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-

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

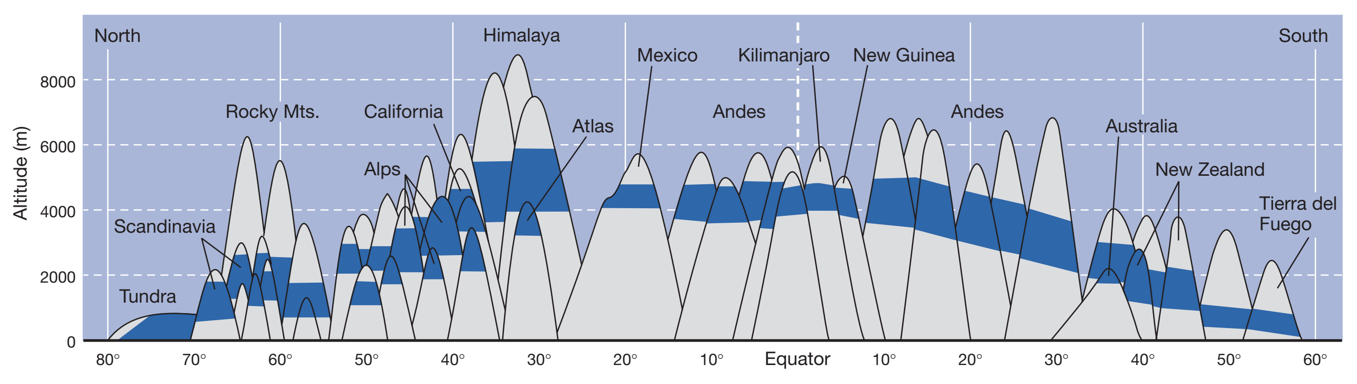

Fig. 2: Altitudinal position of the alpine life zone across latitude [from 3].

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.

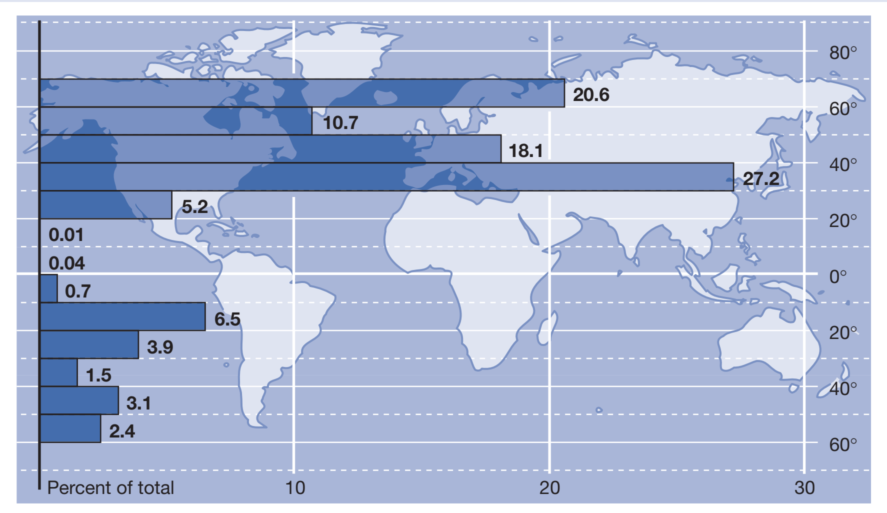

Fig. 3: The relative contribution of each 10 degree latitudinal range to the total global area covered by alpine vegetation. Modified from C. Koerner's chapter, Alpine plant diversity: A global survey and functional interpretations, in [4].

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.

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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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