Dynamics of metal adaptation in riverine chironomids.

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Summary

Virtually all research on metal adaptation is carried out in more or less stable environments. However, it is hypothesised that the level of metal adaptation in the river inhabiting chironomid *Chironomus riparius* is subjected to fluctuations, because changing water discharge influences the level of contamination and, therefore, the selection pressure. Furthermore, drift of chironomid larvae and, hence, gene flow is a natural feature in river inhabiting insects and may also shape the population structure of metal-adapted strains. The interaction between selection pressure and transport rate is likely to be observed as a variable metal adaptation in riverine chironomids. This dynamics has rarely been analysed and is examined here following five main questions.

- **How similar are seasonal dynamics of chironomids inhabiting polluted and reference sites, and is larval drift of quantitative importance?**

In order to get insight into the potential inbreeding between metal exposed and non-exposed chironomids, a detailed year round field study was conducted. Every fortnight, seasonal population density and structure were examined by comparing larval instar composition and density patterns of metal exposed and non-exposed populations. Furthermore, the number of midge larvae directly entering the metal-exposed zone were measured, to estimate immigration of non-exposed individuals. Results indicated a massive input to the standing stock at metal contaminated downstream sites and it was concluded that drift of non-tolerant larvae might substantially dominate the seasonal dynamics of midges downstream. Accordingly,

uniform seasonal life cycle dynamics of chironomids inhabiting upstream and downstream sites is expected most of the time.

- **Is metal pollution reflected in morphological measures for development?**

Hypothetically, the severe metal influx might negatively affect local developmental stability of chironomids. Therefore, the level of disturbance was analysed in eight different midge populations and their offspring, cultured under clean conditions, by analysing mouthpart aberrations like fluctuating asymmetry and the occurrence of mentum gaps. Both morphological parameters were highly increased in midges from contaminated field sites and less so in larvae sampled at upstream reference sites. In the first generation progeny the high incidence of mentum deformities were lost, indicating the direct effect of metals on mouthpart aberrations and suggests that the metal-exposed chironomids are under stringent natural selection. Furthermore, a residual heritable effect of increased asymmetry levels is argued to reflect genetic stress emerging from interbreeding between metal adapted and non-adapted chironomids.

- **Is metal adaptation expressed in the metal handling capacity of chironomids?**

Metal accumulation in larvae and the fate of metals during metamorphosis were investigated in metal-exposed midge populations in the field and compared with their non-exposed conspecifics. To this purpose, zinc and cadmium content was measured in simultaneously sampled larvae and imagoes of *C. riparius*, allowing the estimation of metal shedding rates in situ. In contrast to the large interpopulation differences in larval cadmium and zinc content, cadmium body burdens in imagoes vanished to background levels for all midge populations. This suggest that any cadmium accumulated in larval stages was lost during metamorphosis. Body burdens of zinc in imagoes showed interpopulation differences even between metal-exposed sites, indicating differences in shedding capacity for zinc. Clearly, the highly efficient shedding of accumulated metals reflect local adaptation to metals in exposed chironomids. However, based on the differences in zinc accumulation and shedding rate between the two metal-exposed sites it is suggested that population differentiation due to metal stress is of degree, rather than of kind.

- **How persistent is the actual level of metal adaptation in metal-exposed chironomids?**

The consequences of gene flow in metal-adapted chironomid populations, which were expected to be expressed as temporal fluctuations in the degree of metal adaptation, were investigated by following certain life-history characteristics during a five-month period. Populations were examined in experiments using clean cultured first generation progeny and differences among populations can, therefore, assumed to be at least partly genetically determined. In midge populations originating from downstream metal-contaminated field sites, several parameters showed substantial temporal variation, whereas reference populations displayed stability in all characteristics studied. These observations showed that the actual level of metal adaptation varies considerably both in time and space.

- **Is it possible to crossbreed midge strains and what is the influence of experimentally simulated gene flow on the level of metal adaptation?**

Chironomids need monospecific swarms to mate and therefore it is difficult to crossbreed midge strains under laboratory conditions. In an attempt to overcome these practical problems, an emergence trap was developed in which individual, freshly emerged midges could be caught. Virgin midges with a certain background could then be combined in artificial swarms and inbred lines produced. This technique proved to be successful in crossbreeding *C. riparius* midges, facilitating research on the heritability of adaptation and allowing to mimic gene flow under experimental conditions. Experiments focused on two closely situated midge populations which were thought to interbreed under natural conditions. Results confirmed the presence of metal adaptation in the metal-exposed population. On the other hand, a rapid loss of metal adaptation in the first generation hybrid progeny was observed. Furthermore, the responses of the reciprocal crosses showed

no clear consistent indications of maternal effects, suggesting a major genetic component for the increased metal tolerance in adapted *C. riparius* populations.

This thesis shows for the first time that metal adaptation in riverine invertebrates is a highly dynamic process determined by selection of metal stress. The findings supplement to the few studies on genetic adaptation to metals in invertebrates showing the impact of gene flow. Results demonstrated that the actual level of metal tolerance in midge populations fluctuates strongly, varying both in time and space. It is therefore concluded that temporal fluctuations in adaptation levels are influenced by several factors, such as population dynamics and current velocity, and the interaction between different factors might even cause a temporary absence of tolerance.