Doctoral Thesis

Patterns, pathways, and trophic transfer of organic matter in a glacial stream ecosystem in the alps

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Publication Date:
2001

Permanent Link:
https://doi.org/10.3929/ethz-a-004105296

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PATTERNS, PATHWAYS, AND TROPHIC TRANSFER OF ORGANIC MATTER IN A GLACIAL STREAM ECOSYSTEM IN THE ALPS

A dissertation submitted to the Swiss Federal Institute of Technology for the degree of Doctor of Natural Sciences

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Zürich 2001
**Chapters 2, 4, 7 and 8 have been published, or are in press:**


**Chapter 3 has been submitted:**

**Chapters 5 and 6 are in preparation for publication:**

Zah R. & Uehlinger U. Spatial modeling of allochthonous inputs of particulate organic matter to a high alpine floodplain.
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Summary

Compared to other stream types the energy supply to glacial streams is limited. Harsh environmental conditions like high turbidity, low temperatures, and migrating channels constrain in situ primary production, while allochthonous inputs of organic matter from riparian ecosystems are low, due to the limited productivity of Alpine forests. The assessment of organic matter pathways in glacial catchments is complicated by the high spatial and temporal variability of these hydrosystems. The goal of this thesis was to quantify organic matter pathways of the Val Roseg glacial stream system (Engadin, Swiss Alps) along an altitudinal gradient from the proglacial area to subalpine forest stands, and across a complex alpine floodplain in the heart of the catchment. For the handling of spatial and temporal data, a Geographic Information System (GIS) was used as the central tool for data management, data analysis and modeling.

The shape and structure of channel systems, so-called stream morphology, are important features of freshwater habitats. However, determination of parameters characterizing the morphology of streams and floodplains with classical methods is very time consuming and sometimes even impossible. Using remote sensing data, channel area, channel length, mean channel width, channel slope, bank inclination, and riparian vegetation density of the Val Roseg floodplain were successfully calculated. Multivariate analysis clustered sites based on morphological parameters into different channel types, thus indicating the high ecological relevance of the results.

The glaciers in the Val Roseg are among the fastest retreating glaciers in Switzerland. However, the quantification of climate change effects on ecosystems is difficult, due to high inter-annual variations and a lack of long-term time series. By using GIS, effects of a 52-year period of substantial glacier retreat on the structure of an alpine floodplain could be shown. No direct relation between glacial movements and floodplain dynamics was found, although the surveyed periods included phases of glacier advance, retreat, and stability. However, flood events induced significant changes in the braiding index and connectivity of the channel network.

For determining litterfall and lateral transport of organic matter, spatially distributed litter traps were sampled over a one-year period. Annual inputs increased from $1.1 \text{ g AFDM m}^{-2}\text{y}^{-1}$ in the «desert-like» proglacial area to $35 \text{ g AFDM m}^{-2}\text{y}^{-1}$ in
the lowest reach where subalpine forests were present. Direct inputs of organic matter decreased exponentially from forests at the floodplain edge to the floodplain center, while lateral inputs of organic matter correlated linearly with distance to trees. Direct litterfall dominated litter input close to the forest, while lateral transport was the major pathway for channels more than 20 m away from the forest.

Organic matter within the hyporheic zone is expected to be an important food source for invertebrate communities of glacial streams, because energy supply on the stream bed is limited. Subsurface organic matter content increased along the altitudinal vegetation gradient from the proglacial area into the zone of subalpine forests. This increase was more pronounced for FPOM and detached POM fractions than for biofilms. A lateral increase of subsurface POM across the floodplain from the main channel towards stable groundwater channels was not found. Hydrological effects were clearly reflected by the distribution of hyporheic FPOM. This fraction was largely absent in the top layers (0 – 30 cm) of the most disturbed main channel reaches, due to frequent bed movement at these sites.

To quantify total organic loadings to the different floodplain channels, field data from organic matter traps were combined with remote sensing data, and the different pathways of allochthonous organic matter were modeled for the entire channel network of the floodplain. Results showed lowest values for direct inputs to the channel network (0.07 tons y⁻¹) and intermediate values for the lateral input (0.48 tons y⁻¹). The major input of organic matter was via lateral erosion of the riparian zone (23.4 tons y⁻¹).

Finally, food sources and trophic structure of the macroinvertebrate community along a longitudinal gradient were examined using analysis of multiple stable isotopes (d¹³C and d¹⁵N). Although isotopic signatures of algae varied widely among sites and dates, it was possible to discriminate between allochthonous and autochthonous food sources using a site-specific approach. Dominant food sources of herbivorous invertebrates in all study sites in the glacier stream were epilithic diatoms and the filamentous gold alga *Hydrurus foetidus*. Allochthonous organic matter was of some importance only in a groundwater-fed stream close to the floodplain margin.
Zusammenfassung


Zur Bestimmung des direkten Eintrages und des oberflächlichen Transportes von allochthonem organischem Material wurden Fallen während eines Jahres beprobt, die über das ganze Untersuchungsgebiet verteilt waren. Im Bereich der Gletscherzungengeh, sich der gesamte jährliche Eintrag auf 1.1 g AFDM m\(^{-2}\)y\(^{-1}\) und stieg bis auf 35 g AFDM m\(^{-2}\)y\(^{-1}\) in der subalpinen Nadelwaldzone an. In der Schwemmebene nahmen direkte Einträge mit zunehmendem Abstand zum Wald exponentiell ab, während der oberflächliche Transport linear zurückging. Nahe beim Waldrand dominierte der direkte Eintrag von organischem Material. Der oberflächliche Transport war aber bereits in einer Entfernung von 20 m zum Wald der bedeutendere Prozess.


Zur Quantifizierung der Transportpfade für organisches Material in die verschiedenen Bachtypen wurden im Feld erhobene Daten mit Fernerkundungsdaten kombiniert. Die Resultate zeigen niedrige direkte Einträge ins Kanalnetzwerk (0.07 t/Jahr) und deutlich höhere Werte für oberflächlichen Transport (0.48 t/Jahr). Der grösste Eintrag erfolgte jedoch durch seitliche Erosion der Uferzone (23.4 t/Jahr).

Die Nahrungsgrundlagen und trophische Struktur der Insekten-Gemeinschaft wurden mittels Analyse stabiler Isotopen (\(\delta^{13}\)C and \(\delta^{15}\)N) bestimmt. Obwohl die Isotopen-Werte der Algen zeitlich und räumlich stark schwankten, war die Unterscheidung von autochthonen und allochthonen Nahrungsquellen dank lokaler Vergleiche möglich. Wichtigste Nahrungsgrundlage an allen Untersuchungsstellen im Gletscherbach waren epilithische Diatomeen und die fädige Goldalge *Hydrurus foetidus*, während allochthones Material nur in einem nahe beim Wald gelegenen Quellbach eine gewisse Rolle spielte.
1. Introduction

Alpine stream ecosystems: human impact and climate change

According to Messerli (1997) mountains are the most sensitive ecosystems to climate and environmental change. Consequently, the reasons for conducting research on alpine stream ecosystems are numerous. Globally, mountain regions provide water to about 50% of the world’s population, both in the mountains themselves and, more importantly, also in many downstream lowlands (Bandyopadhyay et al., 1997). Furthermore, mountains are home to a substantial portion of the planet’s biodiversity of species and ecosystems (Price, 1999). Worldwide expanding economic pressures are degrading mountain ecosystems while confronting mountain people with increasing poverty, cultural assimilation, and political disempowerment (e.g. Stone, 1992; Messerli et al., 1997). In the European Alps pressure on natural ecosystems is high: volume of transit traffic is increasing (Franz, 1994) and tourist activities extend into sensitive alpine regions (Henselmann, 1991). The growing interest in production of renewable energy endangers, in particular, alpine stream ecosystems (Ammann, 1993). However, concerns over the degradation of alpine streams are on the rise in politics, economics, and public opinion. Certificates for labelling sustainable power production in alpine regions are under discussion (Bratrich, Truffer & Jorde, 1999). However, these efforts can only be successful when the interactions between human impacts, morphology, hydrology, and biodiversity of alpine streams are known (Becker & Bugmann, 1996). This emphasizes the need for more information on the functioning of alpine stream ecosystems.

Alpine stream ecology

Alpine streams, and in particular, glacier fed alpine streams have attracted the interest of glaciologists (e.g. Collins, 1989; Collins, 1998), geomorphologists (e.g. Gregory, 1987; Gurnell et al., 1999), and hydrologists (e.g. Marsh & Woo, 1981; Becker & Bugmann, 1996), but they were widely neglected by stream ecologists for many decades. In the early 20th century pioneering studies on the fauna of glacier streams were undertaken (Steinmann, 1907; Steinböck, 1934). The recently re-emerged interest
1. Introduction

in the ecology of glacial and alpine streams resulted in conceptional papers on biology and typology of alpine streams (Ward, 1994), the physical habitat template of glacial streams (Milner & Petts, 1994), and in field studies on macroinvertebrates (e.g. Milner, 1987; Winterbourn & Ryan, 1994). However, functional aspects of alpine and glacial stream ecosystems, for example, energy supply, stream metabolism, or organic matter dynamics are still scarce (Gessner, Robinson & Ward, 1998; Robinson et al., 2000).

The energy base of glacial streams

In contrast to terrestrial ecosystems, where in-situ primary production is the dominant energy source for consumers, biologically available energy in lotic ecosystems originates from two sources: primary production occurring within the wetted channel (autochthonous energy) and terrestrial organic matter entering the stream by aerial litterfall, lateral transport, bank erosion, or exfiltrating groundwater (allochthonous energy). The relative importance of autochthonous and allochthonous production changes along the river continuum depending on stream size and riparian vegetation (Vannote et al., 1980; Minshall et al., 1985) and across biomes (e.g., Fisher & Likens, 1972; Minshall, 1978; Bott et al., 1985). The energy base of headwater streams in forested catchments is mainly leaf litter from the woody riparian vegetation (Cummins et al., 1973; Fisher & Likens, 1973; Ward, 1986; Graca, 1993), whereas desert streams (Jones et al., 1997), antarctic streams (McKnight & Tate, 1997) and arctic tundra streams (Peterson, Hobbie & Corliss, 1986) largely rely upon autochthonous primary production.

Autochthonous production is also expected to be the dominant energy source of most alpine streams (Ward, 1994). In glacial streams high turbidity, low temperatures and instable substrata may impede the growth of benthic primary producers (Milner & Petts, 1994). Algal assemblages in this harsh environment are characterised by low species diversity (Kawecka, 1980). The holarctic chrysophyte Hydrurus foetidus which can form long filaments, is often dominating. If bedload transport is lacking Hydrurus reaches high densities even close to the glacial mouth (Lavandier & Décamps, 1984; Uehlinger, Zah & Bürgi, 1998).

Riparian vegetation above the tree line or in proglacial areas is typically sparse. Therefore, direct and lateral inputs of terrestrial organic matter is expected to be
very small (Ward, 1994). Organic particles transported by wind and subsequently entrained in glacial ice are a potential food source for the aquatic fauna of glacial streams (Steffan, 1971). If slopes are steep, the riparian vegetation changes within short distances from «rock desert» to subalpine forests (Ormerod et al., 1994). This change in terrestrial vegetation is assumed to be paralleled by an increasing input of allochthonous organic matter and thus, reduced autochthonous dominance in ecosystem energetics. Dissolved organic material from hillslope and valley aquifers are also potential energy sources in floodplain reaches (Bishop et al., 1994; Mulholland, 1997).

The energy base of glacial streams can not be evaluated without considering the dynamics of the fluvial hydrosystem, which strongly influence autochthonous production and riparian vegetation. Glacial streams are characterised by high variations in discharge, almost unlimited sediment supply from proglacial areas below receding glaciers, and variable channel slope (Milner & Petts, 1994). These factors result in three unique geomorphic features: (1) highly unstable channels, which are braided, steeply graded and of low sinuosity in the proglacial area (sandurs); (2) wandering channels with an irregular laterally mobile main channel and secondary channels separated by vegetated bars further downstream; and (3) a relatively stable, single-thread channel with a reduced width : depth ratio in the lower reaches of glacial stream segments (Hickin, 1993). A rich supply of coarse sediment in combination with high flow enhances the temporal variability of glacial hydrosystems (Gurnell, 1987; Collins, 1998).

The Val Roseg study system

This study was conducted in the Val Roseg, a side valley of the upper Engadin (Eastern Swiss Alps). Detailed descriptions of the system are given in the various chapters of this thesis. Important system characteristics in the context of this thesis are:

(1) Low human impact: Despite some extensive cattle grazing and hiking tourism during the summer months, the upper part of the catchment has remained in its natural state. However, in the lower 7 km of the Roseg River the channel is stabilized by several sills.
1. Introduction

(2) Geomorphic diversity: Between the glacier terminus and the lower catchment boundary the typical succession of a glacial hydrosystem (Hickin, 1993) can be found. A braided reach in the recent proglacial area (length 500 m) is separated by a single-thread channel incised in glacial till (length 900 m) from the main glacial floodplain (length 2800 m) with a complex channel network (Tockner et al., 1997). The floodplain is followed by a reach constrained by steep valley slopes (length 7200 m).

(3) The fast retreat of the Tschierfa and Roseg glaciers (10 – 60 m y\(^{-1}\) (Haeberli, Hoelzle & Frauenfelder, 1999) has released large amounts of sediments and enhanced the dynamics of the glacial hydrosystem.

(4) Distinct gradient of terrestrial vegetation: The Roseg River flows from the scarcely vegetated proglacial area into the subalpine forest belt in the lower part of the catchment.

(5) The catchment is accessible all-year-long and discharge has been gauged at the lower end of the catchment for more than 45 years. Moreover, aerial photographs of the entire catchment have been taken since 1947.

Fig. 1-1 The multifaceted nature of the Val Roseg project (Ward et al., 1998).
Objectives and organization of the study

This thesis is part of a holistic ecosystem study investigating biodiversity patterns along longitudinal and lateral gradients, structure and dynamics of benthic communities, longitudinal, lateral and vertical ecological connectivity, and groundwater ecology (Fig. 1-1, Ward et al., 1998).

The main objectives of this thesis research were to identify pathways, storage and trophic transfer of organic matter in the Val Roseg stream ecosystem in the context of glacial hydrosystem dynamics. This included assessment of organic matter standing stock, allochthonous organic matter input and changes in the hydrosystem at the landscape level. The size and spatio-temporal heterogeneity of the study system required adaptation of analytical methods developed in terrestrial ecology.

Chapter 2 describes the development of a method for assessing ecologically relevant morphological parameters such as bank inclination, stream width and channel

![Diagram of spatial scales and processes](image)

**Fig. 1-2** The different chapters of this thesis ordered along spatial scales and processes.
1. Introduction

slope by analysis of remotely sensed data. The method was then used to quantify these parameters for the entire channel network of the Roseg floodplain. In Chapter 3 a time series of aerial images was analyzed to assess the impact of glacial movements and peak floods on the morphology of the glacial floodplain during the last 52 years. Chapter 4 deals with the assessment of direct and lateral inputs of terrestrial organic matter along the river continuum and across the main floodplain. Subsurface storage of organic matter is the focus of chapter 5. Chapter 6 portrays spatial modeling of organic matter derived from direct inputs, lateral inputs and bank erosion. In Chapter 7 stable isotope discrimination between allochthonous and autochthonous organic matter was investigated. Based on these results the contributions of the different food items to the diet of the aquatic invertebrates were assessed (Chapter 8). These seven chapters can be ordinated along a spatial axis - from catchment to habitat (Frissell et al., 1986) - and along a process axis - from fluvial dynamics to trophic transfer (Fig. 1-2).

References


References


1. Introduction


References


2. Application of photogrammetry in freshwater ecology: analysing the morphology of a high alpine floodplain


The shape and structure of river channels (channel morphology) are important features of freshwater habitats. However, determination of parameters characterizing the morphology of rivers and floodplains with classical methods is very time consuming and sometimes even impossible. The application of digital photogrammetry reduces the time for data acquisition and allows analysis of complex and remote floodplains: Aerial photographs capture a distinct flow situation, which can be analysed later in the laboratory with high accuracy and without time constraints. In this project, a digital elevation model (DEM) and color-infrared orthophotos were generated at a resolution (DEM: 2 m, Orthophoto: 0.25 m) that allowed the measurement of different morphological parameters of channels in the Val Roseg floodplain (eastern Swiss Alps). Based on these photogrammetric data, channel area, channel length, mean channel width, channel slope, bank inclination, and riparian vegetation density were successfully calculated. The assessment of variability in width and slope of channel segments however was affected by the highly complex floodplain structure and the limited DEM resolution. Multivariate analysis showed that the morphological parameters clustered the channel segments into different channel types, thus indicating the high ecological relevance of the results.
2. Application of photogrammetry in freshwater ecology

Introduction

Knowledge of the physical aspects of streams, in particular geomorphology and hydrology, are important for understanding the functioning of river ecosystems (e.g., Fisher et al., 1998). Geomorphic settings, such as channel size, slope, grain size distribution, the spatial configuration of bars and riparian vegetation strongly influence the structure of fluvial habitats and, as a consequence, biodiversity and ecosystem function. Physical characteristics of rivers can be studied at spatial scales that range from sediment grains of $10^{-3}$ m to drainage systems of $>10^3$ km (Frissell et al., 1986), but stream ecology traditionally has focused on channel processes (Fisher, 1997). This focus determined the scale of observation typically ranging from microhabitat to reach. However, by adopting a landscape perspective, stream ecologists are expanding the scale of their investigations (Johnson and Gage, 1997; Richards et al., 1997; Ward et al., 1999).

At the reach scale, relevant morphological parameters such as channel width, slopes of channels and banks, and riparian vegetation are usually assessed using simple tools such as meter tapes, inclinometers and vegetation classification techniques.

![Spatial Metrics](image)

**spatial metrics**
- mean width
- channel length
- channel area
- channel slope

**spatial diversity**
- width variability
- slope variability
- bank inclination

**riparian zone**
- density of riparian vegetation

Elevation Data (DEM)

*Fig. 2-1 Schematic view of morphological characteristics of a hypothetical stream segment.*
These techniques yield reliable data but become painstaking if the interest is expanded to the channel network of an entire drainage. At this scale, modern photogrammetric methods such as ortho-photographs and digital elevation models (DEMs) in high resolution make it possible to extract morphological parameters, that are of ecological significance for stream habitats. Such parameters include (1) channel length, channel slope, stream area, and mean channel width that define the spatial metrics of the aquatic ecosystem, (2) variability in channel width and slope as indicators of spatial diversity, and (3) bank inclination of the adjacent riparian zone and riparian vegetation density that are correlated with the input of terrestrial organic matter to aquatic systems (Figure 2-1).

The objective of this study was to demonstrate the benefits and limitations of photogrammetry and geographical information systems (GIS) for the assessment of ecologically relevant geomorphic parameters at the floodplain scale. The project was conducted in a high alpine floodplain (Val Roseg, eastern Swiss Alps).

**Methods**

**Study system**

The study system was the Roseg River in the eastern part of the Swiss Alps. About 30% of the drainage basin (area 66.5 km$^2$) is covered by glaciers. Meltwater from the Tschierva and Roseg glaciers is the primary water source of the Roseg River. The most remarkable feature of this system is a glacial floodplain (length 2800 m, about 2100 m a.s.l.) comprising a diversity of channel types. Within this floodplain, the following channel types can be distinguished based on their hydrological connectivity and physico-chemical attributes (modified from Tockner et al., 1997): (1) main channel primarily draining the floodplain that is mainly fed by glacial meltwater of the Tschierva and Roseg glaciers, (2) side channels with upstream and downstream connections to the main channel, (3) intermittently-connected channels permanently connected downstream and intermittently connected upstream to the main channel, (4) groundwater channels fed by alluvial groundwater and only connected downstream with the main channel, (5) groundwater channels fed by lateral groundwater exfiltrating from the edge of the floodplain and only connected downstream with the main channel, (6) tributaries entering the floodplain from side-valleys and fed by hillslope aquifers or small side glaciers.
2. Application of photogrammetry in freshwater ecology

Fig. 2-2a: Part of a high-resolution color-IR-orthophoto, b: digitized coverages for the same area indicating flow paths, stream segments and the riparian bufferstrip.

**Geodetic methods**

Aerial photographs (color film and color infrared film) of the Val Roseg floodplain were taken on 29 July 1998, at 13:00 GMT with a standard aerial camera (WILD 21 NAGIIA-F, focal length 214.74 mm). At this time of the year most floodplain channels have surface flow and the shrub and grass vegetation is well-developed. Coordinates of the signalized control points were determined with GPS before the flight.

Color film was used for the generation of digital elevation models, while orthophotos were created from color infrared images for a better differentiation of vegetation patterns and wet areas (Fig. 2-2a). Both kinds of film were used on two different flight heights. Two high image strips (scale 1:9'500, scan resolution 21 microns) covered the entire valley (floodplain and side-slopes). Two low elevation image strips (scale 1:5'000, scan resolution 21 microns) provided high resolution and accuracy for the floodplain area. The exterior orientation of the images was determined in a bundle block adjustment for each strip separately.

The photogrammetric evaluation was completed with the digital station PHODIS (by ZI-Imaging). The data analyzed by GIS consisted of a DEM with a rasterwidth of 2 m for the floodplain (estimated height accuracy about 0.12 m) and a DEM with a rasterwidth of 10 m for the adjacent valley slopes (estimated height accuracy about 0.25 m). Digital color infrared orthophotos of the floodplain were created with a footprint of 0.25 m. Although the spatial resolution is limited by the
raster-width of the DEM, the higher resolution of the orthophotos ensures that small objects (0.25 - 2.0 m) are preserved and can be analyzed. Orthophotos of the adjacent valley slopes were created with a resolution of 0.5 m, which is sufficient for the assessment of vegetation patterns. Three separate color bands were extracted from the infrared orthophotos to separate six classes of vegetation density (bare gravel, sparse grassland, intermediate grassland, dense grassland, grassland with shrubs, and forest) by applying maximum-likelihood classification.

**GIS analysis**

Photogrammetric data were analyzed with ArcInfo (ESRI, 1994): Coverages were digitized with ArcEdit and raster data were generated and analyzed with ArcGrid. First, a line coverage was created representing the main flow paths of the different channels. Next the channel area of the whole floodplain was digitized as polygons (Fig. 2-2b). Both, flow path and channel area coverages, were split into about 500 segments with a maximum length of 150 m per segment. For each channel segment, all morphological parameters were calculated using combinations of the four coverages: flow paths, channel area, vegetation density, and DEM (Fig. 2-1).

First, each segment was assigned to one of five channel types (main channel, intermittently-connected channel, groundwater channel, lateral groundwater channel, or tributary). As the next step, channel area and channel length per segment were derived from the ArcInfo coverages. Mean channel width was calculated by dividing the area of each channel segment by the channel length of the respective segment. Variability in channel width was determined by intersecting the channel area coverage with parallel lines transecting the floodplain every 2 m. The resulting coverage included replicated channel width measurements that were linked to the respective channel segments. Width variability was calculated as the standard deviation of all width measurements of one channel segment. Direct and indirect methods were used to determine channel slope. In the indirect method, the slope in each raster point of the DEM was calculated as the change in altitude of the neighboring cells (Slope-function of ArcGrid). Next, a point coverage was generated including sampling points every two meters of the thalweg coverage. With this point coverage, slope was measured for all segments every two meters on the main flow path. Finally, mean channel slope and standard deviation in slope were calculated for each channel segment. With
2. Application of photogrammetry in freshwater ecology

Fig. 2-3 Visualization of selected morphological parameters on the channel network of Val Roseg.
Results and discussion

the direct method, mean slope was calculated directly from the DEM: (max. altitude – min. altitude) / channel length * 100. However, this method only yields the mean slope, the determination of slope variability is not possible with the direct method. A 5m-wide, lateral strip along each channel segment was analyzed to generate morphological parameters of the riparian zone. Within this strip, mean vegetation density and bank inclination of the riparian zone were determined using the zonal functions of ArcGrid.

The resulting morphological parameters were visualized on a floodplain map using ArcView 3.1 (by ESRI). To separate channel types, principle component analysis (PCA) was performed using ADF 4-Software (Chessel & Dolédec, 1996).

Table 2-1 Morphological values for the different channel types (mean ± 1 SD).

<table>
<thead>
<tr>
<th>Channel type</th>
<th>Number of segments</th>
<th>Total stream area</th>
<th>Total channel length</th>
<th>Mean channel width</th>
<th>Channel slope (direct method)</th>
<th>Bank inclination</th>
<th>Bank inclination</th>
<th>Riparian vegetation density</th>
</tr>
</thead>
<tbody>
<tr>
<td>main channel</td>
<td>169</td>
<td>69432</td>
<td>12992</td>
<td>5.1 – 2.2</td>
<td>2.4 – 1.2</td>
<td>7.3 – 5.2</td>
<td>1.2 – 0.4</td>
<td>1: bare, 6: forest</td>
</tr>
<tr>
<td>intermittently-connected channel</td>
<td>114</td>
<td>26246</td>
<td>7805</td>
<td>3.3 – 2.5</td>
<td>2.6 – 1.3</td>
<td>6.0 – 2.5</td>
<td>1.4 – 0.4</td>
<td></td>
</tr>
<tr>
<td>alluvial groundwater channel</td>
<td>40</td>
<td>3204</td>
<td>1702</td>
<td>1.6 – 1.2</td>
<td>3.4 – 2.9</td>
<td>9.1 – 4.7</td>
<td>2.4 – 0.8</td>
<td></td>
</tr>
<tr>
<td>lateral groundwater channel</td>
<td>72</td>
<td>5523</td>
<td>2135</td>
<td>2.1 – 1.6</td>
<td>2.3 – 1.5</td>
<td>10.1 – 7.0</td>
<td>2.8 – 1.0</td>
<td></td>
</tr>
<tr>
<td>tributary</td>
<td>93</td>
<td>5734</td>
<td>3346</td>
<td>1.5 – 1.7</td>
<td>5.5 – 6.1</td>
<td>16.2 – 13.8</td>
<td>3.2 – 1.0</td>
<td></td>
</tr>
</tbody>
</table>

Results and discussion

Channel characteristics

Segments of the main channel and of intermittently-connected channels contributed 70% and 20%, respectively, to the channel area of the entire floodplain (Table 2-1); this means that 90% of the channels in the floodplain are directly fed by glacial melt water during summer. The mean width averaged 5.1 m for main channel segments and 3.3 m for intermittently connected channels. Channel types lacking upstream connections to the main channel were on the average ≤ 2 m wide and also showed a lower variability in channel width (Table 2-1).

Channel slope was over-estimated by the indirect method, particularly in narrow channels with steep banks where the inclination of the riparian strip strongly affected estimates of slope. Therefore, these results were not considered for further analysis. Interference with the riparian strip was small with the direct method, and
thus results are more representative for channel slope. Mean slopes of main channel segments, intermittently-connected channel segments, and lateral groundwater channels segments were about 2.5%, while mean slope of alluvial groundwater channels was 3.4% and slope of tributaries averaged 5.5%. The channel types with steeper slopes also showed higher variability in slope (Table 2-1). Slopes of channel segments were remarkably uniform in the middle of the floodplain, while slopes slightly increased towards the upper part and edges of the floodplain (Figure 2-3a).

Because of high connectivity between the main channel segments (braided chan-
Results and discussion

channel pattern, shown in Fig. 2-2a), we failed to determine channel width every two meters and, as a consequence, variability of channel width within channel segments. However, variability in width among channel segments was high for intermittently-connected channels and for the main channel segments, and lower for the other stream types with narrow channels. Channel width was inversely related to channel slope (Fig. 2-4b).

Characteristics of the riparian zone
The lowest bank inclination was found for intermittently-connected channel seg-
ments (6.0%). This channel type also showed the lowest variability among segments. Mean bank inclination for the main channel was 7.3% with a standard deviation of 5.2%. The standard deviation is so high because the main channel was partially eroding the steep valley slopes. Mean bank inclination for alluvial and lateral groundwater channels was 9.1% and 10.1% (Table 2-1). Inclination of the riparian bank was maximum for tributary segments. Inclination was generally higher along the edge of the floodplain than in the middle of the floodplain (Fig. 2-3b). Highest values have been found in the uppermost part of the floodplain where the main channel incised glacial deposits.

Riparian vegetation density along main channel segments was scarce or lacking (Table 2-1, Fig. 2-3c), apparently reflecting low channel stability during high flows and high sediment supply from recent proglacial areas. Vegetation along intermittently-connected channels was nearly as low (Table 2-1). Riparian vegetation density of groundwater channels in the middle of the floodplain was relatively high indicating that these channels are restricted to stable parts of the floodplain. The highest vegetation density was found along tributaries and groundwater channels at the floodplain edge. Density of the riparian vegetation significantly decreased with channel width (Fig. 2-4a). However, Fig. 2-3c shows that some stable spots with dense vegetation existed even in the middle of the floodplain. Our data generally show that restricted channel movement coincided with steep bank slopes. This is reflected by a positive relationship between bank inclination and vegetation density (Fig. 2-4d), both of which are important determinants of the input of allochthonous organic matter in floodplain channels (Chapter 6).

**Channel typology**

In order to cluster the channel types using the morphological parameters, a multivariate analysis (PCA) was performed (Fig. 2-5a). Channel types were mainly separated by the primary axis which explained 55% of the variation. The primary axis was positively correlated with channel width and negatively correlated with vegetation density and channel slope (Fig. 2-5b). The different channel types were aligned along this gradient; main channels and intermittently-connected channels are clustered together on one end of the gradient, followed by alluvial and lateral groundwater channels in the middle, and the tributaries on the other end of the gradient (Fig. 2-5a). The morphological clustering fits the faunistic clustering (Burgherr et al., sub-
mitted) as shown in Fig. 2-5c.

**Conclusions**

By using digital photogrammetry it was possible to calculate a high-resolution DEM and to generate ortho-photographs of a much higher accuracy than by applying a simple rectification with tie points. The photogrammetric method yielded all data necessary for deriving morphological parameters at the scale of the Val Roseg floodplain. However, the spatial resolution of the DEM (2 m footprint) imposed some constraints on the calculation of channel slope. In narrow channels (width < 5 m) with steep banks, channel slope was over-estimated, because the slope function in ArcGrid could not satisfactorily separate channel slope from bank slope. Therefore, the correct DEM resolution for slope calculations should be taken into account early in planning of future projects.

GIS analysis provided data that are considered to determine biotic pattern and processes in stream ecosystems, but that would have been rather difficult to obtain with standard methods with regard to the size and complexity of the investigated system. Another advantage of the methods applied in this project is the high spatial resolution of the data which makes it possible to use statistical methods from landscape ecology and geostatistics for further analysis.

This project showed that standard methods of digital photogrammetry have a high potential to influence scientific progress in other disciplines. The contemporary trend in freshwater ecology towards a landscape approach can benefit from a strong interdisciplinary collaboration with photogrammetry.

**Acknowledgements**

We express our thanks to Plinio Testa and his crew at the Hotel Roseggletscher for their hospitality, to the Schweizer Koordinationsstelle für Luftaufnahmen (KSL) for shooting the aerial photographs, to Peter Burgherr for performing multivariate statistics, and to Chris Robinson for the critical review of this paper. This work was supported by the Swiss National Science Foundation (SNF grant 21-49243.96).
2. Application of photogrammetry in freshwater ecology

References


3. **Effects of glacier movements and floods on the morphology of a glacial floodplain: analysis of aerial images**


Over the last 50 years the Roseg and Tschierva Glaciers (Engadin, Swiss Alps) experienced variable rates of retreat. These glacial movements affected the sediment availability for the meltwater stream, and consequently, the structure of the Val Roseg floodplain. To analyze the changes in floodplain morphology during this period of rapid glacial movements, ten sets of aerial images (1947 to 1999) were rectified and channel network and active floodplain area digitized into a Geographic Information System (GIS). Results showed that changes in floodplain morphology partially correlated with extreme floods but showed no correlation with glacier movements. While the channel network was continuously changing with a mean turnover rate of 25% per year, the overall structure of the Roseg floodplain remained remarkably constant.
3. Effects of glacier movements and floods on floodplain morphology

Introduction

Riverine floodplains are spatially complex ecosystems comprising a variety of geomorphic features that include various channel types with different hydrological connectivity (Leopold, Wolman & Miller, 1964; Stanford & Ward, 1993; Tockner et al., 1997). The immersion of channels and other parts of the floodplain is controlled by floodplain topography and discharge is subject to variation on diel and seasonal scales (Junk, Bayley & Sparks, 1989; Malard, Tockner & Ward, 1999; Tockner, Malard & Ward, 2001). Sediment and discharge driven long-term modifications of the hydro-geomorphic configuration of the floodplain contrast with the stage controlled ecosystem dynamics. These modifications increase habitat heterogeneity, and thus contribute to high levels of species diversity in river floodplains (Ward, Tockner & Schiemer, 1999).

Alpine rivers, glacier-fed rivers in particular, are characterized by high sediment yields and extended periods of high discharge during snow and icemelt. Discharge regime, sediment supply, and riparian vegetation are presumably major determinants of channel dynamics in the river corridor of glacier-fed alpine streams (Gurnell et al., 1999). The discharge regime of glacial streams is characterized by high flow in summer and low flow between autumn and spring. Rainfall induced high-flow events usually occur when the transient snowline is high (August to mid-September; Collins, 1998). During such events, substantial amounts of sediment can be transported. Recent proglacial areas below retreating glaciers can be a rich source of sediments. High sediment yield due to high flow and high sediment availability are expected to parallel deglaciation and the upward shifting snowline (an increase in the snow free portion of a glacier catchment rapidly returns rain to runoff; Collins, 1998). High sediment yield also may be associated with rapid glacier advance, which can shift the meltwater drainage system, and thus provide new fluvial access to stored sediments (Gurnell, 1995). Below rapidly retreating glaciers enhanced sediment yield and flood frequency may increase channel wandering, and thus the width of the active floodplain, although riparian vegetation is expected to constrain the active floodplain width depending on altitude (below or above the treeline; Gurnell et al., 1999).

In this study we focused on the long-term dynamics of the channel network in an alpine floodplain below two valley glaciers. We expected that glacier movements (retreat and advance) and high flow events should be reflected by changes in the
structure of the channel network. Moreover, enhanced sediment yield due to glacier movement should increase lateral channel shifting and result in a widening of the active floodplain. To test these hypotheses, we describe changes in the morphology of the floodplain over a period of 50 years based on a set of aerial images, and we relate these changes to glacier movement and flood events.

Methods

Study site
The study system was the Roseg River in the eastern part of the Swiss Alps (Fig. 3-1). About 30% of the drainage basin (area 66.5 km²) is covered by glaciers. Meltwater from the Tschierva and Roseg Glaciers is the primary water source of the Roseg River. The recently deglaciated, steep proglacial area below the Tschierva Glacier is a major sediment storage zone. The Roseg Glacier ends in a lake, which existed since 1940 and interrupts the transport of coarse sediments from the glaciated Roseg basin to the main floodplain. The main floodplain is about 2800 m long and 100 m to 500 m wide with elevations ranging from 1995 m to 2100 m a.s.l. The floodplain is characterized by a complex channel network. Different channel types can be distinguished based on their hydrological connectivity and physico-chemical attributes (Tockner et al., 1997). Channel types include the main channel, which carries more than 70% of the melt water from the two valley glaciers, side channels of the main channel, channels intermittently connected upstream to the main channel, groundwater channels with no upstream connection to the main channel and side-slope tributaries. The channel network is the habitat of a diverse invertebrate community (Burgherr & Ward, 2001).

Survey and image analyses
Aerial photographs (color film and color infrared film) of the Val Roseg floodplain were taken on 29 July 1998, at 13:00 GMT with a standard aerial camera (WILD 21 NAGIA-F, focal length 214.74 mm). Color film was used for the generation of a digital elevation model (DEM), while orthophotos were created from color infrared images for a better differentiation of vegetation patterns and areas covered by water. Two low elevation image strips covering the whole floodplain area were scanned (scale 1:5000, scan resolution 21 microns). The exterior orientation of the images was de-
3. Effects of glacier movements and floods on floodplain morphology

Fig. 3-1 Middle: Val Roseg catchment, right: Val Roseg floodplain.

termined in a bundle block adjustment for each strip separately, using ground control points that were measured with DGPS and marked prior to the flight. The photogrammetric evaluation was completed with the digital station PHODIS (by ZI-Imaging). The data provided for the analysis with GIS consisted of a DEM with a rasterwidth of 2 m for the floodplain (estimated height accuracy about 0.12 m). Digital color infrared orthophotos of the floodplain were created with a footprint of 0.25 m.

This high-accuracy DEM and the color-IR-orthophotos then were used for the spatial correction of 6 sets of b/w-aerial images (1947 partially, 1955, 1971, 1979, 1985, 1991, resolution: 1m), 2 sets of color-images shot from helicopter (1996, 1997, resolution: 0.5 m), and an additional set of color-IR images (1999, resolution: 0.25 m). All of these spatial corrections were performed using OrthoEngine (by PCI-Geomatics) on a UNIX-workstation.

Using ArcInfo (ESRI, 1994) as the GIS-application, the flow paths of the active channels and the border of the active floodplain were digitized as line coverages for
each of the 10 sampling dates. Further analyses were performed using only these coverages.

**Structure and dynamics of the channel network**

**Braiding index** and **sinuosity index** were calculated for each sampling date as described by Friend and Sinha (1993). \( L_{\text{tot}} \) represents the total channel length of the main channel and the side channels, whereas \( L_{\text{max}} \) is the length of the thalweg (= main channel). \( L_R \), the length of the reach, expresses the north-south expansion of the braided floodplain. The **connectivity index** indicates the ratio of channels with upstream connection to the main channel \( (L_{\text{up.conn}}) \) to channels that are only downstream connected or completely abandoned from the main channel \( (L_{\text{no.conn}}) \).

\[
\begin{align*}
\text{braiding index} &= \frac{L_{\text{tot}}}{L_{\text{max}}} \\
\text{sinuosity index} &= \frac{L_{\text{max}}}{L_R} \\
\text{connectivity index} &= \frac{L_{\text{up.conn}}}{L_{\text{no.conn}}}
\end{align*}
\]

**Turnover of floodplain channels** was determined by comparing two sets of channel coverages and manually marking persistent channels. **Lateral shift of the main channel** was measured for each pair of aerial images across 14 transects along the floodplain (distance between transects 150 and 200 m). The active floodplain border was defined as the border between gravel bars and persistent vegetation cover. **Active floodplain width** was then determined for each of the 14 transects.

**Discharge and glacial movement**

Discharge records (mean daily discharge) were available from a gauging station at the lower end of the Roseg catchment (Fig. 3-1). The record started in spring 1954 (Fig. 3-2). Annual data of glacier movements of Tschierfa and Roseg glaciers since 1900 were provided by the World Glacier Monitoring Service (WGMS).

**Results**

The lengths of Tschierfa and Roseg Glaciers decreased from 1947 to 1999 by 680 m and 1570 m, respectively (Fig. 3-2). In this period, 0.32 km\(^3\) of newly available sediments were exposed by the retreating Tschierfa glacier. Between 1967 and 1987 the Tschierfa glacier advanced by about 220 m. The retreat of the Roseg Glacier slowed between 1974 and 1992. Maximum annual discharge showed no consistent
3. Effects of glacier movements and floods on floodplain morphology

![Graph showing annual peak flows, glacial movements, and dates of aerial surveys in the Val Roseg floodplain.](image)

**Fig. 3-2** Annual peak flows, glacial movements, and dates of aerial surveys in the Val Roseg floodplain.

temporal pattern between 1954 and 1999 and was not correlated with glacier movements. On 22 August 1954, the outbreak of the proglacial lake resulted in a short-term peak flow (< 1h) of about 120 m³s⁻¹. The aerial photographs delimit periods during which glacier movements and magnitudes of high flow events distinctly varied.

Figure 3-3 depicts the development of the channel network and the active floodplain area over the past 52 years. Many channels, especially groundwater channels, do not migrate during long time periods. The high channel density in 1998 can be explained by the exceptionally high discharge (11 m³s⁻¹) during the aerial survey. While the sinuosity of the Roseg river remained constant (1.15 ± 0.01), variation of the braiding index was small (4.6 ± 1.2) (Fig. 3-4a). The connectivity index, in contrast,
Fig. 3-3 Channel network and active floodplain area as derived from the aerial images; bold line indicates Thalweg.
3. Effects of glacier movements and floods on floodplain morphology

Figure 3-4 Sinuosity, braiding index, connectivity index (a) vs. time, and (b) vs. discharge during aerial surveys.

showed high variation (6.6 ± 5.0). One may argue that the variation of the braiding and connectivity indices may reflect different discharges during the aerial surveys rather than the effect of past glacier movements or floods. However, discharge was a weak predictor of the variation of both indices (Fig. 3-4b), explaining only 34% of the variation in the connectivity index and 48% of the variation in the braiding index.

Figure 3-5 Lateral movement of main channel in each section (average ± 1 SD).
Figure 3-3 shows that the main channel shifted almost over the entire floodplain, especially in the upper section. This lateral movement is not a continuous process; the shifting varied distinctly between subsequent observation periods (Fig. 3-5). Periods with lateral channel movement of >100 m were followed by minor shifts of...
3. Effects of glacier movements and floods on floodplain morphology

Figure 3-8 Width of active floodplain on each transect in the 3 sections.

Table 3-1 Results of regression analysis; p-values of linear regressions, * = significant, ** = highly significant.

<table>
<thead>
<tr>
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<th>flood peaks</th>
<th>glacial movement</th>
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<td>active floodplain area</td>
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< 20 m. For assessing the half-life of the channel network, channel turnover for different time periods were calculated (Fig. 3-6) Channel turnover increased with the length of the observation interval from 30% (one-year interval) to a maximum of 70% for time periods > 20 years. The half-life of the channel network is 10 years. The fact that the turnover rate does not exceed 70% can be explained by many former channels, that are disconnected and may persist over time periods > 20 years. The resulting equation from Fig. 3-6 was used to assess annual turnover rates for the different observation periods (Fig. 3-7). The first period (1947-55) showed a high annual turnover-rate of 40%, while annual turnover was 20% - 30% after 1955.

The width of the active floodplain continuously increased in the upper floodplain over the past 52 years except for the uppermost transect (Fig. 3-8). In the middle section, the active floodplain width remained constant. A reduction in active floodplain width in the lower section was observed during the last 10 years, due to dams built from sediments to protect adjacent pastureland. The riparian vegetation in the floodplain consisted of scattered shrubs (*Juniperus communis, Salix sp.*) that occurred in areas not affected by shifting channels for more than 30 years. Tree vegetation (*Larix decidua, Pinus cembra* and *Pinus montana*) was restricted to the valley slopes.

The evaluation of the influence of glacier movement and high flow events on floodplain morphology was based on linear regression analyses. We used the change in length of the Tschierva glacier and maximum peak flow as independent variables (Table 3-1). We found no relationship between length change and main channel turnover, main channel shift or any measured morphological parameters. High flow events correlated significantly with the braiding and connectivity indices. Sinuosity and channel turnover may have been affected by high flow events (borderline cases: p = 0.06 – 0.09). The significance of the results was not increased by combining the two independent variables (Table 3-1).

**Discussion**

This study represents a unique data set documenting change in the channel network of a glacial floodplain over a 52-year period. The quality of such data depends on many factors: For example the quality of the source images was quite different in terms of resolution (0.25 m to 1 m) and color bands (b/w, color, IR-color). The
spatial correction of the aerial images resulted in horizontal position errors of < 5 m
for 95% of the pixels. An additional error of max. 5 m was introduced by manually
digitizing the channel network. The estimated total error is < 7 m. This precision is
adequate for digitizing flow paths of channels, that are 2 m to 15 m wide but not for
digitizing channel areas.

Our investigation showed that during the 52-year period of substantial glacier
retreat, channel turnover, like extent and structure of the channel network, was sur¬
prisingly constant. The only parameter that showed a persistent change was the ac¬
tive floodplain area that continuously increased in the upper section. Although the
surveyed periods included phases of glacier advance, retreat, and stability, no direct
relation between glacial movements and floodplain dynamics was found, as expected
by the model of Gurnell et al. (1999). One reason may be that, for the Val Roseg
catchment, the amount of available sediment is high relative to the catchment size.
The major factor limiting change in floodplain morphology is presumably magni¬
tude and frequency of high flow events rather than sediment availability. Recent
studies on the effects of climate change in the Alps predict an increase of hydrologic
extremes such as floods (Wanner et al., 1997; Imboden, 1998). In the face of the
large sediment storage in the proglacial area of the Tschierva Glacier, we anticipate
an increase in floodplain dynamics in the Val Roseg if current climate trends con¬
tinue.

The active floodplain is relatively large in relation to the current flow regime.
Disconnection and reconnection of former channels (many of the channels persist
for more than 30 years) to the main channel in the upper floodplain section induce
the major changes in the channel network. This is reflected by relatively low turno¬
ver rates (25% mean annual turnover). For example, in a low elevation floodplain
with gravel as the dominating substratum more than 50% of the channel network
can be renewed within one year (Kollmann et al., 1999) due to sheet flow. This is
lacking in the Roseg floodplain where channel erosion and aggradation basically oc¬
curred along the main channel.

The sparse riparian vegetation of the Val Roseg floodplain apparently plays a
minor role in stabilizing the channel system. In relation to the lateral shift of the
main channel, the growth of woody vegetation may be too slow because of high
altitude (300 m below the tree line). However, riparian succession may be constrained
by cattle grazing, that takes place every year for two weeks in late spring and late summer.

**Acknowledgements**

We wish to thank «Schweizer Landestopographie» for access to archived aerial images and the «Koordinationsstelle für Luftaufnahmen» (KSL) for photographing the color-IR aerial images. Many thanks go to Philippe Meuret from the Remote Sensing Lab (RSL) of the Geography Department, University of Zurich, for introducing me to the world of photogrammetry. We also thank F. Malard and C. Robinson for fruitful scientific discussions and comments on this manuscript. This study was supported by a research grant from Swiss National Science Foundation (SNF 21-49243.96).

**References**


3. Effects of glacier movements and floods on floodplain morphology


4. Particulate organic matter inputs to a glacial stream ecosystem in the Swiss Alps


Traps for litterfall and for lateral transport of organic matter were sampled over a one-year period along longitudinal and lateral transects in a glacial stream system (Val Roseg, Swiss Alps), which is characterised by single-thread reaches above and below a braided subalpine floodplain. Annual organic inputs varied from 0.4 g AFDM m$^{-2}$y$^{-1}$ (direct input) and 0.7 g AFDM m$^{-2}$y$^{-1}$ (lateral input) in the proglacial area to 23.0 g AFDM m$^{-2}$y$^{-1}$ (direct input) and 10.7 g AFDM m$^{-2}$y$^{-1}$ (lateral input) in the lowest reach with adjacent subalpine forests. Direct inputs of organic matter decreased exponentially from forests at the floodplain edge to the floodplain centre, while lateral inputs of organic matter correlated linearly with distance to trees. Direct litterfall dominated organic input close to the forest, while lateral transport was the major pathway for channels more than 20 m away from the forest. A conceptual framework has been developed to discuss the influence of terrestrial vegetation and fluvial morphology on organic matter input along the continuum of glacial streams.
4. POM inputs to a glacier stream

Introduction

Organic matter produced in terrestrial ecosystems and primary production in wetted channels provide the energy supporting heterotrophic stream fauna. The relative contribution of both energy sources depends on the availability of terrestrial organic matter and light, which are ultimately controlled by geology, geomorphology, and regional climate (Minshall, 1978; Vannote et al., 1980; Bott et al., 1985; Meyer & Edwards, 1990). In headwaters of forested catchments, riparian vegetation provides large amounts of organic matter to streams and severely impedes primary production by shading (e.g., Fisher & Likens, 1973). With increasing stream size, environmental conditions favor in situ primary production and the relative importance of allochthonous organic matter decreases. In arid environments, the input of allochthonous organic matter is typically small because of narrow riparian corridors and sparse upland vegetation (Cushing, 1997; Schade & Fisher, 1997), but environmental conditions favor high rates of primary production (e.g., Minshall, 1978; Cushing & Wolf, 1984; Lamberti & Steinman, 1997).

The climatic conditions in alpine catchments result in a range of riparian vegetation types from sparse grasslands to shrubs, generally providing low amounts of organic matter. The supply of allochthonous organic matter is expected to increase substantially when a stream enters the belt of subalpine forests. The anticipated longitudinal trend of organic matter input is contrary to deciduous forest settings outlined by Vannote et al. (1980), where headwaters are densely canopied and allochthonous inputs decrease towards the lower reaches. To our knowledge inputs of allochthonous organic matter have not been previously investigated in alpine streams.

Alpine streams may be kryal, krenal or rhithral in nature (Ward, 1994). Glacial (kryal) streams differ from non glacial alpine streams and, in particular, from subalpine or mountain streams in some key features influencing allochthonous organic matter input:

1. During summer, glacier melt results in high flow, high bed mobility (Milner & Petts, 1994), and, depending on geomorphic settings, in the formation of braided proglacial streams (Fenn & Gurnell, 1987). The wide active channel zone of such braided systems constrains the formation of woody riparian vegetation close to channels (Gurnell et al., 1999) which therefore lack shading by riparian vegetation. Auto-
Chthonous energy fixation is presumably far more important than in canopied headwaters and lateral transport by wind may be the dominating pathway for allochthonous inputs (Teeri & Barrett, 1975).

2) Glacial headwaters in the Alps are located close to treeline where forest productivity is generally low (Bray & Gorham, 1964). Additionally, many glaciers in the Alps are retreating, resulting in extended proglacial areas devoid of vegetation. Terrestrial vegetation in these systems is scarce or even lacking close to the glaciers but increases downstream (Burga, 1999; Gurnell et al., 1999; Zah et al., 2000a).

3) Subalpine forests are mainly made up of conifers. This may lead to a less marked seasonal pulse of organic matter input (Campbell et al., 1992). Because of their physical properties, the aerial and lateral transport of needles is presumably limited in space compared to leaves, leading to a different spatial distribution of abscised needles (Zah, unpublished data). Direct litter fall in coniferous forests has been shown to decline rapidly with distance from the forest edge (Conners & Naiman, 1984).

Although allochthonous inputs to glacial systems are typically low, these inputs may be important as an energy source due to limited algal growth in the cold, turbid, and unstable glacial channels (Ward, 1994). Generally, allochthonous inputs in glacial streams are expected to be low close to the glacier terminus but to increase downstream as woody riparian vegetation and forests develop.

The goal of this study was to quantify temporal and spatial patterns in the input of particulate terrestrial organic matter into a morphologically complex glacial stream system that also included a large active floodplain. We hypothesized that the input of allochthonous organic matter would substantially increase longitudinally from the glacier to the end of the catchment and laterally from the middle of the floodplain towards the edge of the valley. Furthermore, we expected direct litterfall to be the major pathway of particulate organic matter entering stream channels close to the forests, while towards the middle of the floodplain organic matter would be increasingly imported by lateral transport. The rational for these hypotheses was based on the assumption that organic matter input would be mainly controlled by the structure of the riparian zone. This structure changed in our study catchment longitudinally from almost barren recent glacial sediments to subalpine coniferous forests, and also laterally across the floodplain from subalpine hill-slope forests to non-vegetated gravel bars along the active floodplain channels.
4. POM inputs to a glacier stream

Fig. 4-1 Description of the Val Roseg glacial hydrosystem, showing positions of traps for measuring direct input and lateral transport of allochthonous organic matter. The map shows only the upper part of the study sites. Nine direct traps and 2 lateral traps were located in the lower reach.
Methods

Study area

The study was conducted in the Val Roseg located in the Bernina Massif (Upper Engadin, Eastern Switzerland, 9°53’57” E, 46°29’28” N, Fig. 4-1). The catchment area above the lowest sampling point is 67.4 km², with elevations ranging from 1768 to 4049 m a.s.l. About 30% of the drainage basin is glaciated. Meltwater from Tschierva and Roseg glaciers is the primary water source of the Roseg River. Both glaciers retreated by 0 – 84 m y⁻¹ during the last 10 years (Haeberli, Hoelzle & Frauenfelder, 1999). In July and August mean daily discharge measured at the end of the catchment ranged from 2.0 – 46 m³/s, between December and March mean daily discharge varied between 0.007 and 0.66 m³/s (Tockner et al., 1997).

Four morphologically different reaches characterise the study system (Fig. 4-1): a partially braided reach in the proglacial area of the Tschierva Glacier (length 650 m, elevation 2080 – 2160 m a.s.l.), a single-thread channel incised in glacial till (length 700 m, elevation 2020 – 2080 m a.s.l.), the main braided glacial floodplain (length 2800 m, elevation 1990 – 2020 m a.s.l.), and a reach that is mainly constrained by steep valley slopes (length 7200 m, elevation 1768 – 1990 m a.s.l.) at the lower end of the catchment. The floodplain reach (Fig. 4-1) comprises various channels of different hydrology, chemistry (Tockner et al., 1997), and morphology (Zah, Niederöst & Uehlinger, 2000b).

Tree line elevation in the Val Roseg is 2100 to 2300 m a.s.l.. Terrestrial vegetation varies from no woody vegetation close to the terminus of the Tschierva glacier (2160 m a.s.l.) to subalpine forests covering the valley slopes below the proglacial reach (Fig. 4-1). Dominant tree species were the conifers Larix decidua (Miller), Pinus cembra (L.) and Pinus mugo (Miller). Early successional stages of a subalpine larch forest characterise the plateau along the incised reach. Within the active floodplain, vegetation patches of different successional stages can be distinguished, corresponding to the vegetation described for the adjacent Morteratsch valley (Burga, 1999). The active channel area is characterized by gravel bars with initial stages of pioneer plants such as Epilobium fleischerii (Hochst.), Oxyria digyna (L.) and Linaria alpina (L.). Less disturbed areas show denser plant communities (e.g. Rumex scutatus-Poa nemoralis communities). Close to the floodplain border dense grassland with patches of Juniperus communis (L.) can be found; hill slopes are covered with coniferous forests dominated by Larix decidua, Pinus cembra and Pinus mugo.
4. POM inputs to a glacier stream

Fig. 4-2 Devices used to collect allochthonous organic matter. (a) direct trap: white bucket with 30 cm diameter and 0.5 mm holes in the bottom mounted on iron sticks 20 cm above ground. (b) lateral trap: 1 – plastic tube 50 cm x 10 cm, 2 – metal net (0.25 mm mesh-size), 3 – metal plate 50 cm x 50 cm, 4 – tubing for FPOM and DOC collection in additional bottle. (c) snow corer: plastic tube with 10 cm diameter and iron sawtooths at the lower end for cutting ice sheets.

Methods

Trap Samples

Direct litter input was monitored with 70 0.06-m² traps (Fig. 4-2a) placed 20 cm above ground along a longitudinal gradient from the glacier terminus to the lower end of the catchment and along perpendicular transects across the floodplain (Fig. 4-1). Lateral transport of particulate organic matter > 0.25mm was determined with 26 lateral traps (Fig. 4-2b) constructed according to Moser (1991). In the floodplain, four replicated lateral traps were placed at two different bank inclinations (flat: 10° ± 6°; steep: 33° ± 8°) in three riparian vegetation types: pioneer plants, dense grass cover and forest. Three lateral traps were placed in the proglacial area and 2 lateral traps were placed at the lower end of the catchment. Originally the lateral traps were designed to collect CPOM, FPOM and DOM. However, FPOM and DOM sampling was discontinued due to algal growth in the FPOM buckets. Therefore, only fractions > 0.25 mm were analyzed. The position of each trap was determined with differential GPS (error < 1 m). ARC/INFO software (ESRI, 1994) was used to determine the distance from each trap to the closest tree. Information on wind speed, precipitation, and snowfall during the sampling period was based on data from the nearest meteorological station (Samedan, 1721 m.a.s.l.) 10 km north of the floodplain. Discharge was measured continuously at a gauging station at the lower end of the Val Roseg catchment.
Results

The traps were used over a one-year-period and emptied monthly during the vegetation period from June to September and two times in October during the abscission of Larch needles. During the winter period, one survey was performed with a snow-corer (Fig. 4-2c) in order to collect direct litterfall stored within the snow (February 1999, Fig. 4-3a). All samples were frozen immediately upon returning to the laboratory. During the sampling period, damage to some direct and lateral traps occurred from cattle, human tampering, and floods. Damaged or obviously disturbed traps were immediately replaced.

In the laboratory, samples were thawed and dried for 3 days at 60°C before being sorted into 6 fractions: larch needles, pine needles, wood, leaves, grass, and remaining material. Ash free dry mass (AFDM) of the larch-, pine-, wood-, leaf-, and grass-fractions was calculated using previously determined regressions between dry matter and AFDM. The remaining material was ashed for 4 hours at 500°C assessing AFDM of the non-identifiable organic fraction and dry mass of the inorganic fraction.

Data analysis

Results from direct traps were transformed to g AFDM m² yr⁻¹ and lateral transport data were transformed to g AFDM m⁻¹ yr⁻¹. To calculate lateral input, lateral transport rates were divided by channel width. Resulting lateral input is expressed as g AFDM m² yr⁻¹ and may be compared with direct input. ANOVA was applied to analyze variance in lateral trap samples (Röhr, 1997). The semi-variance of aerial inputs and lateral inputs was assessed using the geostatistical method of semi-variance (VARIOWIN software, Pannatier, 1996). Unlike other methods, this approach treats samples as spatially dependent such that the variance of sampling sites at short lag distances is small, but increases with the distance between the pairs of sampling points. At a distance referred to as the range, the semi-variance attains a relatively constant value. This implies that beyond this range distance, the variation in the measured parameter is no longer spatially correlated (Journel & Huijbregts, 1978). Semi-variograms were calculated using a maximum distance of 500 m. Depending on the number of sampling sites, 50 m was selected as optimal lag, leading to 11 values of semi-variance for each variable.
4. POM inputs to a glacier stream

Fig. 4-3 Total input of allochthonous organic matter, and climatic and hydrologic variables during the sampling period in the Val Roseg.

Results

*Temporal patterns*

The average direct input of particulate organic matter, all sites combined, was less than 0.1 g m\(^{-2}\)d\(^{-1}\) between winter (February 1999) and summer and peaked in autumn at 0.85 g m\(^{-2}\)d\(^{-1}\). The average lateral input ranged from 0.07 g m\(^{-1}\)d\(^{-2}\) during spring to 0.21 g m\(^{-2}\)d\(^{-1}\) during autumn. Lateral input dominated organic matter input in June and July but direct inputs were two to four times higher during autumn (Fig. 4-3a). The autumnal litterfall coincided with intense precipitation in early October 1998 (Fig. 4-3b). Strong winds that could trigger needlefall were lacking between June 1998 and February 1999 (Fig. 4-3c). The autumnal litterfall occurred after two high flow events while discharge was receding (Fig. 4-3d).
The direct input of needles from larch, a deciduous conifer, peaked in early October and remained low during spring and summer (Fig. 4-4). The lateral input of larch needles was one magnitude lower except in spring. The direct input of pine needles displayed a similar temporal pattern as larch needles but seasonal variation was less distinct. Temporal variation of direct input and lateral input of wood, leaves and grass was more stochastic. Direct and lateral inputs of leaves and grass were relatively low. Lateral input of non-identifiable organic matter exceeded direct input two to ten times and did not vary seasonally.

**Input to the main channel: longitudinal trends**

Direct annual input of particulate organic matter increased from only 0.4 g m⁻²y⁻¹ in the proglacial area to 23 g m⁻²y⁻¹ at the end of the catchment (Fig. 4-5a). However, between the glacier and the end of the floodplain direct input averaged only 2 g m⁻²y⁻¹. Lateral annual transport of particulate organic matter increased almost linearly from 2.3 to 81 g m⁻¹y⁻¹ between the glacier and the end of the catchment (Fig. 4-5b). Assessed lateral inputs to the main channel, however, showed higher values.
Fig. 4-5 Direct input (a), lateral input, and lateral transport (b) of allochthonous organic matter collected with traps along the main channel (mean values of all traps ± 1 SD). (c) and (d): relative contributions of the different fractions to the total inputs at the respective sites. Trap locations are indicated above each panel (PG = proglacial reach, IN = incised reach, FP = floodplain reach, LR = lower reach).
Fig. 4-6 Left panels: allochthonous organic matter inputs across the floodplain. Right panels: relative contributions of different fractions to the total input.
4. POM inputs to a glacier stream

![Graph showing semi-variance of POM inputs](image)

Fig. 4-7 Standardised semi-variance ($\gamma_s$) of allochthonous organic matter inputs (annual means) to all direct and lateral traps.

than direct inputs in the floodplain reach, but only slightly increased towards the end of the catchment (Fig. 4-5b).

The dominant fractions of particulate organic matter in the direct traps of the proglacial reach, incised reach, and floodplain along the main channel were grass and non-identifiable material. In the lower reach however, needles were the dominant fraction (Fig. 4-5c). The organic material in the lateral traps was dominated by non-identifiable organic matter in the upper reaches, and larch and pine needles in the lower reach (Fig. 4-5d).

**Input across the floodplain**

Direct inputs of particulate organic matter decreased exponentially from the forests on the valley slopes to the middle of the floodplain (Fig. 4-6a). While direct inputs at the forest edge were > 50 g m$^{-2}$y$^{-1}$, direct inputs averaged only 8 g m$^{-2}$y$^{-1}$ about 50 m away from the forest edge. The semi-variance of direct inputs leveled off ($\gamma_s > 1$) at a distance of 150 m (Fig. 4-7). Beyond this distance, the variation in direct input was no longer spatially correlated. The lateral input of particulate organic material also declined with increasing distance from the forests, but the relation was approximately linear (Fig. 4-6b). A similar relation was found for lateral transport (Fig. 4-6c). Variance in organic matter input to lateral traps could not be explained either by riparian slope ($p = 0.17$) or by vegetation density ($p=0.07$), but lateral inputs of larch and pine needles were correlated with riparian slope ($p < 0.05$) and vegetation density ($p <0.01$). The semi-variance of lateral inputs was close to the correlation level ($\gamma_s = 1$), indicating no spatial dependence. The relatively low sample number probably caused the fuzzy pattern of the lateral semi-variance, because the benchmark of 30 sample...
Table 4-1 Total direct and lateral inputs into the different reaches of the Val Roseg catchment compared to literature data. 1: Canada Stream, Antarctica (McKnight et al., 1997); 2: Kuparuk River (Peterson, Hobbie & Corliss, 1986), Monument and Caribou Creeks, Alaska (Irons III, 1997); 3: coniferous forest streams, Oregon (Sedell, Triska & Gregory, 1982); 4: different desert streams, southwestern U.S. (Benfield, 1997).

<table>
<thead>
<tr>
<th>Stream</th>
<th>direct input (g·m⁻²·y⁻¹)</th>
<th>lateral input (g·m⁻²·y⁻¹)</th>
<th>total litter input (g·m⁻²·y⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Val Roseg, proglacial area</td>
<td>0.4</td>
<td>0.7</td>
<td>1.1</td>
</tr>
<tr>
<td>Val Roseg, floodplain</td>
<td>2</td>
<td>8</td>
<td>10</td>
</tr>
<tr>
<td>Val Roseg, lower reach</td>
<td>23</td>
<td>11</td>
<td>34</td>
</tr>
<tr>
<td>antarctic stream¹</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>tundra streams²</td>
<td>0 - 62</td>
<td>0 - 500</td>
<td>0 - 500</td>
</tr>
<tr>
<td>desert streams³</td>
<td>3 - 242</td>
<td>3 - 18</td>
<td>3 - 242</td>
</tr>
<tr>
<td>coniferous forests⁴</td>
<td>218 - 730</td>
<td>667 - 1111</td>
<td>218 - 1678</td>
</tr>
</tbody>
</table>

The quality of the direct inputs changed with distance from the forest (Fig. 4-6d). In the forest and at the forest edge, larch needles, pine needles, and the wood fraction were dominant. Five to 30 m away from the forest edge, needles were still dominant while wood was negligible and at distances more than 30 m away from the forest, grass and non-identifiable organic matter became major components. The lateral input in the forest and at the forest edge consisted of pine and larch needles, wood, and non-identifiable organic matter (Fig. 4-6e). Non-identifiable organic matter and grass were the most important components at distances of more than 15 m from the forest. In contrast to the direct inputs, larch and pine needles were still found 100 m away from forests.

Discussion
The results of this study demonstrated a significant increase in the input of allochthonous particulate organic matter from the glacier terminus to the end of the catchment, supporting our first hypothesis. This increase reflected to some extent
4. POM inputs to a glacier stream

the altitudinal change in terrestrial vegetation at the catchment scale. The results also indicated that a geomorphic feature such as a floodplain can modify organic matter input at the reach scale and, as a consequence, the longitudinal pattern in allochthonous matter supply. In the floodplain, the relative importance of lateral input increased with increasing distance from the forest edge, as predicted by our second hypothesis.

Temporal patterns

In the Val Roseg, the overall annual patterns of direct and lateral inputs were similar to those of temperate deciduous forests (e.g., Weigelhofer & Waringer, 1994; Pozo et al., 1997) mainly because of the autumnal abscission of larch needles. When litterfall occurs before the winter snow, as during this study, more allochthonous organic matter may reach the stream and serve as an important food source for macroinvertebrates (Robinson et al., 2000). The coincidence of needle abscission with low discharge is apparently a feature of alpine streams and contrasts with streams, where spates may occur during or shortly after the period of leaf abscission (Gonzalez & Pozo, 1996; Uehlinger & Naegeli, 1998). The amount of litter input during the period of snow cover was relatively low compared to a high arctic catchment (Teeri et al., 1975). If winter snow cover commences in October (this occurred two times in the Val Roseg

Fig. 4-8 Conceptual model of the influence of floodplains on direct and lateral input of allochthonous organic matter to glacial streams in the Alps. Solid line: hypothesised input without floodplain; dotted line: hypothesised input modified by a floodplain.
between 1980 and 1999), and when intense precipitation and storms are lacking, peak needlefall may be delayed until November. Under this scenario, the major fraction of autumnal litter input will be stored in the snow pack and is not available as a food source for aquatic invertebrates. During spring snowmelt this material will be released into the channel network and rapidly transported downstream by higher flow.

**Spatial patterns**

The total input of terrestrial litter to the investigated glacial stream was low (Table 4-1). The total annual input of organic matter in the proglacial area was 1.1 g AFDM m⁻²y⁻¹, which is in the lower range of data reported from streams draining catchments with grass or shrub vegetation (Table 4-1). Lower values may be expected in biomes lacking most terrestrial vegetation as, for example, in Antarctica (McKnight & Tate, 1997; McKnight et al., 1999). At the end of the catchment, where the Roseg River flows through subalpine forests, the annual input averaged only 34 g m⁻²y⁻¹. The coniferous forests of the subalpine zone are apparently a poor source of particulate organic matter compared to coniferous forests in the western United States or in the boreal zone of North America (Table 4-1). The low litter production of the larch and pine trees presumably reflects the harsh environment (low average temperatures, short vegetation period) that constrains forest productivity (Körner, 1999).

The Roseg floodplain seemingly reduced the expected increase of organic matter inputs between the proglacial area and the beginning of the constrained reach. Terrestrial vegetation in major parts of the floodplain was in an early state of succession or even lacking because of high channel turnover (about 25% per year, Zah et al., 2000b). Forests on the valley slopes produced relatively large amounts of organic matter compared with the floodplain vegetation but the average aerial transport distance (10 – 15 m) of this material was short compared to the floodplain width (150 – 500 m). Cessation of significant direct inputs within a few meters of the forest edge is a characteristic of coniferous forests (this study, Conners et al., 1984). The semi-variogram analysis indicated that large-scale parameters such as distance to forest or grass vegetation were major factors controlling direct organic matter input. The lateral transport of organic matter across the floodplain also declined with distance from the forest, but because this decrease was less pronounced, lateral transport became the dominant pathway of organic matter input to the floodplain 10 - 20 m away from the forest edge.
4. POM inputs to a glacier stream

The quality of the imported organic matter changed from the glacier to the end of the catchment and across the floodplain. Larch and pine needles dominated close to the forest and non-identifiable material prevailed in the proglacial area and, apart from grass litter, in the floodplain. All of this organic matter is a potential food for benthic invertebrates. A stable isotope study showed that allochthonous organic matter was an important food source in a groundwater fed stream located close to the forest at the floodplain margin (Zah et al., 2001). In the main channel, however, invertebrates preferentially fed on autotrophic biofilms, which are considered to be a more suitable food source than needle or leaf litter (Lamberti & Moore, 1984).

**Structure of the river corridor and allochthonous inputs**

In the preceding paragraphs the role of terrestrial vegetation and fluvial morphology for organic matter input to a glacial stream ecosystem has been discussed. Here we expand our conceptual view on general patterns of allochthonous organic matter input in glacier fed streams of the Alps, by emphasising the role of stream corridor morphology. If the glacier terminus is above treeline and the stream channel is constrained, direct and lateral organic matter input increases moderately from the terminus to the treeline. Below treeline litter production intensifies, and as consequence, litter input increases (solid lines in Fig. 4-8). A floodplain above the treeline has a minor influence on the generally low direct and lateral inputs (Fig. 4-8a,b). If a floodplain is below but close to the treeline as in the Val Roseg, direct input remains low until the end of the floodplain (Fig. 4-8c). In a floodplain with pioneer vegetation, lateral inputs are expected to increase because the channel network expands the riparian zone, thereby enhancing the transport of organic matter to floodplain reaches (Fig. 4-8d). For example, the shoreline of the channel network in the Val Roseg floodplain is more than eight times longer than for a single-thread channel system. A vegetation-free floodplain reduces lateral inputs. If the floodplain is located distinctly below the treeline, direct inputs will increase towards the upper end of the plain and subsequently drop to a low level within the floodplain reach (Fig. 4-8e). Lateral inputs will generally increase because of the expanded shoreline (Fig. 4-8f upper curve). However, if the canopy in the constrained reach is dense, a floodplain may also lead to a decrease in lateral inputs due to lower inputs from the side slopes (Fig. 4-8f lower curve).
Acknowledgements

We wish to thank G. Herzog, H. Zah, C. Ermert, B. Fasnacht, B. Känel, and the Val Roseg Group for helping with fieldwork. We also thank Prof. J.V. Ward and C. Robinson for critically reviewing this manuscript. This study was supported by a research grant from the Swiss National Science Foundation (SNF 21-49243.96).

References


4. POM inputs to a glacier stream


References


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5. **Structure and particulate organic matter content of glacial stream sediments**

Grain size structure and organic matter content of subsurface sediments were assessed along an altitudinal gradient and across an alpine floodplain of a glacier stream (Val Roseg, Switzerland). Sediment porosity and fine fractions of inorganic sediments (0.25 - 4 mm) significantly increased with depth. The total POM-reservoir in this glacial hydrosystem ranged from 1.8 to 4.8 g dm$^{-3}$, which is 2 - 4 x lower than in low-elevation streams. Organic matter content in the hyporheal increased along the altitudinal vegetation gradient from the proglacial area into the zone of subalpine forests. This increase was more pronounced for fine organic matter and detached organic fractions than for biofilms. A predicted lateral increase of subsurface POM from the highly disturbed main channel to the stable groundwater channels in the floodplain was not found. Hydrological effects were clearly reflected by the distribution of fine organic matter. This fraction was largely absent in the top layers (0 – 30 cm) of the most disturbed main channel reaches, indicating frequent bed movement at these sites.
5. Subsurface storage of POM in a glacier stream

Introduction

Primary production in the wetted channel and allochthonous inputs of organic matter produced on the floodplains and uplands provide the energy base driving lotic ecosystems. Environmental extremes such as high flow or drought may severely reduce the autotrophic energy capturing capacity of the ecosystem (Biggs & Close, 1989; Uehlinger, Bührer & Reichert, 1996). In such a case, an alternative energy source is needed to sustain ecosystem functioning. In streams with dense woody riparian vegetation, resistance against disturbance is assumed to be high, because a large reservoir of allochthonous organic matter prevents a shortage of energy (Cummins et al., 1973; Ward & Aumen, 1986; Graca, 1993). In a prealpine river draining a forested catchment, Naegeli et al. (1995) found evidence that the pool of organic matter stored in the sediments is replenished during spates. This relatively stable pool is assumed to sustain the energy supply at the ecosystem level after removal of benthic algae by bed moving spates (Naegeli, Huggenberger & Uehlinger, 1997; Uehlinger & Naegeli, 1998).

Glacier streams in the Alps are characterised by harsh environmental conditions. High turbidity and bedload transport during summer high flow constrain primary production to periods of 4-6 weeks in late spring and in autumn before the onset of winter snow cover (Uehlinger, Zah & Bürgi, 1998). The sparse vegetation of the alpine zone contributes little allochthonous organic matter (Zah & Uehlinger, 2001b), and, due to this lack of woody debris, movement of bed sediment is not expected to enhance transport of particulate organic matter to the sediments. Therefore, organic matter stored in sediments is expected to be low unless the stream flows through the zone of subalpine forests, which are a relatively rich source of allochthonous organic matter (Zah & Uehlinger, 2001b). The lack of substantial allochthonous organic matter input and extended periods of high flow during summer are expected to deprive uppermost sediments from particulate organic matter. However, fine particulate organic matter may accumulate in sediments not affected by bed movement. This material may be a food source for invertebrates unless vertical migration is impeded by small pore size (Carling, 1984; Cunningham, Anderson & Bouwer, 1987).
The amount and spatial distribution of organic matter stored in the sediments depends on the input of organic matter, channel stability, hydraulic conditions and sediment structure (Brunke, 1998). A geomorphic element such as a floodplain is expected to modify these factors by influencing riparian vegetation, grain size distribution, or channel diversity with respect to stability, hydraulic conditions, and hydrological connectivity (Tockner et al., 1997; Ward et al., 1999).

In this study we focused on organic matter stored in the uppermost sediment layers of a glacier stream in the Swiss Alps. Along the continuum of this stream, the riparian vegetation changed from sparse pioneer plants in the proglacial area to subalpine forests in the lower parts of the catchment. A remarkable feature of this system is a large glacial floodplain with a hydrologically diverse channel network. Our first objective was to test the hypothesis that sediment organic matter will reflect the change in riparian vegetation along the main stream channel. Our second objective was to explore to what extent organic matter stored in the sediments may reflect channel stability, hydrology and organic matter input. For this, we focused on the floodplain, which in this respect offered an array of different channel types. We expected that concentrations of organic matter would be highest in stable channels close to the floodplain margins because of low discharge and proximity to the densely vegetated valley slopes. Moreover, some of these channels were also fed by small streams draining the valley-slope forests. Minimum organic matter storage was expected in the main channel, which is subject to high flow and bedload transport during summer and which receives minor amounts of terrestrial organic matter because of the sparse riparian vegetation along the unstable banks. Sediment organic matter in channels intermittently connected with the main channel were located between these extremes. Finally, we expected that channel stability and differences in organic matter supply should also be reflected by the vertical distribution of organic matter, i.e. organic matter content of the uppermost sediment of the groundwater channels should be higher than in the sediments of the highly disturbed main channel.
Fig. 5-1 Map of the Val Roseg hydrosystem. Middle panel: locations of sampling sites for the altitudinal aspect; right panel: Sampling sites used for the floodplain aspect.
Study system

This study was conducted in the Roseg Valley located in the Bernina Massif (Upper Engadin, Eastern Switzerland, 9°53′57″ E, 46°29′28″ N, Fig. 5-1, left). The catchment area above the lowest sampling reach is 67.4 km², with elevations ranging from 1768 to 4049 m a.s.l. About 30% of the drainage basin is glaciated. Meltwater from Tschierva and Roseg glaciers is the primary water source of the Roseg River. Both glaciers retreated by 0 – 84 my⁻¹ during the last 10 years (Haeberli, Hoelzle & Frauenfelder, 1999). In July and August mean daily discharge measured at the end of the catchment ranged from 2.0 – 46 m³s⁻¹, between December and March mean daily discharge varied between 0.007 and 0.66 m³/s (Tockner et al., 1997).

Four morphologically different reaches characterise the study system (Fig. 5-1, middle): a partially braided reach in the proglacial area of the Tschierva Glacier (length 650 m, elevation 2080 – 2160 m a.s.l.), a single-thread channel incised in glacial till (length 700 m, elevation 2020 – 2080 m a.s.l.), the main glacial floodplain (length 2800 m, elevation 1990 – 2020 m a.s.l.), and a reach that is mainly constrained by steep valley slopes (length 7200 m, elevation 1768 – 1990 m a.s.l.) at the lower end of the catchment. Within the floodplain, different channel types can be distinguished based on their hydrology, chemistry, and morphology (Tockner et al., 1997): the main channel (M), that is mainly fed by glacial meltwater of the Tschierva and Roseg glaciers, side channels (S) with upstream and downstream connections to the main channel, and groundwater channels (G) fed by alluvial groundwater and only connected downstream with the main channel (Fig. 5-1, right).

Treeline elevation in the Val Roseg is 2100 to 2300 m a.s.l. Terrestrial vegetation varies from almost absent on bare gravel close to the terminus of the Tschierva glacier (2160 m a.s.l.) to subalpine forests covering the valley slopes below the proglacial reach (Fig. 5-1). Dominant tree species were the conifers Larix decidua (Miller), Pinus cembra (L.) and Pinus mugo (Miller). In the floodplain, the main channel and side channels form the active channel area (braided corridor) where the riparian zone is characterized by gravel bars with initial stages of pioneer plants such as Epilobium fleischerii (Höchst.), Oxyria digyna (L.) and Linaria alpina (L.). Less disturbed areas show denser plant communities (e.g. Rumex scutatus-Poa nemoralis communities). Close to the floodplain border dense grassland with patches of Juniperus communis (L.) can be found; hill slopes are covered with coniferous forests dominated by Larix decidua, Pinus cembra and Pinus mugo.
5. Subsurface storage of POM in a glacier stream

Methods

Sampling sites
Five sampling sites were selected along the main channel: one site in the proglacial area (M1), two sites in the floodplain reach (M2, M3) and two sites in the constrained reach (M4 and M5, Fig. 5-1). In the floodplain we additionally sampled two side channels sites (S1, S2) and two groundwater channels sites (G1 and G2, Fig. 5-1). At each of these sites three to five replicated freeze cores were extracted in September 1998 during medium flow conditions, resulting in a total of 39 cores. For the longitudinal aspect we referred to the 5 sites along the main channel (M1 – M5). For the floodplain aspect we grouped the results for the two replicated sites of the main channel (M2, M3), side channels (S1, S2), and groundwater channels (G1, G2) and we referred to three sites along a lateral gradient (M, S, G).

Fig. 5-2 Patterns of porosity. a: across the floodplain, b: along the altitudinal gradient, c: porosity vs. depth (mean values ± 1 S.D.).
**Freeze coring**

Freeze cores were taken to a sediment depth of 50 cm and were cut into five sections of 10 cm and stored at -23° before analysis (Stocker & Williams, 1972). First, the total volume of each sample was determined by displacement water. Rocks greater than 64 mm were excluded from further analysis as recommended by Adams & Beschta (1980) in order to reduce the effect of extreme values for relatively small amounts of sediment. The sediment was then thoroughly agitated and rinsed with a standardized volume of water. The fraction of organic matter > 0.063 mm which was only loosely associated with the sediment (loosely associated organic matter, LOM) was elutriated according to Pusch & Schwoerbel (1994) and ash-free dry mass was determined (APHA, 1992). Ash-free dry mass of the organic matter which remained on rinsed sediment, i.e. the OM-fraction strongly associated with the sediment of the grain sizes 0.063 - 16 mm (strongly associated organic matter, SOM) was determined by drying and combustion (Pusch & Schwoerbel, 1994). The fraction < 0.063 mm, containing small detached organic particles and organic matter attached to small inorganic particles, was designated fine organic matter (FOM). This fraction was subsampled, and ash-free dry mass was determined according to APHA (1992) after filtration through glass-fibre filters (Whatman GF/F). After POM determination,

![Logarithmic plot of total grain size fractions vs. depth; asterisks indicate significant gradients (p < 0.05, linear regression analysis of untransformed values).](image)

Fig. 5-3 Logarithmic plot of total grain size fractions vs. depth; asterisks indicate significant gradients (p < 0.05, linear regression analysis of untransformed values).
Fig. 5-4 Spatial distribution of grain size fractions. Top panels: altitudinal aspect, lower panels: floodplain aspect.
Fig. 5-5 Spatial distribution of organic matter fractions. Top panels: altitudinal aspect, lower panels: floodplain aspect.
the remaining mineral sediment was fractionated by dry sieving into the following size classes: 64 – 16 mm, 16 – 4 mm, 4 – 1 mm, 1 – 0.25 mm, 0.25 – 0.063 mm and < 0.063 mm.

The porosity of core samples (%) was calculated as the volume of pore water divided by the volume of the saturated core sample times 100. The pore water volume was determined as the difference between wet and dry weight of the core sample. The results of the sediment analyses were expressed as g dm\(^{-3}\). Finally, linear regressions were calculated for analysing gradients, and ANOVA’s with Tukey’s HSD post-hoc tests were calculated to compare results from different sites.

**Results**

**Sediment structure**

Porosity of the core samples varied between 8.6 % and 22.9 %. Along the main channel porosity showed no significant trend (linear regression: \( r^2 = 0.04 \)) although average values of the three upstream reaches were lower (only site M4 significantly differed from sites 1 and 3: ANOVA \( p < 0.01 \), Fig. 5-2 b). Average porosity slightly decreased across the floodplain from main channel sites (17.8 %) to side channels (14.7 %) and groundwater channels (13.7 %) but differences between sites were not significant (\( r^2 = 0.02 \), ANOVA: \( p = 0.19 \), Fig. 5-2 a). Linear regression analysis showed

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**Table 5-1** Organic matter content of sediments (0 - 0.5 m depth) at the different sampling sites (mean values ± 1 S.D.).

<table>
<thead>
<tr>
<th>site</th>
<th>POM-fractions</th>
<th>total POM</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>LOM</td>
<td>SOM</td>
</tr>
<tr>
<td></td>
<td>g AFDM dm(^{-3})</td>
<td>g AFDM dm(^{-3})</td>
</tr>
<tr>
<td>proglacial area</td>
<td>0.06 ± 0.17</td>
<td>1.87 ± 1.47</td>
</tr>
<tr>
<td>floodplain: main channel</td>
<td>0.44 ± 0.65</td>
<td>2.10 ± 1.08</td>
</tr>
<tr>
<td>floodplain: side channels</td>
<td>0.52 ± 0.76</td>
<td>2.27 ± 1.04</td>
</tr>
<tr>
<td>floodplain: groundwater ch.</td>
<td>0.17 ± 0.23</td>
<td>2.15 ± 0.94</td>
</tr>
<tr>
<td>constrained reach</td>
<td>0.49 ± 0.50</td>
<td>2.63 ± 1.12</td>
</tr>
</tbody>
</table>
Results

a significant increase of porosity with depth for all sites ($r^2 = 0.16$, ANOVA: $p = 0.04$, Fig. 5-2 c).

The average grain size distribution in different depths is depicted in Fig. 5-3. All fractions < 4 mm increase significantly with depth, the 4-16 mm fraction does not change but the 16-64 mm fraction significantly decreases. The site-specific vertical grain size distributions are shown in Fig. 5-4. At the upper main channel sites (M1, M2, M3) finer fractions (< 4 mm) increased with depth. At the main channel sites in the constrained reach (M4, M5), however, size distribution hardly changed with depth. The vertical size distribution changed across the floodplain. At the main channel sites small size fractions increased with depth but this trend was less distinct at the side channel sites and almost lacking at groundwater channel sites. Porosity exhibited a significant positive correlation with different fine fractions: 0.064 – 0.25 mm ($r^2 = 0.39$), 0.25 – 1 mm ($r^2 = 0.45$), 1 – 4 mm ($r^2 = 0.35$).

Organic matter distribution

The major organic matter fraction in this study was SOM (organic matter strongly associated with particles > 0.064 mm). This fraction made up to 75 % of all particulate organic matter stored in the uppermost 50 cm of the bed sediments (Fig. 5-5). LOM (loosely attached particulate organic matter) consisted mainly of root fragments and accounted for 15 % of the total particulate organic matter. About 10 % of the total particulate organic matter was FOM (< 0.064 mm).

Total particulate organic matter was lowest in the proglacial area (Table 5-1). In the floodplain, total particulate organic matter concentrations were higher, but similar among the different floodplain sites. Highest concentrations of total particulate organic matter were found in the lower reach. LOM was widely absent at the proglacial area, and low in the groundwater channels. The other sites, which were all affected by bedload transport, showed higher values of LOM. The concentrations of SOM paralleled the general trend of total particulate organic matter, while FOM was mainly found in the lowest reach (Table 5-1). At the main channel sites FOM concentrations decreased with depth (Fig. 5-5). In side and groundwater channels vertical distribution of FOM was relatively homogeneous. The vertical distribution of SOM and LOM showed no consistent pattern throughout the catchment.
5. Subsurface storage of POM in a glacier stream

Discussion

The results of this study support the hypothesis that organic matter stored in bed sediments increases from the glacier to the end of the catchment. This gradient apparently reflected the large-scale altitudinal change in terrestrial vegetation and allochthonous organic matter inputs. The data were not in accordance with our second hypothesis, in which we predicted increasing sediment organic matter from the unstable main channel to stable groundwater fed channels at the floodplain border. However, the vertical distribution of FOM appeared to be influenced by sediment stability and flow. FOM increased with depth at the main channel sites, which were subject to high flow and bedload transport. Side channels and groundwater channels, which were rarely disturbed, exhibited a homogenous FOM distribution with depth. Generally, subsurface distribution of particulate organic matter reflected flow conditions rather than the supply of allochthonous organic matter supporting the results of other studies in this thesis (Zah et al., 2001a; Zah & Uehlinger, 2001b).

In the Roseg River, sediment porosity was positively correlated with the relative contribution of fine fractions (0.25 - 4 mm) of sediment. This result can be explained by the fact that sediments with small pores (e.g. clay or silt) generally have a higher porosity (Gibert, 1994; Brunke & Gonser, 1997). Referring to the distribution of grain sizes and porosity, we postulate that the hyporheic zone of the Roseg stream is a suitable habitat for both permanent hyporheic and epigean communities, providing lateral, longitudinal, and vertical connectivity (Stanford & Ward, 1993). This has been confirmed by Malard et al. (2001), who demonstrated, that subsurface sediment is the major habitat of oligochaetes in the Val Roseg catchment, and benthic assemblages of oligochaetes are primarily controlled by vertical migration of hyporheic populations.

Although the glacier streams draining the Roseg catchment transport huge amounts of inorganic suspended solids (60 ± 25 mg l⁻¹) (Tockner et al., 2001) the stream sediments are not clogged by these fine particles. This might have two explanations. First, colmation is reduced under natural conditions by bed-moving floods (Schächli, 1992). Secondly, we hypothesize that the dominance of the coarse sediment fraction and the bulky form of the crystalline particles (Malard, Tockner & Ward, 1999) result in a high permeability. As consequence, the transport of glacial
flour through the sediments is hardly impeded and thus prevents clogging of the streambed.

In this study we discriminated three organic matter fractions: (1) the fraction of loosely attached particulate organic matter (LOM) consisted mainly of fragments of allochthonous origin like roots or woody particles. Consequently, this fraction was widely absent in the proglacial area due to the absence of allochthonous inputs. It was also nearly absent in the groundwater streams, because bed-moving flow, during which particulate organic matter can be transported into the sediments (e.g., Naegeli et al., 1995), were lacking. LOM is presumably an important energy source for microbial communities. For example LOM was significantly correlated with oxygen consumption in a mountain stream (Pusch & Schwoerbel, 1994) and also in the Roseg River (Uehlinger, unpublished data). (2) the fraction of strongly associated organic matter (SOM), which made up 75% of total subsurface organic matter. This fraction presumably consisted of epilithic biofilms, which are known to be dominated by the polysaccharid matrix (Leichtfried, 1988). SOM does not correlate with oxygen consumption (Uehlinger, unpublished data). The origin of this fraction may be autochthonous (algal exudates) and allochthonous (groundwater DOC). (3) the so-called FOM fraction (diameter < 0.064 mm), that might be of allochthonous or autochthonous origin. Such fine organic particles are a valuable food source for the interstitial fauna (Bärlocher & Murdoch, 1989). FOM was found at the proglacial area where allochthonous inputs are low, therefore suggesting autochthonous origin. However, highest FOM-concentrations were found in the constrained reach, where allochthonous inputs were high. The amount of the FOM-fraction was low in the uppermost sediments of sites that were exposed to bed movements, presumably because this mobile fraction is removed during bedload transport.

The total reservoir of particulate organic matter in the Val Roseg ranged from 1.8 to 4.8 g dm⁻³. This is low compared to other studies. In the subalpine Necker river, a total POM reservoir of 4 - 10 g dm⁻³ was found (Naegeli, 1997). Leichtfried (1991) and Metzler & Smock (1990) reported values 2 - 4 x higher than in the Val Roseg. However, the subsurface reservoir of particulate organic matter is much greater than the annual input of allochthonous organic matter into the Val Roseg study area (Chapter 6). LOM correlated significantly with respiration (Uehlinger, unpublished
5. Subsurface storage of POM in a glacier stream

data) indicating the ecological relevance of subsurface organic matter for microbial communities in the Roseg River. We assume that sediment organic matter is a major food source also for the benthic and hyporheic invertebrates of this harsh glacial stream, presumably even more important than for invertebrates in non-glacial streams (Bretschko & Leichtfried, 1988; Eglin, 1990; Naegeli, 1997).

Acknowledgements

We wish to thank the Val Roseg Group, Dave Arscott, Mäggi Hieber, and Matthias Brunke for helping with freeze core sampling. This study was supported by a research grant from the Swiss National Science Foundation (SNF 21-49243.96).

References


5. Subsurface storage of POM in a glacier stream


6. Spatial modeling of allochthonous inputs of particulate organic matter to a high alpine floodplain

The Val Roseg floodplain (elevation 2000 m a.s.l.) is located 1.5 km downstream of the termini of two valley glaciers in the Swiss Alps. As part of a holistic research project, we studied the pathways of allochthonous organic matter (OM) into the complex channel network of this floodplain system. Sources of allochthonous OM were the floodplain vegetation, subalpine forests on the valley slopes, and organic particles entrained within the two glaciers. Pathways examined included direct and lateral transport of terrestrial OM, and stream transport of terrestrial OM eroded by shifting channels. To quantify organic loadings in floodplain channels, we combined field data from organic matter traps and grab samples with remote sensing data (high resolution airborne images and digital elevation models). Using a geographic information system we modeled the different pathways of allochthonous OM for the entire channel network of the floodplain. Results showed lowest values from direct inputs to the channel network (0.07 tons y\(^{-1}\)) and intermediate values from lateral input (0.48 tons y\(^{-1}\)). The major input of organic matter was by bank erosion of the channel network (23.4 tons y\(^{-1}\)). Forty percent of the direct inputs and twenty percent of the lateral inputs ended up in the main channel. However, the tributaries, although covering only a small channel area, received even a higher amount of direct and lateral inputs.
6. Spatial modeling of allochthonous organic matter pathways

Introduction

Allochthonous particulate and dissolved organic matter are important energy sources for heterotrophic communities in lotic ecosystems. This is especially true for streams with a strong spatial connection to productive terrestrial ecosystems, like forested headwaters (Vannote et al., 1980), for intermittent streams with alternating terrestrial and aquatic phases (Webster et al., 1987), or for floodplains with temporally variable interfaces to terrestrial ecosystems or highly productive floodplain vegetation (Cuffney, 1988; Junk, Bayley & Sparks, 1989; Ward, Tockner & Schiemer, 1999b).

Allochthonous organic matter input to hydrosystems occurs along different pathways (Fig. 6-1). Particulate organic matter may enter the stream by direct aerial transport. This pathway, which is mainly relevant for the transport of freshly abscised leaves and needles, has been investigated in many studies (e.g., Fisher & Likens, 1973; Benfield, 1997; Pozo et al., 1997). Terrestrial organic matter deposited on the ground can be transported towards the stream by wind (Teeri & Barrett, 1975) or by overland flow (Peterson, Hobbie & Corliss, 1986). This so-called lateral transport also entrains parts of herbaceous plants and partially decomposed organic matter. Infiltrating precipitation may leach terrestrial detritus and enrich ground water with dissolved organic matter (Mann & Wetzel, 1995), which may enter the stream in groundwater exfiltration zones. The input of organic matter by bank erosion in active floodplains is a potential pathway but its relative contribution to the overall organic matter input has not been studied thus far. Finally, substantial amounts of particulate or dissolved organic matter may be imported by hydrological transport from upstream locations in the catchment (e.g., Dance, Hynes & Kaushik, 1979; Maamri, Chergui & Pattee, 1994).

Assessment of direct or lateral inputs to single-thread channels is straightforward because the input values can be measured along both shorelines and easily extrapolated to the stream area (Schade & Fisher, 1997). In floodplains characterized by multiple channel networks, assessment of allochthonous inputs becomes more difficult because of the spatial configuration of potential sources of organic matter, which is usually much more complex than for single channel systems (Ward et al., 1999b; Zah, Niederöst & Uehlinger, 2000). Depending on the size and complexity
Introduction

of the system the application of methods derived in landscape ecology may be required.

In floodplains situated in alpine regions, woody vegetation is sparse or even lacking (Gurnell et al., 1999). Furthermore, the high sediment supply in glacial catchments leads to dynamic channel networks with high turn-over rates (Hickin, 1993). These two factors led us to expect that organic inputs by bank erosion are especially important for glacial floodplain ecosystems, due to the limited direct input of allochthonous organic matter.

This study focused on the input of allochthonous organic matter to a floodplain in the Alps that is influenced by glacier runoff. The first objective was to estimate direct and lateral input of particulate organic matter to the channel network of the floodplain. Because of the complex spatial configuration of potential sources of particulate organic matter (forests, grass plots of different vegetation densities), we used a GIS-based model for integrating field data of organic matter traps with high-resolution airborne images and a digital elevation model. The second objective was
6. Spatial modeling of allochthonous organic matter pathways

to quantify the input of organic matter by bank erosion. About 30% of the floodplain channels move laterally several meters per year (Zah et al., 2001b), thereby eroding banks with heterogeneous vegetation coverage. The final objective was to evaluate the relative and absolute inputs of organic matter to the different channel types of this alpine floodplain.

Methods

Study system

The upper catchment of the Roseg River is located in the Bernina Massif (Upper Engadin, Eastern Switzerland, 9°53’57” E, 46°29’28” N). Its area is 49.5 km² with elevations ranging from 1990 to 4049 m a.s.l., about 42% of which are glaciated. Meltwater from Tschierva and Roseg glaciers is the primary water source of the Roseg River. The main floodplain (length 2800 m, elevation 1990 – 2020 m a.s.l.) is about 1.3 km downstream from the terminus of the Tschierva glacier. Floodplain width ranges from about 500 m in the upper section to 130 m in the lower section.

Bare gravel or gravel with initial stages of pioneer plants such as Epilobium fleischerii (Hochst.), Oxyria digyna (L.) and Linaria alpina (L.) characterize the active channel area. Less disturbed areas contain denser plant communities (e.g. Rumex scutatus-Poa nemoralis communities). Close to the floodplain border, dense grassland with patches of Juniperus communis (L.) can be found. Subalpine forests cover the valley slopes along the floodplain. Dominant tree species are the conifers Larix decidua (Miller), Pinus cembra (L.), and Pinus mugo (Miller). The elevation of the treeline is about 2300 m a.s.l.

Within the floodplain different channel types can be distinguished based on their hydrological connectivity and physico-chemical attributes (modified after Tockner et al., 1997): (1) The main channel draining the floodplain is mainly fed by glacial meltwater of the Tschierva and Roseg glaciers and forms, together with (2) side channels, a braided corridor; (3) intermittently-connected channels are permanently connected downstream and temporarily connected upstream to the main channel; (4) alluvial groundwater channels fed by alluvial groundwater have only downstream connections with the main channel; (5) lateral groundwater channels fed by water from the hill slope aquifer also have only downstream connections with the
Fig. 6-2 Data layers used for spatial modelling of organic matter inputs: (a) organic matter traps, channel network, and positions of single trees in the Val Roseg catchment, (b) classification of terrestrial vegetation density, (c) digital elevation model (hillshade visualisation), (d) slope derived from digital elevation model.
Fig. 6-3 Resulting maps of spatial modelling: (a) map of annual direct inputs of particulate organic matter, (b) map of annual lateral transport of particulate organic matter, and (c) map of vegetation density and of areas affected by bank erosion between July 1998 and June 1999.
main channel; and (6) tributaries entering the floodplain from side-valleys fed by hillslope aquifers or small side glaciers. The annual flow variation shifts the floodplain channels from surface (melt) water dominance in summer to a groundwater controlled system in winter (Ward et al., 1999a). This shift is paralleled by a distinct seasonal expansion and contraction cycle of the channel network (Malard, Tockner & Ward, 1999).

**Assessment of organic matter**

Direct input (aerial transport) of particulate organic matter was monitored with 60 traps (Fig. 4-2a) placed along transects across the floodplain (Fig. 6-2a). The traps were exposed over a one-year period (1998/99) and sampled monthly during the vegetation period from June to September and two times in October during the abscission of larch needles. One survey was performed in February (reg. Chapter 4) to collect direct litter fall stored within the snow pack using a snow corer (snow cover lasted from November 1998 to May 1999). Lateral input of particulate organic matter > 0.25 mm was determined with 23 lateral traps (Fig. 4-2b). Apart from the period with snowcover, these traps were sampled at monthly intervals between June 1998 and June 1999. A detailed description of the assessment of lateral and direct inputs to the Val Roseg floodplain has been given by Zah & Uehlinger (2001c).

We determined the organic matter content of floodplain soil for the following three vegetation densities: bare gravel, sparse pioneer vegetation and dense grass cover. In five areas of each vegetation type the top layer (0 – 10 cm) and the bottom layer (10 – 30 cm) were sampled (Fig. 6-2b). Soil organic matter was determined as ash-free dry mass (AFDM) and expressed as g AFDM m\(^2\).

**Remote sensing data**

Aerial photographs (color film and color infrared film) of the Val Roseg floodplain were taken on 29 July 1998, at 13:00 GMT with a standard aerial camera (WILD 21 NAGIIA-F, focal length 214.74 mm). Color photographs were used for the generation of a digital elevation model (DEM), while orthophotos were created from color infrared images for a better differentiation of vegetation patterns and areas covered by water. Two low elevation image strips covering the entire floodplain area were scanned (scale 1:5000, scan resolution 21 microns). The exterior orientation of the images was determined in a bundle block adjustment for each strip separately using
6. Spatial modeling of allochthonous organic matter pathways

ground control points that were measured with DGPS and marked prior to the flight. The photogrammetric evaluation was performed with the digital station PHODIS (by ZI-Imaging). The data analyzed by GIS consisted of a Digital Elevation Model (DEM) with a rasterwidth of 2 m for the floodplain (estimated height accuracy about 0.12 m). Digital color infrared orthophotos of the floodplain were created with a footprint of 0.25 m. This high-accuracy DEM and the color-IR-orthophotos were used for the spatial correction of an additional set of aerial color-IR images that were taken in 1999 (resolution: 0.25 m). Orthophotos were generated with OrthoEngine (by PCI-Geomatics) on a UNIX-workstation.

For 1998 and 1999, the area along the corridor of active channels was vectorized as polygon coverage with ArcInfo (ESRI, 1994). The exact location of direct and lateral traps was determined with differential GPS (TRIMBLE Pathfinder). The orthophotos of 1998 were used to locate single trees on the valley slopes along the floodplain. More than 10000 trees were digitized and stored as point slopes along the floodplain. We distinguished between larch (Larix decidua) and pine (Pinus cembra and Pinus mugo were lumped together, Fig. 6-2a). Three separate color bands were extracted from the infrared orthophotos to produce a vegetation density map of the floodplain and the adjacent valley slopes. Maximum-likelihood classification was applied to separate the following six vegetation classes: channel, bare gravel, sparse pioneer vegetation, dense grass, shrub community and forest (Fig. 6-2b). From the DEM (Fig. 6-2c) slopes were calculated (Fig. 6-2d).

Model description for direct and lateral organic matter input

An exponential decrease of direct litter input (leaves and needles) with distance from the forest edge has been demonstrated by Conners & Naiman (1984) and Zah & Uehlinger (2001c). The relative decrease of litter input with distance from a single tree is described as:

$$\frac{I_D(x)}{I_D(x_0)} = e^{-ax}$$  \hspace{1cm} (1)
Methods

$I_D(x)$ is the direct input (g AFDM m\(^{-2}\) y\(^{-1}\)) at a distance $x$ (m) from a tree; $x = 0$ is $x_0$. The model parameters $I_D(x_0)$ (g AFDM m\(^{-2}\) y\(^{-1}\)) and $a$ (m\(^{-1}\)) were identified for each sampling date using all trap data on this date. These equations were used to generate the matrices describing spatial patterns in the deposition of larch needles, pine needles and other organic matter (twigs, cones, non-identifiable matter) for a single tree (Fig. 6-4). These matrices were combined with actual tree coverage, i.e. the larch matrix was applied to every larch tree in the catchment, the pine matrix to every pine tree, and the matrix for other organic matter to both species. By overlaying all distribution matrices using the grid module of ArcInfo, a 2 m-grid of spatial distribution for the relative (dimensionless) direct organic matter input was generated for each sampling date. The factor to convert relative input rates to absolute rates (g m\(^{-2}\) y\(^{-1}\)) was obtained by linear regression of trap data on relative input rates, which were calculated for each trap site. To evaluate the modeling of direct input rates, we randomly selected 50\% of the trap sites and determined the conversion factor. This was then used to predict input rates for the remaining trap sites. Predicted and measured rates were compared using linear regression analysis. Direct input was calculated for each grid-point in monthly intervals for the period June 1998 to June 1999.

Lateral transport to stream channels is highly variable because local factors such as vegetation density, bank inclination (transport by gravity) or wind patterns prevail (Comiskey et al., 1977). Organic matter, which is deposited by aerial transport (di-

Fig. 6-4 Standardized spatial distribution of direct needle input. Left panel: larch trees, right panel: pine trees.
6. Spatial modeling of allochthonous organic matter pathways

![Graph A](image)

![Graph B](image)

![Graph C](image)

Fig. 6-5 Direct allochthonous organic matter inputs during July 1998: Correlation of modeled data with field results, a) larch, b) pine, c) remaining particulate organic matter (POM).

rect input) to areas close to stream channel, is also subject to lateral transport. Equation 2 describes the general model used for calculating lateral transport $I_L$ (g m$^{-2}$y$^{-1}$).

$$I_L = a + bV + cS + dI_{DC}$$

(2)

$V$ is the dimensionless vegetation density, $S$ is bank inclination ($\%$), $I_{DC}$ (g AFDM m$^{-2}$y$^{-1}$) is the calculated direct input at the trap site. The following values were attributed to $V$: channel = 1, bare gravel = 2, sparse pioneer vegetation = 3, dense grass = 4, shrubs = 5 and forest = 6. The model parameters $a$ (g AFDM m$^{-1}$y$^{-1}$), $b$ (g AFDM m$^{-1}$y$^{-1}$), $c$ (g AFDM m$^{-1}$y$^{-1}$) and $d$ (m) were identified for each sampling date (using all trap data from this date), and lateral transport then calculated for each square of the 2m-grid in the floodplain. Transport rates in squares touching a chan-
Results

Table 6-1 Linear regression coefficients for the exponential model (equation 1) describing direct inputs of organic matter during the period May 1998 to June 1999.

<table>
<thead>
<tr>
<th></th>
<th>Larch</th>
<th>Pine</th>
<th>Other OM</th>
</tr>
</thead>
<tbody>
<tr>
<td>May</td>
<td>0.70</td>
<td>0.82</td>
<td>0.46</td>
</tr>
<tr>
<td>June</td>
<td>0.72</td>
<td>0.71</td>
<td>0.44</td>
</tr>
<tr>
<td>July</td>
<td>0.46</td>
<td>0.84</td>
<td>0.21</td>
</tr>
<tr>
<td>August</td>
<td>0.89</td>
<td>0.55</td>
<td>0.43</td>
</tr>
<tr>
<td>September</td>
<td>0.81</td>
<td>0.55</td>
<td>0.38</td>
</tr>
<tr>
<td>October</td>
<td>0.86</td>
<td>0.57</td>
<td>0.32</td>
</tr>
<tr>
<td>November</td>
<td>0.76</td>
<td>0.35</td>
<td>0.21</td>
</tr>
<tr>
<td>February</td>
<td>0.58</td>
<td>0.23</td>
<td>0.25</td>
</tr>
<tr>
<td>June</td>
<td>0.63</td>
<td>0.50</td>
<td>0.45</td>
</tr>
</tbody>
</table>

channel were divided by channel width to obtain input rates (g AFDM m² y⁻¹) for the respective channels. Lateral input was calculated in monthly intervals for the snow free period between June 1998 and June 1999.

**Input of soil organic matter**

The mobilization of organic matter by channel erosion was assessed by overlaying orthophotos of the floodplain taken in July 1998 with orthophotos taken in June 1999. A map of the area eroded during this period was obtained by subtracting the active channel area of 1998 from that of 1999. This map was combined with the vegetation density map to calculate the proportions of different vegetation cover lost by erosion. Finally, soil organic matter content was correlated with the vegetation density and the total amount of organic matter that had been eroded over one year was calculated.

**Results**

**Direct inputs of POM**

The exponential model (equation 1) explained between 46% and 89% of the variation in direct input rates for larch needles, between 23% and 84% for pine needles, and between 21 and 46% for other organic particles (Table 6-1). The relative weak correlation between pine needles and distance from trees may be explained by the fact that the direct traps were located in larch stands with relative low abundance of pine trees. On average 90% of the larch needles were deposited within 20 m of the
6. Spatial modeling of allochthonous organic matter pathways

Table 6-2 Multiple linear regressions of results from lateral input model with field data. a/b/c/d are the resulting parameters for the multiple linear equation, asterisks indicate significant models.

<table>
<thead>
<tr>
<th>month</th>
<th>a</th>
<th>b (veg)</th>
<th>c (slope)</th>
<th>d (aerial)</th>
<th>r²</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>May 98</td>
<td>168.00</td>
<td>-29.73</td>
<td>0.39</td>
<td>0.21</td>
<td>0.04</td>
<td>0.38</td>
</tr>
<tr>
<td>June 98</td>
<td>-399.98</td>
<td>186.78</td>
<td>-6.97</td>
<td>-0.14</td>
<td>0.26</td>
<td>0.09</td>
</tr>
<tr>
<td>July 98</td>
<td>-151.65</td>
<td>65.87</td>
<td>2.82</td>
<td>-0.05</td>
<td>0.22</td>
<td>0.19</td>
</tr>
<tr>
<td>Aug 98</td>
<td>0.80</td>
<td>9.95</td>
<td>1.26</td>
<td>0.01</td>
<td>0.38</td>
<td>0.03*</td>
</tr>
<tr>
<td>Sept 98</td>
<td>-78.40</td>
<td>28.64</td>
<td>9.04</td>
<td>-0.02</td>
<td>0.29</td>
<td>0.05*</td>
</tr>
<tr>
<td>Oct 98</td>
<td>40.88</td>
<td>-35.80</td>
<td>21.34</td>
<td>-0.01</td>
<td>0.33</td>
<td>0.04*</td>
</tr>
<tr>
<td>May 99</td>
<td>294.28</td>
<td>-62.30</td>
<td>1.63</td>
<td>0.05</td>
<td>0.11</td>
<td>0.28</td>
</tr>
</tbody>
</table>

larch trees, while 90% of the pine needles were deposited within only 8 m (Fig. 6-4). Cross validation of the larch ($r^2 = 0.83$) and pine needle model ($r^2 = 0.56$) indicated that the exponential model may be adequate for describing needle input as a function of distance from trees (Fig. 6-5). The correlation between other organic matter (twigs, cones, non-identifiable matter) and distance from trees, however, was poor ($r^2 = 0.40$). Compared to needles, the input of a twig or a cone to a trap was more stochastic. Moreover, non-identifiable matter also may originate from sources other than trees, such as shrubs or from soil litter.

Fig. 6-3a shows spatial patterns in the annual direct input of organic matter to the Val Roseg floodplain. Only channels flowing close to the edge of the floodplain received substantial direct inputs of organic matter (lateral groundwater channels: 1.3 g AFDM m²·y⁻¹, tributaries: 3.4 g AFDM m²·y⁻¹). Direct inputs to channels located more than 20 m from the floodplain edge were low; for example, calculated inputs to main and side channels averaged only 0.2 g AFDM m²·y⁻¹. Total annual input to the floodplain channels was calculated to be 0.5 g AFDM m²·y⁻¹ or 0.068 t AFDM y⁻¹ (Table 6-3).

**Lateral inputs of POM**

Vegetation, bank inclination and aerial input proved to be weak predictors of lateral input (Table 6-2). However, between August and October 1998, when lateral inputs were greatest, the model produced significant results. The generally low correlation might be explained by the fact that lateral inputs of particulate organic matter are influenced by local factors such as small-scale wind patterns, topography and vegeta-
Results

Fig. 6-6 (a) eroded area for the respective vegetation density classes; (b) AFDM content of soil samples from different vegetation densities.

tion structure, which are difficult to assess. Moreover, the number of lateral traps was three times lower than the number of direct traps used in this study.

In contrast to direct inputs, the relative importance of lateral inputs is low close to forests but greater in the floodplain. Spatial patterns of lateral input are highly variable (Fig. 6-3b). The model predicted relatively high inputs at the edge of the floodplain, as well as in channels with steep bank slopes in floodplain areas that were not affected by laterally shifting channels for several years (Zah et al., 2001b). Calculated lateral inputs were low along the braided corridor of the main channel, where vegetation density, bank inclination and aerial inputs were low. Lateral input to the entire floodplain channel network was estimated to be 3.5 g AFDM m⁻²y⁻¹ resulting in a total input of 0.48 t AFDM y⁻¹ (Table 6-3).

Input of organic matter by channel erosion

The floodplain area subjected to bank erosion between July 1998 and June 1999 was restricted to the braided corridor (Fig. 6-3c), where vegetation density was generally low. Erosion mainly occurred in reaches where the main channel crossed the floodplain. About 4500 m² of the eroded area was bare gravel and only 200 m² of the eroded area was densely vegetated (Fig. 6-6a). The organic matter content of the top soil layer (0 – 10 cm) was six times greater in densely vegetated areas than in areas
6. Spatial modeling of allochthonous organic matter pathways

Table 6-3 Summarized allochthonous organic matter inputs (total and per m²) for all channel types.

<table>
<thead>
<tr>
<th>Channel type</th>
<th>direct input (kg·y⁻¹)</th>
<th>lateral input (kg·y⁻¹)</th>
<th>erosion input (kg·y⁻¹)</th>
<th>direct input (g·m⁻²·y⁻¹)</th>
<th>lateral input (g·m⁻²·y⁻¹)</th>
<th>erosion input (g·m⁻²·y⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>main channel</td>
<td>26.7</td>
<td>69.4</td>
<td>19005</td>
<td>0.3</td>
<td>1.0</td>
<td>202</td>
</tr>
<tr>
<td>intermittently connected</td>
<td>2.5</td>
<td>92.8</td>
<td>4409</td>
<td>0.1</td>
<td>4.3</td>
<td>202</td>
</tr>
<tr>
<td>alluvial groundwater</td>
<td>1.1</td>
<td>61.9</td>
<td>0</td>
<td>0.2</td>
<td>9.0</td>
<td>0</td>
</tr>
<tr>
<td>lateral groundwater</td>
<td>9.2</td>
<td>69.8</td>
<td>0</td>
<td>1.3</td>
<td>10.0</td>
<td>0</td>
</tr>
<tr>
<td>tributaries</td>
<td>29.0</td>
<td>165.8</td>
<td>0</td>
<td>3.4</td>
<td>19.3</td>
<td>0</td>
</tr>
<tr>
<td>total</td>
<td>68.0</td>
<td>480.0</td>
<td>23415</td>
<td>0.5</td>
<td>3.5</td>
<td>169</td>
</tr>
</tbody>
</table>

covered by bare gravel (ANOVA, p < 0.005, Fig. 6-6b). In the deeper layer, differences in soil organic matter content were small but still nearly significantly different between bare gravel and densely vegetated areas (p = 0.051). The annual input of soil organic matter to the channels in the floodplain was estimated to be 169 g AFDM m⁻²·y⁻¹ or 23.4 t AFDM y⁻¹ (reg. Table 6-3).

Discussion

In this study, we measured an average direct input of POM to the floodplain channels of 0.5 g AFDM m⁻²·y⁻¹ and an average lateral input of 3.5 g AFDM m⁻²·y⁻¹. These results stand in contrast to studies on single-thread channels, where total inputs are generally higher and direct input is usually the dominant pathway (Benfield, 1997). In this study, however, we also were able to quantify organic matter inputs by bank erosion. This pathway for all floodplain channels averaged 169 g AFDM m⁻²·y⁻¹ and was 40 x higher than direct and lateral inputs together.

Total fluxes of the three modeled organic matter pathways to the different channel types, based on model output, are displayed in Table 6-3. Both direct and lateral inputs were lowest in the main glacier channel and highest in tributaries draining forested hill-slopes. Erosional inputs were restricted to the migrating main and side channels. When comparing total fluxes, input to the main channel is high for direct and lateral fluxes due to the large extent of the glacial main channel. Forty percent of the direct inputs and 20% of the lateral inputs end up in the main channel. However, the tributaries, although covering only a small channel area, receive 42% of the direct inputs and 30% of the lateral inputs.
**Organic matter pathways in the floodplain**

Total pathways of allochthonous organic matter are compared in Fig. 6-7 with hydrological import of DOC and POC (Tockner et al., 2001). Although hydrological inputs and erosional inputs of POM are high, retention within the floodplain may be small because highest inputs occur during floods. Further, we also expect that bioavailability of this material is limited because this suspended POM is mixed with inorganic particles (glacial flour and inorganic soil particles). However, the allochthonous inputs to tributaries and groundwater channels apparently influenced the energy base of benthic invertebrates because of a better food quality (less inorganic particles) and a higher retention of particles in these shallow and slow flowing streams. These assumptions are supported by the results of a stable isotope study, that indicated autochthonous diets for the fauna in the glacial channel and a more allochthonous diet for macroinvertebrates in a groundwater channel (Zah et al., 2001a).

The effect of a floodplain on organic matter dynamics is complex because different channel types receive different amounts of organic matter (Table 6-3), and it is primarily dependent on the spatial configuration of the channel network and of the floodplain and upland vegetation. The dominant pathway of terrestrial organic matter input to the floodplain was lateral input (Fig. 6-7). This contrasts with single-thread channels canopied by woody riparian vegetation, where direct litterfall prevails. We assume that with increasing width of the active channel area lateral transport becomes more important. However, to which extent a floodplain modifies the
6. Spatial modeling of allochthonous organic matter pathways

overall input of terrestrial organic matter depends on the location of the floodplain with respect to the treeline and on the structure of the floodplain vegetation (Zah & Uehlinger, 2001c).

**Evaluation of the method**

The complex spatial configuration of potential sources of particulate organic matter required the use of a GIS-based model that integrated field data from organic matter traps with high-resolution remote sensing data. The spatial modelling of direct inputs apparently worked satisfactorily (Table 6-1), although potential factors like wind or hillslope were not considered. Because needles are deposited only short distances from the trees (Fig. 6-3a), we postulate that these factors usually have a minor influence on the large-scale distribution of the direct inputs, at least in the investigated system. However, it might be possible that storms during the period of larch needle abscission (September – October) can affect the distribution of direct inputs within the floodplain (Zah & Uehlinger, 2001c).

Correlations between measured and lateral transport rates were weak (Table 6-2). The main reason is, that the resolution of the spatial data was 2 m, but lateral transport of organic matter might be strongly dependent on smaller-scale factors like vegetation patches, configuration of single rocks, or stability of the riparian zone. Despite these shortcomings, results of lateral mapping (Fig. 6-3b) were apparently plausible; for example zones of increased lateral transport were identified as valley edges or the riparian zones of incised groundwater channels. Although this kind of spatial models are not yet operational for environmental management purposes (e.g. assessment of organic matter loss due to erosion in agricultural areas), the models allowed an approximate estimate of organic matter fluxes to the complex hydrosystem and gave new insights into the complexity of organic matter dynamics in floodplain systems.

**Acknowledgements**

We wish to thank Klement Tockner for stimulating discussions on the topic. We also thank Chris Robinson for critically reviewing this manuscript. This study was supported by a research grant from the Swiss National Science Foundation (SNF 21-49243.96).
References


6. Spatial modeling of allochthonous organic matter pathways


In a high alpine floodplain system influenced by glacial runoff, stable isotope ratios were used to investigate the relative importances of different organic matter as food resource for benthic macroinvertebrates. Isotope ratios ($\delta^{13}$C and $\delta^{15}$N) were used to delineate types and pathways of allochthonous organic matter (grass, wood, needles), autochthonous organic matter (epilithic and filamentous algae) and benthic invertebrates in various channels along a gradient of increasing allochthonous organic matter input. The preliminary results of this study show a shift in the diet of the invertebrates from food mainly derived of autochthonous algae at sites close to the glacier to a mixed diet at sites further downstream in the zone of subalpine forests. However, isotopic ratios of algae are known to vary highly among sites and further investigations in the Val Roseg are needed for focussing on a site specific analysis of isotopic values.
Introduction

Energy flow through lotic ecosystems is fueled by instream primary production and allochthonous inputs of organic matter from adjacent terrestrial environments. The relative contributions of both kinds of resources to the energy flow vary significantly along the river continuum (Vannote et al., 1980). In alpine catchments above the tree line, terrestrial vegetation is scarce or even lacking. Consequently, the input of allochthonous organic matter is low and benthic primary producers (algae) are presumably the dominant energy source supporting the heterotrophic community (Ward, 1994). Allochthonous organic matter becomes more important when such a stream continues into subalpine forests.

In this study we present preliminary results of an investigation that is focused on the relative importance of autochthonous and allochthonous organic matter for benthic invertebrates along an altitudinal gradient in an alpine stream ecosystem dominated by glacier runoff. For this we analyzed stable isotope ratios of algae and terrestrial organic matter as a tracer for potential food resources of benthic invertebrates.

Study site

Val Roseg is situated in the Bernina Massif of the Swiss Alps (Fig. 7-1). Elevations range from 1775 m a.s.l. (end of the catchment) to 4049 m a.s.l. (Piz Bernina). About 30% of the 67.4 km² drainage basin is covered by glaciers. The primary water source of the Roseg River is meltwater from the Tschierva and Roseg Glaciers (average discharge: 2.8 m³/s). The river exhibits the characteristics of a glacial meltwater stream with discharge being lowest during winter when the stream is only fed by exfiltrating groundwater. Melting of the glaciers is highest during late summer when the stream reaches peak flow.

Five major reaches characterize the Val Roseg: a braided reach in the recent proglacial area of the Tschierva Glacier (length 500 m), a lake outlet downstream from the Roseg glacial lake (length 900 m), a single-thread channel incised in glacial till (length 900 m), the main glacial floodplain (length 2800 m) with various channels of different hydrology and chemistry, and a reach that is mainly constrained by
Fig. 7-1 The Val Roseg Catchment in the Eastern Alps of Switzerland. Indicated are sampling sites, forests, and glaciers.
7. Application of stable isotopes for tracing food sources

Table 7-1 Physico-chemical characteristics of the 4 sampling sites (chemical data from Tockner et al., 1997).

<table>
<thead>
<tr>
<th>Site</th>
<th>L-10</th>
<th>M20</th>
<th>M40</th>
<th>G1</th>
</tr>
</thead>
<tbody>
<tr>
<td>description</td>
<td>main channel below</td>
<td>main channel below</td>
<td>main channel close to</td>
<td>spring close to edge of</td>
</tr>
<tr>
<td></td>
<td>glacial lake</td>
<td>floodplain</td>
<td>mouth</td>
<td>floodplain</td>
</tr>
<tr>
<td>altitude [m]</td>
<td>2159</td>
<td>1998</td>
<td>1768</td>
<td>2020</td>
</tr>
<tr>
<td>catchment [km^2]</td>
<td>18.6</td>
<td>48.3</td>
<td>67.4</td>
<td>4.4</td>
</tr>
<tr>
<td>glacial area [%]</td>
<td>52.0</td>
<td>42.8</td>
<td>30.7</td>
<td>0.0</td>
</tr>
<tr>
<td>forested area [%]</td>
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<td>1.2</td>
<td>5.2</td>
<td>2.1</td>
</tr>
<tr>
<td>distance to the forest [m]</td>
<td>850</td>
<td>65</td>
<td>10</td>
<td>30</td>
</tr>
<tr>
<td>discharge range [m³/s]</td>
<td>0.02 - 14</td>
<td>0.05 - 26</td>
<td>0.1 - 0.34</td>
<td>0.002 - 0.004</td>
</tr>
<tr>
<td>conductivity range [µS/cm]</td>
<td>26 - 73</td>
<td>35 - 91</td>
<td>39 - 86</td>
<td>46 - 136</td>
</tr>
<tr>
<td>turbidity range [NTU]</td>
<td>33 - 130</td>
<td>0.6 - 150</td>
<td>2.3 - 31</td>
<td>0.3 - 3.5</td>
</tr>
<tr>
<td>DOC range [mg/l]</td>
<td>0.1 - 0.5</td>
<td>0.1 - 1.0</td>
<td>0.1 - 1.0</td>
<td>0.3 - 0.9</td>
</tr>
<tr>
<td>POC range [mg/l]</td>
<td>0.1 - 0.6</td>
<td>0.1 - 0.4</td>
<td>0.1 - 0.4</td>
<td>0.1 - 0.2</td>
</tr>
</tbody>
</table>

steep valley slopes (length 7200 m) (Tockner et al., 1997). Subalpine forests, dominated by Larix decidua, Pinus mugo and Pinus cembra, are restricted to the valley slopes.

Four sampling sites were selected along a vegetation gradient from the glacier to the end of the catchment (Fig. 7-1, Table 7-1): L-10 was situated at the lake outlet and received water from the Roseg Glacier; M20 was 3 km downstream within the glacial floodplain where sparse forests are restricted to the valley slopes; M40 was located in the lower catchment, where subalpine forests were relatively dense; G1 was a groundwater-fed spring located near a forest at the edge of the high alpine floodplain. While habitat conditions at the main channel sites (L-10 – M40) are harsh (high flow and bed load transport during summer, snow cover during winter) and subject to distinct seasonal variation (Table 7-1), site G1 exhibits a constant discharge regime.

Methods

Samples for stable isotope analysis were collected in September 1997 with some additional algae samples taken in February 1998. Ten to 20 macroinvertebrates were sampled at each site and for each taxon (Fig. 7-2b). For the determination of the isotope ratios of the woody vegetation we sampled fresh twigs (wood and needles) of 20 cm length. Grass samples consisted of the total above-ground biomass in 0.04 m²
Methods

Fig. 7-2  a) δ¹³C and δ¹⁵N values for terrestrial plants and algae. The dotted lines delineate the respective ranges. b) δ¹³C and δ¹⁵N values for invertebrates. The dotted lines delineate the ranges of plant and algae samples from a).

sampling plots. Algal samples consisted of filamentous green algae and epilithic microalgae. In the upper part of the Val Roseg Hydrurus foetidus formed dense algal mats that were sampled separately. Epilithic algae were brushed from single stones and treated with 1N HCl in order to remove inorganic carbon. Invertebrates were collected in the stream reaches with kick sampling. Ten to 20 individuals for each of 11 abundant taxa (Fig. 7-2b) were pooled for analysis.

All samples were frozen in the field, oven-dried at 60°C in the laboratory, ground, and aliquots of 0.5 - 1.5 mg were retained. Each sample was analyzed for stable isotopes of organic carbon (¹³C) and nitrogen (¹⁵N) on a mass spectrometer coupled in continuous flow with a CE-Instruments NCS2500 following standard methods (Peterson & Fry, 1987). Results are given as ratios relative to the standard (δ¹³C and δ¹⁵N).
7. Application of stable isotopes for tracing food sources

Discriminant analysis was used to identify the variable contributing most to distinguishing between algae and plant samples. The $\delta^{13}$C compositions of plant and invertebrate samples were compared using one-way analysis of variance (ANOVA).

Results and discussion

Carbon isotope ratios of algal samples ranged from -33.0 to -27.4‰, whereas those of terrestrial organic matter ranged from -29.6 to -23.8‰. Based on $\delta^{13}$C and $\delta^{15}$N, algae and terrestrial organic matter can be distinctly separated (Fig. 7-2a); 96% of the plant samples and 84% of the algae samples were correctly classified by discriminant analysis with $\delta^{13}$C being the variable contributing most to the separation. Carbon isotope ratios of invertebrates varied between -33.6 and -24.4‰ (Fig. 7-2b). This range of variation in $\delta^{13}$C is similar to that of algae and terrestrial organic matter. Nitrogen isotopic ratios have been shown to increase by 3 to 5% from one trophic level to the next higher (Minagawa & Wada, 1984; Peterson & Fry, 1987), which may explain the relatively high $\delta^{15}$N of some invertebrates compared to algae.
Carbon isotopic ratios were quite low for the chrysophyte *Hydrurus foetidus* (-33‰), a dominant taxon in the upper catchment (Uehlinger, Zah & Bürgi, 1998). Carbon isotopic ratios of filamentous green algae and algae of relatively thin epilithic biofilms (diatoms and cyanobacteria) were -28‰, which is slightly below δ¹³C of terrestrial organic matter. Larch exhibited significantly lower δ¹³C compositions than pine (ANOVA, p = 0.0007) as it could be expected from other publications (Kloeppe1 et al., 1998). Variability in δ¹³C was highest for grass and moss because these samples were aggregations of different species.

Plant samples lumped together for each site showed no longitudinal trends, whereas pooled invertebrate samples revealed a distinct longitudinal pattern with sites L-10 and M20 having lower δ¹³C compositions than the lower main channel site (M40) or the groundwater stream (G1) (Fig. 7-3, right). A comparison of δ¹³C compositions from terrestrial plants with respective invertebrate compositions for the 4 different sites revealed a highly significant difference between terrestrial samples and invertebrate samples at sites M1 and M2 (ANOVA, p < 0.01), but no significant difference between terrestrial samples and invertebrate samples for sites M40 (p = 0.10) and G1 (p = 0.21).

Differences in δ¹³C of invertebrates between sites become more distinct when focusing on single taxa (Fig. 7-4). These taxa are known as opportunistic feeders being able to consume both attached algae and allochthonous detritus. *Rhithrogena* sp., known as a predominant grazer, showed lower values at all main channel sites,
7. Application of stable isotopes for tracing food sources

whereas Acrophylax cerberus and Ecdyonurus sp. had lowest ratios at the floodplain site M20.

In summary, our preliminary results indicate a shift in the diet of the invertebrates from food mainly derived of autochthonous algae at sites close to the glacier to a mixed diet at sites close to the valley edge and further downstream in the zone of subalpine forests. However, isotopic ratios of algae are known to vary highly among sites. Further investigations in the Val Roseg will therefore focus on a site specific analysis of isotopic values.

References


8. Stable isotope analysis of macroinvertebrates and their food sources in a glacier stream


Food sources and trophic structure of the macroinvertebrate community along a longitudinal gradient were examined in a glacier stream of the Swiss Alps (Val Roseg). Analysis of multiple stable isotopes ($\delta^{13}C$ and $\delta^{15}N$) and measurement of C:N ratios were used to differentiate between allochthonous and autochthonous organic matter. Although isotopic signatures of algae varied widely among sites and dates, it was possible to discriminate between allochthonous and autochthonous food sources using a site-specific approach. Dominant food sources of herbivorous invertebrates in all main channel sites were epilithic diatoms and the filamentous golden alga *Hydrurus foetidus*. Allochthonous organic matter was of some importance only in a groundwater fed stream close to the floodplain margin. Seasonal changes in the $\delta^{13}C$ signature of the macroinvertebrates corresponded with seasonal changes in $\delta^{13}C$ of the alga *H. foetidus*. This indicated that the energy base remains autochthonous throughout the year. Due to limited food sources, feeding plasticity of the invertebrate community was high. Both grazers and shredders fed predominantly on algae, whereas gatherer-collectors seemed to be omnivorous. The overall enrichment of $\delta^{15}N$ was 2.25%o ($r^2=0.99$) per trophic level. On a gradient from the glacier site to a downstream forested site trophic enrichment was constant but variation in $\delta^{15}N$ within trophic levels decreased.
Introduction

In contrast to terrestrial ecosystems, where in-situ primary production is the dominant energy source for consumers, organic energy in lotic ecosystems is derived from different pathways: primary production occurs within the wetted channel (autochthonous energy), whereas terrestrial organic matter enters the stream by aerial inputs, erosion, or exfiltrating groundwater (allochthonous energy). The river continuum concept predicts changes in the relative importance of autochthonous and allochthonous production along the river continuum depending on stream size and riparian vegetation (Vannote et al., 1980, Minshall et al., 1985). The relative importance of autochthonous and allochthonous production also varies across biomes (Minshall et al., 1983). Forested streams receive large amounts of allochthonous organic matter in the form of leaf fall (Cummins et al., 1973; Fisher & Likens, 1973; Ward & Aumen, 1986; Graca, 1993) whereas desert streams, antarctic, arctic, and alpine streams (Minshall, 1978; Jones et al., 1997; Ward, 1994; McKnight & Tate, 1997) rely upon autochthonous production.

High alpine headwater streams lack the substantial input of allochthonous organic matter typical of headwaters in forested catchments (Zah & Uehlinger, 2001). Above the tree line primary production is presumably the most important energy source of streams (Lavandier & Décamps, 1984). If slopes are steep, the riparian vegetation changes within short distances from a «rock desert» to subalpine forests (Ormerod et al., 1994), which provide substantial amounts of allochthonous organic matter. Such a marked change in the terrestrial environment might be accompanied by a shift in the energy base from autochthonous dominance to increasing allochthonous influence.

Both quantity and quality of the organic material (algal biomass, leaf litter, wood, etc.) are expected to influence the feeding habits of the primary consumers. According to the concept of functional feeding groups (Cummins 1973; 1974; Merritt & Cummins, 1996) a shift in the food resources should lead to a shift in the functional feeding groups (FFG) and therefore to a different species composition. On this basis Meritt & Cummins (1996) distinguished six categories: shredders, collectors (filterers and gatherers), grazers, macrophyte piercers and parasites. Although it is common practice to assign benthic taxa to FFGs, the use and usefulness of the FFG concept has been criticized (Lake et al., 1985; Barmuta, 1988). An area of con-
cern has been that many stream macroinvertebrates are opportunistic generalists (Coffman, Cummins & Wuycheck, 1971), and have a highly flexible feeding behaviour (McShaffrey & McCafferty, 1986).

The trophic importance of specific food sources to invertebrate consumers was assessed in this study using the method of dual stable isotope analysis ($\delta^{13}$C and $\delta^{15}$N, Fry, 1991). Isotopic signatures of consumers generally reflect the isotopic signatures of organic matter assimilated. Therefore, isotopic signatures can be used to trace the flow of organic matter through foodwebs if isotopic signatures of different food sources can be distinguished.

In this study we focused on the relative importance of different food sources in supporting primary consumption and structuring the benthic community along a glacial stream in the Swiss Alps. Along this stream, the riparian vegetation changed from alpine meadows to subalpine forests in the lower parts of the catchment. The vegetation gradient was paralleled by a corresponding increase in allochthonous organic matter (Zah & Uehlinger, 2001). We hypothesised that the gradient in allochthonous organic matter supply shifts the energy base of macroinvertebrate consumers from an autochthonous diet to a mixed diet. Further, we hypothesized that this alteration of food supply would be reflected in the trophic structure of the invertebrate community. To test these hypotheses we examined the isotopic discrimination between potential autochthonous and allochthonous food sources of primary consumers and subsequently assessed isotopic signatures of primary and secondary consumers at different sites along the stream, and measured enrichment of $^{15}$N in primary and secondary consumers.

**Methods**

**System**
The study was conducted in the Roseg River, a tributary of the River Inn, located in the Bernina Massif of the Swiss Alps (Fig. 8-1). The catchment area above the lowest sampling point is 67.4 km$^2$ with elevations ranging from 1768 m a.s.l. to 4049 m a.s.l. Meltwater from the Tschierva and Roseg glaciers, which cover about 30% of the drainage basin, comprises the primary water source of the Roseg River. Five major reaches characterise the study system, namely a partially braided reach in the recent proglacial area of the Tschierva Glacier (length 500 m), a lake outlet downstream
8. Isotope analysis of the food web in a glacier stream

Fig. 8-1 The Val Roseg catchment in the Eastern Alps of Switzerland. Indicated are the study sites.
from a glacial lake (Lake Roseg, length 900 m), a single-thread channel incised in glacial till (length 900 m), the main glacial floodplain (length 2800 m) with various channels of different hydrology and chemistry (Tockner et al., 1997), and a reach that is mainly constrained by steep valley slopes (length 7200 m). Annual discharge gauged at the lower end of the catchment (0.5 km downstream of sampling site M40) averaged 2.8 m³s⁻¹. In July and August mean daily discharge ranged from 2.0 – 46 m³s⁻¹, between December and March mean daily discharge varied between 0.007 and 0.66 m³s⁻¹ (Tockner et al., 1997). Terrestrial vegetation ranges from a „rock desert“ close to the terminus of the Tskierva glacier to subalpine forests covering the lower valley slopes. Dominant tree species are the conifers *Larix decidua* (Miller), *Pinus Cembra* (L.), and *Pinus montana* (Miller).

**Sampling sites**

Four sites were sampled (Fig. 8-1), three along the main channel (L-10, M20, M40) and one groundwater fed channel at the edge of the main floodplain (G1). The uppermost site L-10 (river km 0.05, 2159 m a.s.l.) was located in the lake outlet about 50 m downstream of the proglacial Lake Roseg. Grass and a few scattered shrubs (*Salix sp.*) dominated the riparian vegetation. The lack of bedload transport even during summer high flow and maximum water temperatures exceeding 3°C result in a relatively diverse invertebrate community (Burgherr & Ward, 2000), high periphyton biomass and high standing stock of benthic organic matter (Table 8-1). Allochthonous inputs of terrestrial organic matter were small. Site M20 (river km 3, 1998 m a.s.l.) was located in the lower part of the main glacial floodplain, where forests are restricted to the valley slopes. Riparian vegetation was limited to sparse pioneer plant species due to frequent lateral movement of main channel and side channels. Bedload transport during summer high flow limits periphyton accrual (Uehlinger, Zah & Bürgi, 1998) and reduces BOM standing stock (Table 8-1). Input of terrestrial organic matter was small similar to L-10. Site M40 (river km 12, 1768 m a.s.l.) was located in the constrained reach at the lower end of the catchment, where subalpine forests grew close to the channel. This site was characterised by highest aerial inputs of terrestrial organic matter, while periphyton biomass was low and BOM standing stock was 30% higher than at M20. Site G1 (2020 m a.s.l.) was a groundwater-fed spring at the edge of the glacial floodplain. Habitat conditions were characterised by
Table 8-1 Characteristics of sampling sites.

<table>
<thead>
<tr>
<th>site</th>
<th>L-10</th>
<th>M20</th>
<th>M40</th>
<th>G1</th>
</tr>
</thead>
<tbody>
<tr>
<td>description</td>
<td>main channel below glacial lake</td>
<td>main channel in floodplain</td>
<td>main channel near mouth</td>
<td>spring near edge of floodplain</td>
</tr>
<tr>
<td>altitude [m a.s.l.]</td>
<td>2159</td>
<td>1998</td>
<td>1768</td>
<td>2020</td>
</tr>
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<td>distance to forest [m]</td>
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<td>60</td>
<td>10</td>
<td>30</td>
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<tr>
<td>discharge range [m³s⁻¹]</td>
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<td>0.05 - 26</td>
<td>0.1 - 34</td>
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<td>conductivity range [μS cm⁻¹ at 20°C]</td>
<td>26 - 73</td>
<td>35 - 91</td>
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<td>46 - 136</td>
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<tr>
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<td>67.4</td>
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<td>42.8</td>
<td>30.7</td>
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<tr>
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<tr>
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<td>0.1 - 0.4</td>
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<td>210 ± 33</td>
<td>138 ± 32</td>
<td>175 ± 50</td>
<td>119 ± 22</td>
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<td>aerial input of POM [g AFDM m⁻²y⁻¹]</td>
<td>1</td>
<td>4</td>
<td>38</td>
<td>10</td>
</tr>
</tbody>
</table>
Methods

constant flow, low turbidity and high conductivity. Due to low disturbance, periphyton density was constantly high. The riparian vegetation was dominated by dense grass and a few Juniperus communis (L.) shrubs. Input of terrestrial organic matter was higher than at L-10 and M20 but distinctly lower than at M40. The standing stock of BOM was the lowest of all sites. All sites were characterised by low temperatures and low DOC- and POC-concentrations (Tockner et al., 1997, Table 8-1).

Sample collection
Benthic algae and invertebrates were collected in September 1997 and February 1999. At each site 3 - 5 rocks (b-diameter: 8 – 15 cm) with visible biofilms were collected. The filamentous chrysophyte Hydrurus foetidus (Kirch.), which dominated the algal community, was sampled by manually removing slime filaments from the rocks. Epilithon, which could also contain attached cells of Hydrurus foetidus, was sampled by scrubbing the rocks with a metal brush. Benthic invertebrates and stream detritus were collected by repetitive kick-sampling (mesh size: 250 μm) at several sites within each study reach. Smaller fractions were discarded due to high contents of inorganic glacial flour. Allochthonous organic matter was sampled in September 1997. Living and decomposing needles and twigs from the dominant conifers (Larix decidua) and (Pinus Cembra) were collected. Grass samples were taken by cutting the plants at ground level within a 20 x 20 cm square. All samples were frozen and transported to the laboratory for further treatment.

Stream velocity was measured at each collection site with a magneto-inductive probe (Nautilus C2000, R.Ott, Kempten-Germany) during field sampling in 40% depth above the streambed (Gore, 1996). Mean stream velocity for each sampling site was used for data analysis. Water temperature was measured continuously at all sampling sites during the field campaign with instream loggers (Minilog, VEMCO Ltd., Armdale, Canada).

Sample processing
Epilithic algae scraped from rocks were washed in diluted 1M HCl to remove inorganic carbon. Invertebrates were separated manually from filamentous algae and detritus. Detritus was concentrated by repetitive sieving (250 μm mesh size). Terrestrial organic matter was cut into small pieces. Invertebrates were kept alive in containers for 6 h in order to let their guts clear. Individuals which still had full guts
were not included in the analysis. Terrestrial matter, invertebrates, algae, and stream detritus were dried at 60°C. All samples, except invertebrates, were ground to a fine powder from which aliquots of 0.5 - 1.5 mg were used for analysis. Invertebrate samples for isotope analysis consisted of 2 – 5 whole individuals from each of the dominant taxa (Table 8-2). Ground aliquots and invertebrates were transferred into small tin capsules for analysis. We analysed 413 samples (algae: 102, terrestrial organic matter: 101, stream detritus: 17, invertebrates: 193) for stable isotopes of carbon (\(^{13}\)C) and nitrogen (\(^{15}\)N) composition. We used a mass spectrometer coupled in continuous flow with a CE-Instruments NCS2500 following standard methods (Peterson & Fry, 1987). Carbon and nitrogen isotope values (\(\delta^{13}\)C and \(\delta^{15}\)N) are expressed in the conventional delta notation: 

\[
d = \frac{(R_{sample} / R_{standard}) - 1}{1000}
\]

with respect to the Vienna PeeDee Belemnite standard (V-PDB) and atmospheric hydrogen (AIR), respectively.

Table 8-2 Invertebrates: Functional feeding groups and numbers of samples per taxon at each study site and for the summer (S) and winter sampling (W).

<table>
<thead>
<tr>
<th>Functional Feeding Group</th>
<th>Taxon</th>
<th>Code</th>
<th>L-10</th>
<th>M20</th>
<th>M40</th>
<th>G1</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>S</td>
<td>W</td>
<td>S</td>
<td>W</td>
</tr>
<tr>
<td>Shredder</td>
<td>Acrophylax zerberus</td>
<td>ACR</td>
<td>3</td>
<td>11</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Rhabdiopteryx sp.</td>
<td>RDX</td>
<td>5</td>
<td>5</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Protonemura sp.</td>
<td>PNM</td>
<td></td>
<td></td>
<td></td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Nemoura sp.</td>
<td>NEM</td>
<td></td>
<td></td>
<td></td>
<td>5</td>
</tr>
<tr>
<td>Grazer</td>
<td>Baetis sp.</td>
<td>BAE</td>
<td>2</td>
<td>3</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Chironomidae</td>
<td>CHI</td>
<td>3</td>
<td>3</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Ecdyonurus sp.</td>
<td>ECD</td>
<td>3</td>
<td>1</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Filterer-Collector</td>
<td>Simuliidae</td>
<td>SIM</td>
<td></td>
<td></td>
<td></td>
<td>3</td>
</tr>
<tr>
<td>Gatherer-Collector</td>
<td>Leuctra sp.</td>
<td>LEU</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Predator</td>
<td>Rhithrogena sp.</td>
<td>RGN</td>
<td>4</td>
<td>4</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>Dictyogenus sp.</td>
<td>DIC</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Empididae</td>
<td>EMP</td>
<td>3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Isoperla sp.</td>
<td>ISO</td>
<td>4</td>
<td>5</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Perlodes intricata</td>
<td>PER</td>
<td>3</td>
<td>5</td>
<td></td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Dicranota sp.</td>
<td>DCR</td>
<td>5</td>
<td>3</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Rhyacaphila sp.</td>
<td>RHY</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Results

C:N ratios

We calculated C:N mass ratios for all food source samples based on total carbon and nitrogen masses that were obtained from the mass spectrometer analyses.

Statistical methods

All statistical analyses were performed using STATISTICA (Röhr, 1997). Because the data did not significantly deviate from a normal distribution (Kolmogorov-Smirnov test, p = 0.08), no prior transformation was needed. MANOVA was used to test for differences in multiple isotope signatures among food sources and functional feeding groups (dependent variables: \(\delta^{13}C\) and \(\delta^{15}N\)). Subsequent pairwise comparisons were made with Tukey's HSD Test. \(\delta^{13}C\) signatures of invertebrate taxa at the two sampling dates and C:N-ratios of organic matter from different origin were analysed using univariate ANOVA (dependent variable: \(\delta^{13}C\) or C:N-ratio, F-statistics).

Results

Isotope signatures of potential food sources

The \(\delta^{13}C\) signatures of autochthonous material (epilithic algae) varied between \(-37\%o\) and \(-18\%o\) while \(\delta^{15}N\) signatures ranged from \(-8\%o\) to \(2\%o\) (Fig. 8-2a). Dual isotope analysis showed significant differences between Hydrurus foetidus and the other epilithic algae at each site (MANOVA, p < 0.05). For site G1, only the differences in \(\delta^{13}C\) were significant, whereas at the other sites both isotopes exhibited significant differences (Tukey’s HSD test). Among the sampling sites we found highly significant differences for Hydrurus foetidus (p < 0.01) and for other epilithic algae (p < 0.01). The \(\delta^{13}C\) signatures of allochthonous material (conifers and grasses) in the Val Roseg catchment varied between \(-29\%o\) and \(-25\%o\) while \(\delta^{15}N\) signatures varied between \(-3\%o\) and \(5\%o\) (Fig. 8-2b). Differences between sites and taxa were small compared with the autochthonous material. The isotopic composition of potential allochthonous and autochthonous food sources were significantly different at sites M40 (p < 0.01) and M20 (p < 0.01) and G1 (p = 0.03) but not at the lake outlet site L-10 (p = 0.60). Regression analysis indicated no significant relation between \(\delta^{13}C\) signatures of benthic algae and temperature or current velocity (temperature: p = 0.15; current velocity p = 0.22). There was also no relation found between \(\delta^{13}C\) signatures of benthic herbivores and current velocity (p = 0.91).
8. Isotope analysis of the food web in a glacier stream

![Graph A](image)

![Graph B](image)

**Figure 8-2** Isotopic signatures of potential food sources ($\delta^{13}C$ and $\delta^{15}N$ compositions) at the study sites: A) autochthonous organic matter, B) allochthonous organic matter.

Isotopic signatures of stream detritus were located between allochthonous and autochthonous organic material (Fig. 8-3). Repeated kick-sampling did not yield sufficient detritus for isotope analyses at sites L-10 and M20. At site G1 dual isotope analysis separated stream detritus from algae (MANOVA, $p = 0.046$) and terrestrial organic matter ($p = 0.041$) and at site M40 from terrestrial organic matter ($p << 0.01$) but not from algae ($p = 0.52$). For a more distinctive tracing of detrital sources, C:N mass ratios were calculated (Table 8-3). Typically, autochthonous organic matter tends to have ratios of 8:1 (Thorp et al., 1998) to 12:1 (Wetzel, 1983), whereas allochthonous organic matter ranges between 45:1 and 50:1 (Wetzel, 1983) or less, but significantly higher than the ratio for benthic algae (Thorp et al., 1998). In our study, the C:N ratios for terrestrial plants ranged from 13:1 to 44:1 while C:N ratios for algae varied between 7:1 and 10:1 (Table 8-3). The C:N ratios of detritus at sites G1 and M40 were significantly different from C:N ratios of terrestrial plants ($p = 0.05$ and $p = 0.01$) but not significantly different from C:N ratios of algae ($p = 0.88$ and $p = 0.57$).
Figure 8-3 Site-specific $\delta^{13}C$ and $\delta^{15}N$ signatures of potential food sources and invertebrates based on averages of all sampling dates (mean ± 1SD). Shaded boxes: autochthonous organic matter, unshaded boxes: allochthonous organic matter. Black dots: shredders and grazers, white dots: gatherer-collectors, no dots: predators. Invertebrate codes as in Table 8-2.

**Isotope signatures of invertebrates**

Figure 8-3 shows $\delta^{13}C$ and $\delta^{15}N$ signatures of invertebrates at each sampling site. All $\delta^{13}C$ signatures can be found within the range of potential food sources of each site, except for Baeis sp. at site G1. The $\delta^{15}N$ signatures of the consumers and predators
8. Isotope analysis of the food web in a glacier stream

Table 8-3 Mass C:N ratios for specified organic resources and for stream detritus at the sites G1 and M40 (average ± 1 SD).

<table>
<thead>
<tr>
<th>Source</th>
<th>G1</th>
<th>M40</th>
</tr>
</thead>
<tbody>
<tr>
<td>grass</td>
<td>22.6 ± 5.6 (n=6)</td>
<td>13.8 ± 2.9 (n=8)</td>
</tr>
<tr>
<td>Larix decidua</td>
<td>23.2 ± 0.3 (n=3)</td>
<td>23.4 ± 1.8 (n=3)</td>
</tr>
<tr>
<td>Pinus sp.</td>
<td>44.1 ± 16.2 (n=2)</td>
<td>30.4 ± 1.7 (n=3)</td>
</tr>
<tr>
<td>Fontinalis sp.</td>
<td>—</td>
<td>34.5 ± 0.9 (n=2)</td>
</tr>
<tr>
<td>epilithon</td>
<td>8.6 ± 0.9 (n=4)</td>
<td>7.2 ± 0.6 (n=4)</td>
</tr>
<tr>
<td>H. foetidus</td>
<td>9.5 ± 0.7 (n=4)</td>
<td>—</td>
</tr>
<tr>
<td>stream detritus</td>
<td>13.2 ± 6.5 (n=5)</td>
<td>9.1 ± 1.6 (n=5)</td>
</tr>
</tbody>
</table>

were generally higher then those of their potential prey, presumably due to enrichment effects (Fig. 8-3).

At site L-10, δ¹³C signatures of most invertebrate taxa were in the range of *Hydrurus foetidus* suggesting that this alga was the dominant food source, which is also supported by the enrichment of δ¹⁵N (Fig. 8-3). The δ¹³C signature of the caddisfly *Acrophylax zerberus* (Brauer) was in between *Hydrurus foetidus* and epilithic algae, in the range of terrestrial organic matter such as *Salix sp.* and grasses. The variation in the δ¹⁵N of herbivores at site L-10 was high compared to the other sites.

At site M20, the δ¹³C signatures of all grazers and shredders were grouped between those of *Hydrurus foetidus* and the other epilithic algae. The δ¹⁵N enrichment supports the conclusion that algae were the dominant food source. At site M40, the δ¹³C signatures of the invertebrates were grouped between the potential food sources and a tracing of the food base was not possible by using δ¹³C only. However, the δ¹⁵N signatures of the primary consumers were all lower than the δ¹⁵N signatures of the terrestrial organic matter, suggesting that algae and autochthonous detritus were the major food sources. The grazer *Ecdyonurus sp.* exhibited unexpectedly high δ¹⁵N composition in the range of terrestrial organic matter, but δ¹⁵N enrichment over that of *Hydrurus foetidus* suggests this alga as a major food source.

At site G1, potential aquatic and terrestrial food sources were difficult to separate based on δ¹³C signatures because *Hydrurus foetidus* at this location covered the same range as terrestrial organic matter. The very low δ¹³C signature of *Baetis sp.* suggests that these animals fed on algae that were not included in our samples. The δ¹³C signature of chironomids was in the same range as epilithic algae. The shredders *Acrophylax zerberus*, *Protonemoura sp.*, and *Nemoura sp.* were closely grouped together; their δ¹³C signature ranged between those of detritus, *Hydrurus foetidus* and grasses.
Results

Figure 8-4 Seasonal differences in δ¹³C signatures of the alga *Hydrurus foetidus* and macroinvertebrate taxa (mean ± 1SD). Black lines = significant seasonal difference. Invertebrate codes as in Table 8-2.

**Seasonal differences in invertebrate signatures**

We found no significant difference in the isotopic signature of invertebrates between summer and winter when the pooled sites were considered (ANOVA, p > 0.05). Neither were seasonal differences found when univoltine species (one-year life cycle) and semivoltine species (multiannual life cycle) were separated (p = 0.21). However, site-specific and taxon-specific seasonal differences did exist: Fig. 8-4 shows the shift in δ¹³C composition of all taxa, which were collected in both seasons. In the main channel (L-10, M20, M40) δ¹³C signatures of all animals, except the gatherer-collector *Rhithrogena* sp., were significantly lower in winter than in late summer. In the groundwater stream (G1) δ¹³C signatures of 3 out of 4 taxa were significantly higher in winter. At all sites except M40, where *H. foetidus* data is missing, the shift of the δ¹³C signature of animals was paralleled by a corresponding shift of the δ¹³C signature of *Hydrurus foetidus* (Fig. 8-4).

**Change in δ¹⁵N signatures across trophic levels**

δ¹⁵N signatures increased with trophic level at each site (Fig. 8-5), and apart from site L-10 (p = 0.67), increases in δ¹⁵N between trophic levels were significantly different (ANOVA, M20: p < 0.05, M40: p < 0.01, G1: p < 0.01). Average enrichment per trophic level for all sites was 2.25‰ (linear regression analysis: r²=0.99,
8. Isotope analysis of the food web in a glacier stream

Figure 8-5 Site-specific enrichment of $^{15}$N in the trophic cascade (mean ± 1SD).

$p < 0.01$). High algal variation lead to high variation in consumer signatures (L-10), while a low algal variation was reflected by low variation within higher trophic levels (G1). Sites M20 and M40 exhibited overlaps in $^{15}$N signatures between primary consumers and predators. Gatherer-collectors and the grazer *Ecdyonurus* sp. showed the highest $^{15}$N signatures for primary consumers at all sites.

**Discussion**

Although both $^{13}$C and $^{15}$N signatures of algae varied widely between sites and dates, it was possible to discriminate between allochthonous and autochthonous food sources using a site-specific approach. The $^{13}$C signatures of invertebrates analysed were, with the exception of *Baetis* sp. at site G1, within the range of potential food sources at their respective sites. In contrast to our expectations, no evidence indicated that the diet of primary consumers shifted from autochthonous towards an allochthonous diet, as potential terrestrial food sources increased across sites. Allochthonous organic matter seemed to be an important food source only in the springbrook at the floodplain margin. The dominance of an autochthonous food base was further emphasized by the changes in invertebrate $^{13}$C that corresponded to changes in algal $^{13}$C values from summer to winter. Additionally, there were no
Discussion

significant differences in trophic structure between the sites, although variation in δ15N values within trophic levels decreased along the longitudinal gradient.

Alternative food resources
This study focused on aquatic algae and terrestrial POM as potential food resources for primary consumers. However, other sources of organic matter may contribute to the food base of these consumers. Steffan (1971) and Ward (1994), considered aeolic input of fine organic particles transported by wind (e.g. pollen), as a potential food source for glacial headwaters. For the Val Roseg, aerial inputs of organic material, which could not be identified as fragments of terrestrial plants, were very small particularly in the floodplain and the lake outlet area (Table 8-1, R. Zah unpublished data). Tschierva and Roseg glacier however were substantial sources of particulate and dissolved organic carbon (Table 8-1, K. Tockner, unpublished data). Although dissolved organic carbon can be an important food resource (Mulholland, 1997), we believe that these carbon sources were presumably of minor importance in our study system because retention is small in the fast flowing glacier stream and selective feeding on drifting organic particles is difficult due to the high amount of suspended inorganic particles.

Variation in isotopic signatures of benthic algae
In the Val Roseg variation in δ13C signatures of benthic algae was remarkably high (−37‰ to −18‰) matching the range of δ13C signatures of 19 studies in lotic systems (France, 1995). In a recent study Finlay et al. (1999) suggested that variation in δ13C values of algae might result from variation in current velocity, which is considered to be an important factor for the discrimination of 13CO2 by algae. Their conclusion is based not on direct assessment of algal δ13C values but on the observation that δ13C values of invertebrate herbivores varied with current velocity. The lack of any correlation between current velocity and δ13C values of algae and herbivores observed in this study may be explained by the fact that in low productivity streams such as the Roseg River CO2 availability is unlikely to be limited (Finlay, Power & Cabana, 1999). We also found no correlation between algal δ13C signatures and water temperature in contrast to the findings of MacLeod & Barton (1998). However, δ13C signatures of the filamentous alga Hydrurus foetidus were depleted by 2.5‰ in winter (low temperature and low current velocity due to low discharge) at sites L-10
8. Isotope analysis of the food web in a glacier stream

and at M20, while $\delta^{15}$N composition was enriched by 1.5%. This corresponds with both, the findings of France & Cattaneo (1998) who observed a positive correlation between $\delta^{13}$C signatures of filamentous algae and water current, and partially with MacLeod & Barton (1998) who found enrichment in both $^{13}$C and $^{15}$N in periphyton samples in summer relative to autumn samples. The high isotopic variability of autochthonous material appears to be largely influenced by variations in species composition and microhabitat conditions and remains largely unexplained (France, 1995; MacLeod & Barton, 1998). This high variability may lead to misinterpretations, when lumping all algal isotopic values together (Zah et al., 2000). Using a site-specific approach, however, the variability in stable isotopic signatures of different food sources was small enough to apply the dual isotope method as a tracer of organic matter pathways in the Roseg Catchment.

Longitudinal trend in food base

Analogous to the gradual downstream changes proposed by the River Continuum Concept (Vannote et al., 1980), we expected a shift in the food base of invertebrates from a pure autochthonous diet close to the glacier (site L-10) to a mixed diet in the region of subalpine forests (site M40). Our data did not support this initial hypothesis but instead, support the contention of Minshall (1978), that the importance of autotrophy in stream ecosystems is often underestimated. At all main channel sites invertebrates apparently incorporated different forms of available autochthonous organic matter like epilithic and filamentous algae or autochthonous detritus in their tissue. High stream velocity and bed mobility limit the storage capacity for terrestrial organic matter in the main channel of the glacier stream. Except for the summer high flow period, relatively high availability and better quality make algae a more suitable food source than allochthonous organic matter (Lamberti & Moore, 1984), which consisted primarily of refractory needles (Robinson et al., 2000). Allochthonous organic matter had some importance as a food source only at site G1, where proximity to the trees and slow currents favoured input and retention of terrestrial organic matter.

Although $\delta^{13}$C and $\delta^{15}$N values of foods changed significantly between sites, isotopic signatures of consumers fit in the ranges of potential food sources at the respective sites. We therefore conclude that invertebrates of all feeding types were
largely dependent on local food sources consistent with their limited mobility and small foraging range. The only exception were the filter-feeding simulid larvae (Fig. 8-3, M20), which fed on organic matter transported from upstream reaches as also shown for an arctic stream by Finlay et al. (1999).

**Seasonal differences in food base**

Stable isotope signatures integrate carbon assimilation only over a limited time period and isotopic signatures of both, autochthonous and allochthonous food sources change seasonally (Lajtha & Marshall, 1994; McArthur & Moorhead, 1996). Seasonal change in $\delta^{13}C$ of sampled invertebrates (Fig. 8-4) corresponded with observed seasonal change in $\delta^{13}C$ signatures of Hydrurus foetidus (Fig. 8-2a, Fig. 8-4). These results favour the hypothesis that autochthonous organic matter constitutes the main energy base throughout the entire year. Furthermore, the temporal coincidence of animal $\delta^{13}C$ signatures with algal $\delta^{13}C$ signatures, which is stronger for grazers than for gatherer-collectors, indicates a high turnover rate for assimilated carbon.

**Environmental conditions and feeding plasticity**

Harsh physical conditions in the glacier stream and a quantitatively and qualitatively limited energy supply select for invertebrates that can adapt their feeding behaviour to available food sources. Species normally considered as grazers and shredders all fed predominantly on algae and autochthonous detritus, rather than on allochthonous detritus (Table 8-2, Fig. 8-3). So-called detritivores such as Rhithrogena sp. or grazers such as Ecdyonurus sp. were apparently highly omnivorous, as indicated by their high $\delta^{15}N$ values in the same range as predators (Fig. 8-3, Fig. 8-5).

At site G1 discrimination of trophic levels was relatively distinct and variation in $d^{15}N$ within trophic levels was low. This may reflect the more benign environment of the springbrook, where biotic interactions presumably prevail. At the harsh main channel sites (L-10 - M40) high variation and overlapping of isotopic signatures was found, suggesting animals were opportunistic feeders capitalizing on available food sources. The flexibility in functional feeding mode observed in this study has been reported from other field studies (Palmer et al., 1993; Miller et al., 1998) and food preference experiments (Walker & Merritt, 1991; Friberg & Jacobsen, 1994; Burgherr, Robinson & Zah, submitted). In conclusion, our results indicated that a plastic feed-
8. Isotope analysis of the food web in a glacier stream

ing behaviour is a key factor for benthic macroinvertebrates to persist under the physical extremes in temperature, turbidity and flow conditions prevailing in a glacial stream such as the Roseg River.

Acknowledgements

We wish to thank H. Paul for helping us measuring stable isotopes. We also thank Prof. J.V. Ward and D. Arscott for critically reviewing this manuscript. This study was supported by a research grant from Swiss National Science Foundation (SNF 21-49243.96).

References


8. Isotope analysis of the food web in a glacier stream


9. Synopsis

Spatial complexity as a research focus for stream ecologists

Development of theoretical constructs in stream ecology have been primarily derived to explain the functioning of one-dimensional systems. In many studies, the river is treated as a linear element and research questions are formulated along this continuum (e.g., Perry & Schaeffer, 1987; Marchant, Lake & Doeg, 1991). The multidimensional nature of streams has been emphasized by Ward (1989). The vertical dimension (hyporheic zone) has increasingly attracted the interest of stream ecologists in the last two decades (e.g., Bretschko & Klemens, 1986; Dole-Olivier & Marmonier, 1992; Ward & Voelz, 1997). The importance of the lateral dimension became evident when research focused on floodplain systems (Ward et al., 1999a; Ward, Tockner & Schiemer, 1999b; Tockner, Malard & Ward, in press). Geographic Information Systems (GIS) - a common tool in landscape ecology – has also become familiar to stream ecologists, but most GIS applications were restricted to the analysis of catchment characteristics, whereas streams were still treated as linear elements (e.g., Johnson & Gage, 1997; Richards et al., 1997).

Until recently, the resolution and quality of remote sensing data were not adequate for applications in relatively small braided corridors. Development of multiband sensors, color-infrared photographs, increased resolution (ground resolution of up to 1 m (Zhou & Li, 2000)) due to new satellite technologies, easy-to-use orthocorrection tools, and faster computers together with new releases of user-friendly GIS-Software now allow the application of these techniques to relatively small floodplains and braided rivers. In my investigation of the Val Roseg floodplain system, I used a GIS to combine high-resolution airborne orthophotos with limnological field data to get new insights about organic matter dynamics of this spatially complex hydrosystem. In Chapter 2 the successful use of GIS at a fine spatial scale, not yet considered by stream ecologists, is described. Ecologically relevant morphometric parameters like channel width, channel slope or bank inclination were extracted from remote sensing data as well as riparian vegetation density along the channel network of the flood-
9. Synopsis

plain. Acquiring these data by field surveys is nearly impossible because of the prohibitive amount of effort required.

Impact of climate change on glacial stream ecosystems

Mountain ecosystems are sensitive to climate and environmental change (Messerli & Ives, 1997). This is especially true for glaciated catchments (Oswood, Milner & Hynes, 1991). The glaciers in the Val Roseg catchment are among the fastest retreating glaciers in Switzerland, a trend that has been attributed to increased air temperature since the middle of the 19th century (Greene, Broecker & Rind, 1999). The quantification of climate change effects on ecosystems is difficult due to high interannual variations of ecosystem processes (Extence, Balbi & Chadd, 1999) and a general lack of ecological long-term time series. In Chapter 3, I examined the effect of glacier movements over a 52-year period on the structure of an alpine floodplain using GIS. Retreats and advances of these glaciers were not directly related to floodplain dynamics but floods induced significant changes in the braiding index and the connectivity of the channel network. Recent studies on the effects of climate change in the Alps predict both a further increase of mean annual temperatures and an increase of hydrologic extremes such as floods (Wanner et al., 1997; Imboden, 1998). I anticipate a trend toward increased floodplain dynamics (i.e. increased channel movement and habitat turnover) in the Val Roseg if current trajectories of climate change continue.

Input and storage of organic matter in a glacial floodplain

The inputs of allochthonous organic matter along the altitudinal gradient are reported in Chapter 4. The results demonstrated a significant increase in the input of allochthonous organic matter from the glacier terminus to the end of the catchment. The results also indicated that the expected increase in organic matter inputs was shifted downstream due to the existence of the floodplain. In Chapter 5, I examined subsurface storage of organic matter. Subsurface storage paralleled, to some extent, allochthonous matter input but sediment organic matter was several magnitudes higher than annual allochthonous inputs to the system (Fig. 9-1). In Chapter 6, I compared different pathways of organic matter input to the hydrosystem of the Val Roseg flood-
Input and storage of organic matter in a glacial floodplain

plain: 1) direct litter input, 2) lateral litter input, 3) input of soil organic matter by bank erosion and 4) hydrological import of dissolved and particulate organic matter from upstream areas. Direct and lateral inputs were very small in relation to erosional and hydrological inputs. Different channels of the hydrosystem received different amounts of organic matter (Fig. 9-1), primarily depending on the spatial configuration of the channel network, and of floodplain and upland vegetation.

Fig. 9-1 Schematic visualisation of morphological parameters, hyporheic POM-fractions, and allochthonous pathways. The size of the circles represent the relative contributions of the different fractions for the respective channel types.
9. Synopsis

**Organic matter as food source**

Chapters 7 and 8 are stable isotope studies dealing with the use of autochthonous and allochthonous matter as food for benthic invertebrates. Feeding plasticity of the invertebrate community was high. Grazers and shredders preferentially used algae as a food source despite a substantial increase in allochthonous material concomitant with distance to glacier. These findings contrasted expectations that predicted a downstream shift from autochthonous to allochthonous organic matter (Milner & Petts, 1994).

**Outlook**

Organic matter pathways and trophic energy transfer were studied along the altitudinal gradient of a glacial stream, which represents the first such study. However, glacial streams are highly complex systems (Gurnell et al., 1999), and additional studies in different glacial catchments are needed for a general understanding of organic matter dynamics. First steps were made towards understanding the spatial and temporal complexity of floodplain systems using GIS. Although the application of high-resolution remote sensing in stream ecology is still far from being operational, the rapid technological evolution will improve methods and tools in the near future and finally lead to new insights in floodplain ecology.

**References**


References


9. Synopsis


Terms

AFDM: ash free dry mass: dried mass of organic matter minus mass of ash after furnacing. AFDM is a measure for carbon content of organic matter.

Allochthonous: in the context of aquatic energy budgets, it means that the organic energy has been assimilated in a terrestrial ecosystem and was transported into the aquatic ecosystem in the form dissolved (→DOM) or particulate organic matter (→POM).

Alpine: describing areas situated in the European Alps.

alpine: describing areas above the timberline in mountainous northern regions.

Ash free dry mass: →AFDM

Autochthonous: in the context of aquatic energy budgets, it means that the organic energy has been assimilated by primary producers (algae, macrophytes) within the given aquatic system.

Coverage: A term that refers to a layer of spatial data within a →Geographical Information System.

DEM: digital abstraction or approximation of a surface. Because a surface contains an infinite number of points, some subset of points must be used to define the surface. Each model contains a formalised data structure, rules, and X,Y,Z point measurements that can be used to represent a surface.

Detritus: organic matter produced by the decay or disintegration of an organic substance or tissue.

DGPS: differential GPS or DGPS increases the precision of the GPS-technique by a factor >10 by correcting the data from the rover station using data from a base station with known coordinates.
Digital Elevation Model, Digital Terrain Model, Digital Surface Model: \rightarrow DEM

DOM: dissolved organic matter. The fraction of organic matter less than 0.5 \( \mu \text{m} \).

DTM: \rightarrow DEM

Floodplain: a relatively flat strip of land bordering a river and formed from alluvial material deposited when the river overflows its banks.

FPOM: Fine particulate organic matter. The fraction of organic matter less than 1 mm and more than 0.5 \( \mu \text{m} \).

Geographical Information System: \rightarrow GIS

GIS: A computer system for capturing, storing, checking, integrating, manipulating, analysing and displaying data related to positions on the Earth’s surface. Typically, a Geographical Information System (or Spatial Information System) is used for handling maps of one kind or another. These might be represented as several different layers where each layer holds data about a particular kind of feature. Each feature is linked to a position on the graphical image of a map. Layers of data are organised to be studied and to perform statistical analysis. Uses are primarily government related, town planning, local authority and public utility management, environmental, resource management, engineering, business, marketing, and distribution.

GPS: A satellite based navigational system allowing the determination of any point on the earth’s surface with a high degree of accuracy given a suitable GPS receiver. The network of satellites is owned by the US Department of Defence, and as such, the accuracy of the signal is intentionally degraded for non-US military users. The error introduced into the signal is known as selective availability. Error in the accuracy of GPS derived positions can also be introduced through the nature of local conditions, for example multipath. These errors can be greatly reduced using a technique known as \rightarrow DGPS.

Hyporheal: transition zone between ground water and surface water showing features of both adjacent habitats. The hyporheal is looked as integral part of the fluvial ecosystem.
**Hyporheos**: community of epigean and hypogean organisms colonizing the hyporheal.

**Intermittent stream**: stream that exhibits a discontinuous flow regime. E.g. a stream that falls dry in regular or unpredictable periods.

**Orthophoto**: A modified copy of a perspective photograph of the earth's surface with distortions due to tilt and relief removed.

**POM**: Particulate organic matter. The total fraction of organic matter > 0.5 μm.

**Proglacial**: referring to the area directly in front of or just beyond the outer margin of a glacier or ice sheet, and the deposits or other features formed by or derived from the glacier ice.

**Turbidity**: a measure of the degree of clarity of a solution. Turbidity is an easy-to-measure tracer for glacial meltwater, that exhibits a high turbidity due to suspended glacial flour.
Scientific Achievements

1st author papers


Co-authored papers


Submitted papers

Papers in preparation
Zah R. & Uehlinger U.  Spatial modeling of allochthonous inputs of particulate organic matter to a high alpine floodplain.

**Papers presented at international conferences**


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Verdankung


Gegen Ende der Doktorarbeit war vor allem der intellektuelle Gedankenaustausch wichtig. Ich danke Piet Spaak, Chris Robinson, Andreas Frutiger, Mark Gessner und Heinrich Bührer für die fruchtbaren Diskussionen, die zur
Verbesserung der Arbeit geführt haben. Ganz besonders danke ich meinen Kommilitonen Sandra Lass, Dave Arscott, Mike Monaghan, Mäggi Hieber, Peter Burgherr, Diana Soldo und Heini Eisenmann. Sie haben mich sowohl fachlich als auch persönlich über die Zeit der Doktorarbeit und darüber hinaus begleitet.

Der größte Dank aber gebürt meinen Eltern und meiner Familie, die während meiner Doktorarbeit einige Entbehrungen erduldet hat. Ohne Gabi wäre diese Arbeit nicht möglich gewesen.
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