$ g dry weight, mean ± 1 SD), circular leaf fragments ($d = 1.5$ cm) of alder ($0.11 \pm 0.01$ g), and whole willow leaves ($0.09 \pm 0.02$ g). In the 2nd experiment, willow was replaced by the moss Fontinalis sp. ($0.18 \pm 0.02$ g). At the beginning of each experiment, 4 larvae were placed in each aquarium ($n = 20$ individuals per site). Larvae that died during the experiment were replaced, but usually fewer than 3 died within any one experiment. The experiments were terminated after 4 and 7 days, respectively, because larvae began to pupate. Observations of larvae were made hourly during „daytime“ (light on, 8:00 - 18:00). Larvae were assigned to a certain food type when they were within a respective plastic dish, otherwise they were categorized as „None“. Counts for the 5 aquaria for each site were pooled and expressed as percentages. Data were arcsin(sqrt($x$)) transformed to ensure normality and homogeneity of variance. Two-way ANOVA (site x food type) followed by Tukey’s Honest Significant Test (HSD) for multiple pairwise comparisons (Zar, 1996) were used to test for significant differences among food types. An analysis of food quality was not performed, as the experiments were designed to reveal only whether larvae displayed site specific food preferences that corresponded to the different food resources found at each site.
6.3 Results

Population genetic structure

Allele frequencies, expected ($H_{exp}$) and observed ($H_{obs}$) heterozygosities, population heterozygosities, sample sizes, and deviations from Hardy-Weinberg expectations, are summarized in Table 6.1. Mean $H_{exp}$ per locus ranged between $0.30 \pm 0.07$ (SE) at the Outlet site, $0.32 \pm 0.07$ (SE) at the Willow site, and $0.36 \pm 0.08$ (SE) at the Alder site; no significant differences were observed among sites ($F_{2,18} = 0.154$, $p = 0.86$). Average $H_{obs}$ also were not significantly different among sites ($F_{2,18} = 0.155$, $p = 0.86$). Deviations from Hardy-Weinberg equilibrium were found for 2 out of 7 polymorphic loci (29%) at the Outlet site, 3 out of 7 (43%) at the Willow site, and 4 out of 6 (67%) at the Alder site. With the exception of Ao at the Outlet site, all deviations indicated a deficiency of heterozygotes (Table 6.1). Specific tests for heterozygote excess or deficiency confirmed the results of the calculated exact probabilities. A jackknife estimate of $F_{ST}$ based on all loci was $0.086 \pm 0.038$ (SD). Significant $F_{ST}$ values were observed for all loci except G3pdb, Ao and Mdh (Table 6.2).

Stable isotope analysis

Stable isotope signatures for A. zerberus larvae and potential food resources collected at each site are presented in Fig. 6.2. Average $\delta^{13}C$ values of A. zerberus were $-24.6\%o$ at the Outlet site, $-29.6\%o$ at the Willow site, and $-27.8\%o$ at the Alder site. Respective averages for $\delta^{15}N$ were $-5.2\%$, $-1.9\%$, and $-2.9\%$. Results of ANOVA indicated that carbon and nitrogen isotopic domains of A. zerberus were significantly different among sites ($\delta^{13}C$: $F_{2,27} = 21.03$, $p < 0.001$; $\delta^{15}N$: $F_{2,27} = 27.27$, $p < 0.001$). Pairwise comparisons revealed significant differences for 2 out of the 3 possible combinations for $\delta^{13}C$ (Tukey’s HSD: Outlet vs. Willow $p < 0.001$; Outlet vs. Alder $p < 0.001$; Alder vs. Willow $p = 0.09$), and all combinations for $\delta^{15}N$ (Tukey’s HSD: Outlet vs. Willow $p < 0.001$; Outlet vs. Alder $p < 0.001$; Alder vs. Willow $p = 0.02$).

At the Outlet site, average $\delta^{13}C$ of A. zerberus was nearest to those of grass and Salix sp., followed by epilithic algae (Fig. 6.2). The low concentrations of allochthonous organic matter at this site (R. Zah, unpublished data) suggest larvae fed mainly on epilithon at the Outlet site. Although $\delta^{15}N$ of A. zerberus were $\sim 3\%$ enriched compared to Hydrurus foetidus, the difference in their $\delta^{13}C$ values suggested that animals apparently avoided it in the presence of other food resources at this site. Detritus and, to a lesser extent, willow and grass were identified as major food resources at the Willow site (Fig. 6.2). At the Alder site, the identification of potential food resources was more difficult because of similar $\delta^{13}C$ signatures for the
Genetic structure and feeding plasticity of A. zerberus

Various foods analyzed. However, larvae seemed most likely to feed on epilithon, *Alnus viridis* and grass, whereas the use of *Pinus cembra* and *Larix decidua* as food resources was less clear (Fig. 6.2).

**Table 6.1**: Allele frequencies, observed and expected heterozygosities, population heterozygosities, sample sizes (n), and deviations from Hardy-Weinberg equilibrium (HWE) using exact probabilities (p = 0.05) of *A. zerberus* larvae. **ex** = excess of heterozygotes, **def** = deficiency of heterozygotes.

<table>
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<th>Allele</th>
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<td>0.302 ± 0.103</td>
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<tr>
<td>Willow</td>
<td>0.232 ± 0.104</td>
</tr>
<tr>
<td>Alder</td>
<td>0.232 ± 0.103</td>
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<tr>
<td></td>
<td>Expected</td>
</tr>
<tr>
<td>Outlet</td>
<td>0.303 ± 0.072</td>
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<tr>
<td>Willow</td>
<td>0.322 ± 0.066</td>
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<tr>
<td>Alder</td>
<td>0.359 ± 0.078</td>
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Table 6.2: $F_{ST}$ values for each locus separately, and over all loci. NS = not significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

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<td>$Pgm$</td>
<td>0.070 ***</td>
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<td>$Me$</td>
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<td>$Ao$</td>
<td>0.033 NS</td>
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<tr>
<td>$Mdh$</td>
<td>0.001 NS</td>
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<tr>
<td>Jackknife estimate over loci</td>
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<tr>
<td>Mean ± 1 SD</td>
<td>0.086 ± 0.038</td>
</tr>
</tbody>
</table>

Food preference experiments

In the 1st laboratory experiment, two-way ANOVA showed significant differences in the relative abundance of *A. zerberus* larvae among food types ($F_{4,420} = 92.8$, $p < 0.001$) and for the site x food type interaction ($F_{8,420} = 3.4$, $p < 0.001$), but not among sites ($F_{2,420} = 0.1$, $p > 0.90$) (Fig. 6.3a). Post-hoc comparisons revealed that the proportion of animals not feeding on any of the offered food types (None) was significantly higher at all sites (Tukey's HSD, $p < 0.05$), whereas no significant differences were found among food types within a site (Tukey's HSD, $p > 0.05$). Individual food types also did not differ significantly among sites (Tukey's HSD, $p > 0.05$). In the 2nd experiment, two-way ANOVA revealed a significant effect for food type ($F_{4,490} = 71.9$, $p < 0.01$), but not for site ($F_{1,590} = 0.0$, $p > 0.99$) or the site x food type interaction ($F_{4,590} = 1.7$, $p = 0.15$). The non-significant interaction term indicates no differences either among food types within sites, or within individual food types among sites (Fig. 6.3b).
Fig. 6.2: Plots of dual isotope ratios for _A. zerberus_ larvae and potential food resources at each site. Isotopic signatures of _A. zerberus_ are given as mean ± 1 SD. Open boxes are terrestrial food resources, and filled boxes are aquatic food resources (mean ± 1 SD).
Fig. 6.3: Proportions of *A. zerberus* larvae feeding on different food resources offered during the first (a) and second (b) food preference experiments. Bars represent mean ± 1 SD. In the second experiment *Salix* sp. was replaced by the moss *Fontinalis* sp.
6.4 Discussion

Allozyme electrophoresis was used to test for significant differences in the genetic structure of *A. zerberus* among populations. The high levels of heterozygosity at all sites could be an indication that *A. zerberus* larvae show some life history plasticity to maintain viable populations in different stream types (Robinson *et al.*, 1992). Predictions from population genetic models also suggest high levels of heterozygosity for species living in spatio-temporally heterogenous environments (Hartl, 1980; Hedrick, 1986). Empirical evidence for such a fact has been reported for fishes (Zimmermann, 1987), zooplankton (Weider, 1992), and lotic macroinvertebrates (Hughes *et al.*, 1999). A high spatio-temporal variability in environmental conditions has been demonstrated for the Val Roseg flood plain (Tockner *et al.*, 1997; Malard *et al.*, 1999), and also that benthic macroinvertebrate communities respond to these changes (Burgherr & Ward, in press, b). The overall $F_{st}$ value indicated the possibility of a moderate genetic differentiation among populations. The observed deviations from Hardy-Weinberg equilibrium were high and differed across loci within each local population. This could be a result of the low sample size for some loci, although it is likely that the specific tests for heterozygote excess and deficiency applied here detected real departures from Hardy-Weinberg equilibrium. Excluding this possibility, several other options remain that have been discussed in Schmidt *et al.* (1995). Following the reasoning of these authors and empirical evidence from other studies (Bunn & Hughes, 1997; Hughes *et al.*, 1998), we assume that larval populations in the 3 habitats are likely the product of only a few matings by successfully dispersing adults. In conclusion, our findings suggest that there has been little migration of *A. zerberus* populations among sites in the current generation. Of the little empirical data available on movement distances of caddisflies, the adult stage appears to be most important. Long-distance flights ranging from 1-4 km (Neves, 1979) to 16 km (Coutant, 1982) have been documented, although limited larval dispersal during periods of low, stable flow have been found (Hart & Resh, 1980; Jackson *et al.*, 1999). For example, Neves (1979) showed that *Pycnopsyche guttifer* (Walker) (Limnephilidae) moved out of pools during low flow conditions. However, the harsh environmental conditions in the main glacial channel (high turbidity and bedload movement), and the lack of upstream connections among sites effectively limit dispersal by larvae in our glacial flood plain.

Brachyptery (flightlessness) of adults is known for some populations of *A. zerberus*, and was observed for individuals at the Outlet site (P. Burgherr, personal observation). Brachyptery in insects is known to increase with altitude and latitude (Roff, 1990), and also can be a function of time since deglaciation (Donald, 1985). Our observations support the notion that brachyptery in insects occurs more commonly in stable environments in which long-term persistence is unlikely to require long-distance dispersal (Roff, 1990). For example, the higher temperatures and more stable habitat conditions of the proglacial lake outlet attenuate the otherwise harsh environmental conditions of other glacial streams (Burgherr & Ward, in press, a).
On the other hand, macropterous individuals can disperse among isolated habitats, and therefore, have an advantage when environments are spatially or temporally heterogenous (Roff, 1994), as found at the temporary Willow site. Because brachypterous females are more fecund than macropterous females (Roff & Fairbairn, 1991), the brachyptery allele can spread quickly throughout a population within a particular habitat patch. If habitats are spatially isolated, as in the present study, the brachyptery allele can be passed among local populations only if a dispersing macropterous female mates with a brachypterous male. As a consequence, a population homozygous for the brachyptery allele is more prone to extinction when environmental conditions become unsuitable (Roff, 1994). In streams of alpine glacial flood plains, the ratio of brachypterous to macropterous individuals in local populations may be a function of habitat stability, and thus influence long-term distribution patterns in population structure.

The analysis of multiple stable isotopes provided information of whether food resources limited the distribution of populations within the study sites, and gave insight towards the plasticity in A. zerberus feeding behavior. Traditionally, studies regarding the diet of aquatic insects was based on gut content analyses (Coffman, 1971), field or laboratory observations of feeding, or radio-isotopes as tracers (Rounick & Winterbourn, 1986). These approaches, however, only yield information on recent ingestion, and give no insight on an organism’s feeding history, trophic status (Gearing, 1991) or food web structure that is provided by stable isotope analysis (Rounick & Winterbourn, 1986; Peterson & Fry, 1987). We also used a site specific perspective in this study (sensu Doucett et al., 1996) to compensate for some of the limitations of stable isotope analysis suggested in literature (France, 1995). Isotope signatures indicated a site-specific, omnivorous feeding mode for larvae of A. zerberus, and furthermore, that larvae were opportunistic feeders. This is an important finding, as it indicates the role of behavioural trade offs in sustaining local populations in potentially sub-optimal habitats or in the (re)colonization of isolated habitat patches (sensu Hanski, 1999). Plasticity in diet/feeding minimizes the potential constraints of food resources on the colonization and maintenance of local populations in otherwise suitable habitats.

This idea was tested further by assessing the feeding behaviour of larvae in food preference experiments. The laboratory experiments confirmed the existence of a generalist feeding strategy by A. zerberus that was independent of the food resources available at a specific site. That is, last instar larvae from the different sites similarly consumed available resources in the experimental situation even though these same larvae (as earlier instars) fed on different resources in the field, as inferred from the isotope analyses. These results provide additional evidence that plasticity in feeding behavior is a key factor for allowing dispersal and colonization into lotic habitats with different food resources (quality or quantity), e.g., forested streams with a predominant allochthonous food supply vs. alpine streams with mostly autochthonous food sources. For example, A. zerberus has been shown to capitalize on high quality food such as introduced leaf litter in an alpine stream (Robinson et al.,
1998), or as demonstrated for other stream macroinvertebrates in studies on resource limitation (Dobson & Hildrew, 1992).

Relationships between the genetic structure and life history traits of A. zerberus were not assessed within the framework of the present study. However, the relatively high genetic diversity within A. zerberus populations in the present study can be associated with the observed plasticity in its life history (as implied from A. zerberus feeding behavior). A number of studies have shown positive correlations between genetic variation (e.g., number of alleles per locus, heterozygosity, and polymorphism) and life history traits (Nevo & Yang, 1979 in the tree frog Hyla arborea savignyi; Mitton & Lewis Jr., 1989 for a variety of organisms), whereas others found no such associations (Whithehurst & Pierce, 1991 in the spotted chorus frog Pseudacris clarkii Baird; Hutchings & Ferguson, 1992 in Salvelinus fontinalis Mitchill). These contrasting findings may reflect interspecific variation in the strength of genetic correlations among life history traits (Hutchings & Ferguson, 1992). Similarly, aquatic invertebrates lacking a terrestrial stage often exhibit rather high levels of genetic differentiation among populations (Hughes et al., 1995 for the prawn Paratya australiensis Kemp), whereas stream insects having an adult winged stage tend to show little genetic differentiation at larger spatial scales (Schmidt et al., 1995; Bunn & Hughes, 1997; but see Hughes et al., 1999). Clearly, more research is needed to address the important interplay between genetic structure, life history, and the habitat template on the maintenance and structure of macroinvertebrate populations in lotic ecosystems.

6.5 Acknowledgements

We are especially grateful to Dr. S.M. Bernasconi of the Geology Institute of ETH Zürich for stable isotope analyses, and T. Dambone-Bösch for electrophoretic analyses. Special thanks to Mr. P. Testa and his crew at the Roseg Hotel for their hospitality, and to the villages of Pontresina and Samedan for providing access to the study area. We appreciate the helpful comments of M.T. Monaghan and J.V. Ward that improved the manuscript. This study was partially funded by a grant from the Swiss National Science Foundation (no. 3100-050444.97/1).
6.6 References


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Chapter 7

Synopsis

7.1 Motivation

Why this thesis, or in a broader context, why research on alpine glacial streams? My motivation for doing this research was twofold. First, alpine streams constitute integral landscape components in high mountainous areas, but the diversity and uniqueness of these ecosystems is threatened. Human impacts (i.e., water resource developments, tourism) will be the greatest sources of environmental change in alpine regions in the coming decades, and effects of global warming are predicted to be more pronounced in these areas than in other parts of the world (Chapin III & Körner, 1994). However, there is little known about patterns of diversity and ecosystem functioning of alpine and arctic streams (e.g., Milner & Petts, 1994; Scrimgeour et al., 1994; Ward, 1994), which leads to my second motive: inadequate scientific understanding of alpine streams. In a review, Ward (1994) concluded that almost all investigations of alpine streams are of (1) limited intensity and duration, and (2) that most data were collected in kryal segments, whereas krenal biotopes have been widely neglected. Based on these facts, the ultimate goal of the present thesis was to contribute to the understanding how spatio-temporal habitat heterogeneity affects distribution patterns of macroinvertebrate communities in an alpine glacial stream ecosystem.

The following sections summarize major findings of my research, and view them in the context of the current state of knowledge. Last, I discuss some crucial points of the thesis.

7.2 Longitudinal patterns

Downstream zonation patterns in glacier-fed streams are most distinct and predictable, reflecting adaptations of the aquatic fauna (Ward, 1994; Füreder, 1999). The predominance of the chironomid *Diamesa* in the metakryal zone close to the glacier has been documented by several researchers (e.g., Saether, 1968; Steffan, 1971; Kownacka & Kownacki, 1972; Kownacki & Kownacka, 1973), and provided the foundation for the conceptual qualitative model of Milner & Petts (1994). They related zoobenthic gradients to temperature and channel stability, as a function of distance from the glacier terminus and time since deglaciation (Fig. 7.1). The findings in this thesis (chapters 3 and 4) yielded only partial support for Milner & Petts’
model (1994). Changes in community structure in the main glacial channel during high flow conditions in summer were in accordance with model predictions. In contrast, the model did not fully account for seasonal changes in assemblage structure. In addition to these temporal variabilities in longitudinal response patterns, a similarity in temporal patterns among individual sites along the longitudinal gradient was observed. Overall, results suggest that zoobenthic gradients are not solely a function of temperature and channel stability. Seasonal shifts in water sources (i.e., balance between glacial meltwater and ground water), and periods of favourable environmental conditions (in spring and late autumn/early winter) also strongly affect zoobenthic distributions. In conclusion, this thesis demonstrated that only comprehensive year-round studies can lead to a better understanding of the spatial and seasonal dynamics in glacier-fed rivers. However, before developing new or modifying existing models, more research is clearly needed to encounter the variability among different types of glacial streams; e.g., streams fed by the extant glaciers in the Colorado Cordillera remain clear all year (Ward, 1994), whereas differences in geology, topography and riparian vegetation among river basins can cause considerable differences within and among geographic regions (e.g., Gislason et al., 1998).

Milner & Petts (1994) also discussed how tributaries, changes in valley confinement, and lakes disrupt downstream patterns. In chapter 2 the influence of the proglacial Lake Roseg was investigated, by comparing macroinvertebrate assemblages between the lake outlet stream and a kryal stream. As predicted by Milner & Petts (1994) the outlet channel differed in numerous abiotic characteristics from the kryal channel; i.e., temperature was higher, a relatively stable single-threaded channel was attained, and the flow regime was attenuated. This reduction in environmental harshness resulted in a more diverse and less fluctuating community structure than in the kryal stream. In other words, a proglacial lake can compress the typical faunal gradient observed in a kryal stream (Fig. 7.1).

### 7.3 Heterogeneity of zoobenthos across habitat gradients

Differences in lotic zoobenthos among different alpine stream types have received little attention (e.g., Kownacki, 1991; Füreder et al., 1998), and hardly anything is known regarding spatial dynamics among streams in glacial flood plains (Tockner et al., 1997). Following the rationale of the intermediate disturbance hypothesis (Connell, 1978) and its adaptation to lotic freshwaters (Ward & Stanford, 1983), alpine flood plains are positioned on the descending limb of the harshness-diversity curve (Fig. 7.2a). Considering seasonal changes in spatial habitat heterogeneity (Tockner et al., 1997; Ward et al., 1998; Malard et al., 1999), a two-dimensional habitat templet can be obtained for the 3 different habitat types compared in chapter 5 (Fig. 7.2b). From this templet, scale-specific predictions about distribution patterns of their benthic communities can be made.
Whole flood plain: High habitat heterogeneity increases overall ecosystem stability by providing numerous refugia (after Tockner et al., 1997).

Among channel types: More stable habitats (i.e., groundwater channels) exhibit the lowest fluctuations in densities and community structure, and highest levels of species diversity (Burgherr & Ward, submitted).

Within channel types: Channel types encompassing a greater spatial heterogeneity (e.g., groundwater channels) (Ward et al., 1999) also show distinct differences in their benthic assemblage structure.

The study on how habitat heterogeneity affected lotic zoobenthos in the Val Roseg flood plain (see chapter 4) supported the above predictions. However, these findings can only be considered as preliminary. Future studies are needed to test these predictions in glacial floodplain systems with different geology and in different geographical regions.

**Fig. 7.1:** Left side: characteristic zonation of macroinvertebrates predicted in a glacial river by the model of Milner & Petts (1994). Right side: modified situation as it was found in the outlet stream of the proglacial Lake Roseg.
Fig. 7.2.: (a) Alpine streams are positioned on the descending limb of the harshness – diversity curve. (b): Within the glacial flood plain, groundwater channels are characterized by a high spatial but low temporal heterogeneity. In contrast, the main channel and intermittently-connected channels exhibit a high temporal but low spatial heterogeneity. The diameter of the ellipses represents within channel type variability.
7.4 Dispersal and life history plasticity

The value of studies analyzing distribution patterns and responses of biotic communities across environmental gradients is essential to determine what underlying processes may control the structure of riverine communities and to generate hypotheses that can be tested experimentally in the field or in the laboratory. Chapters 2 to 5 of this thesis analyzed patterns in macroinvertebrate community structure in respect to longitudinal and habitat gradients, whereas chapter 6 tested specific hypotheses derived from these investigations.

The extreme environmental conditions in alpine glacial streams exert a severe constraint on successful colonization and persistence for many aquatic macroinvertebrate species; indicating the occurrence of a particular species is a direct expression of this species' ability to tolerate or adapt to the thermal regime and other life history traits (Ward, 1992; Füreder, 1999). Specifically, the complex channel network formed by different stream types in the glacial flood plain is expected to constrain dispersal and to influence other life history traits of aquatic macroinvertebrates. This array of questions was examined in chapter 6. Results of this study suggested that dispersal of the limnephilid caddisfly Acrophylax zerberus most likely occurs through flying adults in the glacial flood plain of Val Roseg. Furthermore, results were indicative of a generalist feeding strategy by A. zerberus, suggesting feeding plasticity may be a key factor for the successful dispersal and persistence of this patchily distributed species. Additional evidence that feeding plasticity may be a relatively common feature in macroinvertebrate species inhabiting the glacial flood plain of Val Roseg, was found for Simuliidae (chapter 4), and in a stable isotope study (Zah et al., in press). Clearly, more research is needed to address the important interplay between genetic structure, life history, and the habitat templet on the maintenance and structure of macroinvertebrate populations in harsh environments such as glacial streams. The combination of allozyme electrophoresis or related techniques to examine genetic structure, and of stable isotope analysis and laboratory food preference experiments used here, may provide a promising approach for future studies.

7.5 Critical remarks

Generally, field studies are hampered by the fact that one can never take as many replicate samples as one would like, and the need to avoid pseudoreplication (e.g., Hurlbert, 1984; Hairston, 1989; Scheiner & Gurevitch, 1993). Some preliminary analyses revealed no significant reduction in sample variability if the number of replicate Hess samples was increased from 3 to 5. Samples were generally taken in riffle/run habitats to make samples more comparable. The use of 3 replicates also allowed a higher number of sampling sites to be more intensively investigated. A
further limiting factor was the use of 100 µm mesh size, instead of the usual 200 µm or more, which substantially increased sample processing time. In total, 145,196 macroinvertebrates were sorted, enumerated and identified. However, it was worth the effort. First, many studies in alpine glacial streams underestimated total densities because coarser mesh sizes were used. Second, most Nematoda, Harpacticoida and Ostracoda that constitute major components of the benthic communities in groundwater channel habitats would have been missed.

Multivariate statistical techniques comprise a thread through the data analyses in this thesis. These methods provide an invaluable tool for the joint analysis of faunal-environmental relationships. The literature on this topic is tremendous, but for example Doledec & Chessel (1991), ter Braak & Verdonschot (1995), and Blanc (2000) provide excellent overviews of common methods in aquatic sciences. Clearly, a full understanding of ecology is no longer possible without some knowledge of multivariate analyses. However, multivariate methods are no panacea, they also have opened a Pandora’s box (James & McCulloch, 1990). Consequently, their adequacy should be checked in every single case to minimize misapplications and misinterpretations of results, and they also should be accompanied by more „simple measures“ and/or graphical representations of the data, yielding a more complete and comprehensive picture.

7.6 References


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Verdankung

Ein herzlicher Dank gebührt Prof. Dr. J.V. Ward, der die Arbeit als Doktorvater stets kritisch begleitet und zu deren guten Gelingen viel beigetragen hat.

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North American Benthological Society (NABS)
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Manuscripts in press


**Submitted manuscripts**


**Other publications**


**Papers presented at scientific meetings**

**Burgherr, P.** (1997) Heterogenität der bentthischen Makroinvertebraten-Gesellschaft in einem komplexen, alpinen Fliessgewässersystem. Annual meeting of the Swiss Hydrological and Limnological Society (SGHL), La Chaux de Fonds, Switzerland


Posters presented at scientific meetings
