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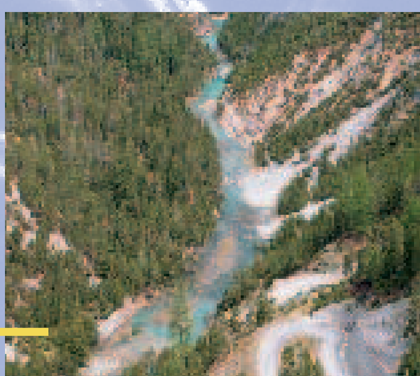
Alpine Streams



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Alpine Streams

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Editorial

Alexander J.B. Zehnder
Director of the EAWAG

Although the critical role of alpine areas for the hydrological cycle and river discharge dynamics has long been recognized, knowledge on the biological, chemical, and physical dynamics of alpine streams has been scarce. A number of innovative scientists have been attracted by these "dull" environments with apparently low biodiversity and limited interaction between the physicochemical environment and the biota. James V. Ward was one of them.

When he joined us at EAWAG in 1995, we had done little research in alpine areas. He gathered together a group of young enthusiastic scientists to start research on the ecology of alpine streams. Fieldwork was carried out throughout the year rather than being restricted to the warmer summer months. This approach allowed the group to have a broader view and provided many new insights. The gained knowledge will help us in taking measures to protect alpine aquatic systems for the safety of densely populated regions at lower altitudes, and in preserving the aesthetic value and biodiversity of mountain ecosystems. In this issue, James Ward and his collaborators summarize their work – a fascinating story about the structure and functioning of alpine aquatic systems.

The United Nations has proclaimed 2002 as the International Year of the Mountains. The goal is to foster international awareness of the global importance of mountain ecosystems, which are increasingly threatened by modern civilization. Global Change research and the recently increased incidence of disasters originating from alpine regions (avalanches, massive floods) have clearly shown that alpine regions – thought to be pristine for a long time – are also seriously impacted by human activities. Rising temperatures for example have shifted the limits of permafrost to higher altitudes and have thus destabilized mountain slopes. In the Alps above tree line, heavy precipitation in the fall used to accumulate as snow. The water now runs off instantly and occasionally provokes large floods in lower regions.

James V. Ward is retiring soon. His uncompromising commitment to science and particularly to stream ecology has made him a fine and exceptional scholar. Just as his review article in 1994 in *Freshwater Biology* on the *Ecology of Alpine Streams* sparked the interest of many, I am sure the work presented here will further increase understanding of these ecosystems and help us appreciate the value of alpine streams, both in Switzerland and elsewhere. I hope the work reviewed in this issue of EAWAG news will make a lasting contribution to the goals proclaimed by the United Nations.

The Ecology of Alpine Streams

The raw beauty of the alpine life zone, present on all continents, has long held the fascination of geographers and naturalists. Scientific work in alpine tundra has focused on glaciology, hydrology, terrestrial ecology and climatology, with surprisingly little previous research on stream ecology. We initiated a comprehensive study of alpine stream ecology involving a year-round sampling program. Our findings demonstrate much greater levels of environmental heterogeneity than previously reported and document the major roles of floodplain dynamics and groundwater aquifers in structuring habitat conditions. In glacial streams, optimal conditions for biological activity occur during late autumn/early winter.

Alpine streams are among our most valuable water resources. These fascinating aquatic systems, although by no means unaffected by humans, are nonetheless much less impacted by anthropogenic activities than lowland running waters. Alpine catchments have high scientific and aesthetic values (Fig. 1) and alpine stream ecosystems are purported to be sensitive indicators of environmental change [1]. Yet the alpine remains "one of the least studied ecosystems in the world" [2]. In an attempt to help fill this knowledge gap, the Limnology Department of the EAWAG launched a major research initiative to investigate the ecology of alpine streams.

This introductory article provides a general overview of alpine stream ecology. Subsequent articles in this issue report on the major findings from various research projects conducted in stream ecosystems situated above or near treeline in the Swiss Alps.

What is an Alpine Stream?

The term "alpine" has two quite different meanings. When the word is capitalized, **Alpine streams** refer to running waters of the Alps, at any elevation. When not capitalized, **alpine streams** refer to running waters of the alpine zone above treeline, anywhere in the world. Here I adopt the latter context, focusing on the ecology of streams situated between the treeline and the permanent snowline.

Global Distribution of Alpine Streams

The alpine life zone is present on all continents; treeline ranges in elevation from near sea level at high latitudes to about 4000 m a.s.l. in tropical mountains (Fig. 2). The portion of alpine tundra colonized by vegetation occupies 4 million km^2 or about 3% of the total land surface [4]. From this total, 16% is in tropical or subtropical regions, 21% is situated at latitudes >60 degrees, with the remaining 63% in the mid-latitudes (Fig. 3). The total area of the alpine zone, including areas devoid of vegetation, covers nearly 6 million km^2.

In mountains ascending above the permanent snowline, alpine streams may be fed directly by glacial meltwater. Snowline elevation, ranging from >5000 m a.s.l. in the tropics to sea level in the arctic, is largely a function of latitude modified by continentality, aspect (orientation) and precipitation. Lewis glacier on Mount Kenya near the Equator, although only 0.25 km^2, is the largest glacier on the African continent. Glaciers covered 32% of the land surface during the last ice age of the Pleistocene, whereas today about 10% of the land surface is covered by glaciers [1]. Valley glaciers advanced during the Neoglaciation (from ca. 1550–1850), but the twentieth century was characterized by glacial recession. Glaciers exert major influence on discharge and sediment regimes, which are the primary controls of channel morphology [5] and along with temperature structure the aquatic biota in alpine streams [6].

General Features of Alpine Streams

There are several types of alpine streams, each with distinctive features, as described in the next section of this article. Nonetheless, alpine tundra streams share a common suite of environmental attributes that distinguish them from forested high mountain stream ecosystems (Tab. 1). In contrast to the dense riparian vegetation of forested headwaters, alpine stream banks may consist of bedrock or mineral sediments devoid of higher plants. Under optimal conditions, alpine streams are lined with herbaceous plants and low-growing shrubs. Therefore, the wood debris that structures habitat con-

M. Hieber, EAWAG

Fig. 1: Stream flowing through an alpine tundra landscape.

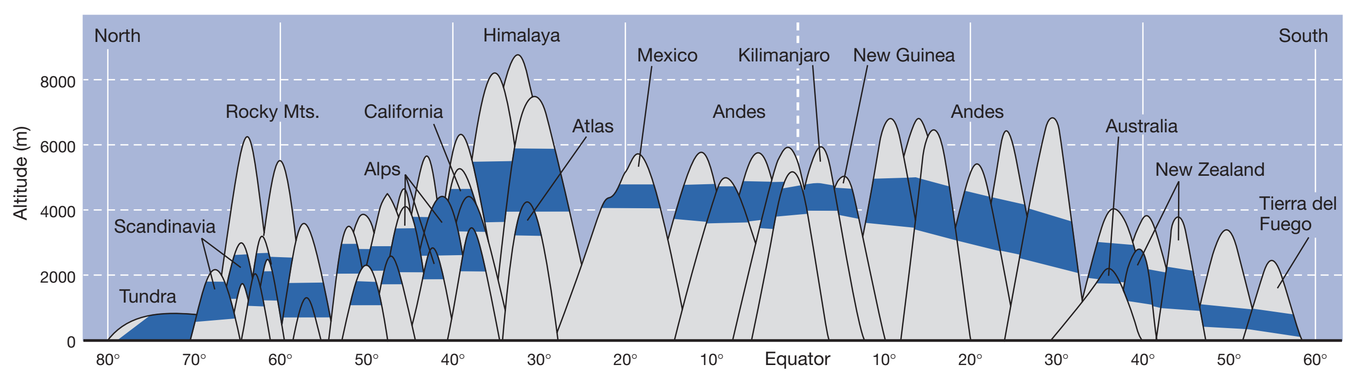

Fig. 2: Altitudinal position of the alpine life zone across latitude [from 3].

ditions and increases retention, and the leaf litter that drives the metabolism of forested headwater streams, are sparse or lacking in alpine streams. Autotrophic production tends to be light limited in heavily canopied forested headwaters, whereas low temperatures and nutrients tend to limit production in alpine streams.

Specific Types of Alpine Streams

Three primary stream types, with distinctly different habitat conditions, flow through alpine landscapes: **kryal** streams fed by glacial meltwater, **krenal** streams fed by groundwater, and **rhithral** streams fed by rainfall and snowmelt [6]. However, the distinctive features of kryal and krenal streams rapidly change downstream as they flow from the source and develop a more rhithral character.

Kryal streams contain the most distinctive fauna and exhibit the most dramatic downstream transformations. Meltwater channels within the glacier, the eukryal zone, are inhabited by heterotrophic microbial assemblages that feed upon organic particles released from the ice mass and the autotrophs, mainly green algae and cyanobacteria, that colonize the walls of the channels. There are even reports of aquatic insect larvae inhabiting englacial channels [7]. The stream that emerges from the glacier, the metakryal zone, is characterized by maximum temperatures ≤2 °C, large diel flow fluctuations in summer, usually high turbidity, and an extremely short growing season. Fishes and higher aquatic plants are absent. The macroscopic filamentous alga *Hydrurus foetidus,* a species confined to cold streams, occurs in glacial streams throughout the Holarctic. The zoobenthos is reportedly restricted to a single genus *(Diamesa)* of chironomid midges. *Diamesa* spp. are the predominant, if not the sole elements of the zoobenthos of the metakryal in the Alps, Scandinavia, Tatras, Balkans, Caucasus, and Rocky Mountains, the Himalayas, and even tropical mountains. *Diamesa* larvae occupy depressions in rock surfaces over which they spin a net, thereby protecting themselves from dislodgement or crushing should the rock overturn. Within a short distance downstream, however, summer temperatures exceed 2 °C and other dipterans and oligochaetes appear in the hypokryal zone. Further downstream, where water temperatures exceed 4 °C, the transition to rhithral conditions occurs and other faunal elements, such as mayflies, stoneflies and caddisflies, are added.

Rhithral headwaters also occur in unglaciated alpine catchments, fed by snowmelt runoff or originating as the outlet streams of lakes. Such rhithral habitats have summer temperatures of 5–10 °C and they lack the severe diel flow fluctuations, unstable bed, high turbidity and paucity of food resources that characterize kryal streams. Fishes are normally present, as are aquatic mosses, lichens, and a relatively diverse algal flora. The zoobenthos contains of a few headwater specialists, but mainly consists of cold-adapted mountain stream species able to occupy a wide range of elevation that are at their upper altitudinal limits in the alpine zone.

Krenal streams, fed by ground water, occur at all elevations. Those originating in alpine tundra provide relatively constant and benign conditions, especially in contrast to kryal streams. They are characterized by relatively warm and clear water and stable substratum. Krenal channels originate as upwelling ground water from the underlying alluvial aquifer (alluvial springs) and from hillslope aquifers that emerge along the edge of the river corridor (hillslope springs). These spring sources provide refugia for aquatic biota in the harsh alpine environment. The alpine landscape often contains a mosaic of kryal, krenal and rhithral habitats, thereby providing a diversity of conditions for aquatic flora and fauna.

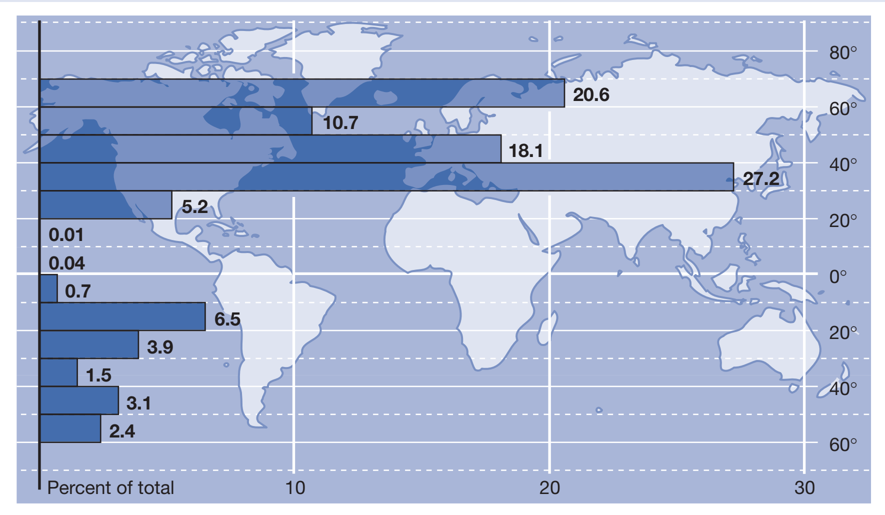

Fig. 3: The relative contribution of each 10 degree latitudinal range to the total global area covered by alpine vegetation. Modified from C. Koerner's chapter, Alpine plant diversity: A global survey and functional interpretations, in [4].

What Have we Learned?

Despite a long-standing interest in high mountain waters, especially in Europe [8], few definitive data were available on alpine stream ecology when the topic was reviewed in 1994 [6]. This contrasts with the rather extensive data on climatology, glaciology, hydrology, and terrestrial ecology of the alpine zone [2, 4]. At that time, the extant ecological research on alpine streams was generally narrow in scope with studies typically limited to the short summer season. For this reason, in 1996 the Limnology Department commenced a comprehensive year-round research initiative that has significantly advanced scientific knowledge of ecological patterns and processes in alpine streams, as summarized in the articles that follow. Other research groups in Europe have also conducted ecological studies of alpine streams over the past few years [9, 10].

Four of Europe's major rivers, the Rhone, Rhine, Po and Danube, have glacial-fed headwaters in Switzerland. The article by C.T. Robinson and U. Uehlinger on page 6 is based on research conducted on six of these glacial streams. Many alpine streams originate from lakes that may or may not be influenced by glaciers. On page 9 M. Hieber and coauthors report on studies conducted in lake outlet streams, to determine to what extent these special running water habitats differ ecologically from alpine streams not associated with lakes. U. Uehlinger's article on page 12 introduces the Val Roseg, a glacier flood plain intensively studied by the Limnology Department. The Val Roseg is the focus of some of the other articles in this issue. K. Tockner and coauthors investigated spatio-temporal habitat heterogeneity in the glacial flood plain of Val Roseg. Their study, summarized in the article on page 14, provided the most comprehensive data set ever collected on habitat dynamics in an alpine stream. The article by F. Malard on page 16 reports on a detailed study of the hyporheic fauna, animals that live in the water-filled sediment interstices within the stream bed, and how they are distributed along a gradient of decreasing glacial influence. An investigation of organic matter dynamics on the Val Roseg flood plain served as the basis for the article by U. Uehlinger and coauthors on page 18. Studies were conducted across scales, from spatial modeling of organic matter flux in the entire stream corridor to decomposition dynamics of individual leaf packs. That article clearly demonstrates the value of year-round sampling for a holistic understanding of alpine stream ecosystems. The article by U. Uehlinger and coauthors on page 20 shows that suitable conditions of discharge, light availability, temperature, and nutrients favor ecological processes and biota during two short periods at the beginning and end of the annual flow pulse. P. Burgherr and coauthors investigated the biodiversity of benthic fauna inhabiting different alpine stream types. The results of their study, reported on page 22, elucidate the strong linkage between habitat heterogeneity and faunal diversity patterns. Alpine streams may be fragmented by both natural and human causes. The study by M. Monaghan and coauthors, summarized on page 24, examined how the genetic diversity of stream insects was affected by fragmentation induced by lakes and reservoirs of different ages. The final article by C.T. Robinson and U. Uehlinger on page 27 reports on a study of the effects of experimental floods conducted in the Swiss National Park. This procedure holds considerable promise as a management technique to restore ecological integrity to regulated streams.

Insights derived from our collective research on alpine stream ecosystems include: (1) recognition that our previous perspective of alpine streams was greatly overly simplified, (2) appreciation of the high level of spatio-temporal heterogeneity that may occur in alpine stream ecosystems, especially those with flood plains and complex channel networks, (3) an elucidation of the important role of aquatic habitat expansion/contraction cycles on habitat conditions and concomitant biotic response, (4) recognition that in glacier streams the period of high biological activity is late autumn/early winter, not during summer when most studies have been conducted, (5) recognition of the important role of ground water – surface water interactions in structuring environmental conditions and biotic communities, and (6) appreciation that effects of habitat fragmentation on gene flow are species specific and reflect glacial history at the catchment scale.

J.V. Ward holds the Chair in Aquatic Ecology at ETH Zurich, and is Head of the Limnology Department at the EAWAG.

Attribute	Alpine tundra streams	Forested mountain streams
Canopy	open	closed
Riparian vegetation	absent/herbs & low shrubs	herbs, shrubs, trees
Large woody debris	absent	important habitat
Snow cover	patchy	deep
Organic matter retention	low	high
Leaf litter	sparse/absent	major energy source
Autotrophic production	temperature/nutrient limited	light limited
Trophic state	autotrophic	heterotrophic

Tab. 1: Some contrasting features of alpine tundra streams and forested high mountain streams.

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Glacial Streams in Switzerland: A Dominant Feature of Alpine Landscapes

Glacial streams are a predominant feature in Swiss Alpine landscapes. Of the relatively few ecological investigations of glacial streams, most have been conducted during summer and usually on only one system. As such, we wanted to know how temporally and spatially variable glacial streams are by examining a number of glacial streams in the Swiss Alps over an annual cycle. An important finding was that glacial streams are more biologically dynamic in autumn/winter than in summer.

The headwaters of all major rivers (Rhone, Rhine, Inn, Ticino) in Switzerland are influenced to some degree by glacial inputs. The diversity of glacial streams in Switzerland is tremendous, ranging from large streams such as the one fed by the Aletsch glacier to much smaller systems coming from the Mutt and Steinlimi glaciers to canyon systems originating from Upper and Lower Grindelwald glaciers where the outflow streams immediately enter a forested flood plain.

Although some recent significant advances have been made, the ecology of glacial streams is poorly understood compared to streams at lower elevations [1]. Recent findings have shown glacial streams to be unique among lotic systems because of the overall dominance of physical forces such as water temperature, large seasonal and diel flow fluctuations, unstable stream beds, turbid water, and the paucity of organic resources. These abiotic factors are a strong controlling force on the biota, particularly in summer [2]. But whether this is the case during other seasons of the year is unknown. In this article, we therefore describe the physico-chemical and biological dynamics of different glacial streams over an annual cycle.

Feature	Kryal	Rhithral
Annual temperature range (°C)	0–4	0–10
Annual cumulative temperature (DD)	<500	500–1000
Annual flow fluctuations	extreme	moderate
Diel flow fluctuations	extreme	moderate
Water clarity (NTU)	2– >1000	0–50
Channel stability	low	high

Tab. 1: General physical features of glacial (kryal) versus non-glacial (rhithral) alpine streams. DD (degree days) = cumulative daily temperature in degrees >0 °C in a year. NTU = nephelometric turbidity.

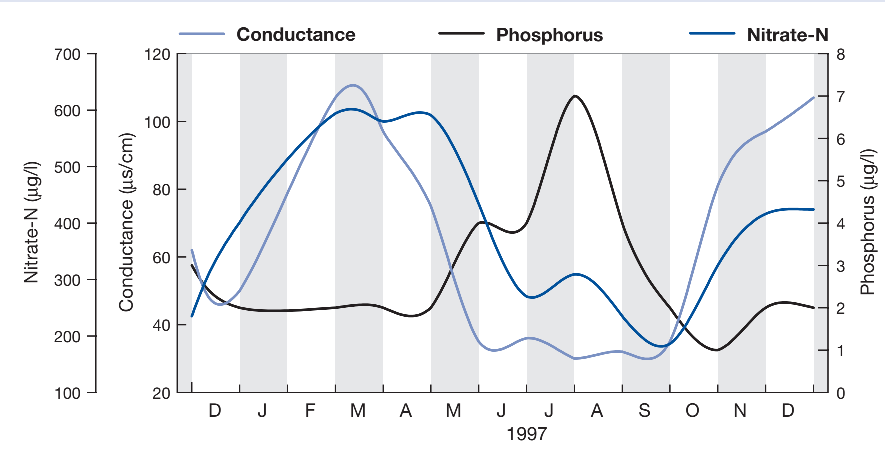

Fig. 1: Annual nutrient patterns as reflected by specific conductance, Nitrate-N, and soluble phosphorus for a typical glacial stream, the Roseg River.

The Glacial Stream Environment

All glacial-fed streams have some common features (Tab. 1). They are characterized by water temperatures <4 °C and extreme changes in flow caused by freeze-thaw cycles. In summer, glacial rivers display strong diel flow fluctuations with peaks in early afternoon. Patterns of melt strongly influence water clarity, being quite clear when flows are minimal to being highly turbid during peak flows in summer [3]. We have recorded turbidity values <10 Turbidity Units in winter to >3000 Turbidity Units during summer [4]. Because most glacial streams are above treeline, terrestrial inputs of organic matter are quite low [5, see also p. 18].

Nutrient Dynamics

Ionic and nutrient dynamics of glacial streams are highly related to the seasonality in glacial influence (Fig. 1). Ionic concentrations, measured as specific conductance, decrease with the increase in glacial melt-

Glacial stream flowing from the Morteratsch glacier.

water in summer. This is also the case for nitrogen concentrations, although they always exceed >150 µg/l. A primary pathway of nitrogen input is atmospheric deposition [6]. In contrast, soluble reactive phosphorus concentrations (SRP) increase in summer to values of up to 7 µg/l (Fig. 1). Throughout the rest of the year, SRP concentrations are about 2 µg/l and are likely to limit primary production in Swiss glacial streams [7]. SRP primarily originates from bedrock.

The Algae

Algal biomass peaks in autumn when glacial streams are most stable and the water is clear, and is lowest during summer (Fig. 2A). If channels remain open, as often occurs at the Morteratsch glacial stream, biomass can remain high all winter (Fig. 2B). The most visible alga, the chrysophyte *Hydrurus foetidus,* can attain high biomass of >25 g ash free dry mass per m^2 in autumn. Some of the more common diatoms include small adnate taxa that are highly resistant to scour and unstable substrates [4]. We observed only one red alga, the rhodophyte *Audouinella violacea,* in the glacial streams studied.

The Macrozoobenthos

Aquatic insects dominate the macrozoobenthos of glacial streams with over 100 species being represented. Year-round sampling revealed an unexpected diverse fauna, including simuliids and other dipteran families, ephemeropterans, plecopterans, trichopterans, and certain non-insect groups such as the predatory flat worm *Crenobia alpina* and oligochaetes. We observed major seasonal changes in macroinvertebrate communities, with substantial increases in abundance, >9000 individuals per m^2, and number of species present in autumn/winter relative to summer (Fig. 3) [8, 9]. Two basic life history strategies were recognized:

- adaptations to the extreme abiotic conditions in summer, e.g., chironomid midges of the subfamily Diamesinae dominate true glacial communities in summer [8–11];

Measure	Nitrogen	Phosphorus
Uptake length (km)	15–45	0.13–2.5
Uptake rate (mg/m^{-2}·h^{-1})	0.01–0.15	0.21–0.51

Tab. 2: Nitrogen and phosphorus uptake measures from a number of glacial streams in the Swiss Alps recorded at different times of the year. Uptake length refers to the length of stream in which a nutrient is in transport before being taken up physically or biologically. Uptake rate is simply the rate at which a nutrient particle is taken up standardized to a unit area of stream.

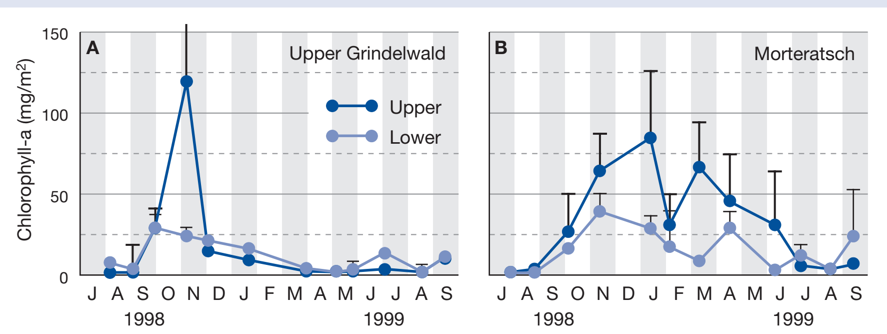

Fig. 2: Seasonal patterns of algal biomass (expressed as chlorophyll-a content in ash-free dry mass) for two glacial streams in Switzerland. Upper and lower sites are presented for each river, illustrating the longitudinal dynamics of glacier rivers. The Morteratsch is usually ice-free in winter, whereas Upper Grindelwald is snow-covered.

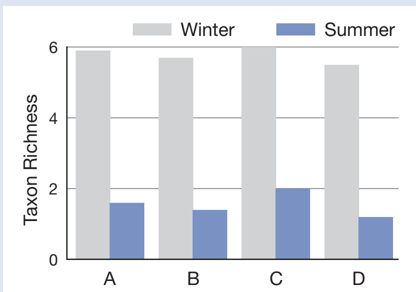

Fig. 3: Seasonal differences in species richness in four glacial rivers (A = Lang, B = Steinlimli, C = Morteratsch, D = Grindelwald) of Switzerland, showing the major increase in the number of species in winter relative to summer.

Glacial stream flowing from the Lang glacier.

■ avoidance of summer with growth and development in winter, e.g., we observed adult midges in snow and ice covered streams in February [10].

Are Glacial Streams Nutrient Limited?

To determine whether algal growth in glacial streams is nutrient limited, we experimentally added nitrogen and phosphorus to different glacial streams in spring, summer and autumn. Nitrogen addition had no stimulatory effect on algal production and the streams essentially retained no nitrogen (Tab. 2). In contrast, a strong response was observed in algal production to nutrient addition (Fig. 4), although only in spring and autumn when instream SRP concentrations were low. We suspect that high turbidity and low substrate stability in summer confounded responses by algae to phosphorus addition. Phosphorus retention was also much greater than nitrogen retention (Tab. 2). The high phosphorus retention rates found in summer are probably due to absorption onto particles of glacial flour.

Conclusion

Glacial streams have some distinct characteristics not shared by other stream types, i.e., low temperature, high loads of suspended solids from glacial flour in summer, and high seasonal and diel fluctuations in flow. Our investigations revealed a strong degree of seasonality in physico-chemical and biological properties, with biological activity being most pronounced in autumn and winter. This high biological activity outside the summer period was shown by the algae which attained high biomass in autumn and by the macrozoobenthos which had higher densities and richness in autumn/winter than in summer.

Christopher T. Robinson is a stream ecologist with the Limnology Department of EAWAG. His primary research emphasis is the ecology of alpine streams.

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U. Uehlinger

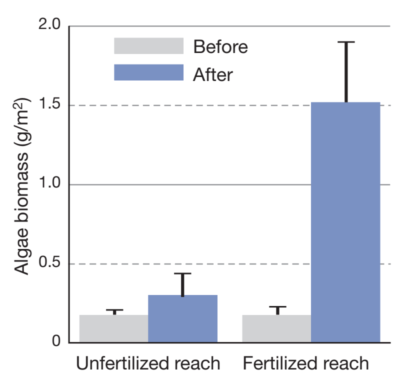

Fig. 4: Response of glacial stream algae to nutrient enrichment with fertilizer pellets containing both nitrogen and phosphorus.

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Alpine Lake Outlets: Distinctive Alpine Stream Types?

Streams flowing from lakes represent unique aquatic environments inhabited by both lake and stream organisms. In alpine areas, lake outlets can be of either rhithral (snow-fed) or kryal (glacier-fed) origin. Although a prominent feature of alpine environments, surprisingly little information exists on the ecology of alpine lake outlets. We have found these distinctive freshwater environments to differ substantially from lowland lake outlets and also from other alpine streams.

Lake outlets are defined as longitudinal transition zones between lake and stream habitats. Depending on size (volume) and flow-through, lakes in lowland areas buffer fluctuations in discharge and temperature, and often supply large quantities of plankton that favor filter-feeding invertebrates in outlet streams [1]. Lake outlets have been widely studied in lowland regions. Virtually nothing is known, however, about the ecology of lake outlets in alpine areas, where they are a frequent feature. Therefore, we launched a research initiative to investigate the habitat and biota of alpine lake outlets. Specifically, we were interested in knowing whether alpine lake outlets differ from other alpine streams and whether they are comparable to lowland lake outlets. We examined 2 kryal and 4 rhithral lake outlets as well as 2 kryal and 2 rhithral streams situated in the Swiss Alps (Fig. 1, for definitions see p. 4).

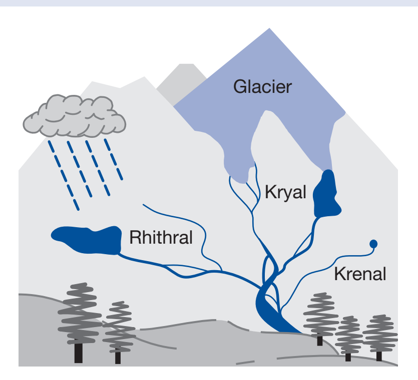

Fig. 1: Alpine stream types with their major water sources [modified from 3, 5].

Habitat Characteristics of Alpine Lake Outlets

Alpine lakes are typically small in size and of limited extent; nevertheless, they have a distinct influence on their outlet streams. For example, water temperature plays a key role in the ecology of aquatic organisms [2, 3], and lakes can markedly affect the thermal regime of outlet streams. We found alpine outlet streams to have higher maximum water temperatures and annual degree days (i.e., accumulated temperature), faster warming rates and lower diel fluctuations than non-outlet streams (Fig. 2) [4]. In addition, proglacial lakes decreased the amount of suspended particles entering their outlets, thus increasing water clarity and decreasing sediment scouring relative to other glacial streams.

Terrestrial inputs of organic material are low in alpine streams, and the energy base is primarily from instream sources such as algae and macrophytes (see also p. 18). In contrast to lowland lake outlets, we found organic matter input from alpine lakes to their outlets to be low. Most alpine lakes are extremely oligotrophic and act more as sinks than as sources of organic matter. However, instream production of organic matter was quite high in rhithral lake outlets, probably resulting from the more stable bed sediments. In kryal systems, organic matter concentrations were similar between streams and lake outlets, both displaying high seasonality with peak abundances during low flow in autumn and spring (see also p. 20).

In general, the examined alpine lake outlets differed in their habitat conditions compared to other alpine streams. However, the presence of a glacier and the seasonality in glacial melt strongly influenced the discharge regime and, thereby, reduced the lake influence on their outlets.

Flora and Fauna of Alpine Lake Outlets

The biota of alpine streams displayed relatively broad geographical distributions [5], although community structure reflected the differences in habitat conditions of the dif-

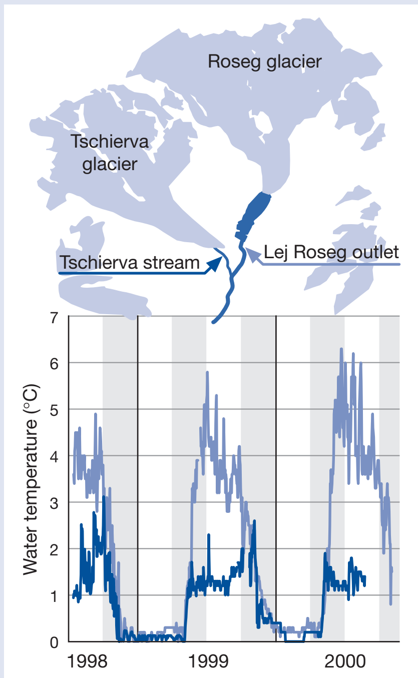

Fig. 2: Average daily water temperature of a kryal lake outlet (Lej Roseg) and an adjacent kryal stream (Tschierva stream).

ferent stream types. Generally, the diversity of stream organisms was lower in kryal than rhithral systems, and lake outlet communities differed from respective streams (Tab. 1).

The aquatic flora typically was dominated by diatoms, blue-green algae and the chrysophyte *Hydrurus foetidus,* a widely distributed cold-water filamentous alga. Algal communities in rhithral systems were characterized by more taxa than those of kryal systems, where species richness and biomass displayed strong seasonal fluctuations usually being low during summer high flows. Among kryal systems, lake outlets had higher algal diversity (especially diatoms) than kryal streams, and rhithral lake outlets were characterized by the presence of aquatic mosses, at times attaining high biomass and providing important habitat for invertebrates [6, 7].

The outlet of the kryal Steinsee.

Invertebrate communities were also more diverse in rhithral than in kryal systems. Common invertebrates included mayflies, stoneflies, caddisflies, true flies (mostly chironomids), flat worms (turbellarians), and oligochaetes. Chironomids (Diamesinae)

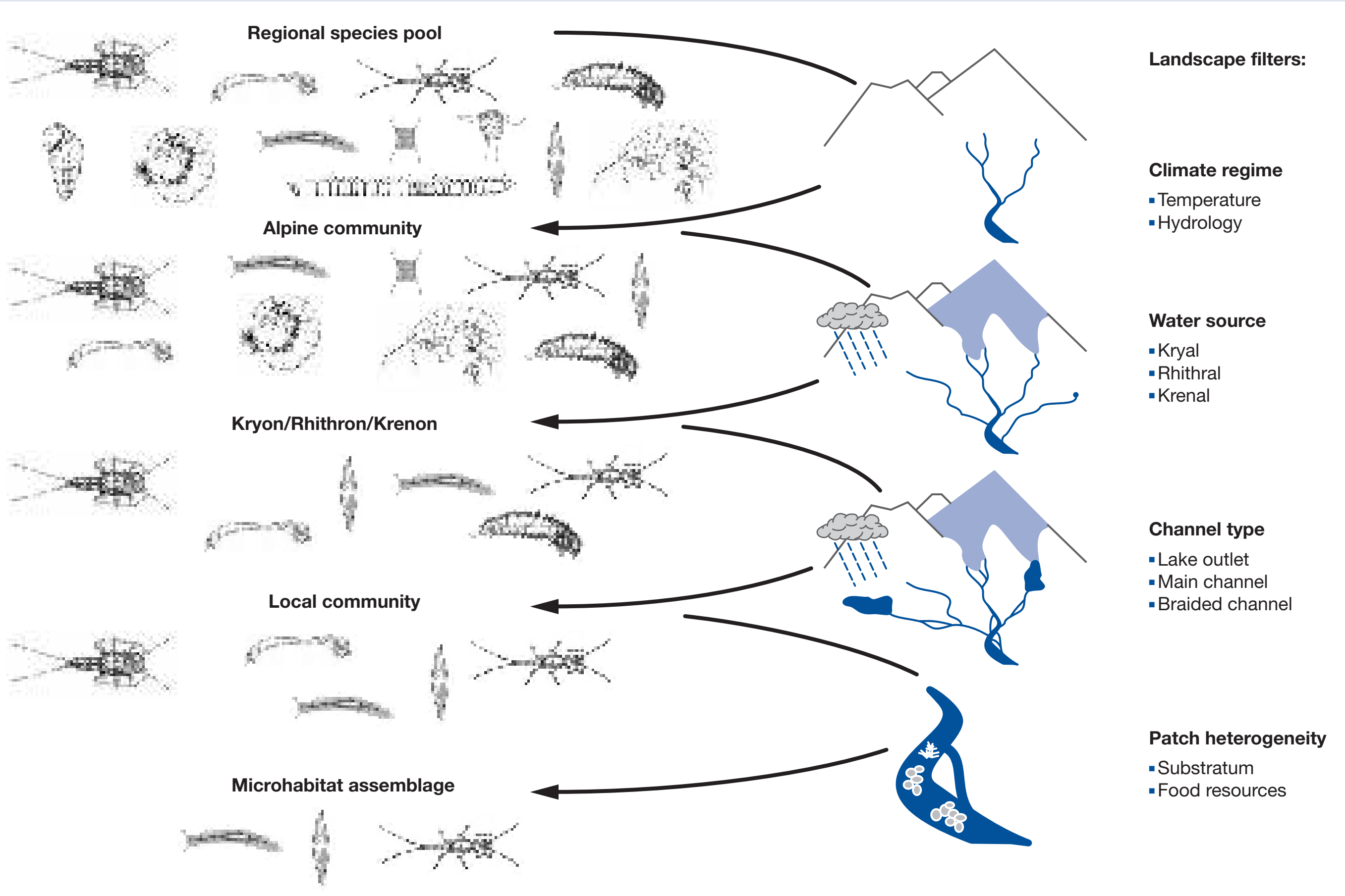

Fig. 3: Conceptual model of how landscape filters [sensu 8, 9] determine the benthic community composition in different alpine stream types. The major environmental factors operating at a given hierarchical level act as filters which determine the species community that occupy the next hierarchical level.

The outlet of the rhithral Lago Bianco.

dominated kryal systems, although mayflies and stoneflies were present during periods of low flow (see also p. 6 and p. 22). Chironomids and non-insect taxa such as oligochaetes, nematodes and copepods were common in rhithral lake outlets, whereas both non-insect as well as many insect taxa were found in rhithral streams and represented a species complex that is characteristic of both kryal and rhithral systems. However, in contrast to expectations of lowland lake outlets, filter-feeding invertebrates were rare or even absent, probably resulting from the low concentrations of transported organic matter in alpine streams.

Extending Ward's [5] general characterization of alpine streams, we provide a summary of environmental and biotic features of rhithral and kryal streams and outlets (Tab. 1).

Are Alpine Lake Outlets Distinctive Stream Habitats?

We found alpine lake outlets to be distinctive habitats having specific biotic communities. Alpine lake outlets can be seen as subclasses of rhithral and kryal systems with the presence of a glacier reducing the influence of an upstream lake. In a sense, the different kinds of alpine streams can be structured hierarchically, with different geomorphic and environmental features acting as nested "filters". These filters effectively "screen" species from the regional species pool based on their biotic traits [8, 9], thereby determining the biotic community within each stream (Fig. 3). Lastly, we found that the distinctiveness of lake outlet communities declines with increasing elevation and glacial influence. We suggest that the successful management of alpine streams and lakes must incorporate the unique ecological features of the individual stream types to sustain native biodiversity.

Mäggi Hieber completed her doctoral research on alpine streams and lake outlets in the Department of Limnology at EAWAG.

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	Rhithral		**Kryal**	
Variable	Stream (n = 2)	Lake outlet (n = 4)	Stream (n = 2)	Lake outlet (n = 2)
Annual degree days	900–1300	900–1500	<300	500–700
Annual temperature range (°C)	0–13	0–17	0–5	0–9
Diel temperature fluctuations	High	Intermediate	Intermediate	Low
Flow regime	High seasonal fluctuations	Intermediate seasonal fluctuations	High seasonal + diel fluctuations	Intermediate seasonal + diel fluctuations
Transparency (NTU)	Clear (0–3)	Clear (0–10)	Turbid (2– >1000)	Turbid (30–400)
Channel stability	Variable	High	Low	Variable
Algae	Diverse diatoms Blue-green algae *Hydrurus foetidus*	Diverse diatoms Blue-green algae Moss	*Hydrurus foetidus* *Chamaesiphon* *Lyngbya* Sparse diatoms	*Hydrurus foetidus* *Chamaesiphon* *Lyngbya* Few diatoms
Macroinvertebrates	Diverse EPTD Non-insects	Non-insects: Oligochaeta Nematoda Chironomidae Few EPT	Diamesinae EP: Baetidae Heptageniidae Leuctridae	Diamesinae EP: Baetidae Heptageniidae Leuctridae

Tab. 1: Idealized environmental and biotic features of rhithral and kryal streams and lake outlets. [modified from 5] E = Ephemeroptera, P = Plecoptera, T = Trichoptera, D = Diptera, n = number of sites sampled.

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Val Roseg: A Glacial Flood Plain in the Swiss Alps

The upper Val Roseg valley in the eastern Swiss Alps hosts a hydro-morphologically diverse stream ecosystem that is strongly influenced by glacial runoff. The distinctive geomorphic feature of the Roseg River corridor is a large glacial flood plain that was subject to a comprehensive ecosystem study.

The effects of future climate change are expected to severely affect alpine stream ecosystems [1] in addition to current human impacts such as tourism, flood protection and water abstraction for power production. Knowledge on the structure and function of alpine streams has been limited until recently (see also p. 3). In the past few years, however, alpine stream ecology has attracted major attention [e.g., 2]. In 1996, the limnological department at EAWAG initiated a comprehensive investigation of the glacial floodplain system in the upper Val Roseg (Fig. 1), a catchment providing a unique diversity of stream types and being accessible throughout the annual cycle. The studies were directed to understand spatial and temporal patterns of periphyton, benthic and hyporheic fauna, production and decomposition of organic matter, and nutrient dynamics in the harsh alpine environment. Some results from the Val Roseg Project will be presented in the following five articles in this EAWAG news issue. This article summarizes some important characteristics of the Val Roseg such as geomorphology, hydrology, temperature regimes, and channel dynamics.

An Alpine River Corridor

The Val Roseg is located in the Bernina Massif of the Swiss Alps. Some important area statistics are summarized in Table 1. Elevations range from 1981 m a.s.l. at the downstream end of the glacial flood plain to 4049 m at the top of Piz Bernina. The Roseg River (mean annual discharge = 2.8 m^3/s) is primarily fed by meltwater from Roseg glacier, which ends in a proglacial lake, and the Tschierva glacier. Five major stream reaches can be distinguished along the corridor of the Roseg River (Fig. 2):

- a 650 m long proglacial reach below the Tschierva glacier,
- a 900 m long lake outlet system below the proglacial lake,
- a 700 m long single-thread channel incised in glacial till downstream of the confluence of the proglacial stream and the lake outlet,
- a 2600 m long and 150–500 m wide main glacial flood plain, where elevation ranges from 1981–2055 m,
- a 7.2 km long reach constrained by valley slopes.

The flood plain include an impressive diversity of different alpine stream types that range from glacial streams to springs [3] (see also p. 14).

Terrestrial vegetation – a potential energy source for benthic organisms (see also p. 18) – varies from almost no vegetation

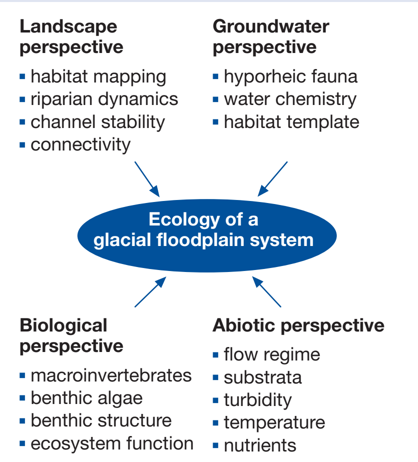

Fig. 1: The multifaceted nature of the Val Roseg Project.

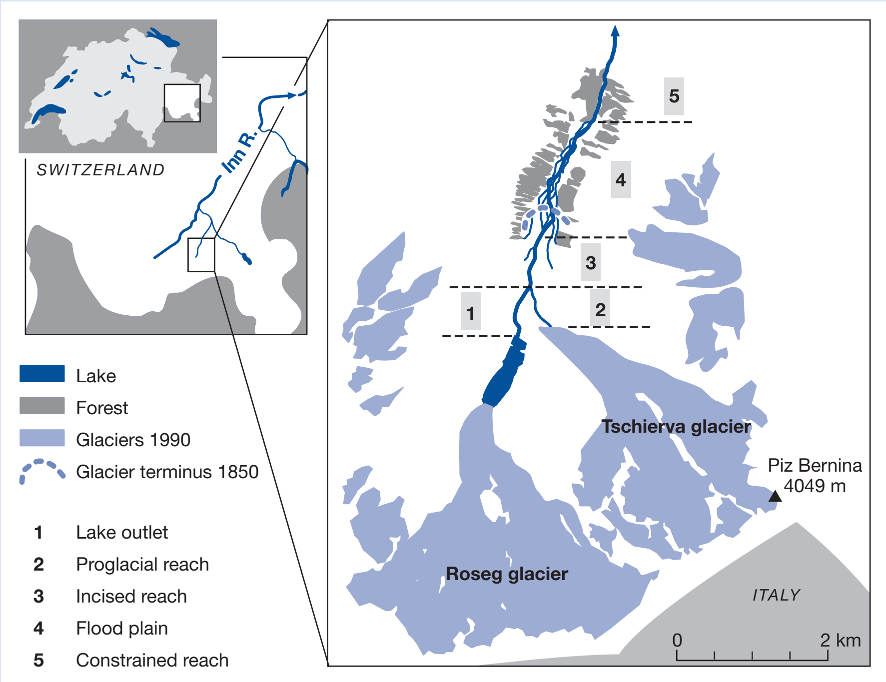

Fig. 2: Upper Val Roseg catchment.

	%	km²
Glaciers	41.7	20.6
Rock	32.3	16.0
Grassland	18.4	9.1
Forest	3.6	1.8
Flood plain	3.4	1.7
Lake	0.6	0.3
Total area		**49.5**

Tab. 1: Area statistics of the upper Roseg valley. Contribution of different landscape elements.

close to the terminus of the Tschierva glacier to subalpine forests covering the valley slopes along the flood plain. The elevation of the treeline ranges from 2100–2300 m a.s.l. In the flood plain, channel dynamics resulted in a dynamic mosaic of different terrestrial vegetation. Bare gravel or gravel with initial stages of pioneer plant communities dominated in 70% of the active floodplain area. The flood plain is free from trees, but contains a few scattered shrubs in relatively small areas not affected by channel migration for more than 30 years.

Flow Dynamics

The glacial flow regime, which is a major factor structuring the physical habitat template of the floodplain system, is characterized by a distinct annual flow pulse. Daily discharge increases from about 0.16 m^3/s in April to more than 10 m^3/s in July and August then declines from late September to November to 0.2 m^3/s (Fig. 3). Superimposed on this highly predictable flow pulse are aperiodic and periodic flow variations. Diel pulses reflect enhanced freeze-thaw cycles during summer. Heavy rainfall results in flow peaks (e.g., in June, August and November 1997, Fig. 3) whereas periods of cold weather reduce the meltwater production (e.g., July and August). The annual flow pulse results in dramatic cycles of habitat expansion, contraction and fragmentation, and affects habitat properties such as water chemistry, turbidity and temperature (see also p. 14) [4, 5].

Thermal Heterogeneity

Temperature is a key factor regulating community structure of aquatic invertebrates and ecosystem function. In addition, there is a strong link between temperature and flow in this glacial system. In spring, air temperature and solar radiation augment water temperature throughout the flood plain. With the onset of snowmelt and icemelt in early June, water temperature in the main channel and in channels with upstream connections to the main channel begins to decrease. In channels lacking upstream connection to the main channel, water temperatures continue to rise until August/September. This results in a high thermal heterogeneity of habitats across the flood plain. Unlike many glacial streams, aquatic habitats with relative high temperature occur in close proximity to the glacier (Fig. 4).

An Alpine Stream Ecosystem in a Changing Climate

Evaluation of aerial photographs taken between 1947 and 1999 showed that about 25% of the channel network is renewed annually [6]. Disconnection and reconnection of former channels in the upper part of the Roseg flood plain induce major changes in the network of wetted channels. There is some evidence that such modifications occur after floods with substantial bedload transport. Roseg and Tschierva glaciers are rapidly retreating like most glaciers in the Alps. In 1934, the Tschierva glacier separated from the Roseg glacier. The Roseg and Tschierva glaciers end today about 3 km and 1.5 km from the terminus of the little ice age in 1850 (Fig. 2). The growing proglacial area below the Tschierva glacier stores large amounts of unconsolidated sediments that are susceptible to fluvial transport into the flood plain during high flow. Increased sediment supply, however, is assumed to accelerate the channel turnover in the flood plain [4] and as a consequence to reduce the average life span of habitats.

Air temperature records from stations in the Alps show an increase in daily minimum temperature of 2 °C since 1901 [7, 8]. The response of stream temperatures to this trend is presumably small unless amplified by receding glaciers. Between the current glacier termini and the 1850 terminus water temperature increases today on the average by about 3 °C during summer. One may infer that since the end of the little ice age, the main channel and surface connected floodplain channels became more favorable habitats, at least with respect to temperature. If the current trend of glacier recession continues, some floodplain channels will continue to warm up whereas channel stability is expected to decline.

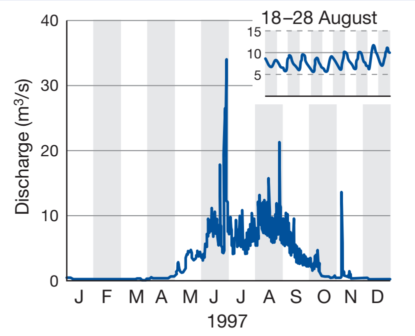

Fig. 3: Hydrograph of the Roseg River. Diel flow variations in August reflect enhanced freeze-thaw cycles during warm weather.

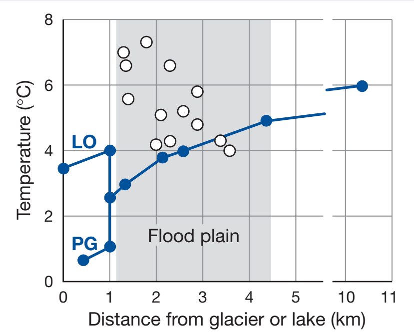

Fig. 4: Average water temperatures in July along the Roseg River corridor. Filled circles = main channel sites, open circles = floodplain channels excluding main channel. LO = lake outlet reach, PG = proglacial reach.

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Habitat Dynamics in the Val Roseg Flood Plain

Flood plains are among the most complex and dynamic but also one of the most endangered ecosystems worldwide. They are characterized by a high level of habitat heterogeneity and diverse biota adapted to this heterogeneity. In the glacial Val Roseg flood plain heterogeneity results from a diversity of channel types and a pronounced expansion and contraction cycle of the entire channel network.

Most investigations on river-floodplain systems have been restricted to large lowland rivers. These studies have shown that flood plains are centers of high biodiversity and bioproduction [1]. Flood plains may, however, develop at different locations along a river corridor. The 2.6 km long flood plain in the upper Val Roseg was formed in the glacial outwash of the Roseg and Tschierva glaciers (Fig. 1 and Fig. 2 p. 12). Does a flood plain at high altitude provide a similar variety of habitats compared to lowland rivers, and does it increase overall regional diversity within an otherwise harsh environment? Hence, a major goal of the Val Roseg project was to quantify the spatio-temporal heterogeneity of the floodplain system and to link it to biological diversity (see article p. 22) and principal ecosystem processes such as transformations of nutrients and organic matter (see article p. 18).

Channel Network Diversity

Six distinct channel types were identified, based on hydrological connectivity with the main channel and the relative proportion of individual water sources (Tab. 1) [2]. In summer, each of these channel types contributes to the total channel network. In winter, however, tributaries, side channels and intermittently connected channels dry up. The remaining mixed and main-channel segments are transformed into groundwater channels lacking upstream surface connectivity. Each of the individual channel types contributes, single and in concert, to the remarkable high biodiversity in this glacial flood plain [3; see also articles p. 16 and p. 22].

Fig. 1: Location of different channel types in the Val Roseg flood plain (upper section): M = main channel, S = side channel, I = intermittently-connected channel, X = mixed channel, G = groundwater channel, T = tributary (see also Tab. 1).

The Flood Plain as an Expanding and Contracting Ecosystem

The Val Roseg flood plain is characterized by distinct expansion and contraction periods that are associated with major changes in channel network length; a common phenomenon in lotic systems that has been given only scant attention by river ecologists. In the Val Roseg flood plain, channel network length increases from about 5 km in winter to more than 20 km in summer. Hydrochemical indicators were employed to link the expansion/contraction cycle with shifts in dominant hydrological processes. Indicators include sodium (groundwater contribution), nitrate (snowmelt water) and particulate phosphorus (glacial meltwater). The relative proportion of the major water sources to total floodplain discharge changes during the annual cycle [4], with subglacial and hillslope ground water dominating in winter, snow-melt water in spring and glacial meltwater in summer (Fig. 2). Based on a mixing model [5], the relative contribution of hillslope ground water to total floodplain discharge ranges from <10% in summer to >70% in winter. Therefore, the entire flood plain shifts from a uniform groundwater-dominated system in winter to a heterogeneous glacial-meltwater dominated system in summer. The seasonal shift in the relative proportion of water sources control the availability of key ecological resources such as nutrients, organic matter and temperature (see article p. 18).

Inundation Dynamics and Floodplain Complexity

Based on the relationship between discharge, channel network length and channel diversity – also called riverscape heterogeneity – we developed a simple model to predict the availability of channel types and aquatic habitat heterogeneity over a 3-year

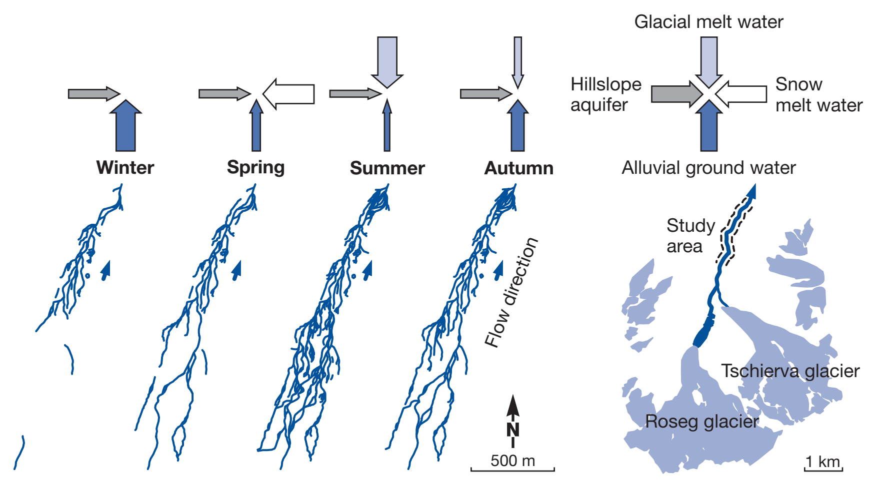

Fig. 2: Expansion and contraction cycle of the channel network of the Val Roseg flood plain (four seasons) and the relative contribution of different water sources to total floodplain discharge.

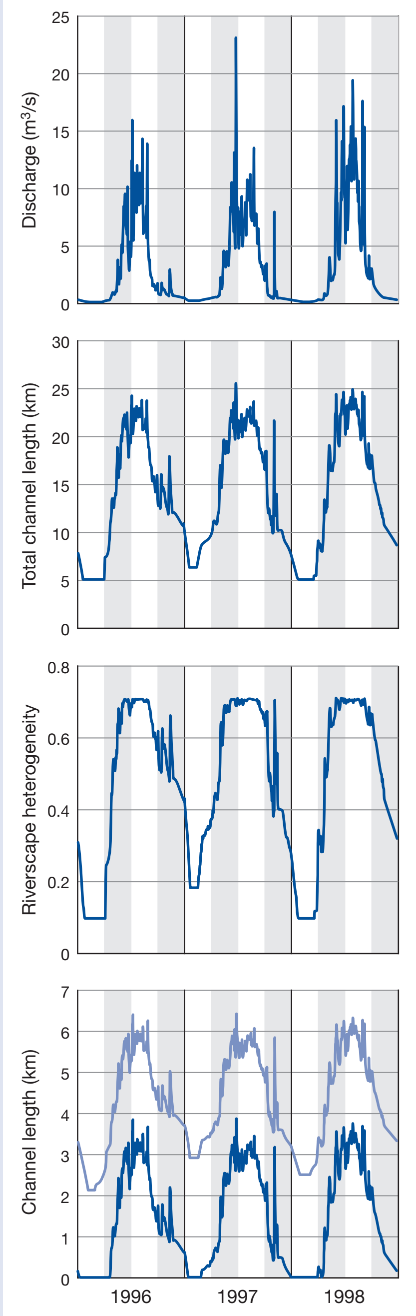

Fig. 3: Seasonal dynamics of daily discharge (A), total channel length (B), riverscape heterogeneity (C). Groundwater (light blue line) and intermittently-connected (dark blue line) channel lengths (D) were predicted from discharge-channel length and discharge-heterogeneity relationships.

period (Fig. 3). Channel heterogeneity was calculated using a diversity index with 8 turbidity classes representing "species" and the proportion of channel length in each class representing "abundance" [4]. Results demonstrate a high seasonal predictability of channel types and diversity. Channel heterogeneity is highest during high flow in summer ameliorating the negative effects of diurnal flow peaks associated with high sediment loads. In contrast to lowland flood plains, the seasonal shift in water sources primarily contributed to the remarkable heterogeneity found in the high alpine Val Roseg flood plain.

Compared to single-thread high alpine rivers, flood plains are presumably more resistant to expected changes in flow regime and land use. Therefore, they provide regional ecosystem stability to otherwise extremely sensitive and rapidly changing ecosystems. Glacial flood plains deserve particular attention in conservation and management programs, as emphasized by the present initiative of BUWAL to inventory the high alpine flood plains that are of national importance.

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Channel type	Parameter					
	Water source	**Temperature (°C)**	**Turbidity**	**Channel stability**	**Nutrients**	**Expected biodiversity**
Main channel (M)	Valley glacier	2–4	High	Low (bedload transport)	Low	Medium–low
Side channel (S)	Valley glacier	2–4	High	Low–medium	Low	Low
Intermittently-connected channel (I)	Valley glacier	2–5	High–medium	Medium–low	Low	Low
Mixed channel (X)	Glaciers, groundwater	3–5	Medium	Medium	Medium	Medium–high
Groundwater channel (G)	Alluvial, hillslope groundwater	4–8	Clear	High	High	High
Tributary (T)	Hanging glacier	4–8	Clear–medium	High	Medium–high	Low–medium

Tab. 1: Floodplain channel types, their characteristics during high summer flow and their expected biodiversity [for detailed information on channel types see 2].

Biodiversity in a Glacial Hyporheic Corridor

Despite the recognition of the hyporheic zone as a key component of stream ecosystems, studies on the diversity and distribution of glacial stream invertebrates have focused on the ecology of surface benthos. Due to the harsh environmental conditions prevailing in the benthic layer, we expected the hyporheic zone to contribute significantly to the diversity of invertebrate assemblages in glacial streams. Recent investigations carried out in the hyporheic zone of the Roseg River revealed the presence of a number of permanent aquatic taxa. Our data suggest that the hyporheic zone acts as the main upstream migration pathway and as a source area from which benthic habitats can be colonized.

The hyporheic zone is the interstitial area extending beneath the stream bed and into the stream banks. It contains a mix of stream water and ground water [1]. Because large amounts of sediments are transported and deposited by glacial water along Alpine valleys, the hyporheic zone forms a corridor that may extend metres vertically beneath the channel and hundreds of meters away from the channel. Surface glacial water downwells into the sediment, travels for some distance (i.e. from cm to km) beneath or along the stream, eventually mixes with ground water, and then returns to the stream [2]. Surface-subsurface hydrological exchanges in streams affect the diversity, production, and distribution of invertebrate communities. However, most of the recent studies on the diversity of glacial stream invertebrates, have focused on the ecology of the surface benthos [3]. In the Val Roseg, we examined the longitudinal pattern of hyporheic invertebrate assemblages. The purpose of the present study was threefold:

- to determine the contribution of the hyporheic zone to the diversity of invertebrate assemblages in a glacial stream,
- to identify key factors affecting the distribution of taxa,
- to examine major differences in the upstream colonization by hyporheic and benthic invertebrates (see also p. 22).

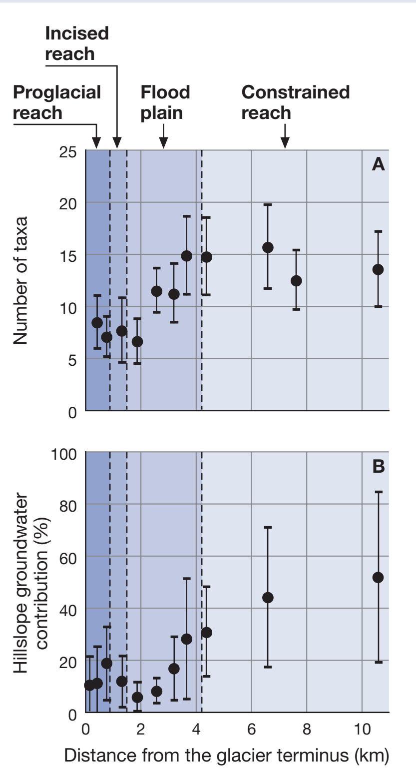

Fig. 1: Longitudinal changes in taxonomic richness of the hyporheos (A, n = 15 samples), average contribution of hillslope ground water to the flow of surface water (B, n = 12 dates). See Fig. 2, p. 12 for the location of the proglacial and incised reaches, the flood plain, and the constrained reach.

Sampling Strategy

Faunal sampling was carried out in September 1996 and in June, August, September and November 1997. Three hyporheic replicate samples were collected at 11 sites located over a distance of 11 km from the glacier terminus in the proglacial and incised reach, the flood plain, and the constrained reaches (see Fig. 2, p. 12). Invertebrates were collected by driving a mobile pipe to a depth of 30 cm below the streambed. Ten liters of interstitial water were immediately extracted using a hand piston pump and filtered through a 100-µm-mesh net. Animals were identified and counted under a dissecting microscope.

The Flood Plain is a Source of Species

A total of 46 taxa were collected from the hyporheic zone of the main channel in the Val Roseg. However, total species richness was strongly underestimated because insect larvae could only be identified to the family level. The number of taxa increased markedly as the main channel entered the lower floodplain reach (Fig. 1A) where groundwater influence also becomes more important (Fig. 1B). This suggests that floodplain habitats originating from the upwelling of ground water act as a major source of species. Sampling at multiple sites within the flood plain showed that the diversity of benthic and hyporheic invertebrate assemblages was distinctly higher in groundwater-fed channels [4; F. Malard, unpublished data]. In addition, at least 12 species of micro-crustaceans collected in the hyporheic layer of the main channel did not occur in the benthic layer and several species of oligochaetes were found to colonize more upstream sites in the hyporheic zone than in the surface stream [5]. These results strongly suggest that the hyporheic corridor acts both as the main upstream migration pathway and as a refuge for several permanent aquatic taxa during the colonization of glacial forelands.

Species are Distributed Along a Gradient of Decreasing Glacial Influence

Longitudinal changes in key environmental factors (e.g., temperature, bed stability, organic matter content of bed sediments) with distance from the glacier terminus are driving forces for glacial stream organisms [3]. In the Roseg River, the spatial niche of 18 hyporheic taxa (out of 42 taxa) deviated significantly from a uniform distribution along a gradient of decreasing glacial influence with distance from the glacier terminus (Fig. 2). Only 2 taxa, the turbellarian *Crenobia alpina* and the harpacticoid copepod *Maraenobiotus insignipes* preferentially colonized the upstream proglacial reach. Most of the taxa present in the proglacial reach were distributed over the entire longitudinal gradient (data not shown). In contrast, several taxa were either restricted to or occurred preferentially in the lower reaches of the River.

In the Val Roseg, temperature has a major influence on the diversity and abundance of hyporheic assemblages. The temperature of hyporheic water is strongly influenced by the direction and intensity of surface water-groundwater exchanges [6]. In particular, inputs of ground water substantially increase mean summer temperatures in the hyporheic zone of the main kryal channel. Higher temperature and physical stability in the hyporheic zone than in the benthic layer enable taxa to persist in glacial-fed channels where they would otherwise be eliminated.

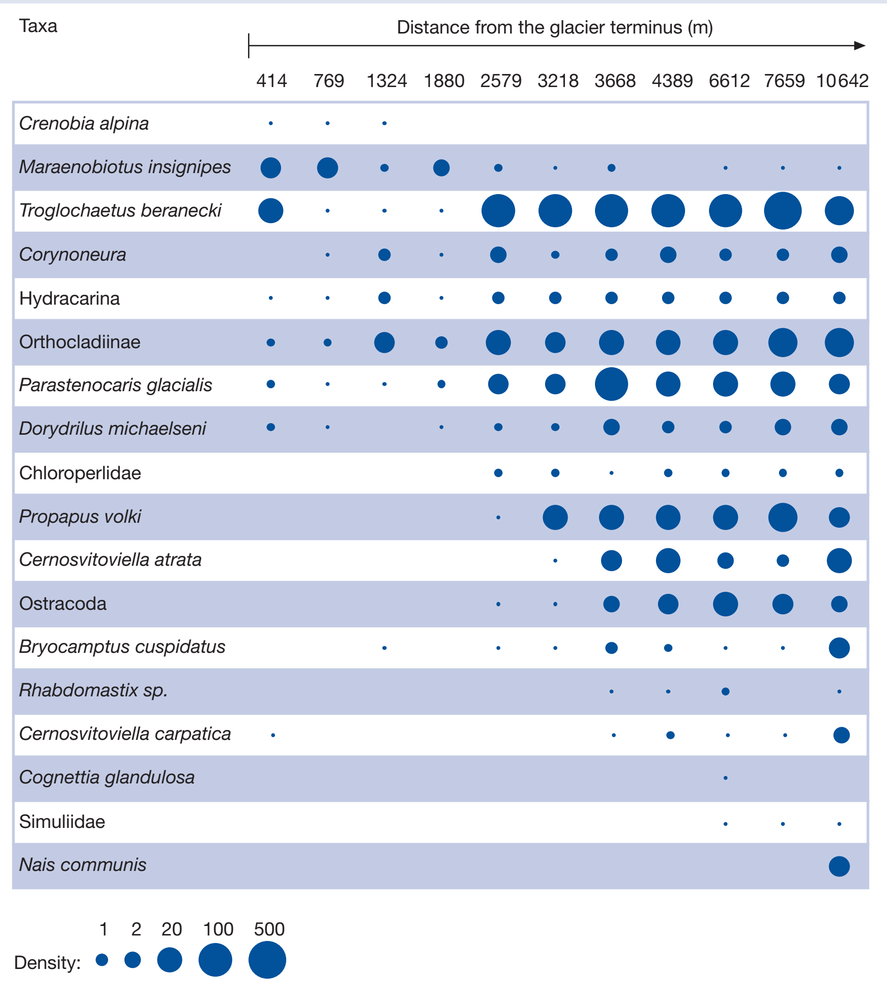

Fig. 2: Longitudinal distribution of 18 taxa in the hyporheic zone of the Roseg River. The size of circles is proportional to the common logarithm (base 10) of the average number of individuals (n >10 samples) in 10 l of intertitial water.

Perspectives

The present study suggests that the colonization process depends partly on the quantity and porosity of alluvium deposited during the glacial retreat. In order to test this hypothesis, similar faunal investigations are being carried out at present. The movement of glaciers and resulting changes in the downstream extent of glacial water influence would modify the distribution range of species. Taxa that are actually restricted to the lower reaches of the Roseg River are expected to colonize more upstream sites if the Roseg and Tschierva glaciers continue to retreat. The present data set can serve as a basis for developing a predictive model of changes in biodiversity induced by the retreat of glaciers. Monitoring long term changes in the longitudinal pattern of hyporheic and benthic assemblages of invertebrates in the Val Roseg would enable us to test our predictions.

Florian Malard, a groundwater ecologist, was a Post-Doctoral fellow at the limnological department of EAWAG from 1996 to 1999. Since 1999, he has been a senior researcher in the Freshwater and River Ecology Research Laboratory of the CNRS in Lyon, France. **The author is indebted to C. Boesch for processing faunal samples, M. Lafont for identifying oligochaetes and to D. Galassi for identifying copepods.**

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Organic Matter Dynamics in Alpine Streams

Benthic algae and organic matter of terrestrial origin provide the energy base for consumers and microbial decomposers in streams. Both energy sources are limited in the Val Roseg catchment, but studies on leaf litter decomposition suggest that the streams' capacity to process organic matter is much greater than currently realized.

Inputs of organic matter from the riparian zone (allochthonous organic matter) and in-stream primary production (autochthonous production) by benthic algae provide the energy base that supports heterotrophic stream organisms such as invertebrates, fish and microorganisms. Forested headwaters receive large amounts of organic matter in the form of leaves and wood, whereas primary production is constrained by shading. Greater light availability favors algal growth in larger streams as the forest canopy opens. Concomitantly, organic matter inputs decline. In alpine streams, however, riparian vegetation is sparse and algal growth is restricted by the cold and turbid water and an unstable stream bed. To answer the question whether alpine streams are driven by allochthonous or autochthonous organic matter, we quantified algal biomass and the input of terrestrial organic matter during one annual cycle and measured processes involved in organic matter turnover in an alpine stream ecosystem, the Roseg River (Fig. 1 on p. 14).

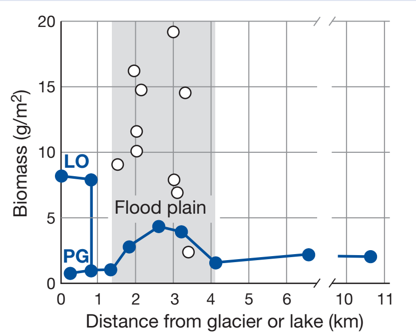

Fig. 1: Average algal biomass between June and September 1997 along the Roseg River corridor. Filled circles = main channel sites, open circles = floodplain channels excluding main channel. LO = lake outlet stream, PG = proglacial reach.

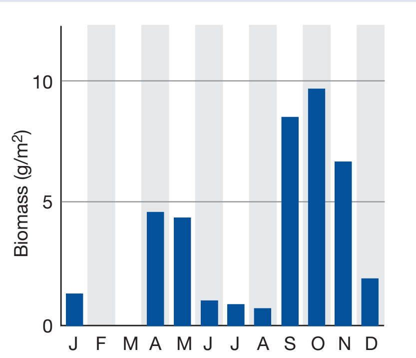

Fig. 2: Seasonal variation of periphyton biomass in the proglacial reach.

A Low Autochthonous Production

The biomass of benthic algae ranged from 0.7 to 19 g ash-free dry mass per m^2 of stream bed during summer (Fig. 1). The proglacial and the constrained reaches had the lowest values, due to abrasion during daily high flow. Biomass was greater in the lake outlet and in the floodplain reach, where discharge is diverted among several channels. The greatest biomass was observed in those floodplain channels that were unaffected by glacial melt water and sediment transport (Fig. 1).

Seasonal patterns of algal biomass were characterized by highest values in spring and autumn (Fig. 2; see article p. 20). If a snow cover on streams is lacking, high biomass may be sustained throughout the winter (see Fig. 2B on p. 7). The highest biomass values observed in the Roseg River come close to those found in the prealpine River Necker.

A Low Allochthonous Input and Retention

The input of particulate organic matter (POM) into the Roseg River was measured with 94 litter traps placed along the river corridor [1, 2]. Depending on the structure of the riparian vegetation, litter included larch and pine needles, twigs, cones, grass and non-identifiable organic matter. The annual input into the proglacial reach averaged 2 g per m^2 and increased up to nearly 40 g per m^2 downstream (Fig. 3). All these values are extremely low compared to other streams below treeline (Tab. 1).

POM-input into the whole flood plain was quantified using a GIS-based model. Trap data were integrated with high-resolution airborne images and a digital elevation model. Most floodplain channels received small amounts of POM, because the floodplain vegetation was in an early state of suc-

Stream	Total input (g·m^{-2}·y^{-1})
Roseg River	2–40
Antarctic stream	0
Desert streams	3–242
Mixed forest streams	37–761
Coniferous forest streams	736–1678

Tab. 1: Total input of particulate organic matter (ash-free dry mass) into different reaches of the Roseg River compared to non-alpine systems [1, 5].

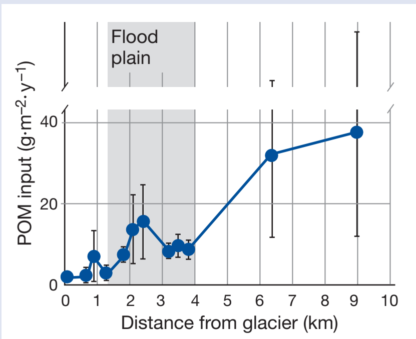

Fig. 3: Annual input of terrestrial particulate organic matter (mean ±standard deviation) into the main channel between the Tschierva glacier and the downstream end of the studied catchment.

cession or even lacking. Although forests on the valley slopes produced up to 300 g per m^2 and year, the average aerial transport distance into the flood plain was only 10–15 m, resulting in a rather low supply of POM also from the valley slopes (Fig. 4).

Alpine Streams are Predisposed to Process Organic Matter

In spite of the absence of significant litter inputs to most stream types in the Val Roseg flood plain, experimentally introduced alder leaves were decomposed at rates not too greatly depressed compared to streams at lower elevations (Fig. 5). Half-lives of decomposing litter ranged from 23 to 239 days with some differences among sites along a physical harshness gradient. Leaves were colonized at all sites by both microbial decomposers (fungi) and leaf-shredding invertebrates known from forest streams [3, 4]. The remarkably fast decomposition in the lake outlet was due to the presence of an effective shredder, the caddisfly *Acrophylax zerberus.* Taken together, these results suggest that alpine streams are predisposed to decompose leaf litter [3]. Upward shifts in tree vegetation as a result of global warming would thus be followed by instant shifts of stream metabolism to the "standard conditions" known from forest streams at lower elevations.

Respiration (oxygen consumption) of near-surface sediments (0–10 cm) measured at 24 sites within the flood plain reflects the processing of organic matter by the aquatic microbial community. Respiration rates were more closely related to channel stability than to distance from dense terrestrial vegetation and were more than one order of magnitude lower than in non-alpine streams. Daily rates averaged 0.34 g O_2 per m^2 in stable channels at the floodplain margin but were only 0.12–0.15 g O_2 per m^2 in the main channel and in surface-connected channels.

Glacial Streams – Energy-limited Ecosystems

Our study indicates that autochthonous organic matter is the primary energy source of the Roseg River. It also shows that the energy base of alpine streams – glacier-fed streams in particular – is distinctly different from forested streams at lower elevations. Inputs of terrestrial POM into headwater reaches are extremely low and even in the zone of subalpine forests inputs are moderate because of relatively wide stream channels. High flow and turbidity during summer, and snow cover in winter, impede algal growth, whereas relatively benign environmental conditions in spring and autumn favor primary production. Glacial streams appear to be energy-limited during summer high flow. However, a complex glacial flood plain provides stream habitats that support high algal biomass throughout the year.

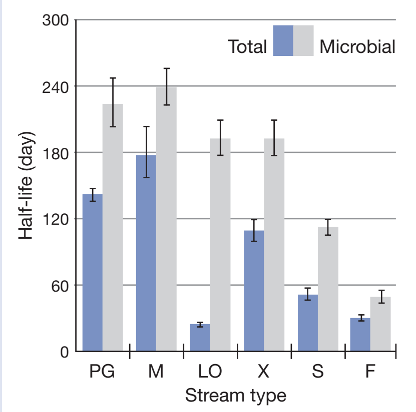

Fig. 5: Variation in half-lives (mean ± standard error) of decaying alder leaves along a physical harshness gradient in streams of the Val Roseg flood plain. The half-life is the time needed to decompose 50% of the organic matter.
"Total" refers to decomposition by microorganisms, invertebrates and possibly mechanical fragmentation. "Microbial" refers to decomposition experiments with fine-mesh bags that exclude leaf-shredding invertebrates. PG = proglacial reach; M = main channel; LO = lake outlet; X = lateral channel carrying water of mixed origin; S = springbrook emanating from valley side slope; F = reference forest stream at 700 m elevation [3, 4].

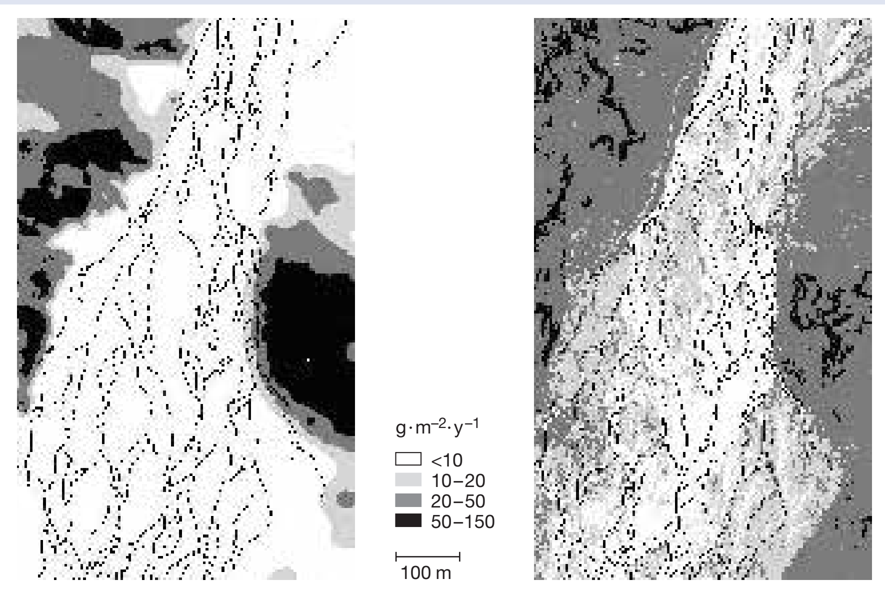

Fig. 4: Spatial patterns of the aerial (left) and lateral (right) annual input of particulate organic matter into the Val Roseg flood plain. Lateral inputs include material transported over the land surface by wind and runoff.

U. Uehlinger (see portrait p. 13)

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Ecological Windows in Glacial Stream Ecosystems

Alpine streams and in particular glacial streams are subject to harsh environmental conditions during most of the year. However nutrient supply, light availability, discharge, and temperature favor ecological processes and biota during two short periods at the beginning and end of the annual flow pulse.

The Alps, a mountain range with rugged topography and steep slopes, are characterized by harsh environmental conditions. With increasing elevation, a growing portion of the annual precipitation falls as snow. Virtually 100% of the precipitation occurs as snow above 3500 m a.s.l. [1]. Snow and glacier ice form a transient water storage that is partly released as a distinct flow pulse during summer, particularly in glacier fed streams (see article p. 6). This radiation and temperature controlled flow pulse is an important factor in determining habitat conditions for algae and invertebrates in addition to climatic constraints such as snow cover or freezing during winter. However, until recently, knowledge on habitat conditions and benthic communities of glacial streams was based on studies typically restricted to the melting season [2]. In this article, we provide a general description of the physico-chemical habitat template of glacial streams using information from year-round studies in the Val Roseg and elsewhere [3] and we discuss the respective implications for benthic organisms.

Summer and Winter: The Unfavorable Seasons

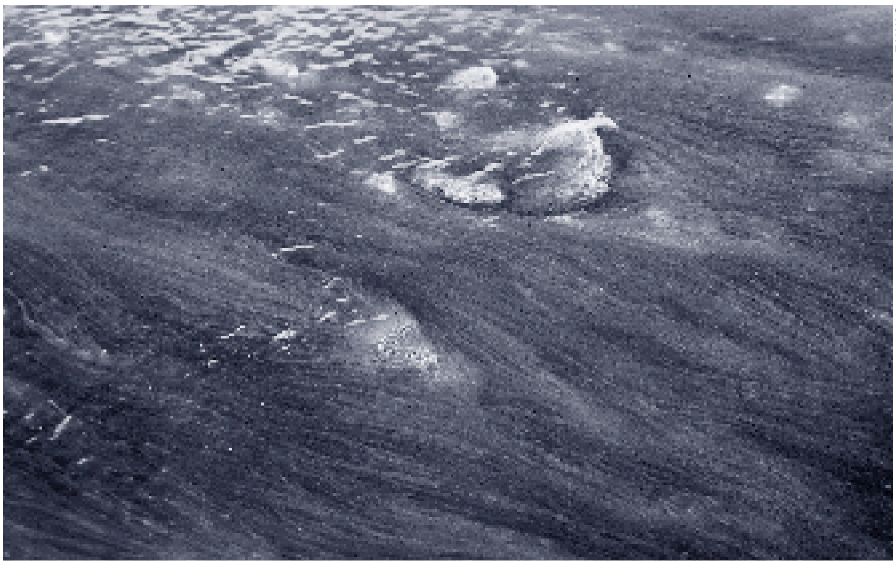
The glacial flow pulse during summer melt-off creates unfavorable habitat conditions in glacial streams (Fig. 1). They result from:

- high shear stress;
- bedload transport and thus low channel stability, especially when slopes are steep and sediment availability is high as in recently deglaciated glacier forefields;
- high turbidity caused by glacial flour, which attenuates light and scours the substratum;
- low concentrations of dissolved phosphorus and dissolved organic carbon [4];
- water temperatures <2 °C near the glacier snout.

High habitat heterogeneity, as for example in the Val Roseg flood plain (see article p. 14), mitigates the detrimental effect of the glacial flow pulse, at least in channels lacking surface connection to the main channel.

From late autumn to the onset of spring, habitat conditions are also harsh but considerably different from summer conditions. Temperatures close to 0 °C extend far downstream, discharge is low, and some streams may even fall dry or freeze to the bottom. No light reaches the stream bottom in snow-covered stream channels. However, exfiltration of relatively warm groundwater may prevent the formation of an ice and snow cover locally despite very low air temperatures, as for example in the Roseg flood plain and other glacial streams in the Swiss Alps [3, 5].

In alpine streams, periods of harsh environmental conditions are highly predictable compared with streams at lower elevation. For example, streams in the northern foothills of the Alps are frequently disturbed by almost randomly occurring spates that reflect the prevailing influence of the Atlantic climate [6].



EAWAG

Dense algal mat formed by the Chrysophyte *Hydrurus foetidus* in the main channel of the Roseg River in January 1998.

Windows of Opportunity

The conceptual diagram (Fig. 1) summarises the relationships between regional climate, the environmental conditions in alpine streams and the response of the stream biota. The abrasive impact of moving bed sediments in summer constrains the abundance of invertebrates [2, 3] and impedes, together with the limited nutrient

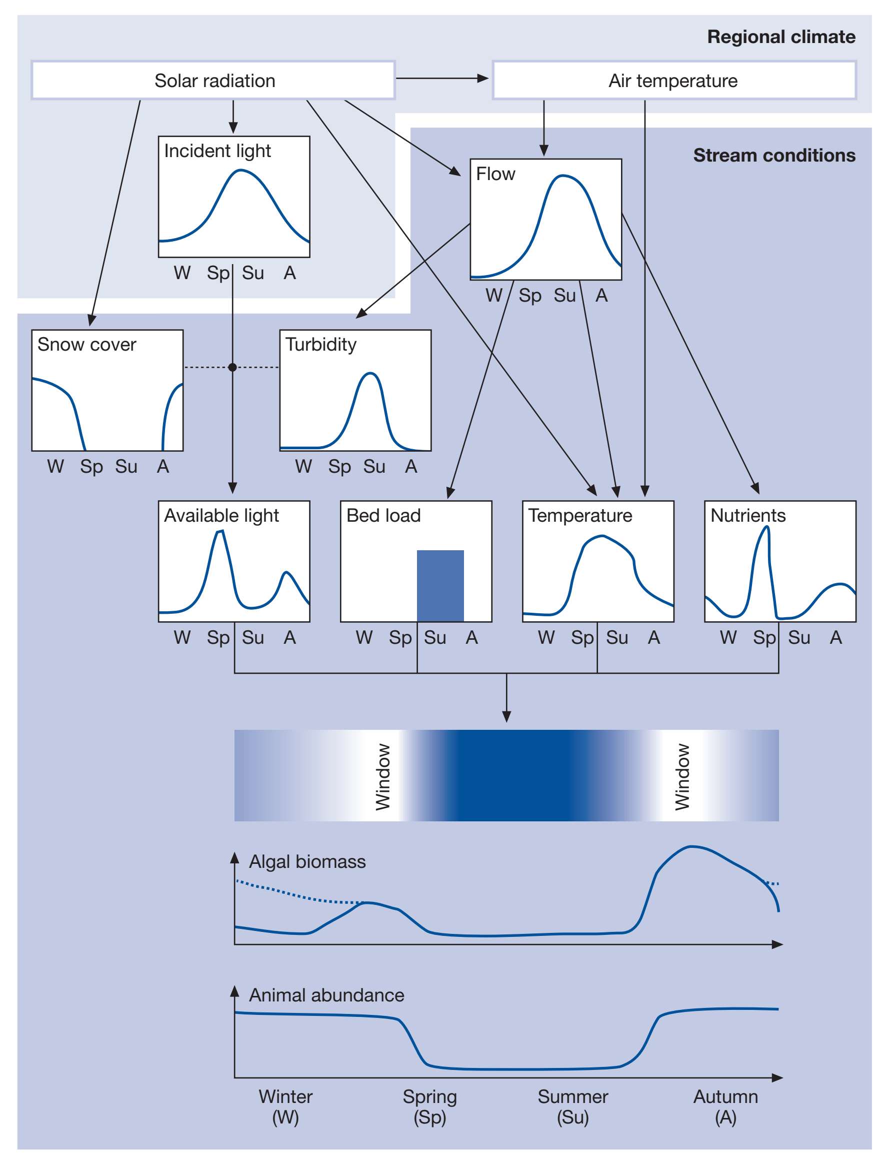


Fig. 1: Windows of opportunity in the physico-chemical habitat template of glacial streams (conceptual diagram). The regional climate characterized by solar radiation and air temperature controls discharge and incident light, and influences water temperature. Rising air temperature and solar radiation increase the release of cold melt water, which halts the vernal increase of water temperature. With the onset of glacial melt, turbidity reaches high levels and bed load transport occurs during periods of high flow. In spring, melting snow releases large amounts of dissolved nitrogen compounds originating from aerial depositions, but during summer large amounts of melt water dilute nutrients. The primary energy source of benthic algae is light. The amount of available light depends on both incident light, which changes seasonally, and light attenuation, which is affected by glacial flour in summer or snow cover in winter (dotted line = algal biomass in streams without snow cover in winter). High flow, bed load transport and suspended solids in summer impose major constraints on the growth of benthic organism in contrast to periods in spring and autumn.

and light availability, the accrual of benthic algae. During the vernal flow increase, however, moderate discharge coincides with relatively high temperatures and nutrient concentrations and low turbidity. In autumn, discharge is again moderate, turbidity low, and temperature slightly lower than in spring. Algae can respond rapidly to these relatively favorable conditions, particularly in autumn but also during spring. Algal biomass in channels covered by snow is low but in open reaches, algae may even proliferate in winter (see photograph). The period from autumn to spring is characterized by maximum invertebrate density and species richness [3, see also article p. 22]. Environmental conditions during winter impose less constrains on benthic invertebrates than on algae; some species even complete their life cycles in snow and ice covered channels.

Global Warming Affects Alpine Streams

In conclusion, sampling during all seasons is necessary to attain a holistic perception of the structure and function of alpine stream ecosystems. This became evident in the Val Roseg Project as well as in other studies [3, 7]. In glacial streams, periods of harsh environmental conditions are separated by relatively short but benign time intervals. This temporal pattern is highly predictable and reflected by corresponding changes in abundance and species richness of benthic organisms. Future climate change scenarios predict a decline of ice-/snowmelt dominated systems. Concomitantly, there will be an increase of streams with snowmelt- and rain-dominated flow regimes. In such streams, the annual flow pulse will already end in early summer and rain-induced floods will become more frequent. The less predictable flow regime and the extension of the autumnal window of opportunity into late summer will affect the structure and dynamics of benthic communities.

Urs Uehlinger (see portrait p. 13)

Coauthors:
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Biodiversity of Zoobenthos in Alpine Streams: The Val Roseg

Alpine glacial streams are common although highly sensitive features of high mountain landscapes. We gaze at their raw and untamed nature in wonder, but are little aware of the diverse and characteristic biota inhabiting these harsh environments. However, the biodiversity of alpine streams is in danger because of their particular sensitivity to climate change and the ever increasing pressure stemming from human activities.

The integrity and biodiversity of alpine stream ecosystems are facing many hazards such as climate change, habitat degradation and loss through land use changes, and generation of hydroelectric power [1]. The assessment and mitigation of these effects requires a good understanding of the complex interplay between environmental conditions and zoobenthic distribution. Despite a well-documented interest in the fauna of high mountain streams at the beginning of the 20th century, [e.g., 2], comprehensive year-round studies are scarce [3]. Therefore, we examined the spatio-temporal patterns of macroinvertebrate distributions in different glacial streams of the Val Roseg (see article p. 12).

Species Inventory in the Roseg River

Currently about 150 benthic macroinvertebrate species have been identified in the glacial flood plain of Val Roseg (Fig. 1). Non-insect species comprise 35 %, with oligochaetes, water mites and Ostracoda having the highest proportions. Insects are dominated by midges with 35 species, whereas the species richness of other groups is distinctly lower. Nevertheless, the number of 8 identified black fly species was higher than expected because glacier-fed streams are considered poor habitats for these animals.

Spatial Phenomena

During the melting season in summer, we observed a longitudinal sequence of macroinvertebrate taxa that typically colonize glacier-fed streams. Chironomids of the cold-stenotherm genus *Diamesa* dominated the fauna in the proglacial reach, making up to 95 % of the community. They remained abundant along the course of the Roseg River. Species richness and density progressively increased with distance from the glacier terminus. Common taxa included other chironomids (Orthocladiinae and Tanytarsini), mayflies *(Baetis alpinus* and *Rhithrogena* spp.), stoneflies *(Leuctra* spp. and *Protonemura* spp.), blackflies and oligochaetes. This longitudinal pattern is most likely attributable to reduced environmental harshness with increasing distance from the glacier and is thus in accordance with the conceptual model of Milner et al. (see box). In contrast to this longitudinal perspective, the spatial dynamics of streams within glacial flood plains have received little attention. The Val Roseg flood plain is characterized by a remarkable degree of aquatic habitat heterogeneity due to the shifting dominance of water sources and flow paths (see article p. 14). We compared the zoobenthic communities of three different channel types reflecting a gradient of increasing channel stability: the main channel, intermittently-connected channels and groundwater channels (see Tab. 1 p. 15). Although alpine streams are extreme environments located on the declining limb of a harshness-diversity curve [4] (Fig. 2), it is this heterogenous mosaic of channel types that enhances overall biodiversity by providing numerous refugia for benthic macroinverte-

Conceptual Model Describing the Zoobenthic Distribution in Glacial Streams

Based on recent research and a literature synthesis, Milner et al. [8] proposed a conceptual model describing macroinvertebrate zonation with increasing distance from the glacier margin and thus decreasing environmental harshness. The model depicts that zoobenthic distribution is controlled by two principle variables, i.e., water temperature and channel stability. Specifically, with increasing water temperature and channel stability also the number of zoobenthic taxa and zoobenthic biomass increase.

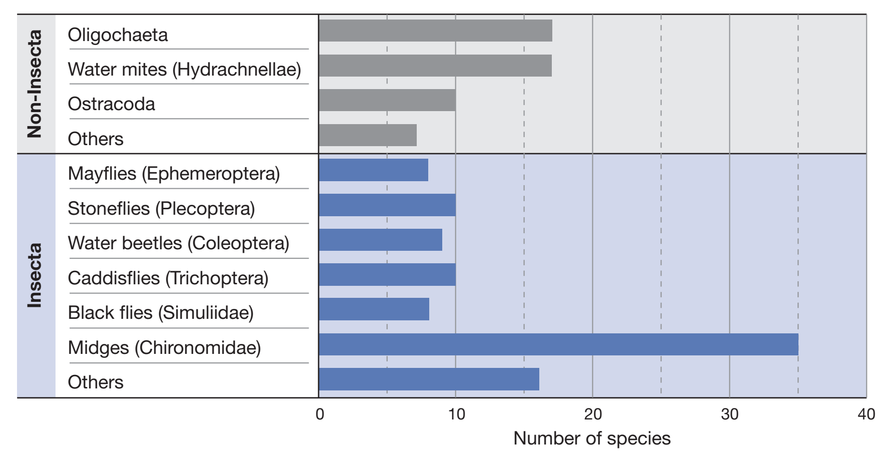

Fig. 1: Species richness and proportions of various taxonomic groups in the Val Roseg flood plain.

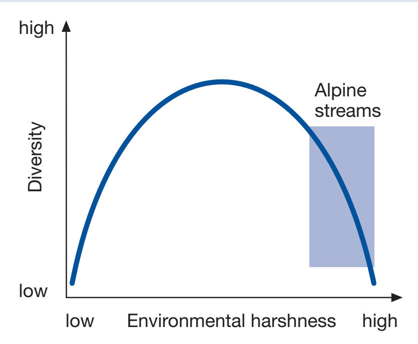

Fig. 2: Alpine streams are positioned on the descending limb of the harshness-diversity curve.

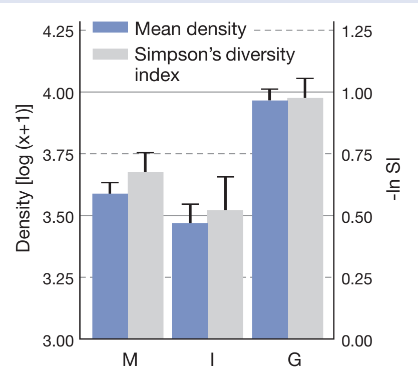

Fig. 3: Mean density and Simpson's index of diversity for the main channel (M), intermittently-connected channels (I), and groundwater channels (G). Error bars represent +1 standard error.

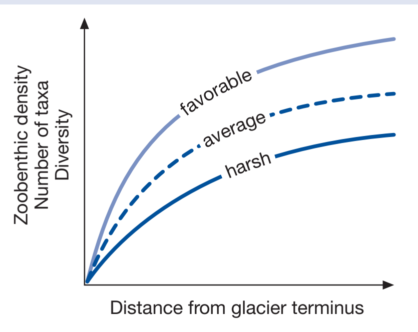

Fig. 4: Conceptual view of changes in density and diversity of zoobenthic communities with increasing distance from glacier terminus. Solid curves represent endpoints when environmental conditions are most harsh or most favorable, whereas the dotted curve is indicative of a theoretical average over an annual cycle.

brates. For example, highly stable habitats such as groundwater channels exhibited high macroinvertebrate density and diversity (Fig. 3), combined with low temporal variability.

Temporal Phenomena

The conceptual model of Milner et al. (see box) predicts macroinvertebrate distribution patterns accurately during glacial melt in summer but does not account for seasonal changes in glacial influence. We found that the longitudinal patterns of zoobenthic distribution varied across seasons. For example, especially in October and November, Ephemeroptera and Plecoptera were found closer to the glacier terminus than predicted by the conceptual model. In addition, maximum species density and diversity occurred during periods of favorable environmental conditions, i.e. in spring and late autumn/early winter (Fig. 4).

Threats to Biodiversity in Alpine Stream Ecosystems

In summary, our results suggest that, besides water temperature and channel stability, a complex interplay of factors determine the distribution of macroinvertebrates in glacial streams [e.g., 5]. Some climate scenarios predict that up to 95% of Alpine glacier mass could disappear by 2100 [6]. However, impacts to alpine streams are difficult to estimate because many of the most

P. Burgherr, EAWAG

Acrophylax zerberus **is a common caddisfly in a variety of habitat types in the Val Roseg flood plain.**

significant consequences will result from changes at the scale of small catchments and are still unresolved by Global Circulating Models. Additionally, about 90% of all streams and rivers in the Alps are affected by human developments [7]. These activities often promote fragmentation of natural and species-rich habitats (see article p. 24). Therefore, more holistic studies like the Val Roseg Project are needed to understand the subtle relationship between habitat changes and biodiversity at various scales.

P. Burgherr completed his PhD in the Limnology Department of EAWAG in 2000 examining zoobenthic distribution patterns in an alpine glacial stream ecosystem. Since 2001, he has been working at the Paul Scherrer Institute.

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Habitat Fragmentation and Genetic Diversity

What We can Learn by Studying Alpine Aquatic Insects

The fragmentation of natural habitats has important implications for the distribution of organisms and the genetic structure of populations. For the past four years, we have studied how fragmentation of alpine streams by lakes and reservoirs affects the dispersal ability and the genetic structure of stream insects. One of two mayfly species studied, *Baetis alpinus,* showed genetic differences between fragmented populations. Adults are poor flyers and generally fly upstream along the water course to lay eggs. The second mayfly, *Rhithrogena loyolaea,* is a better flyer and disperses in all directions, suggesting it can cross the unsuitable habitat between fragments. Interestingly, genetic differences in *B. alpinus* were only detected across geologically old lakes suggesting that human-caused habitat fragmentation may be too recent to detect genetic effects.

The habitats of many species have become fragmented naturally or by humans into smaller "islands". This process of habitat fragmentation can transform one large population into several smaller populations. The reduction of population size is called a genetic bottleneck and can result in a serious loss of genetic diversity within each of the smaller populations increasing the probability of local extinction [1]. It is possible that genetic diversity can be increased by gene flow, defined as the influx of new genetic variation from other populations. But the isolation of populations very often limits the amount of gene flow, thereby confounding the problem.

Does Habitat Fragmentation Affect Genetic Diversity of Stream Insects?

Many aquatic insects are restricted to flowing water habitats. These flowing water habitats can be fragmented into discrete reaches by standing water bodies such as natural lakes and human-made reservoirs (Fig. 1). Aquatic insects living in flowing waters may not be able to transverse lakes, thereby causing population isolation and possible changes in genetic diversity. Over the past four years, we have examined how natural and human-made fragmentation of alpine streams has affected the population genetics of stream insects in the Swiss Alps.

Understanding how fragmentation affects organisms is important in Alpine regions because of their large number of endemic plants and animals.

The Study Sites

We conducted our study in several headwater streams of the Rhine, Inn, and Ticino rivers (Fig. 2). Six streams were fragmented by lakes, 2 streams were fragmented by reservoirs, and 3 of the streams were unfragmented, providing "controls". Organisms were collected from above and below each lake or reservoir or from 2 points along the unfragmented streams (Fig. 2). The purpose of the design was to compare naturally fragmented streams (lakes) with human-fragmented streams (reservoirs), the primary difference being that reservoirs are much more recent features of the landscape. They were constructed mostly within the last 100 years, while most of the lakes we studied were formed by the retreat of Alpine glaciers.

The Study Animals

We investigated two mayfly (Ephemeroptera) species with different dispersal abilities, *Baetis alpinus* and *Rhithrogena loyolaea.* These animals spend most of their lives as larvae on the stream bottom. *Baetis* lives 6–9 months, and *Rhithrogena* 2–3 years in the stream before emerging as flying adults. As adults, they live from only a few hours up to a few days, hence the names *"Eintagsfliegen"* and *"éphémères". B. alpinus* is a wide-

P. Spaak, EAWAG

Fig. 1: Fragmented alpine streams: Natural fragmention by the Jöriseen ...

spread and abundant alpine species [2]. Adults have poor flying ability and generally fly in an upstream direction. *R. loyolaea* also is widespread but occurs at fewer locations. It is considered to be a stronger flyer than *B. alpinus* and other studies of *Rhithrogena* suggests it flies in all directions rather than just upstream.

The Genetic Analyses

We used 2 kinds of genetic analyses to answer questions about the effects of habitat fragmentation. The first technique was allozyme electrophoresis, where genetically different forms of the same enzyme, so-called allozymes, migrate different distances in an electric field (Fig. 3). From this we can examine how many different enzyme forms are present in a population, that is the **genetic diversity,** and how different one population is from another population, that is the **genetic difference** (θ). From this second measure, we can estimate the amount of gene flow that occurs among fragmented populations. Small genetic differences (θ<0.05) between subpopulations indicate that dispersal occurs frequently, whereas large genetic differences (θ>0.05) indicates limited dispersal and low population mixing because animals do not cross the standing water habitat. The second technique was amplified fragment polymorphism (AFLP), a

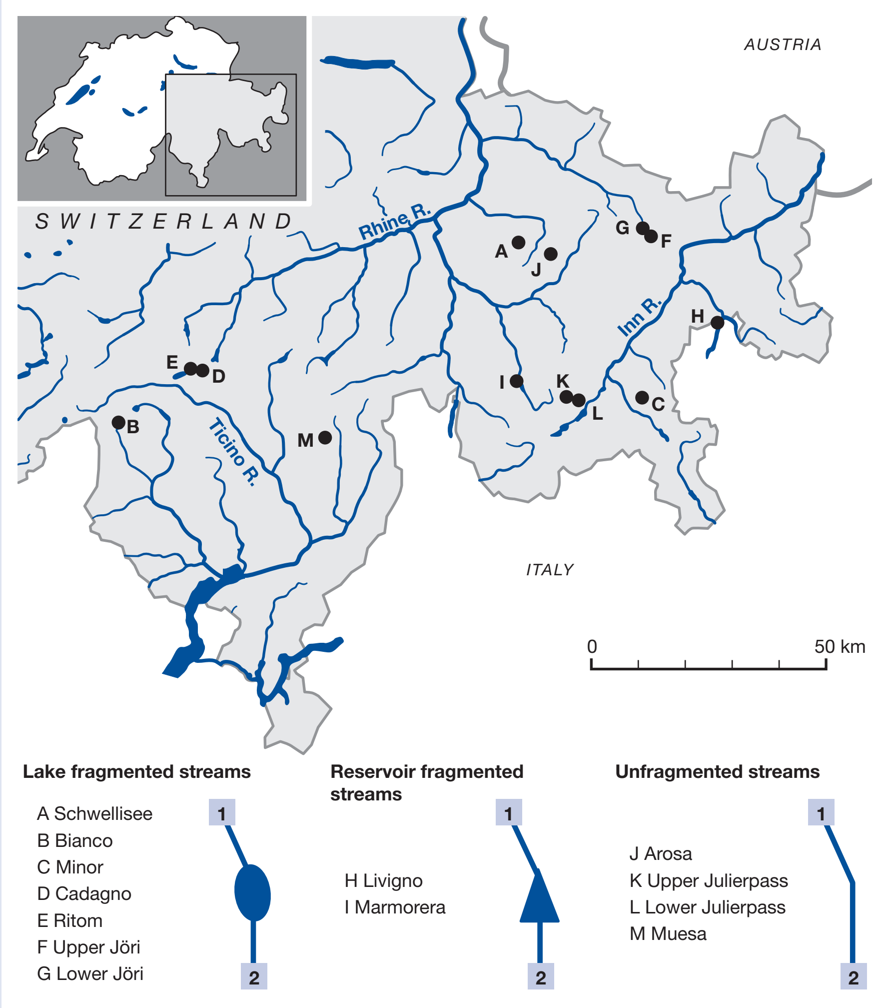


Fig. 2: Location of studied streams. Streams A–G fragmented by lakes, streams H–I fragmented by reservoirs, and control streams J–M without fragmentation. Numbers 1 and 2 indicate the sampling sites.

… and anthropogenic fragmention by the Lago di Livigno.

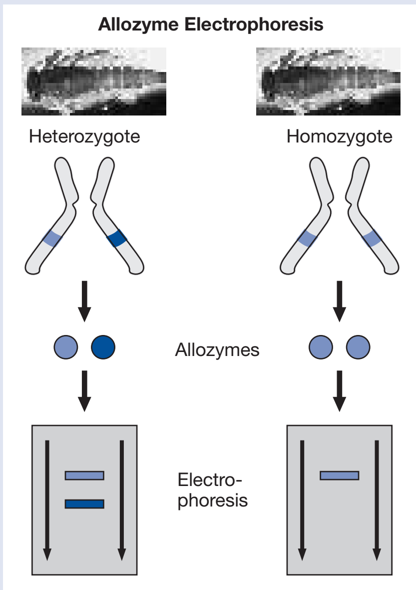
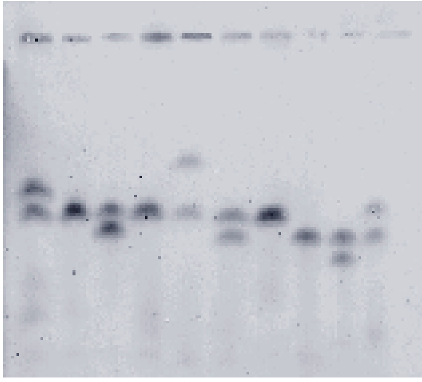


Fig. 3: Principle of allozyme electrophoresis.



The polymorphic allozyme locus *Pep-B* analyzed for 10 individuals of *Baetis alpinus.* Differences in migration distance of dark bands (from the top of the figure) indicate 5 genetically different forms of the enzyme.

DNA "fingerprinting" technique that allows for more sensitive analysis of genetic differences among populations. The data analyses are carried out using specialized programs for population genetics including FSTAT [3] and ARLEQUIN [4].

Limited Dispersal Among Habitat Fragments

The allozyme data indicate no reduction of genetic *diversity* in habitat fragments for either *B. alpinus* or *R. loyolaea.* However, there were large genetic differences between populations of *B. alpinus* within all of the streams fragmented by lakes except for the Jöri lakes (Fig. 4) [5]. These allozyme data were directly supported by the more sensitive AFLP data as well (results not shown). In contrast to *B. alpinus,* there were no detectable genetic *differences* between populations of *R. loyolaea* within any of the study streams.

We attribute the difference among the two species to adult flight and egg-laying behavior. *B. alpinus* normally fly upstream, staying close to the stream course. Upon reaching standing water without exposed rocks to deposit their eggs, they are likely to stop flying and lay their eggs in the stream. This is in contrast to *R. loyolaea,* which flies in several directions, even away from the stream. As a consequence, *R. loyolaea* appears to be able to cross unfavorable habitats such as lakes and disperse among habitat fragments [6].

An unexplained result is the finding that populations of *B. alpinus* were not genetically different across the two Jöri lakes and the two reservoirs (Fig. 4). Our suggestion is that valley history might play an important role in determining the genetic structure of populations and that genetic differences across geologically younger lakes and reservoirs could not be detected within the first 100 to 1000 years of fragmentation. Indeed, the Jöri glacier has remained active throughout the Holocene and extended into one of the study lakes during the Little Ice Age ca 150 years ago. This recent alteration of the stream course may mean that fragmented populations probably have not had enough time to become genetically different. Reservoirs are even more recent, having been constructed in the 20th century.

Conclusions and Next Steps

Two important results from our research are (1) habitat fragmentation can reduce dispersal of alpine stream insects, leading to genetic differences among populations, and (2) human-caused habitat fragmentation may be too recent to detect genetic effects. One important goal of our continuing research is to separate historical from present-day genetic effects to better understand how organisms respond to environmental modification (natural and man-made).

Michael T. Monaghan recently completed his PhD in the Limnology Department of EAWAG studying the effects of habitat fragmentation on genetic diversity and species diversity of alpine stream insects.

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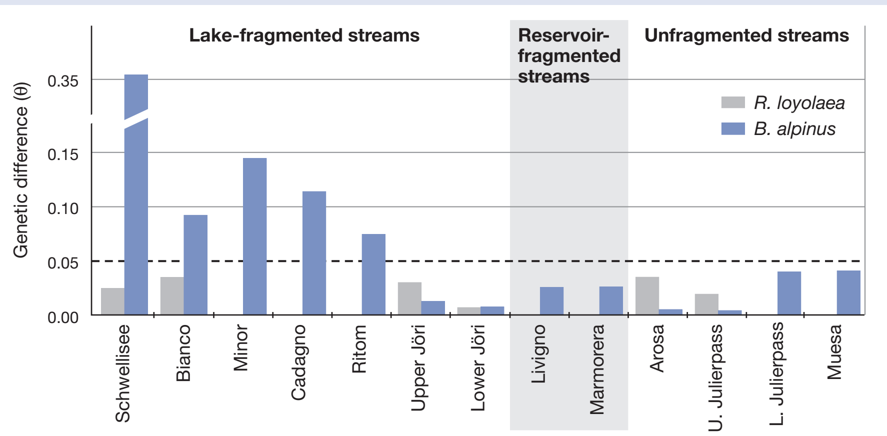

Fig. 4: Genetic differences (θ) between fragmented populations of two mayflies *(Baetis alpinus* and *Rhithrogena loyolaea)* with values >0.05 indicating limited gene flow.

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Stream Response to Experimental Floods

Can artificial flooding restore the ecological integrity of rivers downstream of reservoirs? Experimental flood releases from a large reservoir just outside the Swiss National Park markedly altered the ecology of the receiving river. The response of aquatic flora and fauna to flood disturbance reflected species-specific life histories and the cumulative effects of earlier floods. Results indicate that artificial flooding has great potential as a restoration strategy for regulated rivers.

Large dams (>15 m high) are prominent features of most rivers [1]. Worldwide, about 40,000 large dams are used for power production, irrigation, navigation, water supply, recreation, and just recently, for ecological purposes [2]. Large dams in the Alps are used primarily for power production; streams below these dams have greatly reduced or no flow due to water diversion and therefore become physically altered, e.g., temperature increase and clogging of the streambed by fine sediments [3, 4]. The biota also change in response to the altered habitat, usually showing substantial increases in those organisms favored by more constant environments, concomitant with decreases of organisms adapted to natural flow patterns [5].

The removal of small dams has become increasingly common, especially in North America where around 180 dams have been removed in the last decade [6]. However, most large dams will remain in place for a variety of management purposes, with around 260 new large dams becoming operational each year [7]. Consequently, there is a strong need to restore the natural flow regime of regulated rivers to enhance their ecological integrity [1, 2]. Therefore, we were interested by the possibility to use artificial flooding as a management tool to improve river health below large dams.

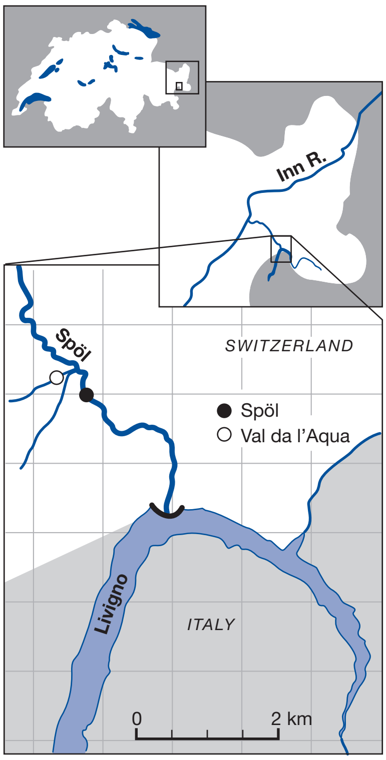

Fig. 1: Location of the Spöl study site in Switzerland.

The Spöl Project: A First in Flood Management

Only one other study examined the effects of an artificial flood on a river below a large dam, this being the Glen Canyon Dam in the USA [3]. Our study was conducted on the River Spöl, flowing below a large dam (Punt da Gall) on the border between Switzerland and Italy through the Swiss National Park (Fig. 1). Operation of the dam since 1974 has resulted in a constant discharge of less than 2.5 m³/s. The reduced flows have caused clogging of the streambed by fine sediments and allowed side-slope debris fans to form in the main channel. A reference stream, Val da l'Aqua, was located nearby to document ecological patterns in an unregulated system. Park authorities and the power company agreed to test whether artificial flooding can restore more natural conditions to the river. It is a multi-disciplinary project involving the Swiss National Park, Engadiner Kraftwerk, University of Berne, Hydra, Graubunden Fish and Game, and EAWAG, each focussing on different components of the system. In this article, we concentrate on the response of algae and zoobenthos, two important groups for assessing biological change, to artificial floods.

The Experimental Flood Regime

Figure 2 shows the discharge regime of the River Spöl during:

- three typical years (1960–1962) before dam construction (full operation in 1974),
- a typical year after dam construction (1999),
- the first year of experimental flooding (2000).

A reduction in residual flow following September 1999 provided enough water for the floods to be a cost neutral experiment. The artificial floods, one each in June, July and August, were comparable to those before dam construction, although being of shorter duration. The fourth flood in October resulted from heavy rain that filled the reservoir, allowing the release of excess water.

General Ecological Affects of the Floods

The First Flood: The first flood was patchy in its effects on stream algae and zoobenthos. Some areas of the stream bed were

Photographs: U. Uehlinger, EAWAG

The Spöl at baseflow and …

highly changed due to scouring and bed movement, resulting in a reduction in algae and zoobenthos, whereas other areas of the stream bed, such as boulders, were less affected and accumulated organisms. These less disturbed areas probably enhanced recovery by providing colonists or propagules, as occurs in unregulated systems. Some stones still had prolific growths of mosses that probably retained and also provided refugia to organisms. Algae and zoobenthos recovered rapidly after the first flood (Figs. 3 and 4), although remaining highly patchy. In Val da l'Aqua, the reference stream, algae and zoobenthos showed little change over the study period.

The Second Flood: The second flood was the largest (Fig. 2) and mobilized most areas of the stream bed. It caused major reductions in algae and zoobenthos (Figs. 3 and 4). Some pools were even filled with deposited sediment. Stones, including boulders, were bare after this flood and little moss cover was found in the channel. Recovery after this flood was delayed and neither algae nor the zoobenthos achieved preflood levels before the next flood. This lack of recovery probably can be explained by the larger impact of the flood, the unfavorable seasonal timing of the flood in respect to the life cycles of the biota, and a change in the composition of the biotic communities (Fig. 5).

The Third Flood: The scouring and disturbance potential of the third flood was markedly reduced because the second large flood had a major "cleaning" effect, transporting many fine sediments downstream. Nevertheless, the third flood also reduced zoobenthos abundances, but had little affect on algae. Although the third flood was similar in size to the first flood, recovery by algae and zoobenthos was more pronounced after the first than after the third flood (Figs. 3 and 4).

Changes in Community Structure from the Floods

Over the flood year, the stream bottom changed from being covered by moss *(Fontinalis* sp.) to being covered by diatoms and filamentous algae, especially *Hydrurus foetidus,* a common filamentous alga of alpine streams in winter. Zoobenthos typical of streams with more constant flows decreased during the flood year, including the turbellarian *Crenobia alpina* and the amphipod *Gammarus fossarum* (Fig. 5). The turbellarian was greatly reduced after the first flood, whereas the amphipod increased in density following this flood but showed lower numbers after the second larger flood. The difference probably is because gammarids are strong swimmers, whereas turbellarians must crawl to refugia. Zoobenthos more typical of unregulated rivers showed a positive response or recovered

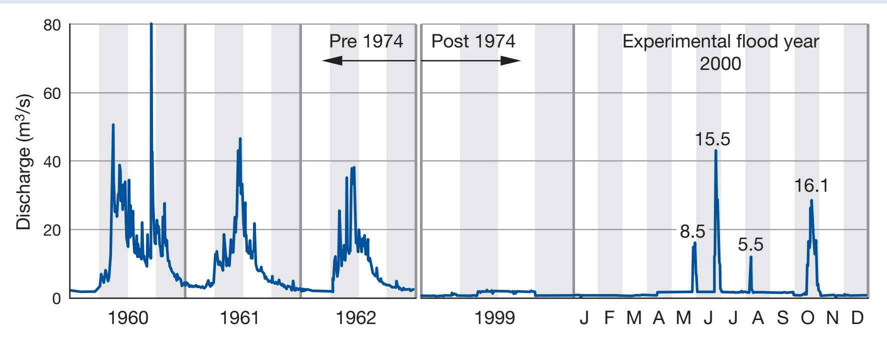

Fig. 2: Typical flow regime of the River Spöl before dam construction (years 1960 to 1962), after dam construction (1999), and during the experimental flood year (2000). The flow in 1999 represents the residual flow maintained below the dam with excess water being diverted for power production. The numbers above the flow peaks in 2000 are the average daily flows in m³/s.

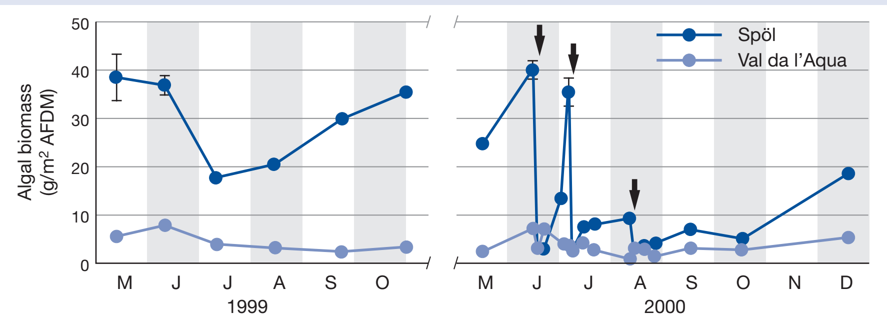

Fig. 3: Mean (±1 SD) algal biomass expressed as mg ash-free dry mass (AFDM) per m² in the rivers Spöl and Val da l'Aqua in the years 1999 and 2000. Arrows indicate the three experimental floods during 2000.

… during the large July flood.

quickly to the floods, and included the midges (Chironomidae), mayflies (Baetidae) (Fig. 5) and black flies (Simuliidae, not shown).

Conclusions

The flow regime is an integral component of rivers and the modification of discharge patterns, including the elimination of floods, is an important disturbance to riverine organisms and can markedly alter biological communities. Our results show that artificial floods can change the abundances of algae and zoobenthos, reducing species favored by river regulation. Additional studies are required to determine the long-term effects of artificial flooding, especially regarding their timing and magnitude, as our results suggest that floods of similar magnitude may have different effects depending on flood history and seasonal changes in population abundances.

Christopher T. Robinson (see portrait p. 8)

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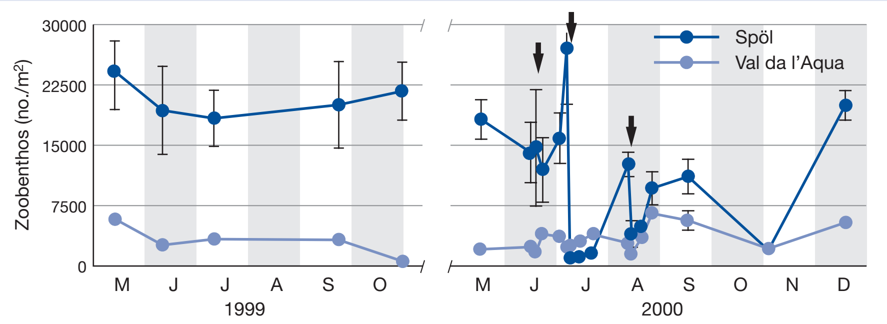

Fig. 4. Mean (+1 SD) zoobenthos density expressed as individual numbers per m² in the rivers Spöl and Val da l'Aqua in the years 1999 and 2000. Arrows indicate the three experimental floods during 2000.

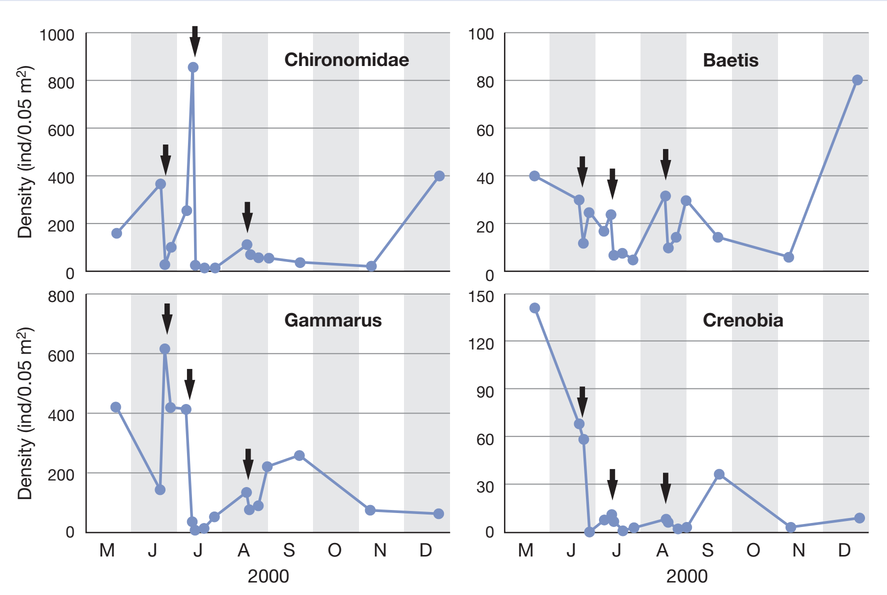

Fig. 5. Mean density (individual numbers per 0.05 m²) of 4 selected macroinvertebrate taxa representing the different response patterns to the experimental floods (arrows). Error bars not shown.

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Limnological Research in the Swiss National Park

Research has been conducted in the Swiss National Park for over 80 years. Botanists and zoologists have been particularly interested in this area because of minimal human impact. It was not until the construction of hydroelectric power plants on the Spöl, creating the Lago di Livigno, that limnologists appeared on the scene. The current project is a "first" worldwide, where artificial flood events are being used in an attempt to revitalize the Spöl. The goal is to optimize the rest water regime and to restore the Spöl to its original condition as closely as possible.

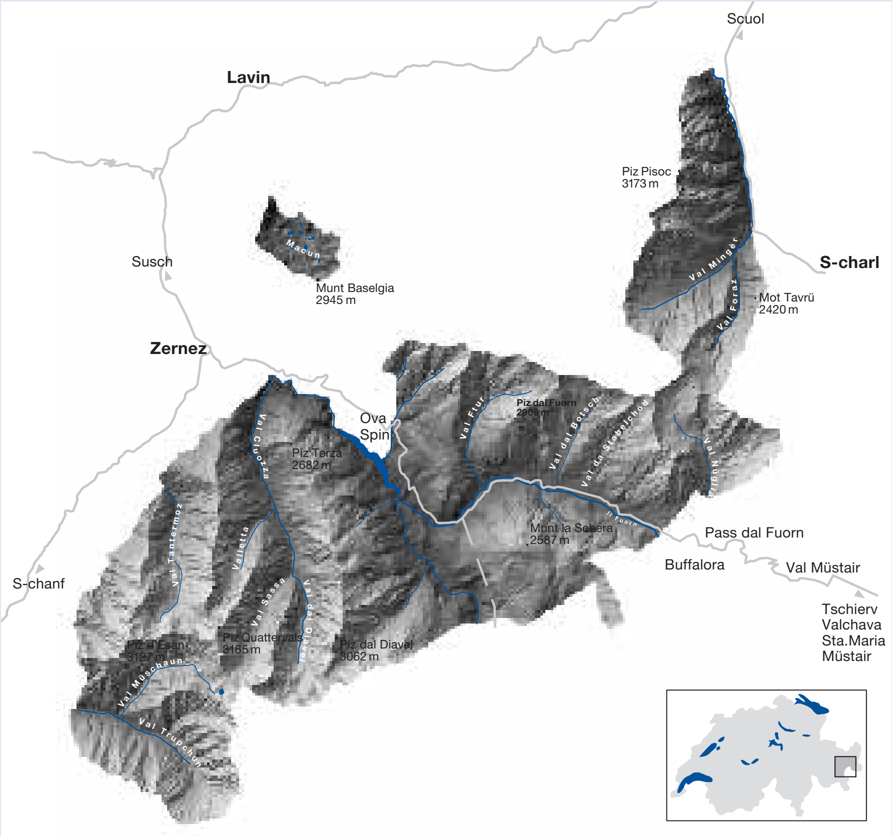
Streams and lakes in Switzerland are highly used and their natural flow regimes are altered to a large degree. Nature reserves are, therefore, especially important, both for studying natural processes and for assessing background impacts of regional and global environmental change (see box). The Swiss National Park, established in 1914, has only gradually assumed the role of a reference area.

Limnological Research Gained in Intensity after 1950

During the first few decades following establishment of the Park, limnological research was mostly limited to hydrobiologists who investigated the algal communities of springs and streams [1]. Limnological research within the National Park increased around 1950 with the onset of the planning process for hyrdroelectric power plants on the Spöl – water protection paradoxically being the trigger for more intensive limnological research even within the National Park. In 1952, a hydrobiological subcommission was formed within the Science Commission of the National Park. After this point in time, extensive chemical/physical investigations were conducted, resulting in the compilation of an inventory of approximately 100 springs in the Fuorn area and the determination of the water quality of these springs [2]. Three hydrological gauging stations were established within the Park in connection with the planning process for the hydroelectric power plants. These gauging stations are still in operation today and provide runoff data for the regulated Spöl and for the two natural tributaries, Ova Fuorn and Ova Cluozza.

Severe Impact: Construction and Operation of the Spöl Hydroelectic Power Plants

Despite strong opposition from environmental organizations and the National Park, the construction of the hydroelectric power plants on the Spöl could not be prevented. It would have been up to the scientific community to investigate the ecology of the Spöl before construction of the power plants and to establish a long-term monitoring program; unfortunately, this was not realized. Research at the time was limited



Map of the Swiss National Park.

to a few sporadic measurements before construction and only a few checks during the construction phase between 1960 and 1970. However, scientists did succeed in gaining a relatively generous rest water regime for the Spöl, providing 35 Million m^3 water per year. Even after the power plants started operations in 1970, research was limited to occasional studies (for example, a limnological study at the Livigno reservoir) and to checks on the biological condition of fisheries.

Dynamic Flow Regime for the Spöl

In 1990, the Engadin Power Plants released deep water from the Livigno reservoir, which provided an opportunity for scientific studies covering a wide range of disciplines. These studies revealed that the section of the Spöl within the National Park below the dam had gradually turned into a series of pools with fairly stagnant water. This development did not appear to be prevented even by occasional flushing events and draining of the reservoir. In addition, it was discovered that the smaller retaining reservoirs within the National Park functionally turned into additional wastewater treatment basins for the Upper Engadin since they received water from the Inn. After extensive discussions, the Science Commission for the National Park decided to revert this stream system, which is significantly impacted by sediment transport and deposition, back to its original condition as far as this is possible under the current conditions. The primary tool available for achieving this are artificial flood events. Due to good relationships between the board of directors for the EKW and the administration of the Canton Grisons, the first flooding experiments were conducted in 2000. Until 2002, three annual high water events are planned for the period between June and August. These experimental floods are accompanied by interdisciplinary research, with intensive collaboration by the Limnology Department of EAWAG (see also article p. 27). The purpose of these preliminary experiments is to optimize the environmental benefit, i.e., to achieve the highest ecological gain with the least amount of water [3].


P. Rey, HYDRA

The heavily impacted Spöl under resiual flow conditions.

The flooding experiments primarily use the monitoring system which was installed in 1996 and provide data for the heavily impacted Spöl and the relatively pristine Ova

Why and What Kind of Research in the National Park?

Research gave the impetus for creating the National Park: a piece of pristine nature was to be protected from human activity to serve as a study object for natural processes. The National Park has, therefore, a research mandate in addition to the environmental preservation mandate, a charge that was passed to the Research Council of the National Park (currently called FoK-SNP) by the Swiss Academy of Sciences (SAS).

Important research goals were and still are:
- **Comprehensive inventory of "nature" within the Park**
- **Observation of natural evolution or regeneration in the Park (long-term research, monitoring)**
- **Comparison with utilized areas outside the Park (reference area)**
- **Recognition of interdependencies between ecosystems (ecosystem research)**

Within this general framework, there are currently several interdisciplinary research foci:
- **The future of the National Park in times of global climate change**
- **The importance of disturbances in ecosystem development**
- **Hooved animals (Ungulates) in alpine habitats**
- **Interactions between society and the National Park**

Further information under: www.nationalpark.ch

Fuorn. The monitoring efforts since 1996 provide the baseline information against which the effects of the artificial flood events will be evaluated. To our knowledge, this is the first time such an experiment has ever been conducted. The National Park provides an ideal setting for such an experiment, since hydroelectric power generation and environmental protection are the only two interests that have to be considered. Initial results indicate that one or two smaller flooding events per year, lasting one day and providing flows of 10–30 m^3/s, yield significant environmental improvements. We can only hope that artificial flooding events will soon be an integral part of rest water management in all of Switzerland.

Impulses from Acid Rain and Global Climate Change

Apart from hydroelectric power plant operations, an additional impetus for limnological research was provided after approximately 1970 by indications that atmospheric conditions are changing. Emerging evidence of acid rain led to chemical measurements and studies of algal vegetation in the Macun lakes in the late 1970s [4]. After the incorporation of these lakes into the National Park in 2000, we now have the opportunity to continuously monitor the condition and dynamics within the plateau containing these lakes, which is situated at an elevation of 2500 m. The Limnology Department of EAWAG will also participate in the development of this monitoring program.

In addition, preparations have been started for a systematic repetition of the measurements conducted in the 1950s, where the water quality of springs was investigated. This is a first step in assessing to what degree atmospheric changes, e.g., increased nitrogen emissions, have an effect on water below the ground. Another question will be, whether and how global warming affects the overall moisture content of mountain ranges.

Opportunity National Park: Reveal Long-term Processes

As the example of the National Park demonstrates, conflicts over water use and atmospheric impacts do not stop at the boundary of nature reserves. Limnological research is a crucial part of research in protected areas in at least two ways: first, long-term environmental changes impact aquatic ecosystems, and we need to know what effect these changes have on the condition of the streams and lakes; second, basic, well-founded information about aquatic ecology – for example that of the regulated Spöl or of the retaining basins – is an prerequisite for effective park management and preventative environmental and water protection. For the most part, we are dealing with questions that can only be answered by long-term investigations or monitoring programs. With respect to the research in the National Park, we hope that EAWAG will continue the current engagement in limnological research in the Park and will contribute to understanding long-term processes.

Thomas Scheurer is executive director of the Research Council of the Swiss National Park (a council of the Swiss Academy of Sciences SAS).

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Aquatic Sciences: Journal Re-launch

The journal "Aquatic Sciences" has been re-launched beginning with volume 64. This is a new era in the development of the journal with an entirely new design, a new Editor-in-Chief and a new and international Editorial Board. "Aquatic Sciences – Research Across Boundaries" deals with natural aquatic systems and the impacts of human activities on these systems spanning the range from molecular-based mechanistic studies to investigations on ecosystem scale. Your research and overview articles are welcome.

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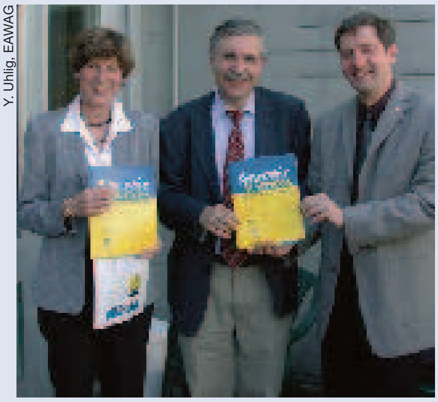
Y. Uhlig, EAWAG

Editor-in-Chief Barbara Sulzberger (EAWAG) and two representatives of Birkhäuser Publishers introduce the "new" Aquatic Sciences.

EAWAG-Workshop: "Reform in Switzerland's Urban Water Management"

It is a worldwide trend to deregulate and privatize services supplying basic needs and to partially relinquish control to the free market. In Switzerland, after deregulation in telecommunications and transportation, reforms in the water supply and wastewater treatment sectors are currently at the center of attention. For this reason, the EAWAG held a one-day workshop on the topic of "Reform in Switzerland's Urban Water Management" in the AudiMax at ETH Zurich. The over 100 participants were treated to an unusual format for this presentation. Instead of a series of talks, the event was held in the form of three panel discussions, featuring renowned personalities: directors of water supply systems and wastewater treatment plants, city council representatives from Switzerland and from abroad, representatives of a private water supply company, directors of cantonal departments, and representatives of NGOs.

The various discussions revolved around the central questions: What are the advantages and disadvantages of the different organizational forms? Is deregulation a tool for increasing flexibility and efficiency, or is it simply a first step towards a private water management industry? Are increased efficiency and ecology mutually exclusive? Can we create sustainable structures by expanding systems to a regional scale?

Information about the workshop can be found at: www.cirus.eawag.ch

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Municipal Water Supply Zurich

EAWAG Advisory Commission: New Member

Since January 2002, Dr. **Ursula Brunner** has been a member of the EAWAG Advisory Board. As an attorney with emphasis on environmental, governmental and administrative law, she is partner of a law firm. Her activities in the area of environmental protection are numerous: she is a coauthor of the Commentary on the Environmental Protection Law, serves as a member of the editorial board for "Environmental Law in Everyday Practice", and was an engaged member and chair of the board of the Association for Environmental Law. In addition, Ursula Brunner has taught in various post-diploma programs on environmental law and has served as expert advisor in the Swiss Priority Program "Environment" initiated in 1992 by the Swiss National Science Foundation.

Fishnet: Entering the Final Phase

The project "Fishnet", which investigates the reasons for decreasing fish catches and health in Swiss streams, is entering its final phase. Out of the total of 75 sub-projects initiated to date, 35 have been completed. A number of results were presented at this year's 4th Science Seminar Fishnet in Fribourg on April 19. The meeting drew a crowd of approximately 170, with representatives from 22 cantons and 5 federal agencies. Topics ranged from colmation and stocking *vs.* natural spawning to hormonally active compounds and impaired reproduction. Based on the preliminary results, six new sub-projects will be initiated in the near future, dealing with issues such as the correlation of relevant environmental factors to regional characteristics and the development of a population model. In addition, work on the final report has begun. The document will summarize the results with practical applications in mind and will contain proposals for further action and improvements that might be possible. A final presentation, which will be open to the public, is planned for November 2003.

More information on the current status of "Fishnet" can be found under: www.fischnetz.ch