Life at the edge: Benthic invertebrates in high altitude Andean streams

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Chapter 7

Concluding remarks

In the General Introduction I depicted aquatic biota in high altitude Andean streams as ‘’life at the edge” and here I would like to reflect on this metaphor. First, the present thesis proved the highly selective force of altitude, showing that the highest sites are inhabited by a unique fauna, as discussed below. The next question was which mechanisms allow these invertebrates to maintain viable populations under conditions that are fatal to so many others. Several adaptation strategies can be envisaged, but this thesis focussed on melanin, and showed that this pigment may protect invertebrates against the adverse effects of exposure to both UV radiation and metals. Melanin synthesis and other traits enabling fauna to cope with life at high altitude are discussed in the second paragraph. The two main factors identified in the present project to drive the composition of benthic invertebrate assemblages in Andean streams were altitude and metals. But do they shape communities as single stressors or do they join into one combined selective force, ‘multi-stress’? This will be discussed in the third paragraph. Finally, the conclusions will be drawn concerning the drivers of the unique fauna inhabiting pristine and metal-rich high altitude Andean streams.

Benthic invertebrates inhabiting high altitude Andean streams: a unique fauna

The uplift and mountain building of the Andes during the late Miocene (~12 Ma) entailed a series of climatological and geological processes, such as glaciations and the closing of the Panama Isthmus, that ultimately drove the diversification of South American fauna (Hoorn, 2010) in a notably different way from that occurring in the Pyrenees, the Alps or the Himalayas (Illies, 1969; Jacobsen et al., 1997). As a result, strong selection and different dispersion mechanisms of each faunal group, modified by regional (e.g. altitude) and local (e.g. physical and chemical) factors, have determined the present day distribution of South American aquatic fauna (Covich, 1988; Sites et al., 2003). In recent years there has been an increasing interest in exploring the Andean benthic fauna, focusing mostly on the Northern (Colombia and Ecuador; Jacobsen, 2008 and references therein) and Southern (Argentina and Chile; Rodrigues Capítulo et al., 2001; Scheibler and Debandi, 2008; Miserendino, 2001; Miserendino and Pizzolón, 2003) regions, but leaving the Central (Bolivian and Peruvian) Andes almost unstudied (Jacobsen and Marin, 2007; Tomanova and Usseglio-Polatera, 2007; Acosta, 2009). This thesis is among the first studies to provide this knowledge by describing the macroinvertebrate fauna in high altitude Andes (chapters 2 and 3) and identifying for the first time the mayfly genera *Thraulodes*, *Americabaetis*, *Dactylobaetis* and *Tupiara* as well as the genetic diversity of chironomid communities using COI sequencing (chapters 5 and 6).

It is generally accepted that invertebrate taxa richness decreases with increasing altitude, mostly because the species’ temperature and oxygen tolerance limits are approached, as seen for Plecoptera, Coleoptera, Heteroptera and Odonata (Illies, 1969;

Jacobsen et al., 1997; Jacobsen, 2004). Yet, in the present study a total number of 55 taxa was identified at 4000 m, in accordance with or even higher than data on invertebrate assemblages from other Andean streams at similar altitude ranges in Ecuador (29–60) (Jacobsen, 2008; Monaghan et al., 2000), Peru (40) (Acosta, 2009), and Bolivia (26) (Jacobsen and Marín, 2007). The major groups of benthic invertebrates, such as Ephemeroptera, Plecoptera, Trichoptera, Diptera, and Coleoptera were well represented among the reference streams, with Baetidae, Perlidae, Limnephilidae, and Chironomidae being the dominant families. The families Hirudidae, Oligochaeta (Annelida), Ephydridae, Chironomidae (Diptera), Ptilidae (Coleoptera), Isotomidae, Sminthuridae, Hypogastruridae (Collembola) and Acari persisted at high pollution levels, while Perlidae (Plecoptera), Ceratopogonidae, Elmidae, Psychodidae, Tabanidae (Diptera), Staphylinidae (Coleoptera) and Amphipoda, Ostracoda, Copepoda (Crustacea) persisted at high altitudes.

Because knowledge of Peruvian stream fauna and South American streams in general is scarce, in the chapters 2 and 3 the taxa could only be identified with certainty to the family level. This came with limitations: in chapter 5 individual mayfly larvae had to be pooled for reliable melanin analysis, but the identity of the species making up the above mentioned families remained obscure, and consequently I could not answer the question if altitude-related differences in melanin concentration were due to changes in community composition or to population differentiation in mayfly species. The latter motivation also held for the chironomid communities, which were present at all sampling sites (chapter 6). Therefore, we decided to progress from traditional morphology-based taxonomy towards genetic identification. Our results showed that the sequenced mayflies and chironomids belonged indeed to these groups, but did not match with known species in Genbank, mainly originating from studies of North American, European and Australian species, while South American species are lacking. These results indicated that most Andean haplotypes probably represent new species not yet morphologically described. Moreover, for two mayfly genera and the chironomid species it was observed that sites at different altitudes and pollution status were inhabited by entirely different species. Thus the benthic invertebrate assemblages in high altitude Andean streams are highly diverse and probably consist of several new species. This unique fauna may have developed during the uplift of the Andean mountain range, yet the present day extreme conditions on these tropical mountains urge for an analysis of factors driving the distribution of species.

Faunal traits to cope with life at high altitude

The development of a unique fauna in streams of the tropical high Andes implies that this fauna has developed traits that provide unique adaptations to local landscapes and local climate. However, even the fauna at the highest altitudes- above 4000 m- comprise many species belonging to diverse taxonomic groups, such as discussed above. Therefore, the faunal traits involved may be equally diverse.

Tomanova and Usseglio-Polatera (2007) suggested that in high altitude Andean streams in Bolivia larval traits, such as feeding habits, respiration activity, maximum body size, adaptation to current flow, and mobility and attachment to substratum, were significantly differing from those reported for temperate and lower areas. But also traits of the flying adults may be at play. Mayflies, caddisflies and chironomids depend on bridal flights depending on local weather and landscape characteristics, especially trees (Finn and Poff, 2008). At altitudes around 4000 m vegetation is sparse though, while at 3000 m streams may pass through mountain forests. The observed distinct differences in mayfly (chapter 5) and chironomid communities (chapter 6), representing a strong altitude zonation, may thus be caused by the prominence of species that either exploit leaf detritus produced by tree species (larval traits), or the support of trees and shrubs for their bridal flight (adult traits) or both.

Oxygen in conjunction with temperature has been considered as a master factor for the evolution of insects in streams (Resh and Rosenberg, 1984). The temperature stability of cool, groundwater fed streams and their equally stable high oxygen concentration has been brought forward as a precondition for an evolutionary diversification of riverine insects such as mayflies and stoneflies (Vannote and Sweeney, 1980). Indeed experimental proof was provided for a limited tolerance of several riverine insect larvae to oxygen concentrations below air saturation in temperate areas (van der Geest et al., 2002), and has also been verified under the extremes of the tropical Andes (Rostgaard and Jacobsen, 2005; Jacobsen and Brodersen, 2008). It is remarkable though that the species-rich mayflies, abounding in well oxygenated streams, are also well represented at altitudes over 4000 m in the Andes where the oxygen level is only half of that at sea level. Moreover, the little oxygen that is present may be activated by light (Souza et al., 2007), even more so by the abundantly present UV radiation, resulting in reactive oxygen species (ROS) that damage cellular processes (Meng et al., 2009). Thus traits of the high altitude fauna in response to oxygen are likely to involve their capacities to cope with low levels high up in the mountains, but meanwhile also their capacity to deal with oxidative stress.

All the mechanisms described above, likely to operate in the high Andes, have not been substantiated yet. A notable trait described in this thesis is melanization of benthic invertebrate taxa producing a vertical zonation of pigmentation. Melanization is a first line defense mechanism described mostly in planktonic crustaceans and serving against the harmful effects of intense sunlight (Sommaruga, 2010). However, the present study is the first to describe this pigmentation in benthic macroinvertebrates in high altitude streams, and it was also commonly found in mayflies and chironomids (chapters 4 and 5). It is tempting to compare pigmentation of the high altitude fauna solely to that of sun-exposed crustaceans at sea level and conclude on the common traits of the invertebrate fauna. The discovery of an even more strong pigmentation in chironomids in metal polluted sites at

3000 and 4000 m altitude revealed an alternative role of the ‘sun screen’ melanin i.e. sequestering of metals and protection against metal toxicity (chapter 4). Now I propose the capacity to synthesize melanin as a trait that is highly effective for insect species in the environment of the high Andes, where quite commonly pockets of metal-rich rock are eroded by water, and a scorching UV radiation dominates upon all the tropical Andes. The example of the trait ‘melanin synthesis’, conveying a two-fold tolerance, may indicate that also for the other challenges for fauna described above (response to oxygen/ROS and exploiting leaf litter or flight zones provided by trees) multiple roles may be associated to seemingly pinpointed traits.

Is life at high altitude determined by single or multiple stressors?

A stressor is defined as a factor, either natural or human-caused, that drives species and populations beyond conditions normally experienced throughout their life history, potentially altering community structure and function, and thus provoking a measurable biological or ecological response (Calow, 1989, Statzner, 2010). In nature, the fitness of species may be affected by a single stressor, e.g. a heat wave, or by multiple stressors, e.g. heat, toxicants and food shortage acting together (Folt et al., 1999; Heugens, 2001). Joint effects of stressors may potentially be weaker than predicted from single action, they may be antagonistic, or may be stronger than expected or synergistic. In the present study I have observed primarily community composition, a feature that emerges from the selection of individual species under local conditions. Multiple stressors are likely to be altitude bound UV radiation and oxygen regime, while at some places increased metal exposure was evident. In the most extreme cases of metal polluted streams at 3000 and 4000 m high the community of invertebrates was reduced to 4-8 species (chapter 3) and to a single abundant chironomid taxon (chapter 6). These reduced species numbers are probably the result of few available species capable of persisting under the local multi-stress. It was argued in chapter 6 that metal contamination was so strong to overrule any effect of altitude on chironomid taxa, and in chapter 3 I brought forward that altitude and metal contamination did not interact with the distribution of all invertebrates identified at the genus level. Yet it can also be argued that the altitudes sampled (3000 and 4000 m) do not encompass the reference of lowland UV and oxygen regimes. Thus the stress factor ‘metals’ cannot be regarded as a single condition selecting the few surviving invertebrate taxa. Metals leaching from rock provide also intrinsically ‘multi-stress’: seven metals (with well-known differences in toxicity and modes of action) were elevated >16x at polluted sites (chapter 6), while pH values < 4.5 and a greatly modified water hardness are known to modify metal availability and toxicity (Gerhardt, 1993; Clements et al., 2000).

At reference sites on the Andean slopes between 3000 and 4000 m I observed a very strict zonation of putative species of chironomids (chapter 6) and also genetic characteristics of five genera of the mayfly family Baetidae were distributed over specific altitude ranges between 650 and 4000 m (Chapter 3). These distribution patterns were linked to the single factor ‘altitude’, but certainly this factor is composed also of a multitude of individual parameters, including UV radiation, oxygen regime, scouring currents and food availability. The last factor (food) is not commonly regarded as a stress factor, but food shortage is so and food supply in mountain streams is subject to (episodic) disturbance (Tomanova et al, 2006). Indeed, the common ability of generalist macroinvertebrates to exploit changing resources in tropical streams may potentially contribute to the maintenance of population stability against natural fluctuations (Hart and Robinson, 1990).

In conclusion it is argued that ‘multi-stress’ rules the selection and distribution of invertebrate species at all altitudes in the Andes, but nevertheless is most evident at high altitude and high metal exposure: at ‘the edges of life’.

General conclusions

High altitude Andean streams harbor a quite diverse benthic community, represented by the major groups of invertebrates. Evidence is provided that abundant insect species have not been described taxonomically and that unique genotypes occur, probably as a result of the geological history of the Andes and the strong selection for high altitude tolerance. Cuticular pigmentation of larvae was demonstrated to form an inducible sunscreen against scorching UV radiation, but the pigment melanin was also effective in mitigating metal stress. Thus a single trait of the fauna enabled species to cope with the combined stressor UV radiation and metal exposure from leaching rock. The only species from the stress tolerant chironomid that survived the most harsh condition of a metal-rich, UV blasted site was a non-identifiable chironomid, characterized as a new haplotype. Most likely the vertical zonation of insect fauna on the slopes of the Andes below the most hostile ‘edge of life’ was also strong and multiple stress factors such as the mountainous oxygen regime, high UV radiation and lack of leaf detritus from montain forest were indicated as drivers.