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).

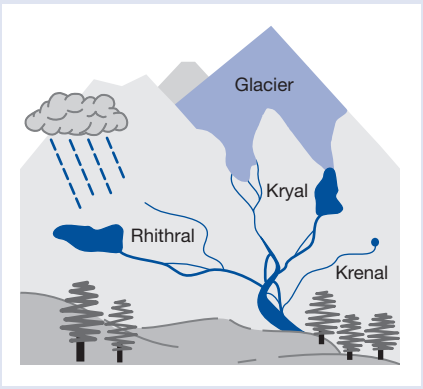

Fig. 1: Alpine stream types with their major water sources [modified from 3, 5].

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-

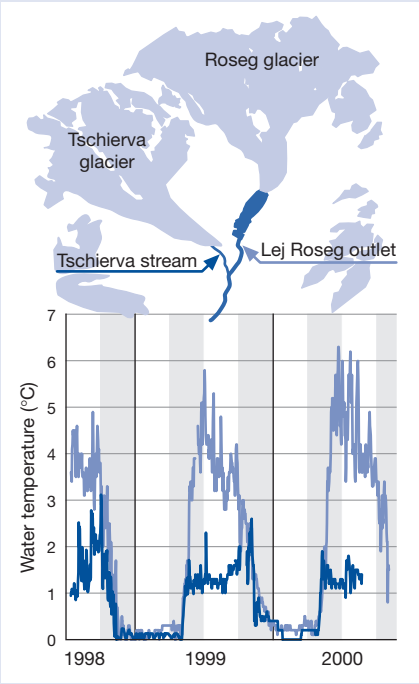

Fig. 2: Average daily water temperature of a kryal lake outlet (Lej Roseg) and an adjacent kryal stream (Tschierva stream).

Photographs: M. Hieber, EAWAG

The outlet of the kryal Steinsee.

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].

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)

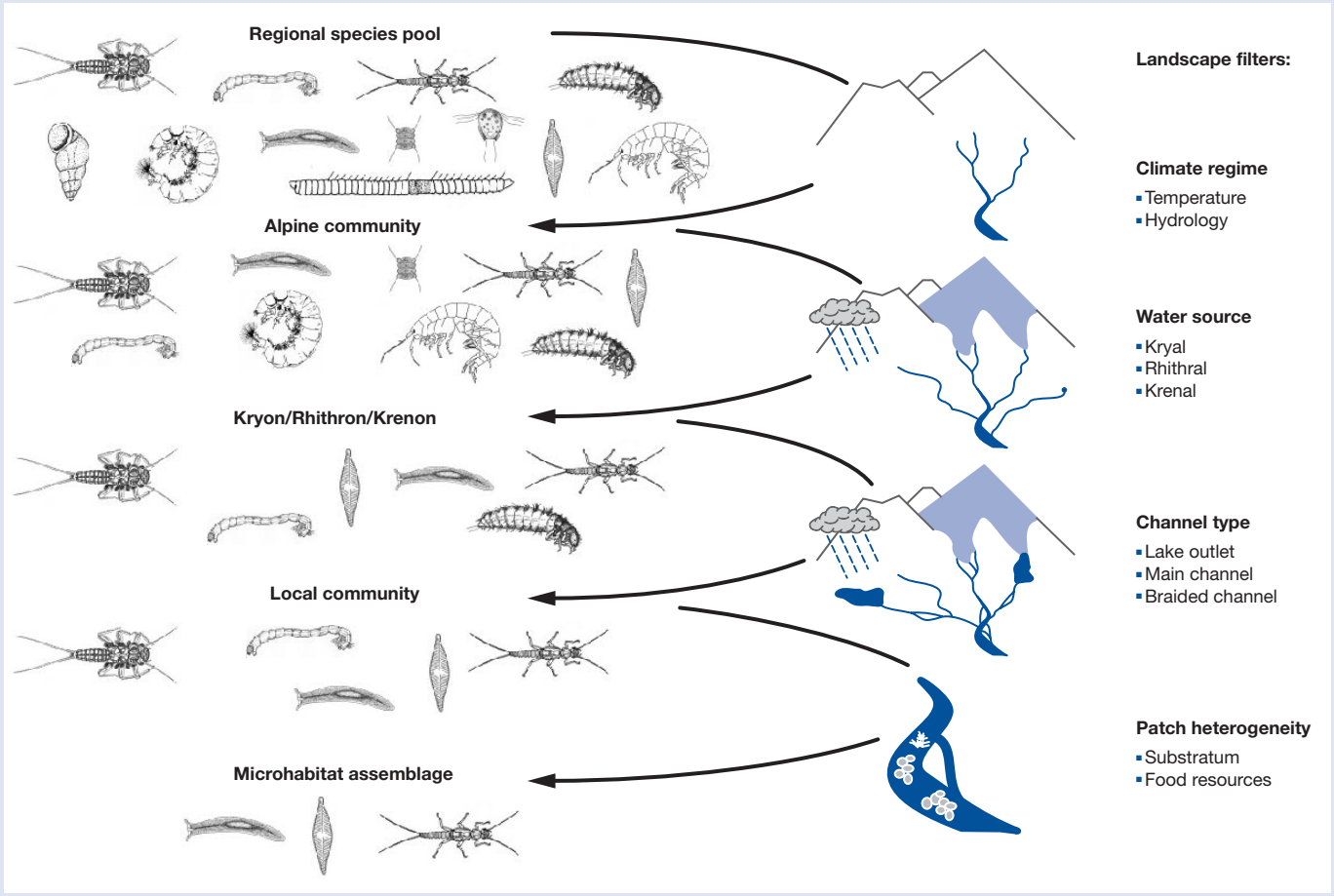

Fig. 3: Conceptual model of how landscape filters [sensu 8, 9] determine the benthic community composition in different alpine stream types. The major environmental factors operating at a given hierarchical level act as filters which determine the species community that occupy the next hierarchical level.

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.

	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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[1] Richardson J.S., Mackay R.J. (1991): Lake outlets and the distribution of filter feeders: an assessment of hypotheses. Oikos *62,* 370–380.
[2] Ward J.V., Stanford J.A. (1982): Thermal responses in the evolutionary ecology of aquatic insects. Annual Review of Entomology *27,* 97–117.
[3] Füreder L. (1999): High alpine streams: cold habitats for insect larvae. In: Margesin R., Schinner F. (eds.) Cold-Adapted Organisms – Ecology, Physiology, Enzymology and Molecular Biology. Springer, Berlin, p. 181–196.
[4] Hieber M., Robinson C.T., Uehlinger U., Ward J.V. (2002): Are alpine lake outlets less harsh than other alpine streams? Archiv für Hydrobiologie *154,* 199–223.
[5] Ward J.V. (1994): Ecology of alpine streams. Freshwater Biology *32,* 277–294.
[6] Kawecka B. (1980): Sessile algae in European mountain streams. I. The ecological characteristics of communities. Acta Hydrobiologica *22,* 361–420.
[7] Hieber M., Robinson C.T., Rushforth S.R., Uehlinger U. (2001): Algal communities associated with different alpine stream types. Arctic, Antarctic and Alpine Research *33,* 447–456.
[8] Tonn W.M. (1990): Climate change and fish communities: a conceptual approach. Transactions of the American Fisheries Society *119,* 337–352.
[9] Poff N.L. (1997): Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological Society *16,* 391–409.