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A conceptual model for niche differentiation of biota within an extreme stream microhabitat

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Introduction

A comprehensive biodiversity study of streams in a 10 km² glacial catchment (PSENNER et al. 2003) revealed one very distinct but ephemeral microhabitat in the main stream and side channels of the Rotmoosache, Austria (RM). It is characterized by a bloom of the chrysophyte Hydrurus recorded annually for about three months in spring. Although these blooms are a frequent phenomenon in fast flowing high alpine streams (UEHLINGER et al 2002) Hydrurus is common in many other streams at all altitudes in the Alps and other mountain areas (PIPP & ROTT 1994). It is a fast growing species well adapted to cope with nutrient limited conditions (ROTT et al. 2000). Theoretically, Hydrurus in RM might be identified as an r-selected pioneer limited by several resources but favoured by moderate physical disturbance in spring and autumn. Pioneer species likely compete more with other species for resources (TILMAN 1982) than profiting from mutual relationships, but degree of competition and mutualism may differ among associated biota. Although macroinvertebrates related to Hvdrurus have been studied from mid-altitudes (MOOG & JANACEK 1991), the structure of the microbial food web, especially in microhabitats of glacial streams above the tree line, is largely unknown. This study is a first attempt to describe the temporal sequences of key biota for a Hydrurus microhabitat observed in a glacial stream.

Key words: benthic algae, macroinvertebrates, bacteria, protozoa, *Hydrurus*

Methods

Samples of benthic biota were taken the same day from the same reach during four seasons in 2001. In addition to stream areas with the thickest algal covers, areas under winter cover and areas completely free of *Hydrurus* were sampled for comparison. Whereas molecular biological methods were applied to study bacterial biodiversity, the diversity of benthic algae, protozoa and metazoa was studied with classical light microscope methods and mounting. Quantitative data comprise surface-related chlorophyll, bacterial numbers and biomass, species and individual numbers of metazoa and total carbon analyses (for details see PSENNER et al. 2003).

Results

Microhabitat

In RM glacial stream *Hydrurus* forms a macroscopically visible, thick mucilage matrix within a short time after the opening of the wintercover from February/March. A few patches (about 100 cm²) are formed first, and larger areas are covered later. Algal biomass in terms of chlorophyll *a* on the richest sites was 86 versus 8 mg m⁻² at bare sites. After a few weeks of growth *Hydrurus* disappeared gradually toward the end of the snow-melt period in May, prior to the annual scour by glacial water pulses in July. Maximum freshweight of *Hydrurus* was $5-20 \text{ kg m}^{-2}$. The mucilage has a variable consistency (from soft to rubber-like) with high water content and 0.5% of organic dry matter.

Host biota

In April 2001 the microhabitat was colonized by the richest community of bacteria, protozoa, microalgae and macroinvertebrates. Compared to the reference situation without *Hydrurus*, bacterial cells embedded in the mucilage showed significantly higher cell volumes yielding > 10 times higher bacterial biomass (34 versus 2.6 mg C m⁻²). The taxonomic composition of bacteria differed highly between *Hydrurus* and non-*Hydrurus* samples, with a high portion of unidentifiable cells on stones without *Hydrurus* (*Eubacteria* EUB338 detection rates 100% versus 69% of total bacterial cell counts). The relative dominance of the taxonomic group *beta-proteobacteria* (Bet42a) and



Fig. 1. Phase model of the *Hydrurus* microhabitat in a glacial stream.

the cytophaga-bacteroides cluster (CF319a) however, showed similar patterns (Bet42a 51 versus 48%; CF319a 38 versus 40%). The pioneer diatom Achnanthes minutissima was the predominant species (> 70%) on stones without Hydrurus, whereas several other diatoms were associated with it, such as Fragilaria arcus, a typical rheobiontic taxon. The species richness (total number of taxa) of ciliates was much higher on stones with Hydrurus (20 taxa) than on comparable stones without it (4 taxa). Ciliates belonged to the orders Hymenostomata, Cyrtophorida, Gymnostomatea, Prostomatida and Peritrichia. Although almost all benthic invertebrate groups were found under both situations, Microcrustaceans (mainly Harpacticoida) and chironomid densities were much higher in the Hydrurus patches in relation to the reference situation. For chironomid larvae this difference was particularly pronounced, with densities 80 times higher than those on stones and gravel bare of *Hvdrurus* (> $2 \ 10^5$ compared to 3 10^3 Ind. m⁻²). Microcrustaceans showed a > 10 times increase in the Hydrurus masses in relation to the reference situation. These findings are the basis to formulate the following preliminary model.

Phase model scenario for Hydrurus and related biota (Fig. 1)

Phase 1: Origination of a bloom (February/ March). Reduced but constant flow, clear water, some nutrient supply, rising water temperatures (SCHÜTZ et al. 2001) and high light allow *Hydrurus* growth on sheltered places (mesolithal) leading to visible patches. Epiphytes, grazers and bacteria have no negative impact on *Hydrurus* growth.

Phase 2: Climax (April). *Hydrurus* masses allow highest diversity of host biota. Epiphytes are settling and growing on top of the mucilage masses. Enhanced bacterial growth is based on the organic matter excreted by other biota and on the mucilage of *Hydrurus*. Grazers and other functional guilds (mainly ciliates, heterotrophic flagellates and chironomids) find food and shelter. Insect larvae can passively be trapped by *Hydrurus* masses and/or invade it from the hyporheic interstitial attracted by excreted aromatic substances. Coexistence of grazers is facilitated by rich resources and extended space.

Phase 3: Patch disintegration of *Hydrurus* starts with the loss of pigments (bleached aspect) and reduced growth. Mechanical scouring

is facilitated. Finally the mucilage is flushed away completely (May/June). As soon as the mucilage becomes softer, epiphytes drift away. Grazers are partly still actively grazing, favouring the decaying algal matter or actively/passively drift away. Some zoobenthos species migrate laterally into slow flowing areas (e.g. *Rhithrogena loyolaea*), while others move vertically into the substrate (e.g. *Harpacticoida*).

Discussion

Although the Hydrurus bloom seems to be a simple microhabitat, it allows an aggregation of several temporal niches for different elements of biota (algae, bacteria, protozoa, metazoa). The niche of Hydrurus is difficult to fully understand, especially the relationship to other algae when classical theories, such as the resource based competion theory (McCORMICK 1996), are applied. It remains unclear whether *Hydrurus* can be identified as a pioneer species (UEHLINGER et al. 2002) because although fast growing and confined to flow, it has large cells and is mechanically affected by strong hydraulic disturbance. Even during bloom formation it has variable effects on other algae, at first seeming to compete successfully with small basal layers of epilithic microalgae by overgrowing them, but later facilitating the growth of epiphytes.

The relationships of *Hydrurus* to heterotrophic organisms seem even more complex. The macroalga offers an accumulation of organic matter as potential food source for bacteria and grazers and a physical structure that is expanded into the flow, but what are the benefits to *Hydrurus* from the host communities? The enhanced densities and higher diversity of the host bacteria, macroinvertebrates and protists within the climax phase of the *Hydrurus* bloom give a strong indication that saving resources through mutual relationships must be effective, and seems to be a common phenomenon for biota under harsh situations (SANDVIK et al. 2002).

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