



## Natural recovery and restoration of acidified shallow soft-water lakes: Successes and bottlenecks revealed by assessing life-history strategies of chironomid larvae

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### Abstract

Acidification has led to a strong decline of species characteristic of shallow soft-water lakes. In spite of reductions in acidifying deposition, natural recovery of biodiversity is modest or even absent, suggesting that the impact of acidification is difficult to reverse. We compared recovery from acidification in non-restored and restored lakes using data from 1983 and 2004. In restored lakes, accumulated organic matter was removed and alkaline water was supplied, resulting in an increase in pH and alkalinity and a decrease in ammonium, sulphur and aluminium. For evaluation of biotic changes we selected chironomid larvae (Diptera). In restored lakes, rarefied species richness increased, chironomid species composition changed and responses of chironomid taxa and their life-history strategies indicated a shift towards pre-acidification assemblages. Species adapted to dynamic and stressful environments decreased in favour of those with life history strategies suitable for more benign environments. In non-restored lakes, chironomid response did not indicate a recovery, despite an improved water chemistry in terms of decreased acidity and sulphur (not ammonium and aluminium). Instead, stressful conditions related to oxygen shortage became more prevalent as a decrease was observed in the chironomids least adapted to periods with low oxygen availability. Acidification has inhibited decomposition, resulting in the accumulation of organic material. Natural recovery from acidification resumed and increased the decomposition of this accumulated organic material, resulting in release of nutrients, consumption of oxygen and a decline of sensitive bottom-dwelling fauna such as chironomids. Therefore, active restoration by removal of accumulated organic matter from sand bottoms is essential for a recovery of chironomid assemblages.

### Zusammenfassung

Der Säureeintrag hat in seichten, schwach gepufferten Gewässern zu einem großen Verlust an Arten geführt. Trotz reduzierten Emissionen von versauernden Substanzen ist die natürliche Wiederherstellung der Biodiversität sehr beschränkt oder sogar nicht existent, was darauf hindeutet dass die negativen Auswirkungen der Versauerung nur schwer rückgängig zu machen sind. Wir haben die natürliche Wiederherstellung von sanierten und nicht-sanierten Seen mit Hilfe von Daten aus den Jahren 1983 und 2004 verglichen. In sanierten Seen wurde angesammeltes organisches Material entfernt und basisches Wasser zur Verfügung gestellt, woraus ein Anstieg des pH-Wertes und der Alkalinität und eine Abnahme der Ammonium-, Schwefel- und Aluminiumgehalte

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resultierte. Für die Evaluierung der biologischen Veränderungen haben wir Chironomiden-Larven (Diptera) ausgewählt. In sanierten Seen nahm die Artenvielfalt zu und die Artenzusammensetzung der Chironomidenlarven verschob sich. Diese Arten und die Life-history-Strategien der Chironomiden wurden der Gemeinschaft vor der Versauerung ähnlicher. Arten, die an dynamische und stressreiche Bedingungen angepasst sind, nahmen zum Vorteil solcher Arten ab, deren Life-history-Strategien an eine günstigere Umwelt angepasst sind.

In den nicht-sanierten Gewässern wies die Reaktion der Chironomiden auf keine Erholung hin, trotz der verbesserten Wasserchemie hinsichtlich der verringerten Azidität und einem abnehmenden Schwefelgehalt (Aluminium- und Ammoniumgehalt sanken nicht). Stattdessen wies die Abnahme der Abundanzen von Chironomiden, die am schlechtesten an Perioden mit geringem Sauerstoffgehalt angepasst sind, auf einen periodischen Sauerstoffmangel, ausgelöst durch stressige Bedingungen, hin. Die Versauerung führte zu einer Akkumulation organischen Materials, da die Aktivität von Mikroorganismen verringert war. Während der natürlichen Wiederherstellung von versauerten Seen zersetzt sich dieses organische Material, was zur Freisetzung von Nährstoffen führt; Sauerstoff wird verbraucht und die sensible bodenbewohnende Fauna wie Chironomiden nimmt ab. Deshalb ist eine aktive Renaturierung durch die Entfernung der organischen Sedimente notwendig, um die vollständige Erholung der Chironomidengemeinschaften zu ermöglichen.

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## Introduction

Acidification has had strong impacts on water quality and aquatic biodiversity of soft waters in the Holarctic region (Leuven, Kersten, Schuurkes, Roelofs, & Arts 1986; Leuven, Van der Velde, & Kersten 1992; Stoddard et al. 1999; Monteith et al. 2005). While reductions in acid deposition have been effective in improving the water chemistry of lakes and streams (Skeffington & Brown 1992; Stoddard et al. 1999), biological recovery is more modest or lagging behind (e.g. Stockdale et al. 2014). Such hysteresis suggests that the impact of acidification on biota is difficult to reverse, which applies more generally to reversing degradation of ecosystems (Schröder, Persson, & De Roos 2005). Natural recovery may proceed slowly or may be impeded even after the degrading influences have been removed (Bradshaw 1996). A delay in biological improvement can result from dispersal limitation or incomplete restoration of habitat conditions (Hildrew & Ormerod 1995; Bradley & Ormerod 2002). Recovery rates of aquatic insects from acidification are lower for lakes than for streams (Stockdale et al. 2014). As dispersal limitation is less likely for insects from standing waters (Ribera, Foster, & Vogler 2003), a habitat condition in these lakes other than pH constrains the biological recovery.

Shallow soft water lakes are especially vulnerable to acidification because primary production is carbon limited (Lucassen, Smolders, & Roelofs 2012). Consequently, acidification stimulates primary production by dissolving bicarbonate in the catchments, enhancing levels of dissolved carbon dioxide. Simultaneously, acidification suppresses microbial decomposition and nitrification, causing organic matter and ammonium accumulation (Leuven & Wolfs 1988; Kok & Van der Velde 1994). Acidification reduced diversity of plankton (Geelen & Leuven 1986), macrophytes (Arts & Leuven 1988; Arts, Van der Velde, Roelofs, & Van

Swaay 1990), macroinvertebrates (Leuven, Van der Velden, Vanhemelrijk, & Van der Velde 1987), fish (Leuven & Oyen 1987) and amphibians (Leuven, Kersten, Christiaans, & Heijligers 1986). Reductions in acidifying deposition resulted in chemical recovery in terms of pH, alkalinity, and ammonium, nitrate and sulphate content (Van Kleef et al. 2010). Decreased acidity simultaneously enhanced decomposition of accumulated organic matter, resulting in internal eutrophication and turbid water (Smolders, Lamers, Lucassen, Van der Velde, & Roelofs 2006; Van Kleef et al. 2010). There is extensive experience with the active restoration of acidified shallow softwater lakes (Brouwer, Bobbink, & Roelofs 2002). Restoration requires reinstating carbon limitation by removal of accumulated organic matter from the mineral sandy bottom and re-establishing soft water conditions through the inlet of alkaline water or catchment liming. With these measures recovery of abiotic conditions and characteristic plant communities can be achieved.

We hypothesise that biotic recovery from acidification requires both a reduction in acidifying deposition and active restoration efforts (removal of accumulated organic sediment and inlet of alkaline water). To test this hypothesis, chironomid assemblages were studied in these two groups of soft-water lakes, using a before-after-control-impact (BACI) design: (1) restored lakes where characteristic plant species recovered, and (2) non-restored lakes where only acidifying deposition was reduced. Chironomids are a species-rich family of Diptera with aquatic larvae. Due to their high dispersal ability and fecundity, they respond quickly to environmental change. In addition a wide range of environmental tolerances and different adaptations to specific types of impairment (Carew, Pettigrove, Cox, & Hofmann 2007), make chironomids very suitable to understand causal mechanisms in the responses of species to decreased acidification or restoration. Changes in chironomid assemblages were

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