

A close-up photograph of a pond with reeds and a spider web. The water is still, reflecting the surrounding greenery. A spider web is visible in the foreground, partially submerged. The background shows a dense thicket of reeds and other vegetation, creating a natural, somewhat blurred setting.

Identifying and crossing thresholds in managing moorland pool macroinvertebrates

HEIN VAN KLEEF

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in managing moorland pool macroinvertebrates

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Henricus Hubertus van Kleef

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Promotor:

Prof. dr. ir. A.J. Hendriks

Copromotores:

Dr. R.S.E.W. Leuven

Dr. G. van der Velde

Manuscriptcommissie:

Prof. dr. H. Siepel (voorzitter)

Prof. dr. J.G.M. Roelofs

Prof. dr. M.G.C. Schouten (Wageningen UR)

Paranimfen:

W.C.E.P. Verberk

G.A. van Duinen

To my parents

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Sampling of aquatic macroinvertebrates in the Vaarvennen by the author. In this complex of moorland pools from 1983 to 2005 pH increased with 1.7 units. Photo: Douwe Schut.

Chapter 1

Introduction

Hein van Kleef

Changing moorland pools

Moorland pools are especially common on the higher Pleistocenic sand grounds in the north, east and south of the Netherlands. Created by large scale natural processes, such as movement of glaciers, drifting of sands and meandering of streams, these pools have soils and water poor in nitrogen and phosphorus (Roelofs et al. 1984, Arts et al. 1988). The amount of carbon is also often limited (Roelofs et al. 1984, Smolders et al. 2002) and determined by the ratio in which moorland pools are supplied by rainwater and calcareous groundwater (Brouwer 2001). Isoetid plant species, such as *Littorella uniflora* (L.) Ascherson, *Isoetes echinospora* Durieu and *Echinodorus ranunculoides* (L.) Ascherson and aquatic macroinvertebrates, such as the midge *Pagastiella orophila* (Edwards, 1929), the water beetle *Hygrotus novemlineatus* (Stephens, 1829) and the caddisfly *Molanna albicans* (Zetterstedt, 1840) are common in these nutrient poor water bodies. Many aquatic macroinvertebrate species depend on the development of shore vegetation for habitat (Harrison 2000, Harrison et al. 2004). Succession often proceeds slowly under natural conditions and these communities may persist up to several centuries (Smolders et al. 2002).

Historically, moorland pools have been used by humans for a variety of purposes (Table 1). Most pools and in particular their catchments have been drained for afforestation (Arts et al. 1988). On the other hand, many moorland pools have been supplied with water, often from nearby streams, enabling fish culture or recreational activities, such as swimming and skating. In these cases, the inlet water had a higher nutrient content and alkalinity than the original moorland pools often resulting in eutrophication and alkalisation and the disappearance of isoetids (Arts & Leuven 1988). To prevent ongoing nutrient enrichment, water inlet has been ceased in all but a few

Table 1 Frequency of occurrence (%) of the most common types of land use in Dutch moorland pools over the period ca. 1850-1980 (adjusted from Arts et al. 1988).

Human activities	Occurrence
Drainage	85-98%
Water inlet	30-43%
Swimming	45%
Skating	32%
Fishing	34-36%
Sand digging	28%
Dredging	19%
Peat digging	13-34%
N	47

moorland pools. Occasionally, succession has been reset by peat cutting, dredging or sand excavation, creating initial succession stages anew.

Over time approximately fifty percent of the Dutch moorland pools have been lost to land reclamation. At the moment nearly all remaining pools are located in protected nature reserves (Arts et al. 1989). Despite their protected status, characteristic flora and fauna (i.e. species that occur more often in these pools than in other water types) in the moorland pools continued to decline as a result of acidification, eutrophication and desiccation (Roelofs 1983, Schuurkes 1987, Leuven 1988, Arts 1990). Acidification was the result of emissions of NO_x , NH_x and SO_x . Nitrogen emissions and nutrient

enrichment of groundwater by agricultural activities in catchments contributed to the eutrophication of moorland pools.

Eutrophication lifted limitation of phosphorus and/or nitrogen, increased primary production and resulted in the accumulation of organic matter and anaerobic conditions. Acidification caused that soil bound bicarbonate was turned into CO_2 and leached from the catchments. This process temporarily eliminated carbon limitation and increased primary production of *Juncus bulbosus* L. and *Sphagnum* ssp. (Roelofs 1983, Arts & Leuven 1988). Strong acidification resulted in reduced degradation of cell walls, fragmentation of leaf material and therefore reduced leaching of nitrogen and phosphorus (Brock et al. 1985, Kok et al. 1990a, 1990b, 1992). Decomposition rates were further reduced when fungal decomposition took over from bacterial decomposition, pectic enzymes involved in the decomposition process were inhibited and detritivore abundance was reduced (Kok et al. 1992, Kok & Van der Velde 1991, 1994). Thus acidification resulted in a strong accumulation of poorly decayed organic material. Desiccation resulting from drainage or lowering of groundwater tables may enhance acidification and eutrophication by increasing the frequency with which sediments become exposed to the air, hereby increasing aeration. Under aerobic conditions mineralization of organic sediments increases resulting in acidification and eutrophication through the release of protons and nutrients (Schuurkes et al. 1988). Consequently, decreasing natural dynamics combined with increasing scale and intensity of anthropogenic pressure have resulted in a severe loss of moorland pool biodiversity.

Moorland pool conservation and restoration

Efforts to prevent the loss of biodiversity from moorland pools and other ecosystems use two different approaches. (1) Reduction of degradation by developing policy and measures to reduce emissions of acidifying and eutrophying compounds and regulate drainage to reduce desiccation. Although the targets have not been reached yet, significant results have already been achieved (Milieu & Natuur Compendium 2008). From 1981 to 2006 deposition of NO_x , NH_x and SO_x has decreased by 31, 26 and 73%, respectively. Phosphorus supply to surface waters has decreased by 71 % between 1996 and 2006. Reversal of desiccation, on the other hand, has been achieved only rarely as only 3% of the in 1990 desiccated area was restored in 2000. (2) Local measures to mitigate the effects of acidification, eutrophication and desiccation have been developed (Bellemakers 2000, Brouwer 2001). These measures were initially developed to allow characteristic communities to persist under ongoing environmental stress and not necessarily to restore them. Only after a number of years when they had proven to be effective and durable, they gradually became accepted as a means of restoring moorland pool communities. The rationale in moorland pool restoration is to recreate suitable starting conditions for autonomic succession. This is achieved by removing accumulated nutrients and enhancing reduced alkalinity (i.e. the legacy of degradation), thus reinstating nutrient limitation (Roelofs et al. 2002), if possible in combination with elimination of local sources of degradation. Typical restoration measures are removal of nutrient rich sediments often including macrophyte swards (Figure 1), supply of calcareous water or catchment liming (Arts et al. 1988, Brouwer et al. 2002, Roelofs et al. 2002, Dorland et al.



Figure 1 Moorland pool restoration in practice. Left: nutrient enriched pool with dominance of *Phragmites australis*. Middle: the pool has been drained to facilitate dredging and looks like this a few days after restoration. Right: after a year characteristic vegetation has recovered.

2005), cessation of agricultural activities, deforestation or conversion of pine to deciduous forest and removal of drainage systems.

To some extent both approaches yielded positive results for water quality, diatoms and higher plants of moorland pools (Brouwer et al. 1996, Van Dam 1996, Brouwer & Roelofs 2002, Brouwer et al. 2002, Roelofs et al. 2002, Brouwer et al. 2009). A limited number of studies on the short term effects of sediment removal on fauna in lakes is available and all report decreasing species richness and/or densities, e.g., for macroinvertebrates (Butler et al. 1992, Darby et al. 2005) and herpetofauna (Aresco & Gunzburger 2004). In moorland pools such studies have not been performed and the effects of moorland pool restoration on macroinvertebrates were unknown until this study.

Managing moorland pool fauna

Restoration measures for moorland pools were initially developed to prevent the extinction of characteristic species until degradation sources have been reduced below critical levels. As nowadays emission and deposition of acidifying substances have been strongly reduced one might wonder whether spontaneous recovery is possible or restoration efforts remain necessary due to restoration thresholds, i.e. barriers that prevent the autonomous recovery of degraded ecosystems. Therefore, effective management requires the identification and elimination of restoration thresholds (Hobbs 2007). Restoration thresholds can be biotic or abiotic in nature. Moorland pool restoration traditionally tackles abiotic thresholds, i.e. accumulated nutrients, elevated nutrient availability and reduced alkalinity. Most aquatic macroinvertebrates are not directly influenced by these abiotic triggers. Instead, most species are expected to respond indirectly through mediation of plant growth. This is because, plants either directly fulfil habitat requirements such as the availability of oxygen, shelter, ovipositing sites and food or indirectly influence the number of predators, competitors and prey an animal encounters. Therefore one might expect that restoration of moorland pools through a bottom-up approach will simultaneously benefit fauna diversity. However, the spatial and temporal configuration of habitat conditions a species requires, is species specific, depends on the species' biological traits (Verberk et al. 2008), and may very well differ from those induced by restoration measures.

Barring a few exceptions (Brouwer et al. 2002, Smolders et al. 2002) little attention has been paid to biotic thresholds, such as trophic interactions, damaged species pool and feedbacks by non-characteristic or non-native invasive species. For macroinvertebrates

biotic thresholds may be important in determining restoration success as suitability of their habitat largely depends on biotic interactions. Due to the extensive reclamation and degradation of moorland pools, it is possible that the regional species pool is no longer intact and characteristic species are no longer able to colonise restored pools despite the fact that many macroinvertebrates are mobile.

Goal and outline of this thesis

The goal of this thesis is: “*to assess effectiveness of moorland pool nature management in conserving and restoring communities of characteristic aquatic macroinvertebrates and to help nature managers to improve effectiveness of their practices by developing knowledge and tools*”.

Achieving this goal requires knowledge on the presence or absence of restoration thresholds. In this thesis abiotic and biotic thresholds are examined including restoration practices which may themselves act as possible barriers for complete recovery (Figure 2).

The emissions of acidifying compounds have been considerably decreased. Chapter 2 explores the reversibility of acidification, presence of abiotic restoration barriers and possibility of spontaneous recovery. This is done by comparing water chemistry data from the 1980s and from recent years and determining whether reduced acidity is accompanied by changes in other water chemistry parameters. Chapter 3 describes the response of chironomids to reduced acidification as well as restoration management. Species are grouped into life history tactics by biological trait combinations with a similar adaptive function. These life history tactics thus are a species' integrated response to naturally occurring environmental conditions. Changes of life history tactic abundance should therefore provide information on environmental changes responsible for species' responses. This chapter along with chapters 4 and 7 also addresses the completeness of the local species pool.

While chapter 3 describes the effects of restoration measures over a period of multiple years, in chapter 4 the direct and short term effects of restoration on macroinvertebrates are analysed. The response of individual ecological traits is used to identify facilitating and limiting conditions in the restoration process. Whether moorland pool restoration is hampered by biotic interactions is studied in chapter 5. This chapter examines whether restoration success is influenced by invasions of non-native pumpkinseed sunfish (*Lepomis gibbosus*) and if there is a relationship between invasiveness of pumpkinseed and nature management practices. Chapter 6 explores an alternative type of moorland pool management. This management is inspired by historical land use and seems to be a promising way of protecting a number of highly endangered species.

In chapter 7 a synthesis of the preceding chapters is given. It describes what barriers aquatic macroinvertebrates encounter in the conservation and restoration of moorland pools. The results are discussed in the face of contemporary restoration concepts. Finally recommendations for improving the output of restoration efforts are given.

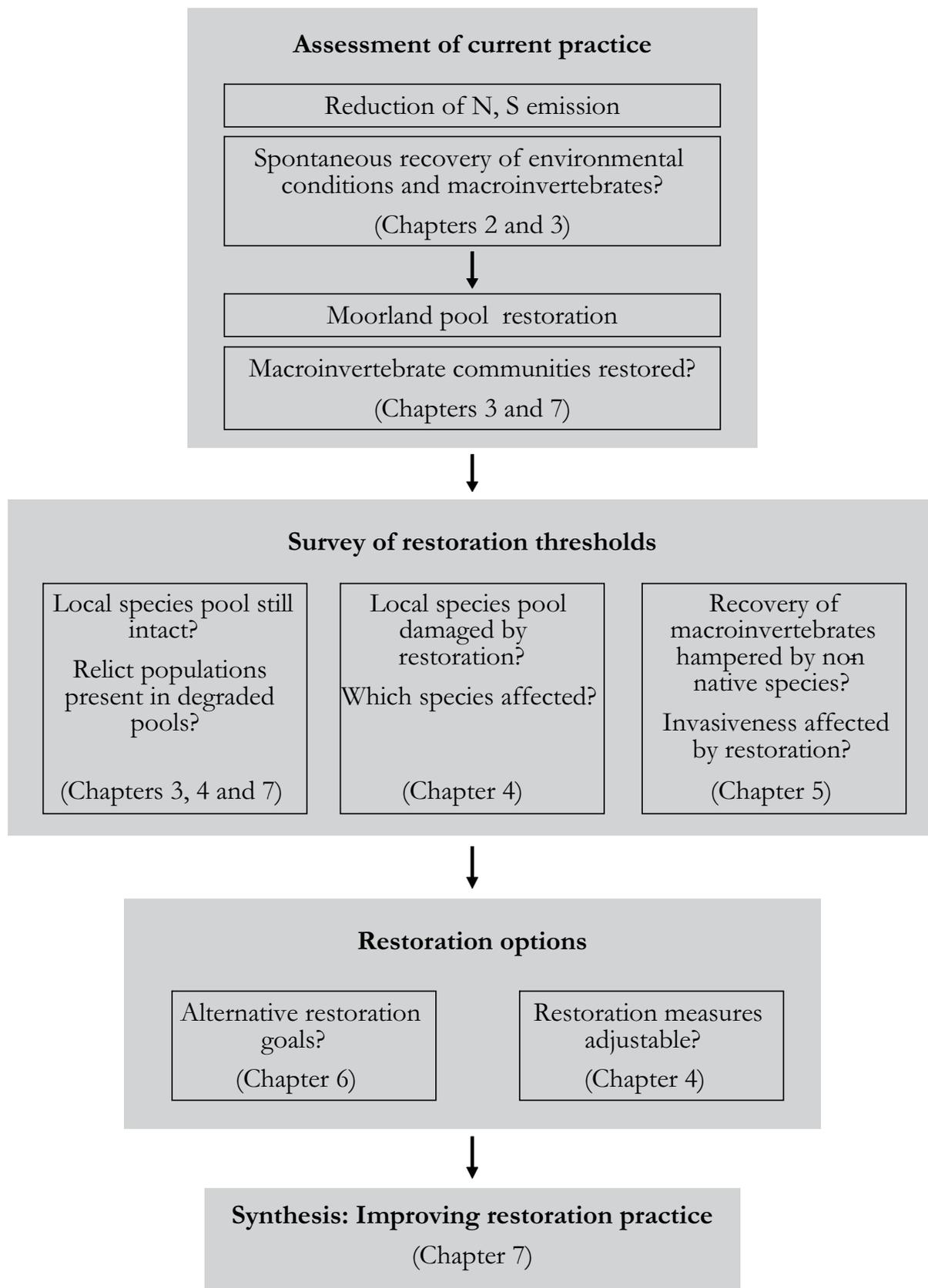


Figure 2 Schematic representation of the coherence of the research presented in the chapters of this thesis.

References

- Aresco MJ & Gunzburger MS (2004) Effects of large-scale sediment removal on herpetofauna in Florida wetlands. *Journal of Herpetology* **38**: 275-279.
- Arts GHP & Leuven RSEW (1988) Floristic changes in shallow soft waters in relation to underlying environmental factors. *Freshwater Biology* **20**: 97-111.
- Arts GHP, Schaminée JHJ & Van de Munckhof PJJ (1988) Human impact on origin, deterioration and maintenance of Littorelletalia-communities. *Proceedings of the 5th symposium on synanthropic flora and vegetation, 1988. Martin, Czechoslovakia*: 11-18.
- Arts GHP, De Haan AJ, Siebum MB & Verheggen GM (1989) Extent and historical development of the decline of Dutch soft waters. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen. Series C: Biological and Medical Sciences* **92**: 281-295.
- Arts GHP (1990) Deterioration of Atlantic soft-water systems and their flora, a historical account. *Thesis, Radboud University, Nijmegen*.
- Bellemakers MJS (2000) Reversibility of the effects of acidification and eutrophication of shallow surface waters. *Thesis, Radboud University, Nijmegen*.
- Brock TCM, Boon JJ & Paffen BGP (1985) The effects of the season and of water chemistry on the decomposition of *Nymphaea alba* L.; weight loss and pyrolysis mass spectrometry of the particulate organic matter. *Aquatic Botany* **22**: 197-229.
- Brouwer E, Bobbink R, Meeuwse F & Roelofs JGM (1996) Recovery from acidification in aquatic mesocosms after reducing ammonium- and sulphate deposition. *Aquatic Botany* **56**: 119-130.
- Brouwer E (2001) Restoration of Atlantic softwater lakes and perspectives for characteristic macrophytes. *Thesis, Radboud University, Nijmegen*.
- Brouwer E, Bobbink R & Roelofs JGM (2002) Restoration of aquatic macrophyte vegetation in acidified and eutrophied softwater lakes: an overview. *Aquatic Botany* **73**: 405-431.
- Brouwer E & Roelofs JGM (2002) Oligotrophication of acidified, nitrogen-saturated softwater lakes after dredging and controlled supply of alkaline water. *Archiv für Hydrobiologie* **155**: 83-97.
- Brouwer E, Van Kleef H, Van Dam H, Loermans J, Arts GHP & Belgers D (2009) Effectiviteit van herstelbeheer in vennen en duinplassen op de middellange termijn. *Dienst Kennis, Ministerie van Landbouw, Natuurbeheer en Voedselkwaliteit, Ede*.
- Butler RS, Moyer EJ, Hulon MW & Williams VP (1992) Littoral zone invertebrate communities as affected by a habitat restoration project on Lake Tohopekaliga, Florida. *Journal of Freshwater Ecology* **7**: 317-328.
- Darby PC, Valentine-Darby PL, Percival HF & Kitchens WM (2005) Florida apple snail (*Pomacea paludosa* Say) responses to lake habitat restoration activity. *Archiv für Hydrobiologie* **4**: 561-575.
- Dorland E, Van den Berg LJJ, Brouwer E, Roelofs JGM & Bobbink R (2005) Catchment liming to restore degraded, acidified heathlands and moorland pools. *Restoration Ecology* **13**: 302-311.
- Harrison SSC (2000) The importance of aquatic margins to invertebrates in English chalk streams. *Archiv für Hydrobiologie* **149**: 213-240.
- Harrison SSC, Pretty JL, Shepherd D, Hildrew AG, Smith C & Hey RD (2004) The effect of instream rehabilitation structures on macroinvertebrates in lowland rivers. *Journal of Applied Ecology* **41**: 1140-1154.
- Hobbs RJ (2007) Setting effective and realistic restoration goals: Key directions for research. *Restoration Ecology* **15**: 354-357.
- Kok CJ, Meesters HWG & Kempers AJ (1990a) Decomposition rate, chemical composition and nutrient recycling of *Nymphaea alba* L. floating leaf blade detritus as influenced by pH, alkalinity and aluminum in laboratory experiments. *Aquatic Botany* **37**: 215-227.
- Kok CJ, Van der Velde G & Landsbergen KM (1990b) Production, nutrient dynamics and initial decomposition of floating leaves of *Nymphaea alba* L. and *Nuphar lutea* (L.) Sm. (Nymphaeaceae) in alkaline and acid waters. *Biogeochemistry* **11**: 235-250.

- Kok CJ & Van der Velde G (1991) The influence of selected water quality parameters on the decay rate and exoenzymatic activity of detritus of *Nymphaea alba* L. floating leaves in laboratory experiments. *Oecologia* **88**: 311-316.
- Kok CJ, Haverkamp W & Van der Aa HA (1992) Influence of pH on the growth and leaf maceration ability of fungi involved in the decomposition of floating leaves of *Nymphaea alba* L. in acid water. *Journal of General Microbiology* **138**: 103-108.
- Kok CJ & Van der Velde G (1994) Decomposition and macroinvertebrate colonization of aquatic and terrestrial leaf material in alkaline and acid still water. *Freshwater Biology* **31**: 65-75.
- Leuven RSEW (1988) Impact of acidification on aquatic ecosystems in The Netherlands, with emphasis on structural and functional changes. *Thesis, Radboud University, Nijmegen*.
- Milieu & NatuurCompendium (2008) Retrieved December 1, 2008, from <http://www.milieuennatuurcompendium.nl/>.
- Roelofs JGM (1983) Impact of acidification and eutrophication on macrophyte communities in soft waters in the Netherlands. I. Field observations. *Aquatic Botany* **17**: 139-155.
- Roelofs JGM, Schuurkens JAAR & Smits AJM (1984) Impact of acidification and eutrophication on macrophyte communities in soft waters in the Netherlands. II. Experimental studies. *Aquatic Botany* **18**: 389-411.
- Roelofs JGM, Brouwer E & Bobbink R (2002) Restoration of aquatic macrophyte vegetation in acidified and eutrophicated shallow soft water wetlands in the Netherlands. *Hydrobiologia* **478**: 171-180.
- Schuurkes JAAR (1987) Acidification of surface waters by atmospheric deposition. *Thesis, Radboud University, Nijmegen*.
- Schuurkes JAAR, Kempers AJ & Kok CJ (1988) Aspects of biochemical sulphur conversions in sediment of a shallow soft water lake. *Journal of Freshwater Ecology* **4**: 369-381.
- Smolders AJP, Lucassen ECHET & Roelofs JGM (2002) The isoetid environment: biogeochemistry and threats. *Aquatic Botany* **73**: 325-350.
- Van Dam H (1996) Partial recovery of moorland pools from acidification: indications by chemistry and diatoms. *Netherlands Journal of Aquatic Ecology* **30**: 203-218.
- Verberk WCEP, Siepel H & Esselink H (2008) Life history tactics in freshwater macroinvertebrates. *Freshwater Biology* **53**: 1722-1738.



*Acidified moorland pools like this one often still harbour characteristic macroinvertebrate species.
Photo: Hein van Kleef.*

Chapter 2

Effects of reduced nitrogen and sulphur deposition on the water chemistry of moorland pools

Hein van Kleef, Emiel Brouwer, Rob Leuven, Herman van Dam, Ankie de Vries-Brock, Gerard van der Velde & Hans Esselink

Abstract

To assess changes as a result of reduced acidifying deposition, water chemistry data from 68 Dutch moorland pools were collected during the periods 1983-1984 and 2000-2006. Partial recovery was observed: nitrate- and ammonium-N, sulphur and aluminium concentrations decreased, while pH and alkalinity increased. Calcium and magnesium concentrations decreased. These trends were supported by long term monitoring data (1978-2006) of four pools. Increased pH correlated with increases in ortho-phosphate and turbidity, the latter due to stronger coloration by organic acids. Increased ortho-phosphate and turbidity are probably the result of stronger decomposition of organic sediments due to decreased acidification and may hamper full recovery of moorland pool communities. In addition to meeting emission targets for NO_x , NH_x and SO_x , restoration measures are still required to facilitate and accelerate recovery of acidified moorland pools.

Introduction

Emissions of nitrogen and sulphur compounds by agriculture and from the burning of fossil fuels have led to acid deposition in parts of Europe, North America and Asia (Jenkins 1999, Lynch et al. 2000, Carmichael et al. 2002). The Netherlands and the southern part of the country in particular is among the areas in the Northern hemisphere to have received the highest N load (Holland et al. 2005, Milieu & NatuurCompendium 2008). Acid precipitation has caused the acidification of moorland pools in the Netherlands (Van Dam & Kooijman-van Blokland 1978, Roelofs 1983, Leuven et al. 1986a, 1989). Acidifying deposition initially increased mobilisation of cations and bicarbonate from the catchment, increasing concentrations of Ca, Mg and CO_2 in the water layer (Roelofs et al. 1984, Haynes & Swift 1985, Bergkvist 1986), as well as leading to acidification and mobilisation of Al. As a result of the increased CO_2 concentrations primary production of *Sphagnum* species and *Juncus bulbosus* L. in moorland pools temporarily increased strongly (Roelofs 1983). With ongoing N and S deposition, bicarbonate reserves became depleted, followed by Mg and Ca bound to soil particles (Kirchner & Lydersen 1995). Subsequently, concentrations in the water decreased strongly. Due to the acidification, decomposition of organic matter and production of organic acids became inhibited (Kelly et al. 1984, Leuven & Wolf 1988) accumulating organic matter (Brouwer et al. 1996) and increasing water clarity. Acidification led to the decline of characteristic macrophytes (Arts & Leuven 1988), phytoplankton and zooplankton (Geelen & Leuven 1986), macroinvertebrates (Leuven et al. 1986a), fish (Leuven & Oyen 1987) and amphibians (Leuven et al. 1986b).

Since the early 1980s European and Dutch policy makers have aimed at reducing acidifying deposition by reducing emissions of NO_x , NH_x and SO_x . As a result, the atmospheric deposition of these substances in the Netherlands has decreased by 31, 26 and 73%, respectively between 1981 and 2006 (Milieu & NatuurCompendium 2008). In the Netherlands N emissions have undergone the largest decrease of all European countries (Fowler et al. 2007). Reductions in sulphur emissions in Northern Europe and North America have led to a recovery of surface water chemistry (i.e. pH, acid neutralising capacity (ANC), SO_4^{2-} and Al) in streams and lakes (Stoddard et al. 1999, Forsius et al. 2003, Davies et al. 2005, Skjelkvåle et al. 2005). On the other hand, reduced acidification

has been hypothesized to enhance concentrations of dissolved organic carbon (Evans et al. 2005, 2006, Monteith et al. 2007).

Moorland pools have morphological and chemical characteristics that make them vulnerable to acidification, but also likely to rapidly respond to reduced N and S emissions (Table 1). The pools are small and shallow. They are formed on impermeable soil layers and thus fed by a combination of rain and local groundwater. The catchments supplying groundwater are relatively small and located on mineral soils covered by heath or forest. Due to the high permeability of the catchment soil, they drain rapidly and oxidation processes dominate. The catchments are poor in calcareous deposits and nutrients leading to limitation of C, N and P in the pools. A slow but gradual spontaneous recovery from acidification was recorded in mesocosms (Brouwer et al. 1996), whereas Van Dam (1996) reported a partial recovery from three pools. Since then emissions of N and S have further decreased and ongoing recovery probably has occurred.

Table 1 Reference values of morphological and chemical moorland pool characteristics. Adapted from Arts (2000).

Parameter	Range	Parameter	Range
pH	4.5 - 6.5	Surface area (ha)	0.25 - 85
Alkalinity (meq l ⁻¹)	< 1.0	Depth (m)	< 1.5
Ortho-PO ₄ ³⁻ (μmol l ⁻¹)	< 0.55	Catchment : pool area ratio	0.5 - 10
NH ₄ ⁺ (μmol l ⁻¹)	< 20	Sediment	Sand
NO ₃ ⁻ (μmol l ⁻¹)	< 20	Water supply	Rain- or groundwater
S (μmol l ⁻¹)	20 - 200	Drainage	Seepage

The objectives of this chapter are (1) to document changes in moorland pool water chemistry associated with decreased deposition of acidifying compounds and (2) to identify the mechanisms for the observed changes in water chemistry.

To assess changes in water chemistry, chemical data were collected from sixty eight pools during the period 2000-2006 (period 2) and compared to data from 1983-1984 (period 1, i.e. high acidifying deposition) (Kersten 1985, Leuven et al. 1986a, 1989). Correlation analyses were performed in order to determine whether recovery from acidification was accompanied by changes in other water chemistry parameters. The results were supported by comparison with long term monitoring data (1978-2006) of four moorland pools.

Material and methods

Data sets and study sites

For this study three data sets were used. Two sets are formed by water chemistry data from 68 moorland pools from two time periods: 1983-1984 (period 1) and 2000-2006 (period 2). These pools were selected from a previous survey (Kersten 1985, Leuven et al. 1986a). Pools were selected if pH in period 1 did not exceed 5.5, if in the pools themselves no restoration measures were applied since 1983 and if no factors other than atmospheric deposition were identified which might have influenced water chemistry (e.g. colonies of black-headed gulls (*Larus ridibundus* L.) and inlet of alkaline surface water). All studied pools are located in the southern part of the Netherlands (Figure 1). Reference conditions for hydromorphological and chemical characteristics are summarized in Table 1. With potential acid depositions of 5590 and 3050 mol ha⁻¹ yr⁻¹ in 1984 and 2006 respectively, this area is among the most acid impacted regions in the world (Bleeker &

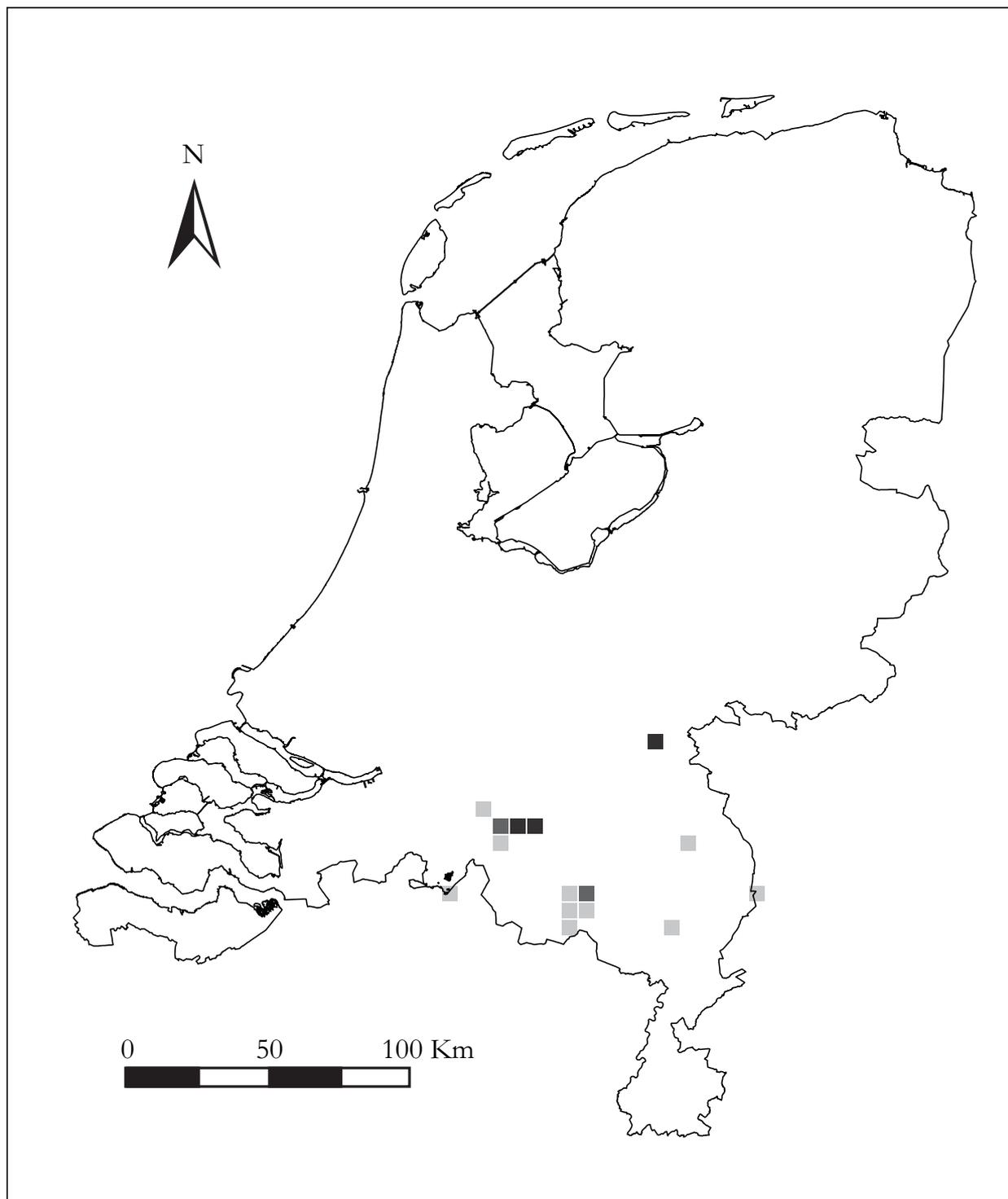


Figure 1 Locations of the study sites in the Netherlands in squares of 25 km². Light grey: 1-2 sites; grey: 3-5 sites; Dark grey: >5 sites.

Erisman 1996, Milieu & NatuurCompendium 2008). The third data set contains long term water chemistry monitoring data (1978-2006) of four moorland pools situated in the same part of the Netherlands (i.e. Achterste Goorven 51°33'50.0" N, 5°12'49.9" E, Groot Huisven 51°34'39.4" N, 5°15'44.7" E, Middelste Wolfspuutven 51°34'32.1" N, 5°13'10.5" E and Schaapsven 51°33'31.8" N, 5°9'34.7" E). The Achterste Goorven and Groot Huisven were also part of the other data sets.

Data collection

In period 2, surface water samples of 68 pools were taken between July and September. Water samples were collected in iodated polyethylene bottles. The pH, alkalinity, colour (extinction at 450 nm; Shimadzu spectrophotometer UV-120-01) and turbidity of surface water samples were measured within 24 h after collection. After filtering (Whatman GF/C filter) and adding 1 mg of citric acid per 25 ml of water, samples were stored at -20 °C until further analysis. The following concentrations were determined colorimetrically; NO₃⁻ according to Kamphake et al. (1967) and NH₄⁺ according to Grasshoff & Johanssen (1972), using a Bran & Luebbe, TRAACS 800+, ortho-PO₄³⁻ according to Henriksen (1965), using a Technicon AA II system, and Cl⁻ according to O'Brien (1962), using a Technicon AA III system. Na⁺ and K⁺ were determined by a Technicon Flame Photometer (Technicon Autoanalyzer Methodology: N20b, 1966). Total concentrations of Ca, Mg, Mn, Si, Fe, Al, P and S were measured by inductively coupled plasma emission spectrometry (Jarrell Ash IL Plasma-200).

Data collection in these pools during periods 1 has been described in detail by Kersten (1985) and Leuven et al. (1986a). Collection of the long term water chemistry monitoring data has been described by Van Dam (1996). In the Achterste Goorven surface water samples were taken at least four times every year (every season). In order to reduce the effects of within year variation, the yearly median was calculated for each parameter. The Groot Huisven, Middelste Wolfspuutven and Schaapsven were sampled once every four years in September/October.

Data calibration

Variation as a consequence of methodical differences was minimized as follows: (1) In period 1 pH was measured in the field, whereas in period 2 pH measurements were performed in the laboratory. Linear regression analysis of pH measured on the same sample in the field as well as in the laboratory revealed the relationship $\text{pH}_{\text{laboratory}} = 0.978 \times \text{pH}_{\text{field}} - 0.043$ (linear regression analysis, $R^2 = 0.943$, $N = 170$, $P < 0.001$, G. van Duinen unpublished data). Laboratory measurements gave significantly lower values than field measurements of 0.06 units on average ($P < 0.001$, $N = 170$, Wilcoxon Signed Ranks test). This difference was not related to pH_{field} (linear regression analysis; $R^2 = 0.009$, $P = 0.231$, $N = 170$). To correct for the discrepancy between field and laboratory measurements, 0.06 units were added to $\text{pH}_{\text{laboratory}}$ -data from period 2. (2) In period 2 concentrations of total-S were measured, which is a good proxy for SO₄²⁻ in these waters. Kersten (1985) and Leuven et al. (1986a) measured SO₄²⁻ colorimetrically with Barium, a method which has a detection limit of 200 μmol l⁻¹. Therefore, differences in S between both periods are only calculated for waters where SO₄²⁻ concentrations in period 1 exceeded 200 μmol l⁻¹. (3) Spectrophotometrical analysis of ortho-PO₄³⁻ is influenced by the concentration of organic acids (Verheggen 1991). However, ortho-PO₄³⁻ data of period 1 were not corrected for organic acids and might have been overestimated. It is not possible to make these corrections afterwards because data on organic acid concentrations were not available for this period. Therefore, ortho-PO₄³⁻ concentrations were compared between periods with correcting only ortho-PO₄³⁻ data from period 2 for organic acids (i.e. average correction of -0.23 μmol l⁻¹) and were discussed considering this discrepancy. Ortho-PO₄³⁻ concentrations were corrected for organic acids following Verheggen (1991) as $[\text{ortho-PO}_4^{3-}]_{\text{corrected}} = [\text{ortho-PO}_4^{3-}]_{\text{measured}} - 3.28 \times \text{Extinction at 450 nm}$.

Data analysis

Changes in water chemistry between periods 1 and 2 were tested using paired Wilcoxon Signed Ranks tests. The change between both periods was calculated for each parameter. The relation of these changes to a shift in pH, was studied using Spearman rank correlations.

In order to assess the contribution of water coloration by organic acids to the turbidity of the water, for period 2 a Spearman rank correlation was performed on data of water coloration and turbidity. A Spearman rank correlation was performed on water coloration in period 2 and the change in pH from period 1 to 2, in order to determine whether changes in turbidity between both periods could be attributed to water coloration by organic acids.

Differences in changes in ortho-PO₄³⁻ between period 1 and 2 were tested for different classes of pH change between these periods (< 0, 0 - 0.5, 0.5 - 1 and > 1) using Mann-Whitney-U tests. The change in ortho-PO₄³⁻ from period 1 to 2 within each class was tested using paired Wilcoxon Signed Ranks tests.

To confirm the findings from the comparison of water chemistry data between periods 1 and 2, trends in water chemistry are presented for four moorland pools (Achterste Goorven, Groot Huisven, Middelste Wolfspuutven and Schaapsven) for the period 1978 to 2006. Trends in water chemistry of these pools were analysed with Spearman rank correlations. Water table data were only available from the Achterste Goorven from August for the period 1989 to 2006. Concentrations of water chemistry parameters from the Achterste Goorven were normalised by log-transformation. In order to distinguish time trends in concentrations of water chemistry parameters from direct and prolonged effects of dry summers, multiple regression analyses were performed on year and concentration using water tables at year (0), year (t-1) and year (t-2) as co-variables.

Table 2 Water chemistry (mean, standard error, minimum, maximum) in moorland pools in the periods 1 and 2. * Measurements of ortho-PO₄³⁻ in period 1 not corrected and in period 2 corrected for organic acids.

	Period 1 (1983-1984)			Period 2 (2000-2006)			N
	Mean	SE	Min-max	Mean	SE	Min-max	
pH	4.25 ^A	0.07	3.4-5.5	4.78 ^B	0.07	3.8-6.6	68
Alkalinity (meq l ⁻¹)	0.022 ^A	0.004	0.00-0.16	0.076 ^B	0.012	0.00-0.55	68
S (μmol l ⁻¹)	336 ^A	39	210-1020	127 ^B	23	23-493	25
NH ₄ ⁺ (μmol l ⁻¹)	95.2 ^A	9.3	4.0-315.0	22.3 ^B	6.1	1.9-299.5	67
NO ₃ ⁻ (μmol l ⁻¹)	10.3 ^A	2.3	1.5-130.0	1.2 ^B	0.4	0.0-18.0	68
Ortho-PO ₄ ³⁻ (μmol l ⁻¹)*	0.74	0.14	0.1-9.5	0.84	0.16	0.0-8.3	68
Total-P (μmol l ⁻¹)	1.97	0.69	0.3-10.9	1.94	0.55	0.3-6.6	15
Turbidity (ppm)	6.3 ^A	0.5	2.0-18.0	14.8 ^B	1.9	2.0-40.0	64
Al (μmol l ⁻¹)	14.9 ^A	2.2	0.2-133.6	6.6 ^B	0.6	1.2-28.2	67
Fe (μmol l ⁻¹)	10.7	0.9	2.5-39.0	13.0	1.3	1.5-50.7	67
Mg (μmol l ⁻¹)	61.0 ^A	6.4	13.0-390.0	35.0 ^B	3.9	6.9-255.3	67
Na ⁺ (μmol l ⁻¹)	231 ^A	15	99-880	282 ^B	24	86-1370	67
K ⁺ (μmol l ⁻¹)	57.7	3.1	15.0-145.0	58.1	6.0	11.9-288.4	67
Mn (μmol l ⁻¹)	3.11 ^A	0.26	1.1-17.8	1.08 ^B	0.11	0.1-5.9	67
Ca (μmol l ⁻¹)	75.2 ^A	8.1	18.0-490.0	65.6 ^B	9.3	14.5-501.0	67
Cl ⁻ (μmol l ⁻¹)	284	17	145-1020	310	29	103-1596	67
Si (μmol l ⁻¹)	15.0	7.6	1.0-108.3	12.9	4.5	0.4-67.5	15

Different letters (^A, ^B) indicate significant differences (paired Wilcoxon signed ranks tests, $P < 0.05$).

Results

Comparison of water chemistry between study periods

Since the 1980s, NH_4^+ , NO_3^- and S concentrations in moorland pools decreased (Table 2). Average S and N concentrations in surface water decreased by 62.1 and 77.7 %, respectively. Alkalinity and pH both increased significantly. Base cation (Mg, Ca, Mn) and Al concentrations decreased from period 1 to 2, whereas turbidity and Na^+ increased.

Water chemistry changes in relation to decreased acidification

The most acid pools exhibited the strongest increase in pH, as pH in period 1 was negatively correlated with the change in pH from period 1 to 2 (Spearman rank correlation: -0.506 , $P < 0.001$). Changes in pH were positively correlated with changes in alkalinity, ortho- PO_4^{3-} , total-P, turbidity, Fe and K. Changes in Mg were negatively correlated with the change in pH. Changes in other parameters (S, NH_4^+ , NO_3^- , Ca, Mn, K^+ and Na^+) were not related to changes in pH.

In period 2 turbidity and water coloration (i.e. extinction at 450 nm, a measure for organic acids) were strongly correlated (Spearman rank correlation: 0.771 ; $P < 0.001$). Water coloration in period 2 was also correlated with the change in pH from period 1 to 2. (Spearman rank correlation: 0.256 , $P = 0.037$). These are indications that increased turbidity from 1983-1984 to 2000-2006 is the result of higher concentrations of organic acids.

In period 1 highest ortho- PO_4^{3-} concentrations were measured in pools with a higher pH (Spearman rank correlation: 0.510 , $P < 0.001$), whereas in period 2 in the same pools the lowest ortho- PO_4^{3-} concentrations were recorded (Figure 2, Spearman rank

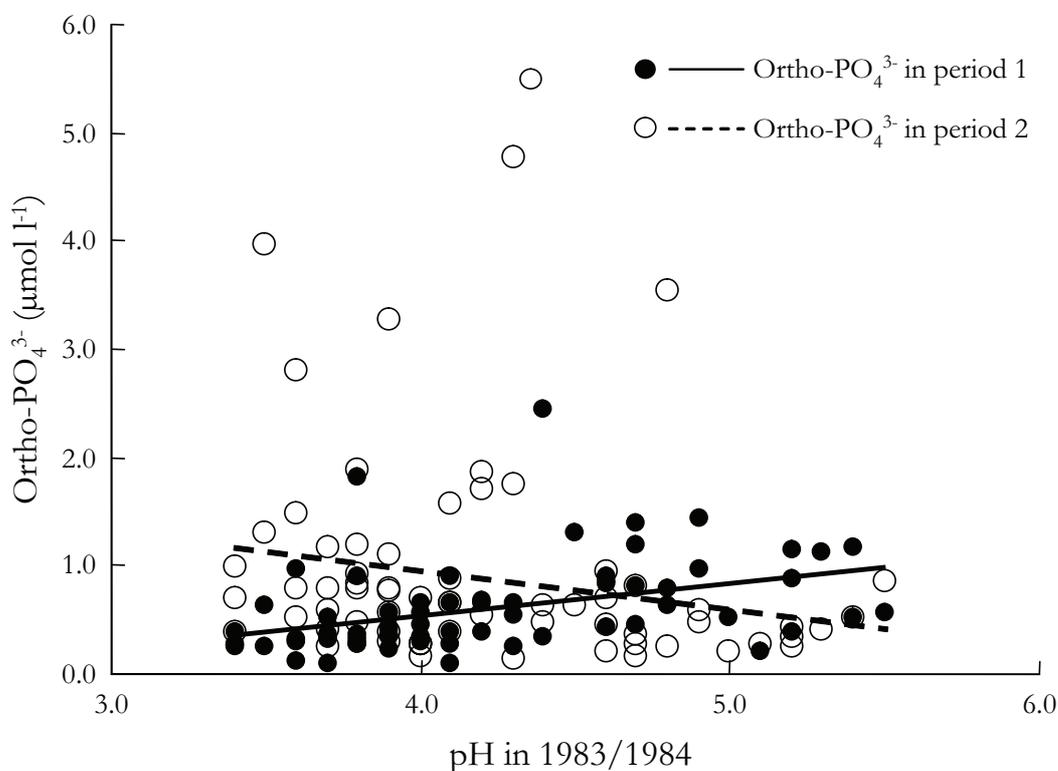


Figure 2 Ortho- PO_4^{3-} concentrations measured in moorland pools in periods 1 and 2 in relation to pH in period 1. Measurements of ortho- PO_4^{3-} in period 1 not corrected and in period 2 corrected for organic acids.

Table 3 Spearman rank correlations of changes from period 1 to 2 in pH and water chemistry parameters.
* Measurements of ortho-PO₄³⁻ in period 1 not corrected and in period 2 corrected for organic acids.

Change in pH vs.	N	Spearman rank correlation
Alkalinity (meq l ⁻¹)	68	0.679 ***
S (μmol l ⁻¹)	25	0.020
NH ₄ ⁺ (μmol l ⁻¹)	67	0.210 *
NO ₃ ⁻ (μmol l ⁻¹)	68	0.005
Ortho-PO ₄ ³⁻ (μmol l ⁻¹)*	68	0.445 ***
Total-P (μmol l ⁻¹)	15	0.618 **
Turbidity (ppm)	64	0.336 ***
Al (μmol l ⁻¹)	67	- 0.078
Fe (μmol l ⁻¹)	67	0.434 ***
Mg (μmol l ⁻¹)	67	- 0.250 **
Na ⁺ (μmol l ⁻¹)	67	0.406 ***
K ⁺ (μmol l ⁻¹)	67	0.384 ***
Mn (μmol l ⁻¹)	67	- 0.178
Ca (μmol l ⁻¹)	67	- 0.097
Si (μmol l ⁻¹)	15	0.350

Significance of correlations: * $P < 0.10$, ** $P < 0.05$, *** $P < 0.01$.

correlation: -0.356 , $P = 0.004$). As a result average ortho-PO₄³⁻ concentrations did not change significantly from period 1 to 2 (Table 2), although ortho-PO₄³⁻ concentrations in period 1 may have been lower because they could not be corrected for organic acids. From period 1 to 2 ortho-PO₄³⁻ increased with increasing pH (Table 3). In pools where pH decreased from period 1 to 2, ortho-PO₄³⁻ appeared to decrease significantly, whereas when pH increased by more than one unit ortho-PO₄³⁻ increased (Figure 3). However, concentrations in period 1 were not corrected for organic acids and organic-acid corrected changes would probably have been smaller. Therefore, the observed ortho-PO₄³⁻ decrease at decreasing pH (Figure 3) may in reality be less pronounced and the observed increase in pools with a large increase in pH is likely to have been higher.

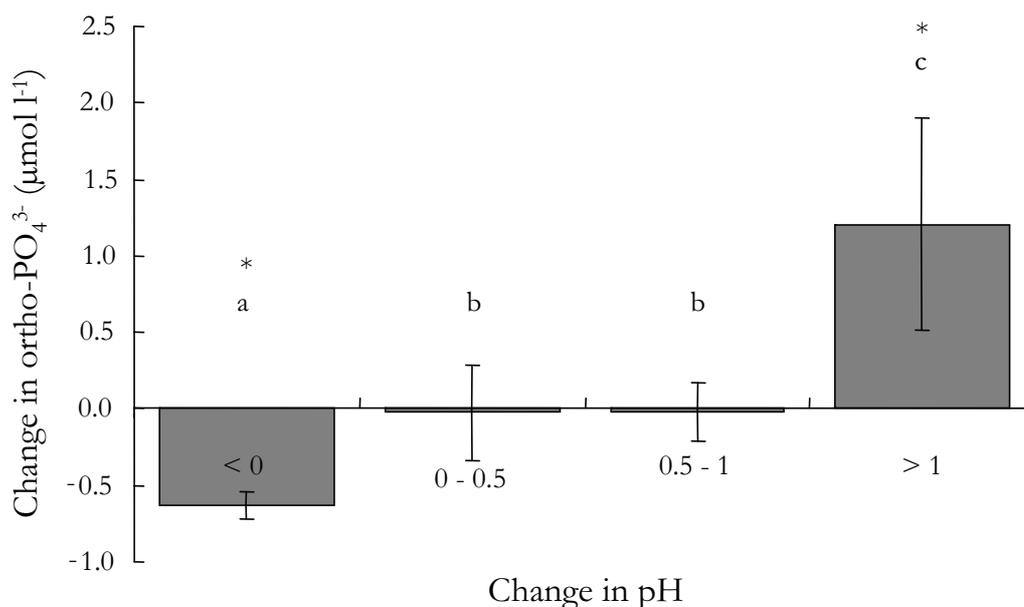


Figure 3 Average change (\pm SE) in ortho-PO₄³⁻ concentrations from period 1 to 2 in moorland pools in relation to the change in pH of these pools. Different letters indicate significant differences ($P < 0.05$) between classes (Mann-Whitney-U tests). * indicates a significant ($P < 0.05$) decrease or increase from period 1 to 2 (Wilcoxon signed ranks test). Measurements of ortho-PO₄³⁻ in period 1 not corrected and in period 2 corrected for organic acids.

Comparison with water chemistry time series

The changes in the Achterste Goorven (Table 4) are similar to the observed changes between periods 1 and 2 (Table 2). From 1978 to 2006, NH_4^+ , SO_4^{2-} and base cation concentrations decreased in this pool (Figure 4). Dissolved organic carbon (DOC) and

Table 4 Spearman rank correlations of time (year) and water chemistry parameters in four time series (1978-2006) from four moorland pools.

	Achterste Goorven	Groot Huisven	Wolfspuiven	Schaapsven
pH	0.716 (N=29) ***	0.663 (N=8) *	0.655 (N=7)	0.826 (N=8) **
SO_4^{2-}	-0.755 (N=29) ***	-0.683 (N=9) **	-0.898 (N=8) ***	-0.862 (N=9) ***
NH_4^+	-0.450 (N=29) **	-0.263 (N=10)	-0.405 (N=8)	0.151 (N=9)
NO_3^-	-0.240 (N=29)	-0.482 (N=10)	-0.578 (N=8)	0.427 (N=9)
Total-P	0.459 (N=16) *	-0.143 (N=6)	N.D.A.	-0.400 (N=4)
DOC	0.601 (N=29) **	0.333 (N=8)	0.536 (N=7)	0.922 (N=8) ***
Al	-0.480 (N=29) ***	-0.367 (N=9)	-0.623 (N=8) *	-0.650 (N=9) *
Fe	0.328 (N=29) *	0.762 (N=9) **	0.762 (N=8) **	0.217 (N=9)
Mg	-0.764 (N=29) ***	-0.633 (N=9) *	-0.898 (N=8) ***	0.067 (N=9)
Na^+	-0.663 (N=29) ***	-0.250 (N=9)	0.548 (N=8)	0.317 (N=9)
K^+	-0.527 (N=29) ***	-0.530 (N=9)	-0.190 (N=8)	0.527 (N=9)
Ca	-0.666 (N=29) ***	-0.594 (N=9) *	-0.802 (N=8) **	-0.034 (N=9)
Cl	-0.862 (N=29) ***	-0.533 (N=9)	0.048 (N=8)	0.267 (N=9)

Significance of correlations: * $P < 0.10$, ** $P < 0.05$, *** $P < 0.01$.

N.D.A.: No data available.

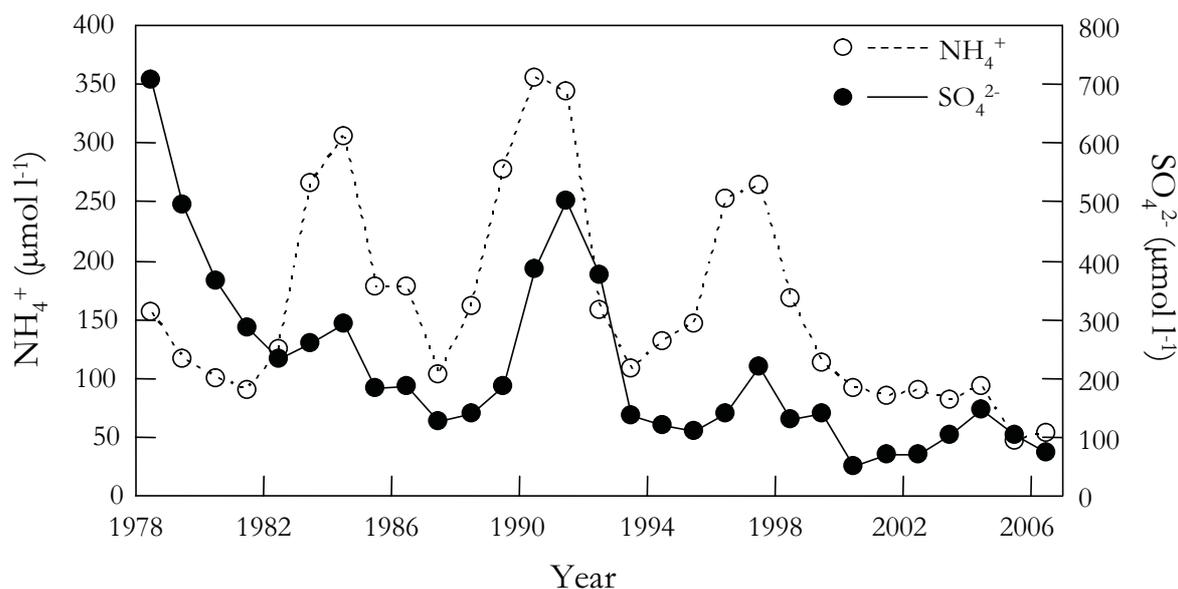


Figure 4 Concentrations of NH_4^+ and SO_4^{2-} in the Achterste Goorven from 1978 to 2006.

pH increased (Figure 5), whereas increases of total-P and Fe concentrations were marginally insignificant ($P = 0.074$ and $P = 0.083$, respectively). Low water level periods in 1989, 1990, 1996 and 2004 were followed by temporary increases of NH_4^+ and SO_4^{2-} and decreases of pH and DOC. Fluctuations in these parameters have become less pronounced in recent years. A multiple regression analyses with water tables from the present and previous two years as explanatory variables was used in order to distinguish drought induced and temporal effects. With the exception of Al, trends in water chemistry also proved to be consistent after correcting for water tables (Table 5).

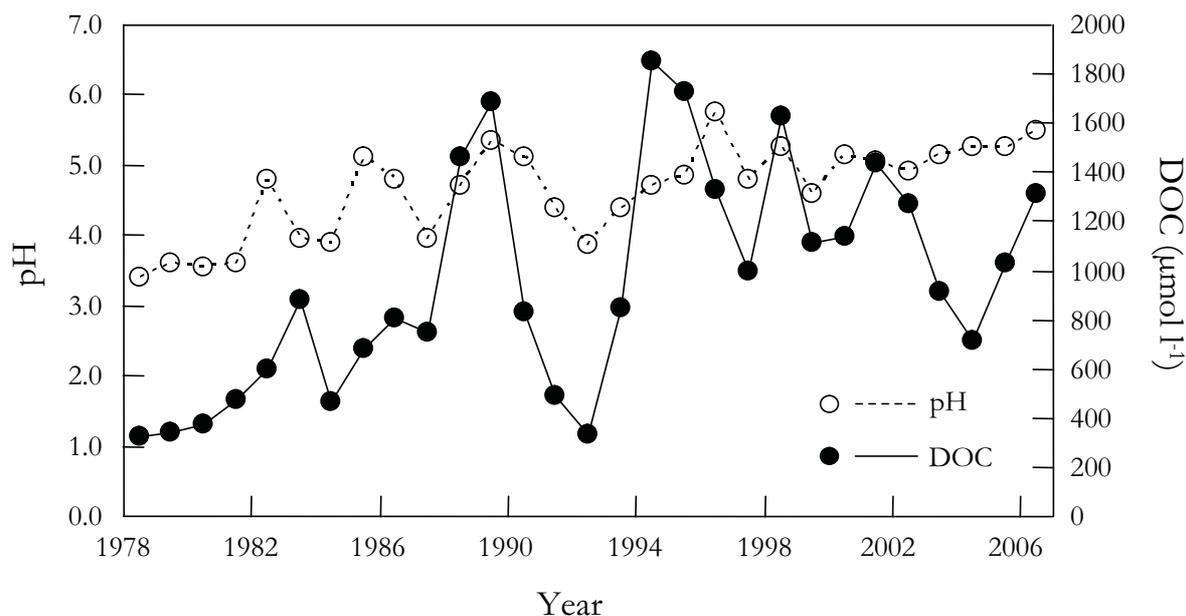


Figure 5 Concentrations of pH and DOC in the Achterste Goorven from 1978 to 2006.

Table 5 Univariate and multivariate regression analyses of water chemistry time series from the Achterste Goorven (1981-2006). In the multivariate analyses, August water tables at year (0), year (t-1) and year (t-2) were used as co-variables.

Parameter	Univariate analyses			Multivariate analyses		
	%	Slope	<i>P</i>	%	Slope	<i>P</i>
pH	46.9	0.053	< 0.001	46.3	0.046	< 0.001
SO ₄ ²⁻	51.0	-0.054	< 0.001	72.6	-0.057	< 0.001
NH ₄ ⁺	16.0	-0.029	0.020	45.6	-0.043	< 0.001
NO ₃ ⁻	2.5	-0.024	0.206	-	-0.015	0.505
Total-P	27.6	0.089	0.021	9.6	0.090	0.041
DOC	30.8	0.035	0.001	42.4	0.033	0.002
Al	10.6	-0.023	0.051	2.3	-0.011	0.337
Fe	0.8	0.015	0.278	-	0.020	0.219
Mg	37.0	-0.027	< 0.001	51.2	-0.025	< 0.001
Na ⁺	42.3	-0.014	< 0.001	50.8	-0.013	< 0.001
K ⁺	20.1	-0.022	0.010	8.2	-0.019	0.057
Ca	24.1	-0.027	0.002	39.4	-0.023	0.008
Cl ⁻	66.4	-0.015	< 0.001	62.0	-0.015	< 0.001

%; Percentage variance accounted for by the model.

Changes in the other three pools (Groot Huisven, Wolfspuiven and Schaapsven) were less pronounced. These pools were less frequently sampled, which combined with the effects of occasional water level fluctuations resulted in a relatively low statistical power. Concentrations of SO₄²⁻ decreased in all three pools, whereas NH₄⁺ and NO₃⁻ did not change. Significant increases in pH and DOC were observed only in pool Schaapsven. Decreases in Mg and Ca were significant in the Wolfspuiven and marginally insignificant in the Groot Huisven (*P* = 0.067 and *P* = 0.092, respectively). Fe concentrations increased in the Groot Huisven, but decreased in the Wolfspuiven.

Discussion

Data considerations

Water chemistry data of 68 moorland pools from two periods were compared. The advantage of the large number of study sites is that disturbances in a single site are unlikely to obscure overall trends. By comparing only few data points in time the results are likely to be influenced by regional processes, such as climate and reduced air pollution. The observed reduced acidity and correlations with other water chemistry parameters suggest that local processes such as decomposition of pool sediments (see below) as well as regional processes such as reduced acidifying deposition are important determinants of moorland pool water chemistry.

Results from the comparison between 1983-1984 and 2000-2006 were supported by the well documented time series of water chemistry in the Achterste Goorven. The less pronounced water chemistry trends in the other pools are probably the result of the larger sampling intervals and variability of parameters due to occasional water level fluctuations.

Partial recovery of water chemistry

Reduced emissions of acidifying substances (NO_x , NH_x and SO_x) since the 1980s have led to a decreased deposition of acidifying compounds (Milieu & NatuurCompendium 2008). Parallel to the reduction of acidifying deposition, we observed a partial recovery of surface water chemistry of moorland pools. Concentrations of N, S and Al decreased, while pH and alkalinity increased (Table 2) to within the ranges normal for moorland pools (Table 1). However, current deposition levels of N of $30.7 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (71 % of which is NH_x) still exceed the critical load of $5\text{-}10 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ for moorland pools (Bobbink & Roelofs 1995). Recovery of these parameters may temporarily become reversed during dry summers as in 1989, 1990, 1996 and 2004 (Figure 4 and 5). During these periods the pools partly dry up and sediments become oxygenated, which leads to S oxidation and acidification. The induced acidification inhibits nitrification, resulting in accumulation of NH_4^+ (Schuurkes et al. 1988, Van Dam 1989, Van Haesebroeck et al. 1997). Over time the effects of dry spells appear to have decreased, indicating a depletion of S stores in the sediment (Laudon 2008).

Studies in lakes and streams in Europe and North America have repeatedly demonstrated recovery of pH, ANC and decreased Ca, Mg and S concentrations, whereas decreased concentrations of NO_3^- are only occasionally reported (Stoddard et al. 1999, Forsius et al. 2002, Davies et al. 2005, Skjelkvåle et al. 2005). The observed changes in H^+ , ANC, SO_4^{2-} , NO_3^- and base cations (Mg + Ca) in Dutch moorland pools correspond to -0.7 , $+2.7$, -5.2 , -0.5 and $-3.5 \text{ } \mu\text{eq l}^{-1} \text{ y}^{-1}$ respectively. This is in line with recovery ranges elsewhere (Stoddard et al. 1999, Davies et al. 2005, Skjelkvåle et al. 2005). Ammonium-N decreased by $-3.6 \text{ } \mu\text{eq l}^{-1} \text{ y}^{-1}$. Comparable data on NH_4^+ are not available from other studies, probably because in most environments N is present as nitrate due to better aeration and higher alkalinity with pH exceeding 4.5. The observed decrease of N in our study is not surprising, as the study area is one of the regions in the Northern hemisphere which has received the highest N load (Holland et al. 2005, Milieu & NatuurCompendium 2008) and has undergone the strongest decrease in N emissions of all European countries (Fowler et al. 2007).

Absence of complete water chemistry recovery

Decreased acidification was accompanied by increases in turbidity and ortho- PO_4^{3-} , both rising above reference levels for moorland pools (Table 1) especially in the pools with the strongest increase in pH (Figure 3, Table 3). Increased turbidity was probably caused by the stronger coloration of organic acids. DOC concentrations have also been reported to increase in streams and lakes in the UK, southern Fennoscandia, northeast North America and Central Europe (Evans et al. 2005, 2006, Vuorenmaa et al. 2006, Monteith et al. 2007). Roulet & Moore (2006) postulate that increases in DOC may be the result of improved ecosystem productivity due to increased NO_x deposition. As the deposition of NO_3^- has actually decreased in the Netherlands, this is unlikely the reason for the observed increase in DOC. Evans et al. (2005, 2006) discuss several other possible explanations for the increased DOC levels (i.e. hydrological change, land-use change, N enrichment, atmospheric CO_2 enrichment, recovery from acidification and temperature change) and conclude that the most plausible mechanisms increasing DOC concentrations are an increased pH and stimulated decomposition by increased temperatures. Monteith et al. (2007) explain the DOC increases by recovery from acidification resulting from reduced SO_x emissions.

The increased concentrations of ortho- PO_4^{3-} in this study (Table 3 and 4, Figure 3) support the hypothesis of Evans et al. (2005) that decomposition has been stimulated. Most other studies deal with water chemistry in ecosystems with large catchments (i.e. lakes and streams) and consequently focus on soil processes in the catchment for explaining enhanced ecosystem productivity. As the catchments of moorland pools are well drained, produced ortho- PO_4^{3-} is strongly retarded in top soils due to binding to oxidised iron. Thus, enhanced productivity in the catchment will not be reflected by water chemistry changes in the pools. Therefore, increased ortho- PO_4^{3-} and probably also DOC is more likely the result of stimulated decomposition of the organic pool sediments. Average temperature in the months March to August was higher in the period 2 than in period 1 (14.0 and 12.9 °C, respectively; Koninklijk Nederlands Meteorologisch Instituut 2008). Simultaneously, in period 2 there was more precipitation than in period 1 (677 and 548 mm year⁻¹, respectively; Koninklijk Nederlands Meteorologisch Instituut 2008) preventing air exposure of shallow shores. Higher temperatures and less oxygenated sediments are likely to have stimulated SO_4^{2-} -reduction and denitrification, anaerobic microbial processes which stimulate decomposition and reduce acidity. Higher temperatures during period 2 may also have stimulated production and leaching of organic acids from the catchment (Evans et al. 2005 and literature therein).

As increases in turbidity and P were most pronounced in moorland pools with the strongest increase in pH, warmer and wetter summers are unlikely to have been the dominant triggers for the observed increase in decomposition. Decreased acidification has been mentioned before as the trigger for increasing concentrations of organic acids (Evans et al. 2005, 2006, Monteith et al. 2007). Proposed mechanisms are increased solubility of organic matter (Clark et al. 2006), reduced Al mobilisation (Schindler et al. 1992) and decreased ionic strength of soil solutions (Evans et al. 1988). Although each of these mechanisms may be involved in the increased coloration of the moorland pools, the observed relation between changes in phosphate and pH indicate another mechanism. A plausible driver is that high proton concentrations no longer inhibit decomposition (Kelly et al. 1984). This process has been predicted by Leuven & Wolf (1988) and supported by Bellemakers et al. (1994) who demonstrated that internal eutrophication was stimulated in

acidified moorland pools with organic soils where lime was added resulting in increased P concentrations. Increased decomposition of organic sediments with decreasing acidity is also supported by the marginally insignificant positive correlation between the changes in NH_4^+ and pH (Table 3, $P = 0.088$). As NH_4^+ is released by decomposition of organic material (Roelofs 1991, Bellemakers et al. 1994), the decrease in NH_4^+ is obscured at high increase in pH. Increased decomposition resulting from reduced acidification has not been reported before as a driver of rising DOC concentrations, but is in line with the observation of Monteith et al. (2007) that reductions in S deposition are closely associated with rising DOC.

Implications for biota and management

The partially improved water chemistry (pH, alkalinity, N, S and Al) of moorland pools is likely to have had beneficial effects of the biota living therein. This is supported by Van Dam (1996) who reported a decrease of the diatom *Eunotia exigua*, an acidification indicator, from 1979 to 1994 and a recovery of pre-acidification diatom assemblages. Also the reproductive success of amphibians is likely to have improved in the studied moorland pools, as the average pH of pools increased above 4.5, which is the lower threshold for egg survival of several *Rana*-species (Leuven et al. 1986b). Aluminium concentrations improved from 14.9 to 6.6 $\mu\text{mol l}^{-1}$. Although there is still discussion about the thresholds of toxic effects of Al for invertebrates (Herrmann 2001), the improvement measured in our study is considerable compared the general toxic range of 3.7 - 11.1 $\mu\text{mol l}^{-1}$ discussed by Herrmann (2001).

On the other hand, acidification has left a legacy in the form of accumulated organic matter in river and lakes (Grahn et al. 1974, Traaen 1980) and also in moorland pools, which normally have mineral sediments (Brouwer et al. 1996). This is the result of lifting of C-limitation leading to increased primary production (Roelofs et al. 1984) as well as reduced decomposition (Kelly et al. 1984, Kok et al. 1990, 1992). Forest plantation on shores of many of the pools in the late 19th and beginning of the 20th century will also have contributed to the accumulation of organic material in the pools (Van Dam & Buskens 1993). This organic layer prevents the return of characteristic plant species, such as isoetids (Bellemakers et al. 1994) and has been predicted to be a source of nutrients in the event of reduced acidification (Leuven & Wolfs 1988). Increased water coloration and P concentrations may affect the growth of submerged plant species. When acidification decreases, increased decomposition of these nutrient reservoirs hampers recovery of chironomid assemblages (Chapter 3) probably as a result of prolonged anoxic conditions in the sediment. Monteith et al. (2007) argue that DOC concentrations are returning to a level characteristic of pre-industrial times. This may indeed be the case for aquatic ecosystems that depend on large catchments with a natural store of organic material. However, in moorland pools where water chemistry is largely determined by internal processes and where in pre-industrial times organic material was scarce, high DOC concentrations are likely to present a new and unprecedented condition with detrimental ecological consequences. It is expected that increased water coloration and P will continue until most of the readily degradable organic matter has been decomposed. It remains unclear if at that time moorland pools will start to recover.

So, reaching emission targets for NO_x , NH_x and SO_x , which in 2006 were still exceeded by 42, 30 and 41%, respectively (Milieu & NatuurCompendium 2008) appears insufficient for the protection and recovery of moorland pool biota in the short term.

Restoration measures may still be required to facilitate and accelerate recovery of acidified moorland pools. Removal of accumulated organic matter is an appropriate measure, if taken with caution to prevent loss of remaining species (Chapter 4, Van Kleef et al. 2006). At many sites this measure should be combined with restoring alkalinity through the inlet of low alkaline water or catchment liming because acid deposition still exceeds critical loads and catchments no longer provide alkalinity (Brouwer et al. 2002, Brouwer & Roelofs 2002, Dorland et al. 2005).

Conclusion

Reduction of nitrogen and sulphur deposition has led to a partial recovery of moorland pool water chemistry (i.e. pH, alkalinity, Al, N and S). However, decreased acidification appears to have stimulated decomposition of accumulated organic material in the pools, resulting in elevated concentrations of ortho-phosphate and organic acids. These processes at least delay complete recovery of water chemistry as well as biotic recovery.

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References

- Arts GHP & Leuven RSEW (1988) Floristic changes in shallow soft waters in relation to underlying environmental factors. *Freshwater Biology* **20**: 97-111.
- Arts GHP (2000) Natuurlijke levensgemeenschappen van de Nederlandse binnenwateren deel 13, Vennen. Achtergronddocument bij het "Handboek Natuurdoeltypen in Nederland". *Expertisecentrum LNV, Ministerie van Landbouw, Natuurbeheer en Visserij, Ede.*
- Bellemakers MJS, Maessen M & Roelofs JGM (1994) Effects of liming on water chemistry in shallow acidified pools in the Netherlands: enclosure experiments. *Water, Air, and Soil Pollution* **73**: 131-142.
- Bergkvist B (1986) Leaching of metals from a spruce forest soil as influenced by experimental acidification. *Water, Air, and Soil Pollution* **31**: 901-916.
- Bleeker A & Erisman JW (1996) Depositie van verzurende componenten in Nederland in de periode 1980-1995. Report 722108018. *Rijksinstituut voor Volksgezondheid en Milieu, Bilthoven.*
- Bobbink R & Roelofs JGM (1995) Nitrogen critical loads for natural and semi-natural ecosystems: the empirical approach. *Water, Air, and Soil Pollution* **85**: 2413-2418.
- Brouwer E, Bobbink R, Meeuwse F & Roelofs JGM (1996) Recovery from acidification in aquatic mesocosms after reducing ammonium- and sulphate deposition. *Aquatic Botany* **56**: 119-130.
- Brouwer E, Bobbink R & Roelofs JGM (2002) Restoration of aquatic macrophyte vegetation in acidified and eutrophied softwater lakes: an overview. *Aquatic Botany* **73**: 405-431.
- Brouwer E & Roelofs JGM (2002) Oligotrophication of acidified, nitrogen-saturated softwater lakes after dredging and controlled supply of alkaline water. *Archiv für Hydrobiologie* **155**: 83-97.
- Carmichael GR, Streets DG, Calori G, Amann M, Jacobson MZ, Hansen J & Ueda H (2002) Changing trends in sulphur emissions in Asia: implications for acid deposition, air pollution, and climate. *Environmental Science and Technology* **36**: 4707-4713.

- Clark JM, Chapman PJ, Heathwaite AL & Adamson JK (2006) Suppression of dissolved organic carbon by sulphate induced acidification during simulated droughts. *Environmental Science & Technology* **40**: 1776-1783.
- Davies JJJ, Jenkins A, Monteith DT, Evans CD & Cooper DM (2005) Trends in surface water chemistry of acidified UK freshwaters, 1988-2002. *Environmental Pollution* **137**: 27-39.
- Dorland E, Van den Berg LJJ, Brouwer E, Roelofs JGM & Bobbink R (2005) Catchment liming to restore degraded, acidified heathlands and moorland pools. *Restoration Ecology* **13**: 302-311.
- Evans Jr A, Zelazny LW & Zipper CE (1988) Division S-7-forest and range soils - Solution parameters influencing dissolved organic carbon levels in three forest soils. *Soil Science Society of America Journal* **52**: 1789-1792.
- Evans CD, Monteith DT & Cooper DM (2005) Long-term increases in surface water dissolved organic carbon: Observations, possible causes and environmental impacts. *Environmental Pollution* **137**: 55-71.
- Evans CD, Chapman PJ, Clark JM, Monteith DT & Cresser MS (2006) Alternative explanations for rising dissolved organic carbon export from organic soils. *Global Change Biology* **12**: 2044-2053.
- Forsius M, Vuorenmaa J, Mannio J & Syri S (2003) Recovery from acidification of Finnish lakes: regional patterns and relations to emission reduction policy. *Science of the Total Environment* **310**: 121-132.
- Fowler D, Smith R, Muller J, Cape JN, Sutton M, Erisman JW & Fagerli H (2007) Long term trends in sulphur and nitrogen deposition in Europe and the cause of non-linearities. *Water, Air, and Soil Pollution* **7**: 41-47.
- Grahn OH, Hultberg H & Landner L (1974) Oligotrophication: a self-accelerating process in lakes subjected to excessive supply of acid substances. *Ambio* **3**: 93-94.
- Grasshoff H & Johanssen H (1972) A new sensitive and direct method for the automatic determination of ammonia in sea water. *Journal du Conseil* **34**: 516-521.
- Geelen JFM & Leuven RSEW (1986) Impact of acidification on phytoplankton and zooplankton communities. *Experientia* **42**: 486-494.
- Haynes RJ & Swift RS (1985) Effects of soil acidification and subsequent leaching on levels of extractable nutrients in a soil. *Plant and Soil* **95**: 327-336.
- Henriksen A (1965) An automated method for determining low-level concentrations of phosphate in fresh and saline waters. *Analyst* **90**: 29-34.
- Herrmann J (2001) Aluminium is harmful to benthic invertebrates in acidified waters, but at what threshold(s)? *Water, Air, and Soil Pollution* **130**: 837-842.
- Holland EA, Braswell BH, Sulzman J & Lamarque JF (2005) Nitrogen deposition onto the United States and Western Europe: synthesis of observations and models. *Ecological Applications* **15**: 38-57.
- Jenkins A (1999) End of the acid reign? *Nature* **401**: 537-538.
- Kamphake LH, Hannah SA & Cohen JM (1967) Automated analysis for nitrate by hydrazine reduction. *Water Research* **1**: 206.
- Kelly CA, Rudd JWM, Furutani A & Schindler DW (1984) Effects of lake acidification on rates of organic-matter decomposition in sediments. *Limnology and Oceanography* **29**: 687-694.
- Kersten HLM (1985) Physico-chemical properties of Dutch soft waters. Report 158. *Department of Aquatic Ecology, Radboud University, Nijmegen*.
- Kirchner JW & Lydersen E (1995) Base cation depletion and potential long-term acidification of Norwegian catchments. *Environmental Science and Technology* **29**: 1953-1960.
- Kok CJ, Meesters HWG & Kempers AJ (1990) Decomposition rate, chemical composition and nutrient recycling of *Nymphaea alba* L. floating leaf blade detritus as influenced by pH, alkalinity and aluminium in laboratory experiments. *Aquatic Botany* **37**: 215-227.
- Kok CJ, Haverkamp W & Van der Aa HA (1992) Influence of pH on the growth and leaf maceration ability of fungi involved in the decomposition of floating leaves of *Nymphaea alba* L. in acid water. *Journal of General Microbiology* **138**: 103-108.

- Koninklijk Nederlands Meteorologisch Instituut (2008) Retrieved December 1, 2008, from <http://www.knmi.nl/>.
- Laudon H (2008) Recovery from episodic acidification delayed by drought and high sea salt deposition. *Hydrology and Earth System Sciences* **12**: 363-370.
- Leuven RSEW, Kersten HLM, Schuurkes JAAR, Roelofs JGM & Arts GHP (1986a) Evidence for recent acidification of lentic soft waters in the Netherlands. *Water, Air and Soil Pollution* **30**: 387-392.
- Leuven RSEW, Den Hartog C, Christiaans MMC & Heijligers WHC (1986b) Effects of water acidification on the distribution and the reproductive success of amphibians. *Experientia* **42**: 495-503.
- Leuven RSEW & Oyen FGF (1987) Impact of acidification and eutrophication on the distribution of fish species in shallow and lentic soft waters: an historical perspective. *Journal of Fish Biology* **31**: 753-774.
- Leuven RSEW & Wolfs WJ (1988) Effects of water acidification on the decomposition of *Juncus bulbosus* L.. *Aquatic Botany* **31**: 57-81.
- Leuven RSEW, Van der Velde G & Kersten HLM (1989) Interrelations between pH, and other physiochemical factors of Dutch soft waters. *Archiv für Hydrobiologie* **126**: 27-51.
- Lynch JA, Bowersox VC & Grimm JW (2000) Acid rain reduced in eastern United States. *Environmental Science and Technology* **34**: 940-949.
- Milieu & NatuurCompendium (2008) Retrieved December 1, 2008, from <http://www.milieuennatuurcompendium.nl/>.
- Monteith DT, Stoddard JL, Evans CD, De Wit HA, Forsius M, Høgåsen T, Wilander A, Skjelkvåle BL, Jeffries DS, Vuorenmaa J, Keller B, Kopáček J & Vesely J (2007) Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. *Nature* **450**: 537-541.
- O'Brien JE (1962) Automatic analysis of chlorides in sewage. *Sewage and Industrial Wastes Engineering* **33**: 670-682.
- Roelofs JGM (1983) Impact of acidification and eutrophication on macrophytes communities in soft waters in the Netherlands. I. Field observations. *Aquatic Botany* **17**: 139-155.
- Roelofs JGM, Schuurkes JAAR & Smits AJM (1984) Impact of acidification and eutrophication on macrophytes communities in soft waters in the Netherlands. II. Experimental studies. *Aquatic Botany* **18**: 389-411.
- Roelofs JGM (1991) Inlet of alkaline river water into peaty lowlands: Effects on water quality and *Stratiotes aloides* L. stands. *Aquatic Botany* **39**: 267-293.
- Roulet N & Moore TR (2006) Browning the waters. *Nature* **444**: 283-284.
- Skjelkvåle BL, Stoddard JL, Jeffries DS, Tørseth K, Høgåsen T, Bowman J, Mannio J, Monteith DT, Mosello R, Rogora M, Rzychon D, Vesely J, Wieting J, Wilander A & Worsztynowicz A (2005) Regional scale evidence for improvements in surface water chemistry 1990-2001. *Environmental Pollution* **137**: 165-176.
- Schindler DW, Bayley SE, Curtis PJ, Parker BR, Stainton MP & Kelly CA (1992) Natural and man-caused factors affecting the abundance and cycling of dissolved organic substances in precambrian shield lakes. *Hydrobiologia* **229**: 1-21.
- Schuurkes JAAR, Kempers AJ & Kok CJ (1988) Aspects of biochemical sulphur conversions in sediment of a shallow soft water lake. *Journal of Freshwater Ecology* **4**: 369-381.
- Stoddard JL, Jeffries DS, Lükewille A, Clair TA, Dillon PJ, Driscoll CT, Forsius M, Johannessen M, Kahl JS, Kellogg JH, Kemp A, Mannio J, Monteith DT, Murdoch PS, Patrick S, Rebsdorf A, Skjelkvåle BL, Stainton MP, Traaen T, Van Dam H, Webster KE, Wieting J & Wilander A (1999) Regional trends in aquatic recovery from acidification in North America and Europe. *Nature* **40**: 575-578.
- Traaen TS (1980) Effects of acidity on decomposition of organic matter in aquatic environments, in Drabløs D & Tollan A (Eds.), Ecological impact of acid precipitation. *Proceedings of the International Conference on the Ecological Impact of Acid Precipitation, SNSF-project*: 340-341.

- Van Dam H & Kooijman-van Blokland H (1978) Man-made changes in some Dutch moorland pools, as reflected by historical and recent data about diatoms and macrophytes. *Internationale Revue der gesamten Hydrobiologie* **63**: 587-607.
- Van Dam H (1989) Acidification of three moorland pools in the Netherlands by acid deposition and extreme drought periods over seven decades. *Freshwater Biology* **20**: 157-176.
- Van Dam H & Buskens RFM (1993) Ecology and management of moorland pools: balancing acidification and eutrophication. *Hydrobiologia* **265**: 225-263.
- Van Dam H (1996) Partial recovery of moorland pools from acidification: indications by chemistry and diatoms. *Netherlands Journal of Aquatic Ecology* **30**: 203-218.
- Van Haesebroeck V, Boeye D, Verhagen B & Verheyen RF (1997) Experimental investigation of drought induced acidification in a rich fen soil. *Biogeochemistry* **37**: 15-32.
- Van Kleef HH, Verberk WCEP, Leuven RSEW, Esselink H, Van der Velde G & Van Duinen GA (2006) Biological traits successfully predict the effects of restoration management on macroinvertebrates in shallow softwater lakes. *Hydrobiologia* **565**: 201-216.
- Verheggen GM (1991) Achtergrondcorrectie voor humuszuurkleuring bij colorimetrische bepalingen. Internal report. *Department of Aquatic Ecology and Environmental Biology, Radboud University, Nijmegen*.
- Vuorenmaa J, Forsius M & Mannio J (2006) Increasing trends of total organic carbon concentrations in small forest lakes in Finland from 1987 to 2003. *Science of the Total Environment* **365**: 47-65.



Although midges (Chironomidae) like this adult male are best known for their mating swarms, they spend most of their life living underwater. Photo: Hein van Kleef.

Chapter 3

Functional response of chironomids to restoration and decreased acidification in formerly acidified moorland pools

Hein van Kleef, Rob Leuven, Wilco Verberk, Frank Kimenai, Gerard van der Velde & Hans Esselink

Submitted

Abstract

Emission of NO_x , NH_x and SO_x have led to the acidification of numerous moorland pools. To prevent further deterioration and to enable rehabilitation of moorland pool communities, national and international policy has been implemented, decreasing these emissions and restoration measures have been taken in acidified pools. Changes in chironomid assemblages as a result of (1) decreased acidifying deposition in non-restored moorland pools and (2) as a result of the removal of organic sediments and the inlet of alkaline water in restored pools were examined. Changes in chironomid assemblages were analysed by comparing data from 1983 and 2004 using species responses, multivariate analyses and life history tactics. In restored pools water chemistry improved (pH, alkalinity, ammonium, sulphur and aluminium). Rarefied species richness increased. Multivariate analyses revealed a directed shift in chironomid species assemblages of restored pools, which was reflected in the decreased relative abundance of *Chironomus* gr. *plumosus* and *C.* gr. *thummi* and increased abundance of *Tanytarsus* ssp. and *Psectrocladius psilopterus*. Responses of these species and chironomid life history tactics indicated a shift towards pre-acidification assemblages. Water chemistry in non-restored moorland pools improved in terms of pH, alkalinity and sulphur. This did not result in consistent changes in species abundance or community structure. In non-restored pools the relative abundance of chironomid species, adapted to low stress and low dynamic environments was negatively correlated with changes in turbidity suggesting increased periodic oxygen stress. Oxygen deficiency is hypothesised to be the result of increased decomposition resulting from reduced acidification. Acidification of moorland pools over the past decades has left a legacy in the form of accumulated layers of organic material. These reservoirs of nutrients appear to hamper natural recovery of acidified pools. Therefore, active involvement in the form of restoration management including the removal of organic sediments remains necessary for the recovery of chironomid assemblages in acidified moorland pools.

Introduction

Elevated anthropogenic emissions of SO_x , NO_x and NH_x have led to the acidification of aquatic ecosystems throughout Europe (Jenkins 1999). European as well as Dutch legislation were implemented in order to reduce the emissions of acidifying substances. As a result acidifying deposition in the Netherlands by sulphur and nitrogen compounds has decreased over the period 1983 to 2004 with 68 and 35 percent, respectively (Milieu en Natuur Planbureau 2007). Restoration due to natural processes may proceed slow or may be impeded (Bradshaw 1996). Recovery from acidification has been demonstrated repeatedly for the water chemistry of lakes and streams (Skeffington & Brown 1992, Stoddard et al. 1999, Forsius et al. 2003, Davies et al. 2005, Skjelkvåle et al. 2005). For macroinvertebrates only partial recovery has been observed (Lancaster et al. 1996, Hynynen & Meriläinen 2005). McNicol et al. (1995) and Ledger & Hildrew (2005) hypothesised on the recovery of invertebrate communities based on data gathered along pH gradients. However, degradation of ecosystems is often difficult to reverse (Carpenter 2003, Schröder et al. 2005) and possibilities for recovery may not always be deduced from studying gradients. This may also be the case for moorland pools, where Van Kleef et al. (2010, Chapter 2) recorded a partial recovery from acidification in terms of pH, alkalinity, NH_4^+ , NO_3^- and sulphur. However, changes in pH were also positively correlated with

changes in turbidity and phosphorus suggesting stimulated decomposition of accumulated organic matter.

In the Netherlands, restoration measures were developed for restoring acidified moorland pools as acidification of these water bodies had led to a strong decline of many characteristic plant and animal species (Roelofs 1983, Leuven 1988, Arts 1990). In moorland pools acidification increases primary production by temporarily lifting the carbon limitation and reducing the decomposition rate. This causes organic matter to accumulate (Leuven & Wolfs 1988). Restoration measures were developed in order to prevent the extinction of characteristic species, until the emissions of N and S compounds have been reduced sufficiently for the natural recovery of affected ecosystems. Restoration of acidified moorland pools aims at restoring nutrient limitation, alkalinity and aerobic substrates. Measures consist of the removal of accumulated organic matter and macrophytes and restoring alkalinity through the regulated inlet of alkaline groundwater or surface water. With these measures the recovery of abiotic conditions as well as characteristic plant communities can be achieved in acidified pools (Brouwer et al. 2002, Roelofs et al. 2002). On a short term (within 2 years) restoration of moorland pools did not increase the number of characteristic invertebrate species (Van Kleef et al. 2006, Chapter 4). However, long term effects of restoration measures on aquatic macroinvertebrates in moorland pools are still unknown.

The objective of this study was to determine whether decreased acidifying deposition and restoration measures have resulted in changes in moorland pool chironomid assemblages. Changes in chironomid assemblages were studied in seven restored moorland pools and seven pools where no measures have been taken (hereafter termed non-restored pools). All pools were sampled in 1983 (Leuven et al. 1987) and 2004. Changes in chironomid assemblages were described in terms of species richness, community structure, species abundance and life history tactics. Recent studies try to explain species occurrences and responses through biological traits (Resh et al. 1994, Townsend & Hildrew 1994, Poff et al. 2006, Van Kleef et al. 2006, Chapter 4). In the life history tactic (hereafter also termed LHT) approach, species are grouped by trait combinations with a similar adaptive function (Stearns 1976, Siepel 1994, Verberk et al. 2008). They can therefore be seen as an integrated response to the environment and studying changes in LHT abundances should provide direct information on how the environment is experienced by the species present.

Methods

Study sites

Fourteen study sites were selected from Leuven et al. (1987). The selected moorland pools were not larger than 4 ha and approximately 1.5 m deep. Selection criteria were: average pH in 1983 ≤ 6 and not higher than in previous periods and an equal number of restored and non-restored sites (Table 1). pH data were obtained from Leuven et al. (1992). Restored sites were only selected if plant species characteristic of moorland pools had recovered or increased after restoration (Van Kleef & Esselink 2005). This criterion was used in order to exclude sites where inappropriate or inadequate measures were taken and had not resulted in ecosystem restoration. In restored sites large scale restoration measures were taken, consisting of the removal of accumulated organic matter and macrophytes and often (except for Leikeven) the controlled inlet of alkaline ground or

Table 1 Study sites with pool numbers (No.), coordinates, year of restoration and average pH before 1983, in 1983 and 2004.

Name	No.	Coordinates		Year of restoration	pH		
		Lat.	Long		<1983	1983	2004
Diaconieven	NR 1	51°34'	5°11'	nr	5.5 ¹	4.0	4.9
Groot Huisven	NR 2	51°35'	5°16'	nr	5.1 ¹	4.3	4.7
Ganzenven	NR 3	51°35'	5°16'	nr	3.8 ²	3.8	4.6
Plakkeven	NR 4	51°38'	5°03'	nr	5.5 ¹	3.9	5.5
Rouwkuilen	NR 5	51°30'	5°55'	nr	5.6 ¹	3.9	4.5
Grote Moost	NR 6	51°18'	5°52'	nr	ND	5.4	5.5
Galgeven	NR 7	51°22'	5°29'	nr	5.4 ¹	5.2	6.2
Staalbergven	R 1	51°34'	5°13'	2003	4.8 ¹	4.3	4.5
Voorste Choorven	R 2	51°34'	5°12'	1995	6.7 ¹	3.8	5.5
Witven	R 3	51°34'	5°12'	1995	5.9 ¹	3.9	5.4
Leikeven	R 4	51°37'	5°02'	1993	5.2 ¹	3.9	4.6
Lobeliabaai	R 5	51°24'	5°38'	1985	4.6 ²	4.1	4.5
Van Esschenven	R 6	51°34'	5°12'	1995	6.6 ¹	5.8	5.9
Bergven	R 7	52°26'	7°01'	1993	5.6 ¹	3.8	4.4

nr: not restored. ¹: average from 1900-1960; ²: average from 1970-1980; ND: no data available from before 1980.

surface water. In the Plakkeven and Grootte Moost organic matter was removed only on a small scale, without inlet of alkaline water and the surface area of open water only increased, without increasing the number and abundance of characteristic plant species. These two pools were therefore classified as non-restored.

Environmental conditions

In spring and summer, surface water was sampled in iodated polyethylene bottles from each pool according to Leuven et al. (1992). The pH, alkalinity and turbidity of surface water samples were measured within 24 h after sample collection. After filtering the water, 1 mg citric acid was added per 5 ml of water and samples were stored at -20 °C until further analysis. Samples were analysed for NO₃⁻, NH₄⁺, Al, and total-S. The following substances were determined colorimetrically; NO₃⁻ according to Kamphake et al. (1967) and NH₄⁺ according to Grasshoff & Johansen (1972). Al and total-S were measured by inductively coupled plasma emission spectrophotometry. Data on the presence of fish were obtained from Leuven & Oyen (1987) and recorded during sampling of chironomids. Chemical parameters were averaged per pool per year. Changes in water chemistry between 1983 and 2004 were tested using paired Wilcoxon Signed Ranks tests.

Chironomid sampling

The sampling method used in 2004 was identical to the method used in 1983 (Leuven et al. 1987). Chironomids were sampled in spring (April/May) and summer (July/August). Two sampling techniques were used. Sampling was done with a 20 × 30 cm pond net with 0.5 mm mesh size using a stratified random sampling procedure. Different habitat elements, such as reedbeds, submerged *Sphagnum* vegetation and mud soils were sampled proportionally to their occurrence in the study site. Total sampling effort differed per site, but was standardised by sorting for a fixed time period of 1.5 h. In addition, chironomids were sampled using a sediment core sampler (8 cm diameter, 10 cm depth). Twenty five samples were taken from different substrates. Within 2 m from the shore 10 samples were

taken from mineral and 10 from organic sediment. Five sediment samples were taken from the centre of the pools. All samples were transported to the laboratory, stored at 4 °C and sorted within 2 days after sample collection. For each type of sediment, samples were mixed, sieved over a sieve with a 0.5 mm mesh width and chironomids were collected from the equivalent of 125 cm² surface area. Collected chironomids were preserved in 70% ethanol until identification, which was done to the lowest taxonomic level possible.

Species data processing

In order to allow comparison of chironomid data from 1983 and 2004, chironomids identified in 2004 were aggregated to the taxonomic level attained in 1983. Chironomid data from 2004 were treated in the same way as in 1983; i.e. collected chironomids from mineral and organic shores and pool centre were pooled with those from net-samples and the abundance of each species/species group was converted to relative abundance for spring and summer separately. Next, spring and summer data were averaged for each site. All further analyses are based on this dataset.

Efficiency of chironomid collection from the samples may have been different for different pools and years. To allow comparison of species richness between years, rarefied richness was determined for each pool. Changes in rarefied richness between 1983 and 2004 were tested using paired Wilcoxon Signed Ranks tests. Changes in community structure were studied using multivariate analyses on species data, performed in Canoco for Windows version 4.0 (Ter Braak & Šmilauer 1998). A preliminary detrended correspondence analysis (DCA) revealed a gradient length exceeding 2.5, indicating that a unimodal response model was most suitable to describe the species response curves. Comparison of a correspondence analysis with a DCA revealed that the data contained an arch effect, which was removed by performing a DCA (Lepš & Šmilauer 2003). The response of individual species was studied by comparing relative abundance in 1983 and 2004 using paired Wilcoxon Signed Ranks tests. In order to interpret observed changes in community structure and species abundance, the Bray-Curtis dissimilarity measure (Bray & Curtis 1957) was used to assess the variation in species composition between pools and compare this similarity with the variation associated with temporal changes in restored and non-restored lakes.

Expected environmental changes and relevant biological traits

Although species possess many different traits, only traits deemed relevant were used in defining LHTs, i.e. traits expected to have a functional relation to changes in abiotic and biotic conditions arising from pool restoration and decreased acidifying atmospheric deposition (Van Kleef et al. 2010, Chapter 2).

Environmental parameters expected to be relevant, were pH, aluminium, oxygen and fish. Both in restored and non-restored moorland pools a raise in pH was expected. Due to a higher pH, aluminium will become less soluble and less toxic. Predation by fishes may become relevant as they will no longer be excluded from the pools by low pH. As pH increases, fungus-dominated decomposition will shift towards a faster bacterial-dominated decomposition (Kelly et al. 1984, Leuven & Wolfs 1988). Increased decomposition is coupled to oxygen consumption and may lead to more frequent oxygen stress. Because in restored pools organic matter was removed, effects of increased decomposition were only expected in non-restored pools.

Biological traits which were expected to be relevant for above mentioned environmental changes in moorland pools, were haemoglobin, tube building activity and larval development synchronised for spring emergence (spring synchronisation). Spring synchronisation allows a species to emerge early in the season, reproduce, have its larvae developing into the final instar at the start of the summer. This is expected to be a way to avoid periods of oxygen stress in summer and an adaptation to decomposing organic sediments. Haemoglobin also is a mechanism to tolerate low oxygen concentrations and simultaneously decreases vulnerability to acid conditions and toxic aluminium concentrations. On the other hand, haemoglobin may enhance a species' vulnerability to predation by increasing its visibility. Chironomids may counteract this by constructing tubes in which they can live. These traits interact with other biological traits such as diet, voltinism and larval size. Data on biological traits were obtained from literature (Vallenduuk & Moller Pillot 2007, Moller Pillot 2009) and supplemented by expert knowledge (pers. comm. HKM Moller Pillot). Some species could not be easily assigned to a LHT, due to missing data on their biological traits, variability within traits (e.g. broad range in number of generations) or because data on a single trait did not correspond to the co-occurrence of other traits. These species were assigned to the LHT that corresponded to most biological traits, where haemoglobin and larval size were given priority over other traits as they are less likely to be biased in literature and expert knowledge.

Defining chironomid life history tactics

Six life history tactics (LHTs) were defined, based on the co-occurrence of sets of biological traits in chironomid species (Table 2). Species belonging to LHT A minimize the age of reproduction and consequently produce many generations per year (up to 6 for *Coryneura scutellata* agg). To allow for a rapid larval development, these species are small and do not show spring synchronisation, which frequently is achieved through quiescence or diapause. In addition, they do not invest time and energy in the construction of tubes. Asexual reproduction does not require time investment in mate searching or mating and is also limited to this tactic. The expected optimal habitat for species in this tactic are not moorland pools, but water bodies in a highly dynamic landscape, characterised by the (periodic) absence of biotic (competition, predation) or abiotic stressors (low food availability, high acidity).

Species of LHT B have no haemoglobin nor spring synchronisation. The absence of spring synchronisation and a relatively small larval size allow species of tactic B to produce more generations than most other tactics. However, rapid larval development is not as stringent as in LHT A and algi- and detritivorous species still invest in protective tubes. The carnivorous species are free-living as they need to be mobile. The expected optimal habitats for species in this tactic are low dynamic water bodies with little abiotic stressors, although short periods of oxygen stress may be avoided by seeking refuge in the vegetation.

Species of LHT C have spring synchronisation, resulting in less generations per year allowing them to grow to a larger size than LHT B. Synchronisation makes these species prepared for periods with stress during summer, such as drying-up of the water body in summer. They lack haemoglobin and thus are poorly adapted to acid conditions. Optimal habitats for species in this tactic have little constant stress with periods of stress in summer, such as shores of moorland pools.

Table 2 Chironomid life history tactics and their associated biological traits. The life history tactics are described in the methods.

Life history tactic	Number of taxa	Haemoglobin	Spring synchronisation	Larval activity	
				F	T
A	3	±	-	3	
B	11	-	-	4	7
C	7	-	+	4	3
D	5	+	-	1	4
E	11	+	+		11
F	5	+	+	5	
U	5				

Life history tactic	Main diet			Average number of generations	Average length final instar (mm)	Expected response	
	A	D	C			NR	R
A	3			3.8	3.8	=	=
B	5	2	4	2.4	7.7	-	++
C	4		3	1.8	9.0	=	+
D	5			2.2	7.4	=	=
E	7	4		2.1	11.5	+	--
F			5	1.7	11.3	-	-
U							

Numbers in the categories larval activity and main diet indicate the number of taxa. Abbreviations: F=free-living, T=construction of tubes, A=algivorous, D=detritivorous, C=carnivorous, NR=non-restored moorland pools, R=restored pools.

Similar to species of LHT B, species of LHT D are relatively small and lack spring synchronisation. They produce slightly less generations, which might reflect a development trade-off: species in tactic D invest in haemoglobin and possibly other physiological mechanisms to tolerate abiotic stress (e.g. low oxygen concentrations, high acidity) at a cost of investments in growth and development. Species of LHT D are expected to perform optimally in habitats with constant abiotic stress such as acid moorland pools.

Chironomids of LHT E both have spring synchronisation and haemoglobin. This allows them to inhabit nutrient rich waters and grow to a large size. Larval size corresponds with adult body size, which in turn is positively correlated with reproductive effort. Therefore, females of these species are capable of producing more eggs (up to 1400 eggs per female) than those belonging to other tactics, allowing them to become dominant in their optimal habitat. Other suitable habitat also includes acid waters. LHT F is similar to tactic E but it includes only carnivorous species. Due to their carnivorous feeding, species of tactic F are free-living. This may make them vulnerable to predation, as they do not build tubes to conceal their conspicuous (i.e. large, haemoglobin pigmented) bodies.

Five chironomid species could not be assigned to one of the life history tactics, described above, due to insufficient information on their biological traits. These species were grouped in tactic U.

In non-restored moorland pools the expected environmental changes are small. Therefore, response of LHTs is expected to be limited to the most sensitive tactics (B, E and F, Table 2). LHT B is expected to decrease, if decreased acidity results in increased decomposition and oxygen stress. LHT E is adapted to this process and is expected to

increase in abundance. Tactic F is expected to decrease when fish species colonise the less acid pools. In restored pools the environmental changes will be more pronounced and the response of LHTs is expected to be accordingly. In restored pools the largest responses are expected from the most sensitive tactics (B, E and F), with LHTs B and E respectively increasing and decreasing in abundance due to removal of organic sediments. LHT F is expected to decrease with increasing fish presence. Tactic C is expected to respond positively to reduced acidity and aluminium. Response of tactic D is difficult to predict as it may react negatively to an increase in pH and positively to removal of organic sediment.

Relative abundance of species belonging to the same tactic was summed and changes from 1983 to 2004 were tested using paired Wilcoxon signed rank tests. Responses of LHTs in non-restored pools were also analysed in relation to observed changes in turbidity using Spearman rank tests. Changes in turbidity were used as a measure for changes in sediment decomposition and were expected to reflect changes in oxygen availability. This is done because the change in decomposition is likely to depend on the extent of previous acidification and change in pH (Van Kleef et al. 2010, Chapter 2.) and thus may vary between pools.

Results

In restored and non-restored moorland pools pH and alkalinity increased and sulphur concentrations decreased (Table 3). Ammonium and aluminium concentrations only decreased in restored pools. In the restored moorland pools fish presence increased. Turbidity increased in non-restored pools, suggesting increased decomposition of accumulated organic material. Concentrations of nitrate did not change significantly.

Rarefied species richness of chironomid assemblages increased significantly from 1983 to 2004 in restored pools (Wilcoxon signed rank test, $P = 0.04$) but not in non-restored pools ($P > 0.05$). A detrended correspondence analysis (eigen values for the first and second ordination axes were 0.478 and 0.313, respectively) revealed that the chironomid assemblages in restored moorland pools changed in the same direction (Figure 1). This is likely the result of the decreased abundance of *Chironomus* gr. *plumosus* and *C.* gr. *thummi* and an increase of *Tanytarsus* ssp. and *Psectrocladius psilopterus* (Table 4). In non-restored pools on the other hand, no significant increase or decrease was observed for individual taxa and species composition appeared to shift randomly (Figure 1).

Table 3 Average values/concentrations (\pm SE) in surface water chemistry parameters and number of fish species of non-restored and restored moorland pools in 1983 and 2004.

	No measures taken		Restoration measures taken	
	1983 N = 7	2004 N = 7	1983 N = 7	2004 N = 7
pH	4.3 \pm 0.3	5.1 \pm 0.2 *	4.2 \pm 0.3	5.0 \pm 0.2 *
Alkalinity (meq l ⁻¹)	0.027 \pm 0.012	0.124 \pm 0.035 *	0.015 \pm 0.011	0.061 \pm 0.009 *
NH ₄ (μ mol l ⁻¹)	61.6 \pm 24.4	23.2 \pm 9.8	89.3 \pm 24.8	14.1 \pm 4.9 *
NO ₃ (μ mol l ⁻¹)	9.4 \pm 3.1	5.9 \pm 2.2	10.6 \pm 2.7	10.6 \pm 3.3
S (μ mol l ⁻¹)	258.0 \pm 32.9	101.7 \pm 15.2 *	330.0 \pm 43.1	188.2 \pm 44.5 *
Al (μ mol l ⁻¹)	5.8 \pm 1.0	8.6 \pm 1.6	15.3 \pm 2.6	7.0 \pm 0.9 *
Turbidity (ppm)	7.7 \pm 1.7	15.2 \pm 1.3 *	3.3 \pm 1.0	4.1 \pm 0.5
Number of fishless pools	3	3	6	1

* indicates a significant difference between years (paired Wilcoxon signed ranks test, $P < 0.05$).

Long term response of chironomids to restoration and reduced deposition

Table 4 Average relative abundance (%) of individual chironomid taxa in non-restored and restored pools in 1983 and 2004.

Taxon	Non-restored pools (n=7)		Restored pools (N = 7)		LHT
	1983	2004	1983	2004	
Chironominae					
Chironomini					
<i>Camptochironomus</i> ssp.	0.00	2.41	0.00	0.03	E
<i>Chironomus</i> gr. <i>plumosus</i>	20.79	5.16	5.93	0.86 *	E
<i>Chironomus</i> gr. <i>ibummi</i>	2.41	7.51	9.86	0.04 *	E
<i>Cryptochironomus</i> ssp.	0.00	1.56	0.01	0.85	F
<i>Cryptocladopelma lateralis</i> Pinder, 1978	0.00	0.66	0.00	0.51	D
<i>Demicryptochironomus vulneratus</i> (Zetterstedt, 1838)	0.08	0.30	0.01	0.22	F
<i>Dicrotendipes</i> gr. <i>lobiger</i>	0.00	0.05	0.00	0.00	D
<i>Dicrotendipes</i> gr. <i>tritonus</i>	0.64	0.00	0.21	0.00	E
<i>Endochironomus albipennis</i> (Meigen, 1830)	0.39	0.99	0.14	3.62	C
<i>Endochironomus</i> gr. <i>dispar</i>	5.62	10.78	0.00	0.87	E
<i>Endochironomus tendens</i> (Fabricius, 1775)	8.70	10.43	4.37	3.62	E
<i>Glyptotendipes paripes</i> (Edwards, 1929)	6.09	9.89	34.69	2.08	E
<i>Lauterborniella</i> ssp.	0.00	0.24	0.00	0.00	A
<i>Microtendipes chloris</i> agg.	3.39	0.70	0.00	0.16	E
<i>Parachironomus</i> gr. <i>arcuatus</i>	0.17	0.00	0.00	0.16	B
<i>Polypedilum uncinatum</i> (Goetghebuer, 1921)	7.73	12.54	8.27	11.64	E
<i>Polypedilum</i> gr. <i>sordens</i>	0.32	6.62	2.43	7.11	D
<i>Tribelos intextum</i> (Walker, 1856)	0.86	0.48	0.18	0.00	E
Pseudochironomini					
<i>Pseudochironomus</i> ssp.	3.23	0.38	6.62	6.55	E
Tanytarsini					
<i>Cladotanytarsus</i> ssp.	0.00	0.60	0.00	0.00	D
<i>Paratanytarsus</i> ssp.	0.77	0.00	0.00	0.13	C
<i>Tanytarsus</i> ssp.	1.99	1.55	1.82	9.13 *	D
Orthoclaadiinae					
<i>Acamptocladus</i> ssp.	0.00	0.00	0.00	0.03	U
<i>Acricotopus lucens</i> (Zetterstedt, 1850)	0.87	0.00	0.00	0.00	B
<i>Chaetocladus piger</i> (Goetghebuer, 1913)	0.00	0.24	0.00	0.00	C
<i>Corynoneura scutellata</i> agg.	0.73	0.00	0.75	0.09	A
<i>Cricotopus sylvestris</i> agg.	2.84	1.20	0.00	5.02	B
<i>Metriocnemus fuscipes</i> (Meigen, 1818)	0.16	0.00	0.00	0.00	U
<i>Metriocnemus birticollis</i> agg.	0.14	0.00	0.00	0.00	B
<i>Nanocladus balticus</i> (Palmen, 1959)	0.00	0.00	0.00	0.29	U
<i>Nanocladus bicolor</i> (Zetterstedt, 1838)	0.08	0.00	0.00	0.00	U
<i>Psectrocladius obvius</i> agg.	0.33	0.00	0.00	0.04	C
<i>Psectrocladius platypus</i> (Edwards, 1929)	11.30	3.27	5.51	5.91	B
<i>Psectrocladius psilopterus</i> Kieffer & Thienemann, 1906	0.52	1.22	0.55	12.25 *	B
<i>Psectrocladius sordidellus/limbatellus</i>	0.23	0.67	0.00	1.53	B
<i>Pseudorthocladus</i> ssp.	0.16	0.00	0.10	0.26	U
<i>Pseudosmittia trilobata</i> (Edwards, 1929)	0.00	0.00	0.15	0.00	A
Tanypodinae					
Coelotanypodini					
<i>Clinotanypus nervosus</i> (Meigen, 1818)	0.15	0.37	0.00	0.00	F
Macropelopini					
<i>Macropelopia</i> ssp.	0.06	0.55	0.00	0.00	F
<i>Psectrotanypus varius</i> (Fabricius, 1787)	0.00	0.07	0.00	0.00	B
Natarsiini					
<i>Natarsia</i> ssp.	2.39	0.00	0.00	0.20	F
Pentaneurini					
<i>Ablabesmyia longistyla</i> (Fittkau, 1962)	0.00	0.75	0.33	4.21	B
<i>Ablabesmyia phatta/monolis</i>	6.64	5.96	8.22	12.28	B
<i>Paramerina cingulata</i> (Walker, 1856)	0.00	0.00	0.00	0.09	B
<i>Telmatopelopia nemorum</i> (Goetghebuer, 1921)	1.48	0.00	1.10	0.16	C
<i>Zavreliomyia</i> ssp.	1.32	0.00	0.00	0.09	C
Procladiini					
<i>Procladius sensulatum</i>	11.18	16.55	8.83	9.98	C

LHT: Life history tactic, letters of life history tactics correspond with table 2 and are described in the methods; * indicates a significant increase or decrease from 1983 to 2004 (paired Wilcoxon signed rank test, $P < 0.05$).

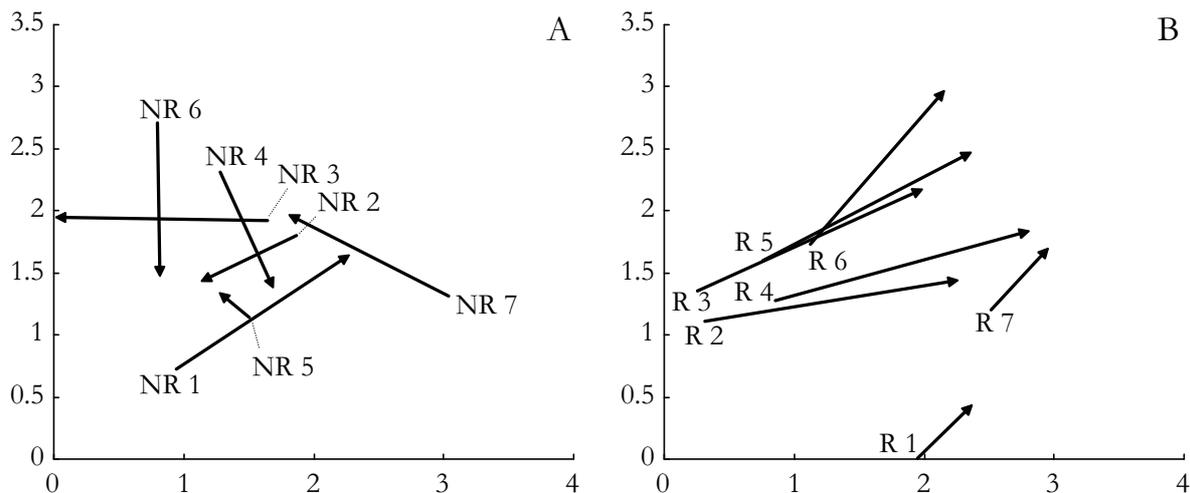


Figure 1 First two ordination axes of the detrended correspondence analysis. Arrows indicate the shift of the chironomid assemblage in a moorland pool. A: changes in non-restored moorland pools. B: changes in chironomid assemblages in restored pools. The starting point of an arrow represents the coordinates of samples taken in 1983, whereas the arrowhead coincides with the coordinates of the 2004 sample from the same pool. Pool numbers as explained in Table 1.

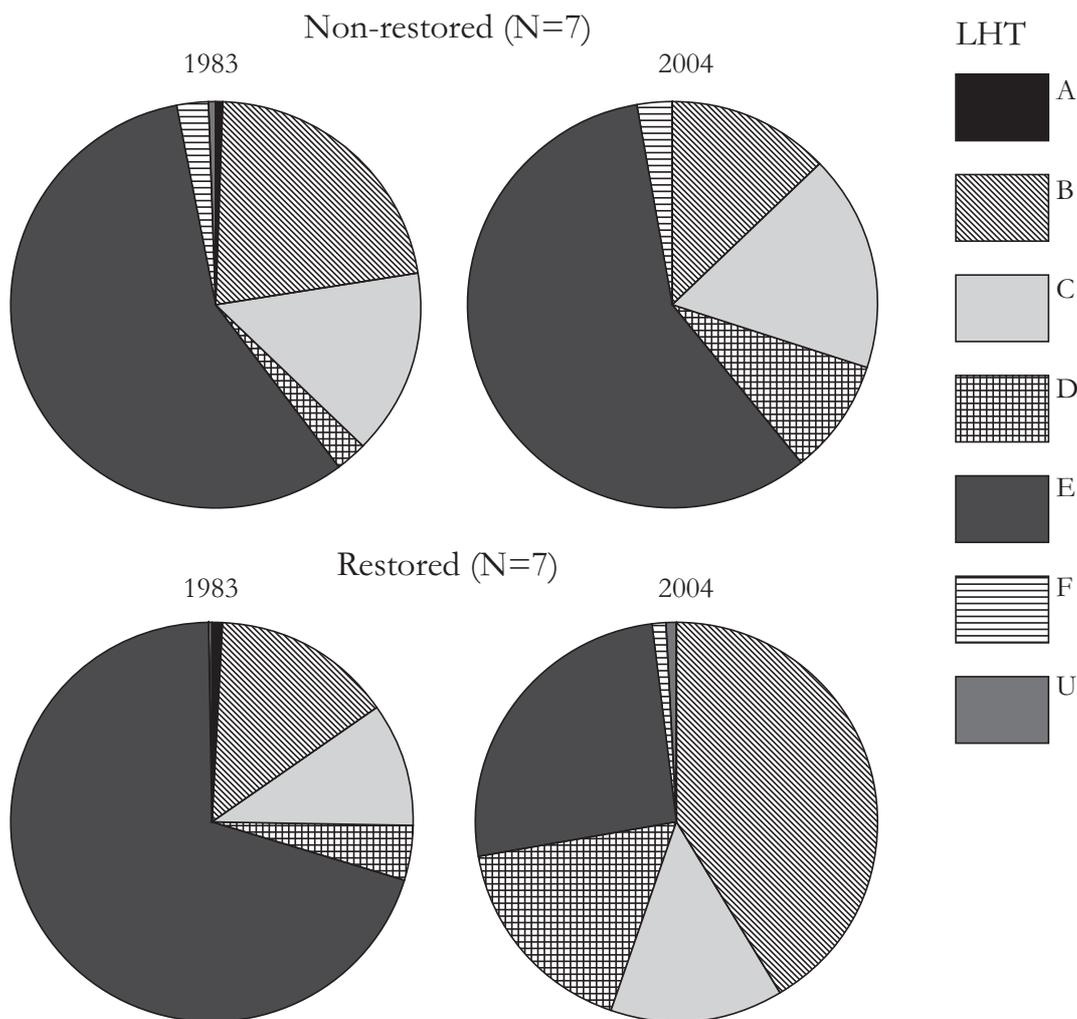


Figure 2 Average relative abundance of different chironomid life history tactics (LHTs) in 1983 and 2004 in non-restored and restored moorland pools. Letters of the legend are explained in table 2 and are described in the methods.

Average dissimilarity between chironomid assemblages in non-restored moorland pools in 1983 was 69% ($\pm 3\%$ SE). In the “to-be-restored” pools average dissimilarity in 1983 was 68% ($\pm 5\%$ SE). From 1983 to 2004 chironomid assemblages on average changed by 74% ($\pm 4\%$ SE) in non-restored pools and by 71 % ($\pm 6\%$ SE) in restored moorland pools.

In 1983 chironomids with LHT E dominated the acidified pools, followed by tactics B and C respectively (Figure 2). Only a small percentage of the chironomids belonged to tactics A, D and F. Chironomids, that could not be assigned to a LHT (U), were scarce or absent in both years. In the restored pools LHT E decreased significantly in favour of tactics B, D and F (Figure 3). Tactic F responded opposite the hypothesised response (Table 2). However the expected negative response could not be achieved as in 1983 this tactic was absent. In non-restored moorland pools no significant changes in the abundance of LHTs occurred. Changes in abundance of LHT B in non-restored moorland pools correlated with changes in turbidity of these pools (Figure 4). The responses of other tactics were not correlated to changes in turbidity (Spearman rank tests, $P > 0.05$).

Discussion

Changes in restored moorland pools

In moorland pools where restoration measures have been taken, water quality improved (pH, alkalinity, ammonium, sulphur and aluminium) and fish presence increased. Water quality improvement can be attributed to the inlet of alkaline ground or surface water resulting in a higher pH, alkalinity and a lower solubility of aluminium as well as removal of organic matter restoring aerobic sediment conditions and stimulating the loss of ammonium through nitrification (Brouwer et al. 2002) as well as decreased nitrogen and sulphate deposition.

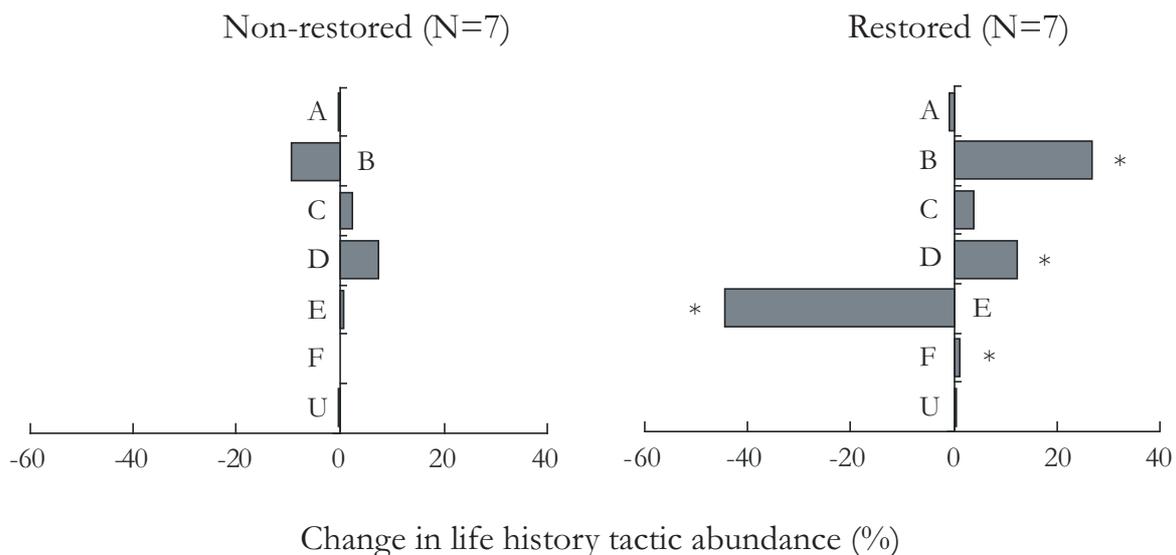


Figure 3 Average changes in chironomid life history tactics relative abundance (%) from 1983 to 2004 in non-restored and restored moorland pools. Letters of life history tactics correspond with table 2 and are described in the methods. *: $P < 0.05$, paired Wilcoxon signed rank test.

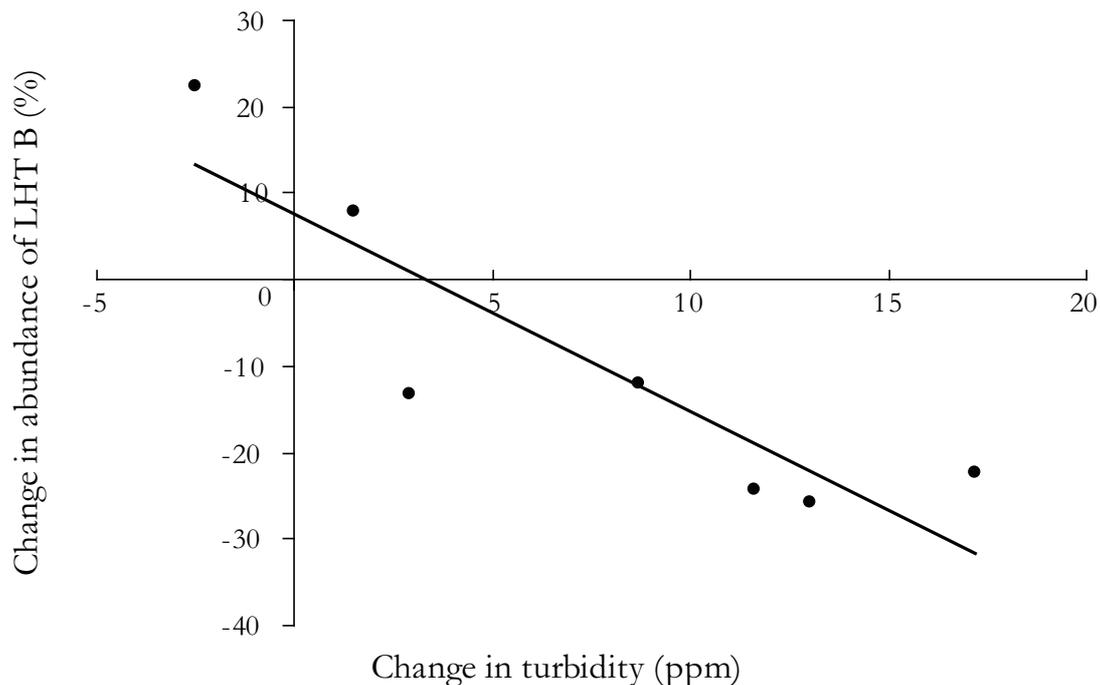


Figure 4 Relation between shift in turbidity and change in relative abundance of life history tactic B in pools where no restoration measures were taken (Spearman rank correlation = 0.857, $N = 7$, $P = 0.014$).

Chironomid assemblages reacted reasonably consistent: two chironomid species increased (*Psectrocladius psilopterus* and *Tanytarsus* spp.) and two decreased (*Chironomus* gr. *thummi* and *Chironomus* gr. *plumosus*). Even in the Staalbergven, which at the time of sampling had been restored in the previous year, species composition had changed in a way similar to other restored pools although it is likely that the change became more pronounced in the following years (Figure 1). Abundance of *Psectrocladius psilopterus* decreased and *Chironomus* spp. increased in acidifying moorland pools during the 20th century (Klink 1986). So, observed species responses in restored pools suggest a recovery of chironomid assemblages. Observed changes in abundance of life history tactics indicated a shift from dynamic, high stress (LHT E) to low dynamic environments (LHTs B and D), also indicating development towards more intact conditions. Increased abundance of LHT B suggests that removal of organic sediment is a more important environmental improvement in the moorland pools than reduced acidity.

Long term (approx. 10 y.) effects of moorland pool restoration on chironomid assemblages contrast with the short term effects which have been reported to be negative (Van Kleef et al. 2006, Chapter 4). On the short term, characteristic species declined or disappeared. Restoration measures in raised bog remnants (i.e. rewetting through rainwater retention) have been reported to result in decreased macroinvertebrate beta diversity due to loss of environmental heterogeneity (Van Duinen et al. 2003, Verberk et al. 2010). This does not appear to be the case for chironomids in restored moorland pools as from 1983 to 2004 rarefied richness increased from 16 to 19. Van Kleef & Esselink (2005) reported that species richness of Trichoptera increased with time since restoration but chironomid richness did not, suggesting that chironomids are not dispersal limited.

Changes in non-restored moorland pools

Water chemistry in non-restored moorland pools improved in terms of pH, alkalinity and sulphur (Table 3) probably as a result of decreased acidifying deposition. For these parameters, reversibility of acidification in aquatic ecosystems has been demonstrated before in moorland pools (Van Dam 1996, Van Kleef et al. 2010, Chapter 2) as well as lakes and streams (Skeffington & Brown 1992, Stoddard et al. 1999, Forsius et al. 2003, Davies et al. 2005, Skjelkvåle et al. 2005).

In spite of improved water chemistry and considerable changes in chironomid species composition in non-restored moorland pools (i.e. 74% on average), no consistent responses in of species richness, species abundance, community structure and life history tactics were observed. In part this may be the result of the large variation in species composition between pools that was observed in 1983 (i.e. 69% on average). It is also possible that abiotic changes in moorland pools are more nuanced and influencing community structure accordingly. Van Kleef et al. (2010, Chapter 2) reported that reduced acidity varied in acidified moorland pools with an average increase in pH of 0.54 units. Changes in pH correlated with changes in turbidity and were hypothesised to be the result of increased decomposition. Changes in turbidity in non-restored pools were negatively correlated with changes in abundance of species adapted to low dynamic, low stress environments (LHT B) suggesting periodic oxygen stress and supporting the hypothesised induced decomposition. However, response of LHT B was not sufficient to explain all of the observed variation in species composition from 1983 to 2004.

In the non-restored pools chironomid communities did not recover and the differential response of tactic B may even be considered as an additional (temporal) degradation. This is in contrast to Hynynen & Meriläinen (2005) who reported a moderate recovery for chironomids in acidified lakes. Other acid-sensitive macroinvertebrate taxa have also been reported to slowly increase in recovering acidified lakes and streams (Lancaster et al. 1996, Tipping et al. 2002, Monteith et al. 2005, Burns et al. 2008, Ormerod & Durance 2009). In moorland pools a recovery of the diatom community towards to a pre-acidification state was observed by Van Dam (1996). Chironomids primarily are bottom dwelling species and hence are especially sensitive to bottom conditions and processes. This may explain the different responses to reduced acidification of moorland pool chironomids and diatoms, the latter being more vegetation and water inhabiting species. Different sediment conditions may also explain different responses of biota of moorland pools and the well-studied streams and lakes. In streams and lakes accumulation of organic sediment as a result of acidification does hardly occur, because organic material is either swept away by water movement or eventually sinks off into the hypolimnion. Rehabilitation of characteristic moorland pool communities thus appears to be delayed by layers of organic material which have accumulated due to acidification. Therefore, active involvement in the form of restoration management including the removal of organic sediments remains necessary for the recovery of chironomid assemblages in acidified moorland pools.

Life history tactics as a tool for understanding ecological change

Known and hypothesised environmental changes could be confirmed by the responses of trait combinations (i.e. tactics) of chironomid species. Expected responses of life history tactics (Table 2) were largely confirmed in restored moorland pools. Observed LHT responses in non-restored pools were more subtle as they appeared to depend on the degree of environmental change in individual pools. The significant LHT changes in restored pools were not solely the result of the response of individual species, but instead were more robust. Changes in tactics B, D and E were more pronounced and significant, than those of the individual species (data not shown). Even after omitting species with a significant change in relative abundance from 1983 to 2004, response of LHT E remained significant ($P = 0.018$, paired Wilcoxon signed ranks test) and LHT B was almost significant ($P = 0.063$).

Interpretation of taxon-based analyses, such as changing species responses and community structure, is not always straightforward as part of the differences in species assemblages between sites may be independent from environmental conditions. For example, there may be differences in the local species pool or species distribution areas (Srivastava 2005) or species that arrive first may occupy niches, making them inaccessible for later arriving species (i.e. community closure; Lundberg et al. 2000). This problem may be circumvented by aggregating species into tactics based on the functionality of biological traits (Verberk et al. 2008). In these life history tactics species are grouped which are adapted to solve environmental problems in a similar way. This is not to say that all species within a tactic are ecologically equivalent. Rather, ecological differences between species of the same tactic are smaller than for species of different tactics. This allows a focus on the main pattern, increasing the signal-to-noise ratio. Because in the LHT approach species assemblages are organized based on their adaptations to a given environment, LHT can provide insight in the causal mechanisms, which are lacking in taxon-based approaches (Lawton 1999). This explanatory power makes the LHT approach a valuable tool for planning and evaluating effects of environmental policy, nature conservation and water management.

Acknowledgements

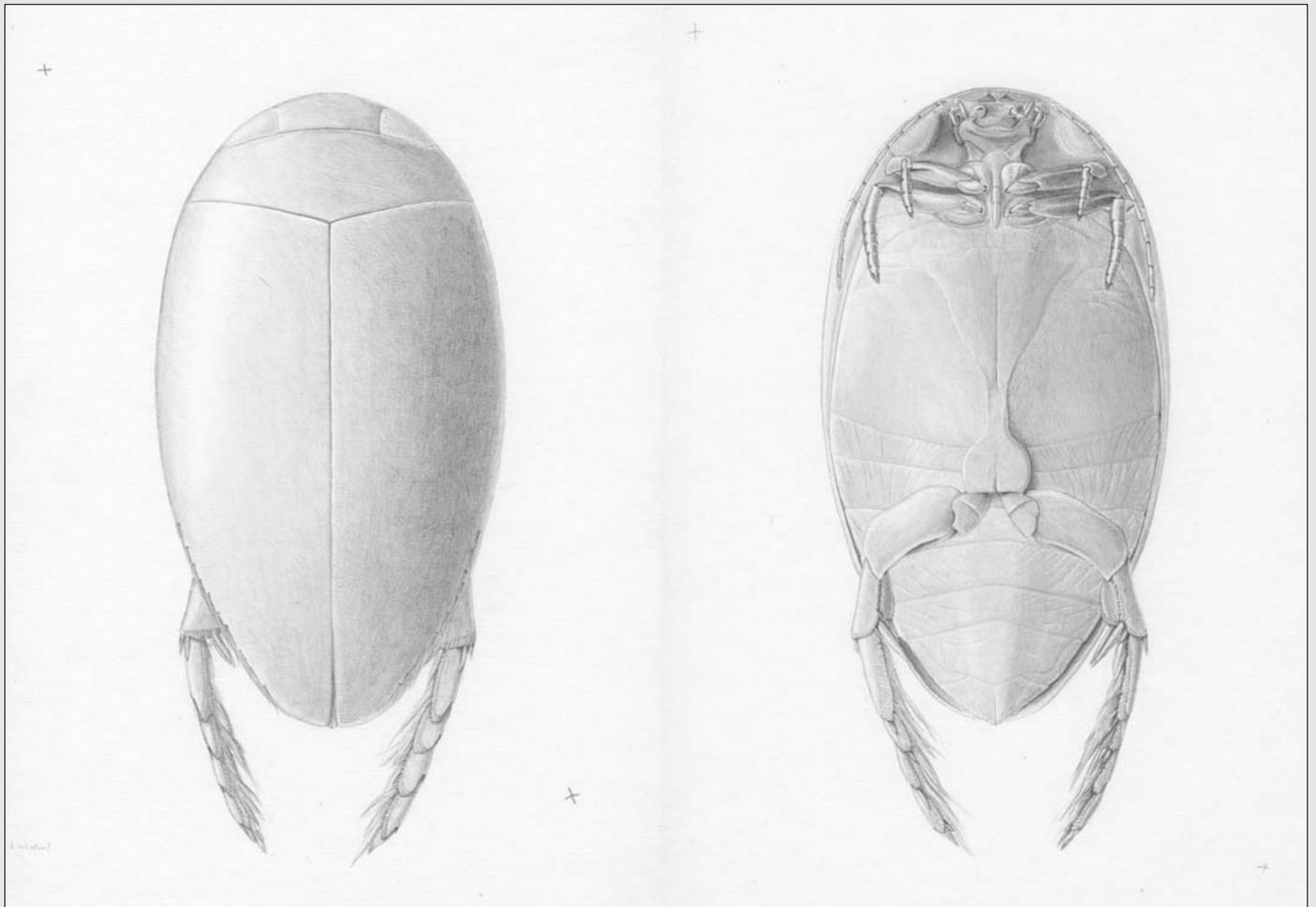
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References

- Arts GHP (1990) Deterioration of Atlantic soft-water systems and their flora, a historical account. *Thesis, Radboud University, Nijmegen*.
- Bradshaw AD (1996) Underlying principles of restoration. *Canadian Journal of Fisheries and Aquatic Sciences* **53**: 3-9.
- Bray JR & Curtis JT (1957) An ordination of upland forest communities of southern Wisconsin. *Ecological Monographs* **27**: 325-349.
- Brouwer E, Bobbink R & Roelofs JGM (2002) Restoration of aquatic macrophyte vegetation in acidified and eutrophied softwater lakes: an overview. *Aquatic Botany* **73**: 405-431.
- Burns DA, Riva-Murray K, Bode RW & Passy S (2008) Changes in stream chemistry and biology in response to reduced levels of acid deposition during 1987-2003 in the Neversink River Basin, Catskill Mountains. *Ecological Indicators* **8**: 191-203.
- Carpenter SR (2003) Regime shifts in lake ecosystems: pattern and variation, in: Kinne O (Ed.), *Excellence in ecology, Vol. 15. International Ecology Institute, Oldendorf/Lube*.
- Davies JJJ, Jenkins A, Monteith DT, Evans CD & Cooper DM (2005) Trends in surface water chemistry of acidified UK Freshwaters, 1988-2002. *Environmental Pollution* **137**: 27-39.
- Forsius M, Vuorenmaa J, Mannio J & Syri S (2003) Recovery from acidification of Finnish lakes: regional patterns and relations to emission reduction policy. *Science of the Total Environment* **310**: 121-132.
- Grasshoff H & Johanssen H (1972) A new sensitive and direct method for the automatic determination of ammonia in sea water. *Journal du Conseil* **34**: 516-521.
- Hynynen J & Meriläinen JJ (2005) Recovery from acidification in boreal lakes inferred from macroinvertebrates and subfossil chironomids. *Hydrobiologia* **541**: 155-173.
- Jenkins A (1999) End of the acid reign? *Nature* **401**: 537-538.
- Kamphake LH, Hannah SA & Cohen JM (1967) Automated analysis for nitrate by hydrazine reduction. *Water Research* **1**: 206.
- Kelly CA, Rudd JWM, Furutani A & Schindler DW (1984) Effects of lake acidification on rates of organic-matter decomposition in sediments. *Limnology and Oceanography* **29**: 687-694.
- Klink A (1986) Geschiedenis van de verzuring in Nederland. Een paleolimnologische studie naar de invloed van verzuring op levensgemeenschappen in enige zwakgebufferde wateren. Rapporten en mededelingen 27. *Hydrologisch adviesbureau Klink BV, Wageningen*.
- Lancaster J, Real M, Juggins S, Monteith DT, Flower RJ & Beaumont WRC (1996) Monitoring temporal changes in the biology of acid waters. *Freshwater Biology* **36**: 179-201.
- Lawton JH (1999) Are there general laws in ecology? *Oikos* **84**: 177-192.
- Ledger ME & Hildrew AG (2005) The ecology of acidification and recovery: changes in herbivore-algal food web linkages across a stream pH gradient. *Environmental Pollution* **137**: 103-118.
- Lepš J & Šmilauer P (2003) Multivariate analyses of ecological data using CANOCO. *Cambridge University Press*.
- Leuven RSEW & Oyen FGF (1987) Impact of acidification and eutrophication on the distribution of fish species in shallow and lentic soft waters in the Netherlands: An historical perspective. *Journal of Fish Biology* **31**: 752-774.
- Leuven RSEW, Van der Velden JA, Vanhemelrijk JAM & Van der Velde G (1987) Impact of acidification on chironomid communities in poorly buffered waters in the Netherlands. *Entomologica Scandinavica Supplements* **29**: 269-280.
- Leuven RSEW (1988) Impact of acidification on aquatic ecosystems in The Netherlands, with emphasis on structural and functional changes. *Thesis, Radboud University, Nijmegen*.
- Leuven RSEW & Wolfs WJ (1988) Effects of water acidification on the decomposition of *Juncus bulbosus* L. *Aquatic Botany* **31**: 57-81.
- Leuven RSEW, Van der Velde G & Kersten HLM (1992) Interrelations between pH and other physico-chemical factors of Dutch soft waters. *Archiv für Hydrobiologie* **126**: 27-51.

- Lundberg P, Ranta E & Kaitala V (2000) Species loss leads to community closure. *Ecology Letters* **3**: 465-468.
- McNicol DK, Bendell BE & Mallory ML (1995) Evaluating macroinvertebrate responses to recovery from acidification in small lakes in Ontario, Canada. *Water, Air, and Soil Pollution* **85**: 451-456.
- Milieu en Natuur Planbureau (2007) Retrieved April 5, 2007, from <http://www.mnp.nl/mnc/i-nl-0184.html>.
- Moller Pillot HKM (2009) Chironomidae larvae. Biology and ecology of the Chironomini. *KNNV Publishing, Zeist*.
- Monteith DT, Hildrew AG, Flower RJ, Raven PJ, Beaumont WRB, Collen P, Kreiser AM, Shilland EM & Winterbottom JH (2005) Biological responses to the chemical recovery of acidified fresh waters in the UK. *Environmental Pollution* **137**: 83-101.
- Ormerod SJ & Durance I (2009) Restoration and recovery from acidification in upland Welsh streams over 25 years. *Journal of Applied Ecology* **46**: 164-174.
- Poff NL, Olden JD, Vieira NKM, Finn DS, Simmons MP & Kondratieff BC (2006) Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. *Journal of the North American Benthological Society* **25**: 730-755.
- Resh VH, Hildrew AG, Statzner B & Townsend CR (1994) Theoretical habitat templates, species traits and species richness: a synthesis of long-term ecological research on the Upper Rhone River in the context of concurrently developed theory. *Freshwater Biology* **31**: 539-554.
- Roelofs JGM (1983) Impact of acidification and eutrophication on macrophytes communities in soft waters in the Netherlands. I. Field observations. *Aquatic Botany* **17**: 139-155.
- Roelofs JGM, Brouwer E & Bobbink R (2002) Restoration of aquatic macrophyte vegetation in acidified and eutrophicated shallow soft water wetlands in the Netherlands. *Hydrobiologia* **478**: 171-180.
- Schröder A, Persson L & De Roos A (2005) Direct experimental evidence for alternative stable states: a review. *Oikos* **110**: 3-19.
- Siepel H (1994) Life-history tactics of soil microarthropods. *Biology and Fertility of Soils* **18**: 263-278.
- Skeffington RA & Brown DJA (1992) Timescales of recovery from acidification: Implications of current knowledge for aquatic organisms. *Environmental Pollution* **77**: 227-234.
- Skjelkvåle BL, Stoddard JL, Jeffries DS, Tørseth K, Høgåsen T, Bowman J, Mannio J, Monteith DT, Mosello R, Rogora M, Rzychon D, Vesely J, Wieting J, Wilander A & Worsztynowicz A (2005) Regional scale evidence for improvements in surface water chemistry 1990-2001. *Environmental Pollution* **137**: 165-176.
- Srivastava DS (2005) Do local processes scale to global patterns? The role of drought and the species pool in determining treehole insect diversity. *Oecologia* **145**: 205-215.
- Stearns SC (1976) Life-history tactics: A review of the ideas. *Quarterly Review of Biology* **51**: 3-47.
- Stoddard JL, Jeffries DS, Lükewille A, Clair TA, Dillon PJ, Driscoll CT, Forsius M, Johannessen M, Kahl JS, Kellogg JH, Kemp A, Mannio J, Monteith DT, Murdoch PS, Patrick S, Rebsdorf A, Skjelkvåle BL, Stainton MP, Traaen T, Van Dam H, Webster KE, Wieting J & Wilander A (1999) Regional trends in aquatic recovery from acidification in North America and Europe. *Nature* **40**: 575-578.
- Ter Braak CJF & Šmilauer P (1998) CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (version 4). *Microcomputer power, Ithaca*.
- Tipping E, Bass JAB, Hardie D, Haworth EY, Hurley MA & Wills G (2002) Biological responses to the reversal of acidification in surface waters of the English Lake District. *Environmental Pollution* **116**: 137-146.
- Townsend CR & Hildrew AG (1994) Species traits in relation to a habitat templet for river systems. *Freshwater Biology* **31**: 265-275.
- Vallenduuk HJ & Moller Pillot HKM (2007) Chironomidae larvae. General ecology and Tanypodinae. *KNNV Publishing, Zeist*.

- Van Dam H (1996) Partial recovery of moorland pools from acidification: indications by chemistry and diatoms. *Netherlands Journal of Aquatic Ecology* **30**: 203-218.
- Van Duinen G, Bobbink R, Van Dam C, Esselink H, Hendriks R, Klein M, Kooijman A, Roelofs J & Siebel H (2004) Duurzaam natuurherstel voor behoud van biodiversiteit. 15 jaar herstelmaatregelen in het kader van het Overlevingsplan Bos en Natuur. *Expertisecentrum LNV, Ministerie van Landbouw, Natuur en Voedselkwaliteit, Ede.*
- Van Kleef H & Esselink H (2005) Monitoring van abiotiek, vegetatie, dansmuggen en kokerjuffers in gerestaureerde zwakgebufferde oppervlaktewateren. Kolonisatie van diersoorten. *Expertisecentrum LNV, Ministerie van Landbouw, Natuur en Voedselkwaliteit, Ede.*
- Van Kleef HH, Verberk WCEP, Leuven RSEW, Esselink H, Van der Velde G & Van Duinen GA (2006) Biological traits successfully predict the effects of restoration management on macroinvertebrates in shallow softwater lakes. *Hydrobiologia* **565**: 201-216.
- Van Kleef HH, Brouwer E, Leuven RSEW, Van Dam H, De Vries-Brock A, Van der Velde G & Esselink H (2010) Effects of reduced nitrogen and sulphur deposition on the water chemistry of moorland pools. *Environmental Pollution* **158**: 2679-2685.
- Verberk WCEP, Siepel H & Esselink H (2008) Life-history tactics in freshwater macroinvertebrates. *Freshwater Biology* **53**: 1722-1738.
- Verberk WCEP, Van der Velde G & Esselink H (2010) Explaining abundance-occupancy relationships in specialists and generalists: a case study on aquatic macroinvertebrates in standing waters. *Journal of Animal Ecology* **79**: 589-601.



Pencil drawings of Laccophilus poecilus. This species probably was once very common in raised bogs, but nowadays is restricted to moorland pools. Artist: Erik Crins.

Chapter 4

Biological traits successfully predict the effects of restoration management on macroinvertebrates in shallow softwater lakes

Hein van Kleef, Wilco Verberk, Rob Leuven, Hans Esselink, Gerard van der Velde & Gert-Jan van Duinen

Abstract

Many shallow softwater lakes are being affected by eutrophication and acidification. In these small lakes decaying organic material usually accumulates and characteristic plant and animal species disappear. In many degraded lakes organic matter and macrophytes are being removed in order to restore the lakes to their original state. To assess the effects of restoration management in softwater lakes on aquatic macroinvertebrates, changes in the species assemblages were studied in four degraded lakes in the Netherlands undergoing restoration measures. The degraded lakes still harboured species characteristic of pristine softwaters. However, most of these species were not recorded after restoration measures were taken. Species' densities declined dramatically during the execution of restoration measures. Swimming and abundant species were more likely to survive the restoration measures than other species. The first years after restoration, the lakes did not meet the habitat requirements for a number of species. Species requiring vegetation for ovipositing, animal food sources and swards of vegetation as habitat declined. Because recolonisation is expected to be restricted, it is recommended to ensure the survival of relict populations when taking measures to restore degraded softwater lakes. This may be achieved by phasing restoration measures in space and time, hereby minimising mortality during the execution of restoration measures and by preserving habitat conditions required by characteristic species.

Introduction

In western Europe, eutrophication, acidification and desiccation have had a tremendous impact on oligotrophic ecosystems. As a result, plant and animal species characteristic of these systems have shown a strong decrease during the last century (Haines 1981, Roelofs 1983, Leuven et al. 1986, Ravera 1986, Arts & Leuven 1988, Leuven 1988, Lamers et al. 1998). In order to prevent these species from going extinct, various restoration measures have been developed (Brouwer & Roelofs 2001, Lamers et al. 2002, Nienhuis et al. 2002). Restoration efforts often focus on restoring the physico-chemical conditions required for the development of communities dominated by characteristic plant and animal species and usually result in the creation of early successional stages. Research on the effects of restoration mostly focuses on physico-chemical conditions and the recovery of vegetation, whereas studies on the effects on fauna are very scarce.

We studied how restoration measures in Dutch shallow softwater lakes affected fauna communities. Historically, these lakes were formed by peat cutting, branching of rivers and brooks and depressions in cover sands (e.g. coastal and ancient river dunes and glacial deposits). Nowadays, Dutch rivers and brooks are strongly regulated, cover sands planted with trees and the cutting of peat has stopped. As a result no softwater lakes are formed any more (Brouwer 2001), emphasizing the need to preserve the existing lakes as these ecosystems harbour a large number of characteristic species. Pristine softwater lakes have a low alkalinity and are nutrient limited, with respect to inorganic carbon, nitrogen and phosphorus. These characteristics make the lakes very sensitive to both acidification and eutrophication. Acidification and eutrophication lift the nutrient limitation of the lakes and increase primary production, because fast-growing plant species are able to become dominant (Bloemendaal & Roelofs 1988). Increased primary production leads to accumulation of organic matter, increased decomposition and anaerobic conditions. Characteristic plant species decline or disappear, because they are out competed for light

and unable to germinate under anaerobic conditions (Bloemendaal & Roelofs 1988). Characteristic fauna species may disappear as a result of oxygen deficiencies and heavy metal toxicity (Henrikson et al. 1982).

Restoration measures in deteriorated softwater lakes aim at restoring nutrient limitation, low alkalinity and aerobic sediments. Generally, these measures are carried out by removal of accumulated organic matter and macrophytes. In order to facilitate restoration activities the water table in these lakes is often lowered until only small pools of water remain. Restoration measures are devised in a way that the recovery of characteristic plant species is ensured, i.e. these species have formed persistent seed banks that are preserved during removal of organic matter. The extent to which recovery of characteristic fauna communities will occur, depends on the ability of species to persist during the draining of the lake and removal of the organic matter and macrophytes, during the recovery of the required habitat characteristics and on the species' ability to colonise the restored lake.

Due to habitat destruction and deterioration as well as the limited dispersal capacity of some species, the importance of colonisation is expected to be limited (Van Kleef & Esselink 2004a). Therefore, this study focuses on the persistence of species during and after the implementation of restoration measures. In four degraded softwaters changes in macroinvertebrate assemblages resulting from restoration efforts are studied. Observed changes in macroinvertebrate community composition are analysed using biological traits of species in order to (1) understand the observed effects of the restoration measures, (2) predict the effects in future restoration projects to anticipate unwanted side effects and (3) provide information on the effects of restoration in similar ecosystems and of similar measures. The persistence of species is studied in two different time periods: (1) when restoration measures are being taken (execution phase) and (2) during the recovery of the ecosystem after measures are taken (recovery phase). During these phases different factors will determine species' performance and species will require a set of different attributes to optimally perform during each phase.

Southwood (1977) hypothesised that the habitat acts as a templet onto which evolution has forged biological traits (the habitat templet concept). Species are adapted to live under certain conditions and can only survive in habitats that meet their requirements. Many studies have tested the habitat templet concept in river systems (Scarsbrook & Townsend 1993, Juget & Lafont 1994, Resh et al. 1994, Richoux 1994, Tachet et al. 1994, Usseglio-Polatera 1994, and others) and used biological traits to understand the distribution of species throughout the catchment. In the present study changes in the species assemblages resulting from restoration measures are related to the biological traits of the species involved. This approach provides us with a tool to predict bottlenecks for species in future restoration projects and to avoid local extinction of characteristic species. Furthermore, it can be used for assessing the performance of species that were not encountered in this study.

We hypothesize that only a limited number of species will be able to survive restoration measures. It is assumed that during the execution phase mobile species will be better able to reach the relative safety of the remaining small water bodies, when the waters are drained. Furthermore, species occurring in large numbers are more likely to persist during this phase. Part of the species that have survived the execution phase will be unable to complete their life cycles during the recovery phase, because the environment does not meet their habitat requirements, yet.

This chapter addresses the following questions:

1. Do deteriorated softwater lakes still harbour species characteristic of pristine softwaters?
2. Are characteristic aquatic macroinvertebrates able to survive the process of restoration?
3. Does the abundance of species prior to restoration determine the chance of survival during the execution phase?
4. Do the changes in species assemblages during the execution and recovery phases correlate with particular biological traits?

Materials and methods

Study sites and restoration measures

Aquatic macroinvertebrates were sampled in four degraded shallow softwater lakes in the Netherlands i.e. lakes Ijsbaan, Verwolde, Grenspoel and Wijnjeterperschar (Figure 1). The surface area of these lakes was 0.67, 0.12, 3.74 and 0.67 ha and the maximum depth 0.5, 0.5, 1.0 and 0.5 m, respectively. Detailed data on water chemistry, vegetation and restoration measures of the lakes are described in Van Kleef & Esselink (2004b). Restoration measures in lakes Ijsbaan, Verwolde and Grenspoel consisted of removal of accumulated organic matter and macrophytes. For these restoration activities, the water table in the lakes was lowered without completely draining the lakes, resulting in shallow pools of approximately 10 cm depth. In lake Wijnjeterperschar restoration measures were carried out without lowering the water table and were phased in space and time: half of the lake was cleared of detritus and vegetation in July 2001 and the other part in spring 2002.

Sampling

For determining changes in species assemblages resulting directly from restoration (during the execution phase), lake Ijsbaan was sampled 1 week before and 1 week after restoration measures were taken. Data on the execution phase for the other lakes are unavailable. In order to determine changes in species assemblages resulting from restoration and changes in habitat (execution and recovery phases combined), each site was sampled twice before and twice after restoration measures were taken, except lake Verwolde which was only sampled once before and once after measures were taken.

Macroinvertebrates were sampled using a 20 × 30 cm pond net with ½ mm mesh size. Different habitat elements, such as reedbeds, submerged *Sphagnum* vegetation and mud soils were sampled proportionally to their occurrence in the study site. Total sampling effort was kept constant at 1.5 m². This ensures that the list of taxa and their numbers reflects the community composition and abundance of the dominant species in the lakes (Van der Hammen et al. 1984).

Samples were transported to the laboratory and stored at 4 °C to minimize mortality. Samples were washed over three sieves with 2, 1, and ½ mm mesh size, respectively and sorted in white trays within 2 days after sample collection and preserved until identification. All macroinvertebrates were identified to the lowest taxonomical level possible (mostly species level).

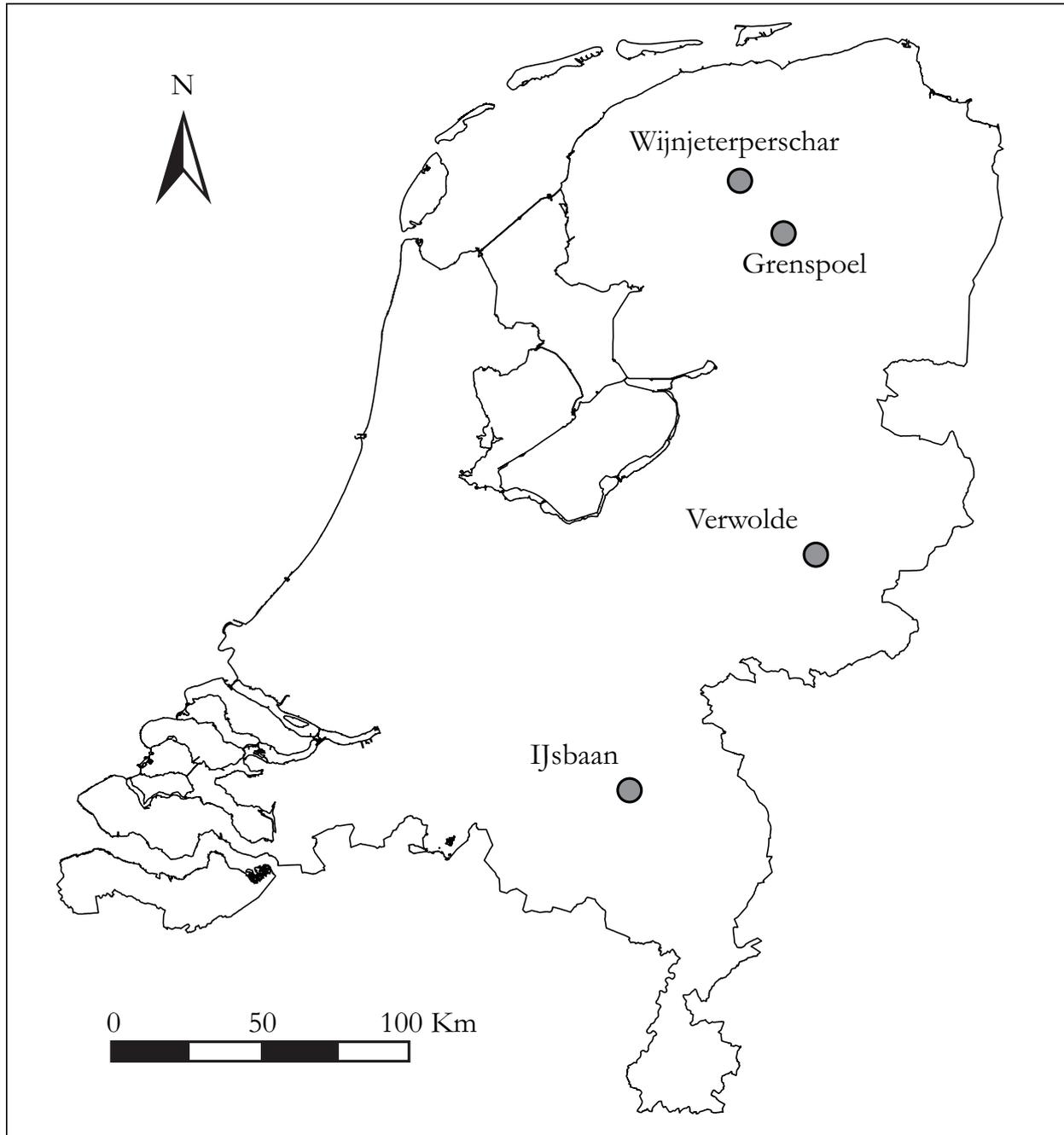


Figure 1 Locations of the study sites in the Netherlands.

Biological traits and coding of information

Biological traits were selected if they were expected to be of importance in determining the performance of species in the restored softwaters. The type of locomotion was expected to determine the ability of a species to reach the remaining patches of open water and to evade the machinery, hereby influencing the survival chances during the execution phase. Species' performance during the recovery phase was expected to be determined by a number of biological traits (Table 1). Specific demands on the environment for completing life cycles (carnivory, ovipositing in aquatic or terrestrial vegetation, inhabiting vegetation and parasitism) were expected to decrease the abundance of species. Delicate respiratory organs (gills and lungs) that may have been damaged

Table 1 Biological traits associated with changes in species density.

Biological trait/ Classes	Code	Not recovered	Decreased	Relatively stable	Increased	New	Prediction
Flight							
Flight	A1	X					> -
Flightless	A2					X	< -
Preferred life history							
Semivoltine	B1		X				< +
Univoltine	B2		X				< +
Multivoltine	B3				X		> +
Diet juveniles							
Detritus	C1				X		> +
Plants/algae	C2				X		> +
Animal	C3		X				< +
Diet adults							
Detritus	D1					X	> +
Plants/algae	D2				X		> +
Animal	D3	X					< +
Irrelevant	D4					X	> +
Reproduction							
Sexually	E1	X					< +
Asexually	E2					X	> +
Parental care							
Eggs in/on vegetation	F1		X				< +
Eggs on solid substrate	F2					X	> +
Eggs fixed terrestrial	F3	X					< +
Eggs on adult	F4			X			> -
Eggs on surface	F5				X		> +
Ovovivipary	F6					X	> +
Respiration juveniles							
Lung	G1					X	< -
Gills	G2			X			< -
Tegument	G3				X		> +
Spiracles	G4	X					> -
Ventilation	G5		X				> -
Respiration water	G6					X	< -
Respiration air	G7				X		> +
Respiration adults							
Lung	H1					X	< -
Gills	H2			X			< -
Tegument	H3					X	> +
Spiracles	H4	X					> -
Respiration water	H5					X	< -
Respiration air	H6	X					> -
Habitat							
Indifferent	I1					X	> +
Anaerobic sediment	I2				X		> +
Vegetation	I3	X					< +
Host	I4					X	< -
Aerobic organic matter	I5					X	> +
Bare sand	I6				X		> +

<: decrease predicted, >: increase predicted, +: predictions confirmed, -: predictions not confirmed.

during restoration were expected to decrease species' performance, whereas species breathing air (terrestrial respiration) were expected to perform better than those with aquatic respiration. Success of species during the recovery phase was also expected to be influenced by their capacity for colonisation (flight capability) and rapid reproduction (number of generations per year and reproduction).

In total eight different biological traits were selected of which three (locomotion, diet and respiration) were defined for juvenile as well as adult stages. Each trait had several classes to which species could be assigned (Table 1). Biological traits of different taxa were obtained from a large number of scientific papers, handbooks, taxonomic literature and information provided by experts (Dr. HKM Moller Pillot and Dr. LWG Higler pers. comm.). For every trait class a score of '0' or '1' was assigned to each taxon (Van Kleef & Esselink 2005). A '0' indicating low or no affinity and a '1' indicating a high affinity with the trait class. Taxa with an equal affinity for multiple classes within one biological trait were coded a '1' for each of these classes.

Data analyses

Because species occurring in low numbers are easily missed in field studies (Foggo et al. 2003), it is nearly impossible to determine whether a species has newly colonised or disappeared from a study site. Therefore, instead of presence-absence data, the performance of species at individual sites was used to analyse changes in species assemblages during and after the execution of restoration measures.

Execution phase

Changes in species assemblages resulting from restoration were analysed by comparing samples from lake Ijsbaan 1 week before and 1 week after restoration measures were carried out. The relation between locomotion type and survival of macroinvertebrates was tested with a Student *t*-test (unequal variance, two-tailed). The Spearman correlation coefficient was calculated between different classes of the density of species before and the chance of recovering of these species after measures were taken.

Recovery phase

For the analysis of species' performance during the recovery phase three cross tables were compiled (Figure 2). Cross table A consists of the species and their biological traits. Species occurring in multiple lakes were included multiple times, because on different locations they were affected by restoration measures in different ways. All taxa identified to species level were included, except oligochaetes, which were omitted because of incomplete knowledge on their biological traits. Cross table A consists of 250 species-site combinations and 54 traits. Next, for each of the lakes, all data collected before measures were carried out were pooled, as well as all data collected after restoration measures were taken. Subsequently, for every site-species combination the change in species density was calculated and assigned to five different categories of density change: (1) not recovered: species found only before restoration measures were taken; (2) decreased: species found before and after restoration measures are taken, exhibiting a decrease in density of at least 25%; (3) relatively stable: species found before and after restoration measures are taken, exhibiting a change in density less than 25%; (4) increased: species found before and after restoration measures are taken, exhibiting an increase in density of at least 25% and (5) new: species found only after restoration measures are taken. Cross table B consists of 250 species-site combinations and 5 categories of density change.

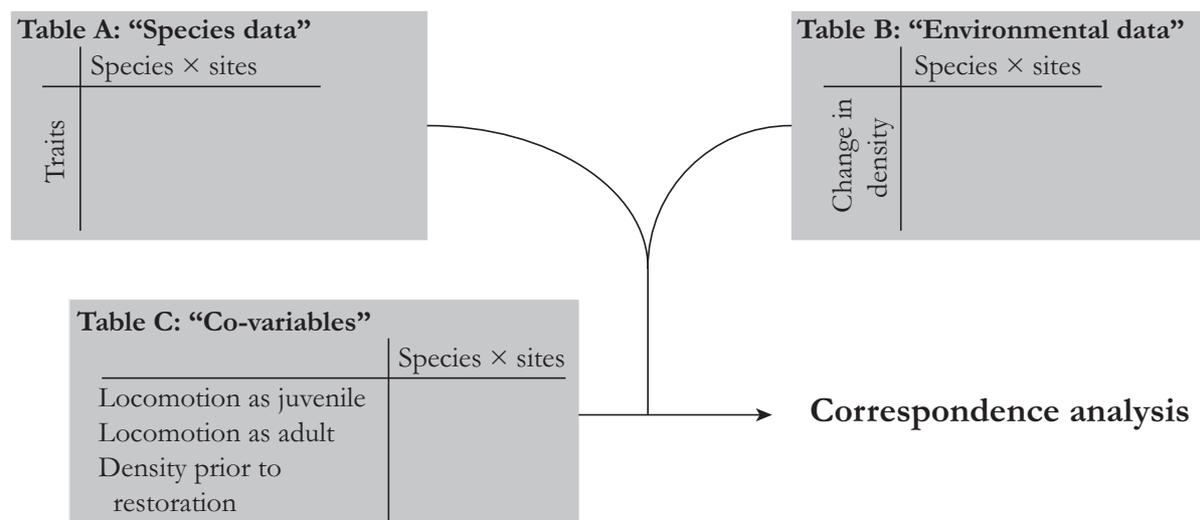


Figure 2 Schematic representation of the analysis of changes in species assemblages taking place during the recovery phase.

Cross table C contains data for each species-site combination on the variables determining survival during the execution phase: locomotion of juvenile and adult stages and the density of the species prior to the execution of restoration measures (Figures 3 and 4). The weight of locomotion type was derived from the effect analysis during the execution phase (Figure 3). Locomotion types related to a low survival of individuals (sprawler, burrower, clinger and crawler) were given a low value (1) and locomotion types related to a higher survival (swimmer and skater) a high value (3). The locomotion type “Skater” was assumed to affect survival of individuals in a similar way as the type “Swimmer”. Furthermore, species with a terrestrial adult stage during the execution of restoration measures were assumed to be the least influenced and were given the highest value (4). For each species the locomotion values for juveniles and adults were calculated as the average weight of the locomotion types. Densities of species in samples taken before measures were carried out were pooled per site and log-transformed ($10 \times \log(\text{average density prior to restoration} + 1)$) in order to normalize the data. Cross table C consists of 250 species-site combinations, their log-transformed starting density and their locomotion type as adult as well as juvenile.

The regular use of ordination techniques is to analyse variation in species composition in a set of samples and identify correlations with environmental variables. In this study ordination techniques are used for a different purpose, i.e. to identify correlations between biological traits and the performance of species. Instead of the normal “species data”, listing the distribution of species in a set of samples, cross table A was used, listing the distribution of traits in a set of species. Cross table B containing data on the performance of the species was used instead of the normal “environmental data”, describing the environmental conditions at the study sites. This part of the analysis requires data on species’ performance during the recovery phase. However, the observed changes in species density (cross table B) as measured before and after restoration measures are the combined effect of the execution and the recovery phase. Therefore it is necessary to include a step that eliminates the variation in the data resulting from the execution phase and allows the analysis of the species’ performance during the recovery phase separately. For this reason variables explaining survival during the execution phase (cross table C) were included as co-variables in the analysis.

In order to identify correlations between the variation in traits and the performance of species an indirect analysis (principal components analysis PCA or correspondence analysis CA) was chosen, because it does not constrain the variation data to the measured species' performance as a direct analysis (redundancy analysis RDA or canonical correspondence analysis CCA) would. In addition, a direct analysis was performed, because it allows these correlations to be tested for their significance (Monte Carlo resampling procedure (500 permutations)).

Because of the large number of species-site combinations and biological traits, the variation in the dataset was expected to be large suggesting a unimodal response curve. This was confirmed in a preliminary detrended correspondence analysis performed in Canoco for Windows version 4.0 (Ter Braak & Šmilauer 1998) which revealed a length of gradient larger than 2.5, indicating that a CA was suitable for data analysis. Therefore, co-occurring biological traits were distinguished and correlated with species' performance using a CA and their significance was tested in a CCA.

In the correspondence analysis the variation in the data is described by Canoco on four ordination axes, with the first axis describing most variation, followed by the second, third and fourth. In order to determine the affinity of the biological traits with the species' performance, classes of biological traits were assigned to the nearest category of density change in the four-dimensional ordination space. Distances between ordination scores of classes of biological traits and scores of categories of density changes were calculated, where the scores were weighted for the amount of variance explained by the four CA-axes calculated by Canoco (Equation 1) with: D_{X-Y} = Distance between class of biological trait X and density change category Y, V_i = Amount of variance explained by axis i, T_{iX} = Score of class of biological trait X on axis i, D_{iY} = Score of density change category Y on axis i. The percentage of variance explained in the distribution of biological traits by the four ordination axes was 12.9, 11.4, 9.2 and 8.2%, respectively.

$$D_{X-Y} = \sqrt{(V_1 \times (T_{1X} - D_{1Y}))^2 + (V_2 \times (T_{2X} - D_{2Y}))^2 + (V_3 \times (T_{3X} - D_{3Y}))^2 + (V_4 \times (T_{4X} - D_{4Y}))^2} \quad (\text{eq. 1})$$

A cluster analysis was performed on the distribution of biological traits over the species in order to visualise the co-occurrence of traits and facilitate the interpretation of the previous analysis. The cluster analysis was performed using Twinspan (Hill 1979).

Execution and recovery phases combined

A list of macroinvertebrate species characteristic of shallow softwater lakes in the Netherlands was obtained from Arts (2000). Arts (2000) describes a characteristic species as a species which occurs more often in shallow softwater lakes than in other water types. A Wilcoxon signed ranks test was used to test if the number of observed characteristic species changed significantly. Relative differences in species' performance between characteristic and non-characteristic species were tested with a χ^2 -test.

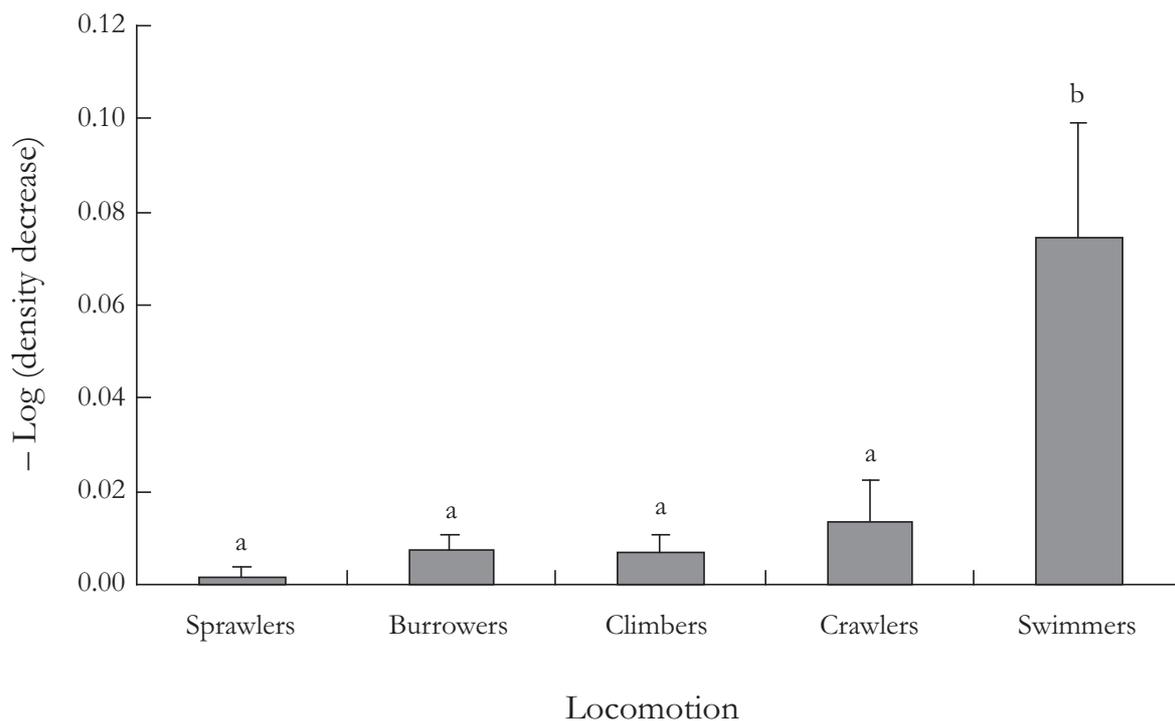


Figure 3 Chance of survival (+SE) in relation to locomotion of macroinvertebrates in lake IJsbahn. Chance of survival is calculated as the $-\log ((\text{density 1 week before restoration} - \text{density 1 week after restoration}) / \text{density before restoration})$. Different letters (a and b) indicate significant differences (Student *t*-test, $P < 0.05$) in the response of locomotion types on restoration measures. Total macroinvertebrate density decreased from 12,436 to 163 individuals m^{-2} .

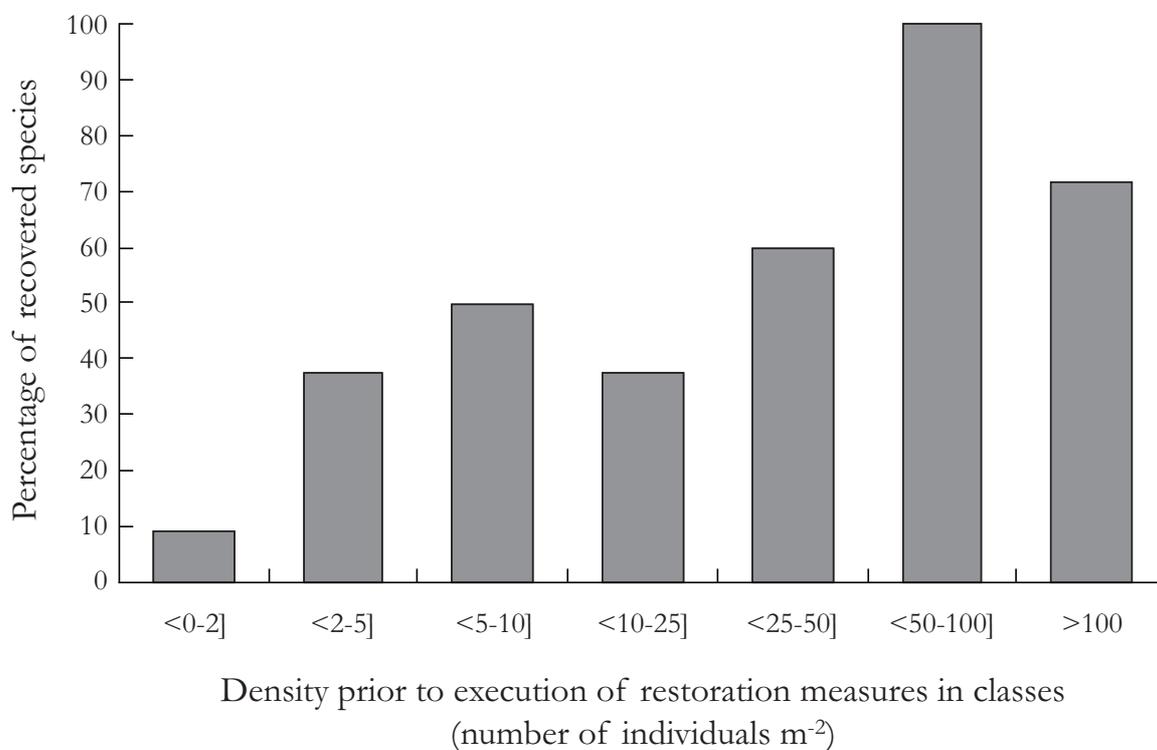


Figure 4 Relation between the number of recovered species in lake IJsbahn and their density prior to restoration. Number of recovered species is expressed in different densities classes (individuals m^{-2}) and is calculated as the percentage of species recorded before restoration that was also recorded after restoration.

Results

One hundred and sixty nine species were identified in this study (Oligochaeta: 6, Hirudinea: 6, Mollusca: 9, Crustacea: 1, Araneae: 1, Hydracarina: 20, Chironomidae: 24, Chaoboridae: 4, Dixidae: 2, Cylindrotomidae: 1, Ephemeroptera: 4, Trichoptera: 8, Neuroptera: 1, Megaloptera: 1, Heteroptera: 25, Coleoptera: 40 and Odonata: 16 species) of which fourteen were characteristic (Table 3).

Execution phase

During the execution phase, abundance of aquatic macroinvertebrates decreased with 99.7% in Lake Ijsbaan. Species in lake Ijsbaan were not equally affected by the restoration activities. Species that were able to swim had a significantly higher chance to survive compared to species with other types of locomotion (Figure 3), indicating that the ability to evade the restoration machinery is important for the survival of macroinvertebrates during this phase. Of the 50 species that were recorded 1 week before restoration measures were taken, only 20 could be recovered one week after measures were taken. The chance of recovering a species showed a significant positive correlation (Spearman correlation, $P = 0.013$) with the density of the species prior to the execution of restoration measures (Figure 4), indicating that abundant species have a higher survival chance than scarce species.

Recovery phase

The categories of changes in species densities “Not recovered” and “New” as well as “Decreased” and “Increased” were plotted opposite of each other and both groups (not recovered/new and decreased/ increased) were plotted perpendicular to each other on the first and second CA-axis (Figure 5). The categories of species densities changes “Not recovered” and “Decreased” correlated significantly (Monte Carlo resampling procedure, $P = 0.016$ and 0.048 , respectively) with the variation in biological traits. After omission of these two variables the category “New” also correlated significantly with the first CCA-axis (Monte Carlo resampling procedure, $P = 0.012$).

Species that were not recovered or decreased in abundance after restoration measures were taken, are mainly semi- or univoltine and reproduce sexually, preventing them from a rapid build up of their numbers (Table 1). They require special habitat features for ovipositing (aquatic or terrestrial vegetation) and nutrients (animal food sources). They also prefer to inhabit swards of vegetation. Other biological traits associated with a negative reaction of species to restoration measures are the ability to fly and respiration by spiracles and ventilation. Biological traits dominating in species that increased in abundance or newly appeared in the treated lakes enable them to rapidly increase their numbers (multiple generations per year, asexual reproduction). Classes of parental care that make a species independent on special habitat features for ovipositing (ovovivipary, depositing of eggs on water surface and solid substrates) are associated with species increasing in abundance. Species profiting from restoration measures inhabit organic sediments, bare sand, host species or have no particular habitat preference. Furthermore, they utilize readily available food such as detritus, algae and terrestrial food sources. Other biological traits associated with a positive reaction of species to restoration measures are the absence of the ability to fly and respiration by lungs and tegument.

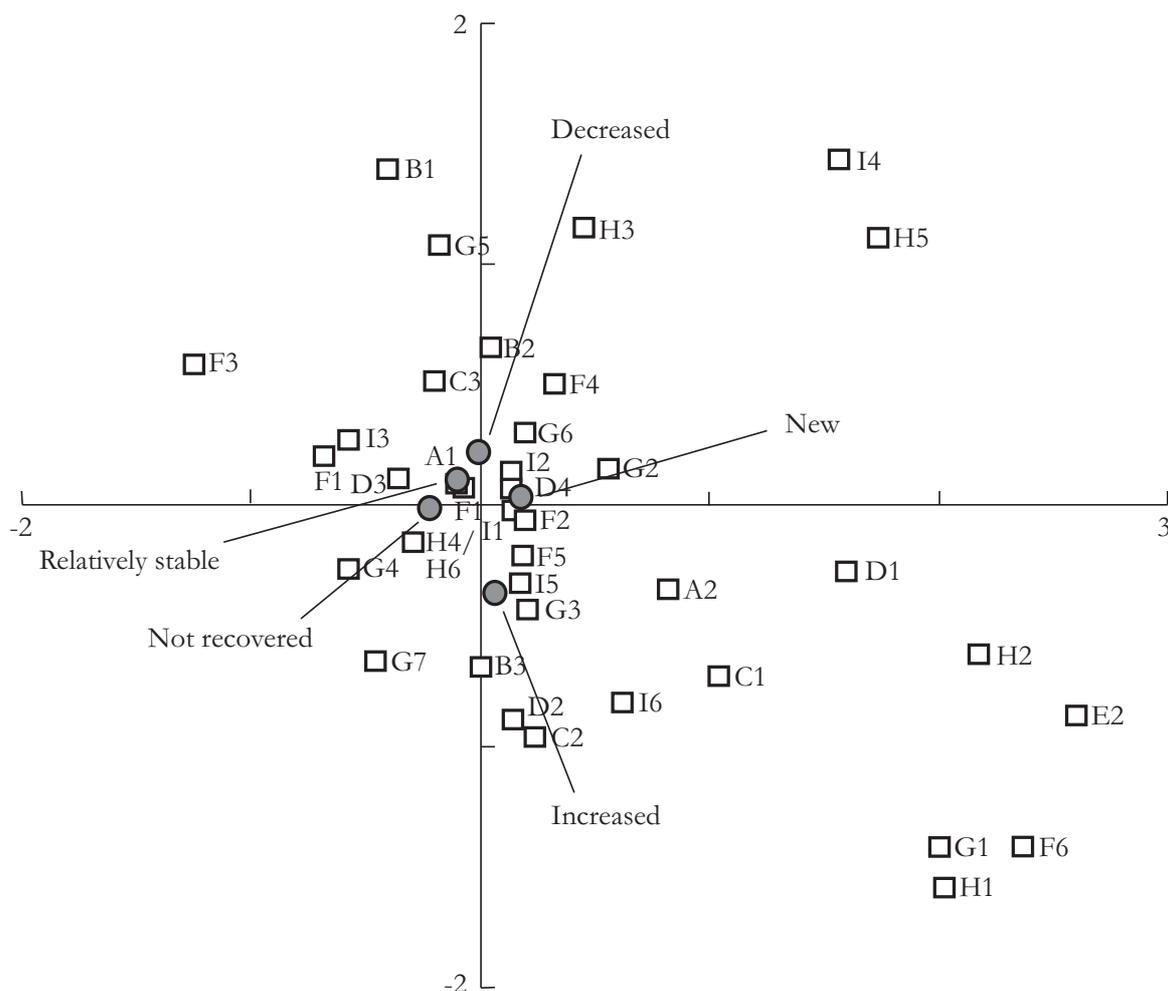


Figure 5 Plot of the first two axes of the correspondence analysis of biological traits. Squares and codes represent classes of biological traits (Table 2): flight capability (A), preferred life history (B), diet of juveniles (C), diet of adults (D), reproduction (E), parental care (F), respiration of juveniles (G), respiration of adults (H) and preferred habitat (I). Changes in the density of species are plotted as open circles: species found only before restoration (“Not recovered”), species with a density decrease of more than 25% (“Decreased”), species with a density change of less than 25% (“Relatively stable”), species with a density increase of more than 25% (“Increased”) and species found only after restoration (“New”).

Nearly all predictions for changes in species densities for the biological traits diet, habitat, parental care, life history and reproduction were confirmed (Table 1). Mainly species with different classes for flight capacity and respiration did not react to restoration measures as predicted. The reason that not all predictions were confirmed is because classes of biological traits were not randomly distributed across species. Species with similar biological traits were grouped together in clusters (Table 2). Flight ability and respiration through spiracles, both expected to induce an increase in abundance, co-occurred with sexual reproduction, which was expected to decrease. The decrease in abundance of species capable of flight may also be induced by carnivory and ovipositing in vegetation, which both occurred solely in flight capable species. Whereas species, unable to fly and breathing by gills or lungs, often featured traits that were expected to induce an increase in abundance (detritivory and asexually reproduction).

Table 2 Co-occurrence of biological traits.

Biological trait	Classes	Code	Cluster										
			I	II	III	IV	V	VI	VII	VIII			
Preferred life history	Semivoltine	B1	0.4										
Diet adults	Irrelevant (adults terrestrial)	D4	1.0	1.0									
Respiration juveniles	Ventilation	G5	0.5	0.1									
Preferred habitat	Aerobic organic matter	I5	0.4	0.3				0.03					
Parental care	Eggs on surface	F5	0.3	0.8		0.04							
Preferred habitat	Anaerobic sediment	I2		0.1									
Preferred habitat	Bare sand	I6		0.1									
Respiration juveniles	Tegument	G3		0.6	0.8				0.2				
Diet juveniles	Detritus	C1		0.6							1.0	0.7	
Respiration juveniles	Gills	G2	0.6	0.2	0.2			1.0					1.0
Preferred life history	Multivoltine	B3		0.8	1.0	1.0	0.03						0.4
Diet juveniles	Plants	C2	0.1	0.6	1.0	0.4	0.1				0.7	0.7	
Preferred habitat	Vegetation	I3	0.7	0.2				0.3					
Flight	Flight	A1	1.0	1.0	1.0	1.0	0.9	0.8					
Reproduction	Sexually	E1	1.0	1.0	1.0	1.0	1.0	1.0	1.0	0.7	0.1		
Respiration adults	Spiracles	H4	1.0	1.0	1.0	1.0	1.0						
Respiration adults	Respiration air	H6	1.0	1.0	1.0	1.0	1.0						
Parental care	Ovoviviparous	F6		0.03							0.3		
Diet adults	Plants	D2			1.0	0.4	0.1	0.1	0.7	0.7			
Respiration juveniles	Respiration air	G7		0.1		0.6	0.3						
Parental care	Eggs in/on vegetation	F1	0.5		0.8	0.1	0.3						
Parental care	Eggs on solid substrate	F2	0.3	0.8	0.2	0.9	0.6	0.9	0.7	0.9			
Respiration juveniles	Respiration aquatic	G6	1.0	0.9	1.0	0.4	0.7	1.0	1.0	1.0			
Diet juveniles	Animal	C3	1.0	0.4		0.6	1.0	1.0					
Preferred habitat	Indifferent	I1	0.2	0.4	1.0	1.0	0.7	1.0	1.0	1.0			
Preferred life history	Univoltine	B2	0.7	0.2				1.0	1.0	1.0	0.6		
Diet adults	Animal	D3				1.0	0.9	0.8					
Respiration juveniles	Spiracles	G4		0.1		1.0	0.9						
Parental care	Eggs fixed terrestrial	F3					0.1						
Parental care	Eggs on adult	F4					0.03	0.1			0.1		
Respiration adults	Tegument	H3						0.2					
Preferred habitat	Host	I4						0.8					
Respiration adults	Respiration aquatic	H5						1.0	1.0	1.0			
Flight	Flightless	A2				0.04	0.1	0.2	1.0	1.0			
Diet adults	Detritus	D1				0.04	0.1	0.1	1.0	0.7			
Reproduction	Asexually	E2								0.3	0.9		
Respiration juveniles	Lung	G1								1.0			
Respiration adults	Lung	H1								1.0			
Respiration adults	Gills	H2										1.0	
Number of species			20	38	6	25	34	25	3	7			

The clusters are groups of species exhibiting a high similarity in biological traits. Clusters and traits are ordered in a way that clusters with a high similarity and frequently co-occurring traits are close together in the table. Numbers indicate the relative number of species within the cluster that features the biological trait.

Execution and recovery phases combined

Species characteristic of softwater lakes were found in all study sites prior to restoration (Table 3). After restoration measures were taken the number of characteristic species did not increase significantly (Wilcoxon signed ranks test, $P = 0.102$). Many characteristic species, recorded after restoration measures were carried out (16 out of 19), were not encountered before restoration, indicating an ability to rapidly increase in abundance

either by reproduction or by colonisation. However, characteristic species present before restoration appear to be negatively affected by restoration measures as most of them (9 out of 12) were not recorded after measures were taken.

Relative numbers of species recorded only before, before and after or only after restoration measures were carried out differed for characteristic and non-characteristic species (Figure 6). Species composition of non-characteristic species was more stable

Table 3 Changes in presence of aquatic invertebrates characteristic for softwater lakes.

Taxa	Ijsbaan	Verwolde	Grenspoel	Wijnjeterperschar
Heteroptera				
<i>Arctocorisa germari</i> (Fieber, 1848)			-	+
<i>Cymatia bonsdorffii</i> (CR Sahlberg, 1819)	+	=	+	+
<i>Glaenocorisa propinqua</i> (Fieber, 1860)			-	+
<i>Notonecta obliqua</i> Thunberg, 1787		+	+	
<i>Notonecta viridis</i> Delcourt, 1909	+		+	
<i>Sigara scotti</i> (Douglas & Scott, 1868)	+		=	+
Coleoptera				
<i>Agabus labiatus</i> (Brahm, 1790)			+	
<i>Helochares punctatus</i> Sharp, 1869	-		=	-
<i>Rhantus suturellus</i> (Harris, 1828)			+	
Odonata				
<i>Coenagrion lunulatum</i> (Charpentier, 1840)				+
Trichoptera				
<i>Holocentropus dubius</i> (Rambur, 1842)				-
Chironomidae				
<i>Polypedilum uncinatum</i> (Goetghebuer, 1921)	+	-	-	-
<i>Telmatopelopia nemorum</i> (Goetghebuer, 1921)				-
<i>Zalutschia humphresiae</i> (Dowling & Murray, 1980)			+	

-, = and +: species was recorded only before, before and after or only after restoration measures were carried out, respectively.

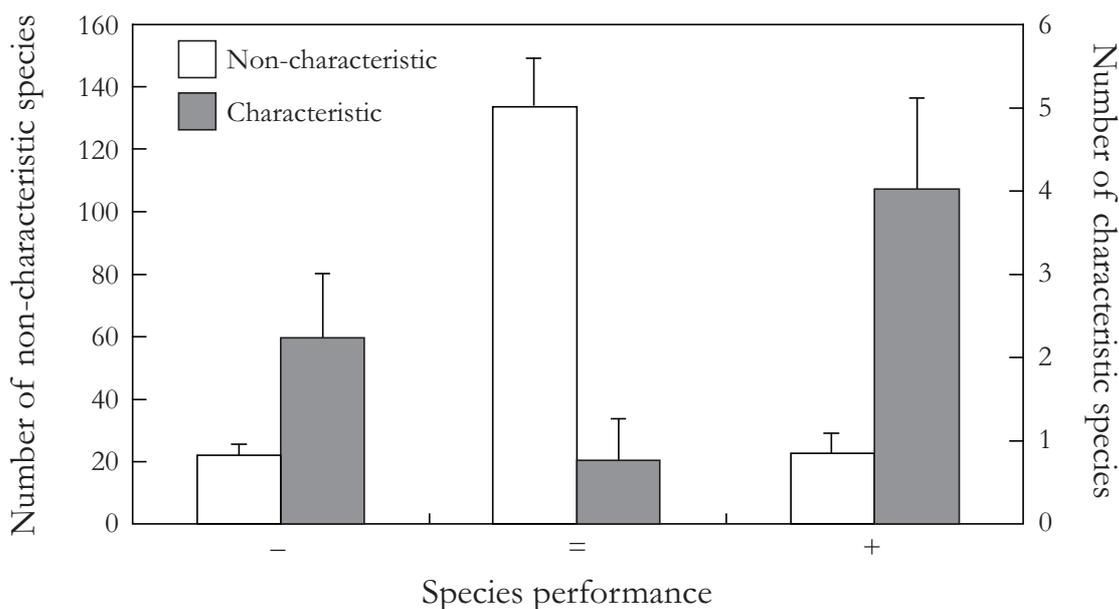


Figure 6 Number of characteristic and non-characteristic species (+ SE) that were recorded only before (-), before and after (=) or only after restoration measures were carried out (+).

than that of characteristic species. I.e. characteristic species, recorded before restoration measures were taken, had a significantly higher chance of not being recorded after restoration, compared to non-characteristic species (χ^2 -test, $P < 0.005$). The relative number of characteristic species observed only after restoration, on the other hand, was higher than that of non-characteristic species (χ^2 -test, $P < 0.01$).

Discussion

Biological traits as a tool for understanding ecological change

Biological traits were used to analyse changes in species abundance and community composition. Results suggest that this approach is suitable for understanding changes in species assemblages during different phases of softwater lake restoration (Figures 3 and 5 and Table 1). Even though the studied lakes differed in morphology, vegetation composition, water quality and in the way the restoration measures were carried out (Van Kleef & Esselink 2004b), the analysis still produced significant results supporting our hypothesis, indicating that this method is very robust. The same approach has also been applied in order to explain and predict the distribution of aquatic macroinvertebrates in the Rhône basin (Juget & Lafont 1994, Richoux 1994, Tachet et al. 1994, Usseglio-Polatera 1994). These studies tested the habitat templet concept, that postulates that species are adapted through biological traits to the spatial and temporal variability in the habitat. Their results, however, only partly confirmed their predictions. Understanding differences in invertebrate community structure between different habitats requires detailed knowledge of the habitats and the adaptations of species to physical, chemical and biological conditions. For example, distasteful secretions from skin glands in water mites are an adaptation against predation (Kerfoot 1982). However, the functionality of this adaptation depends on the predators present as it only protects against fish but not against water bugs, that feed on body fluids. Furthermore, a restriction imposed by the habitat may be tackled by different adaptations (e.g. some dragonflies avoid predation by burrowing in the sediment, while water mites excrete toxins) or prevent a positive response of a trait that otherwise would have been successful in the habitat. The latter possibly occurred in this study, where flight ability and respiration did not react as predicted. They were probably overruled by traits that induced a different response in species.

The analysis of biological traits in this study yielded satisfactory results for two reasons. (1) Species assemblages before and after restoration measures were compared within water bodies instead of comparing differences between study sites. Hereby, the number of factors involved in structuring the communities (e.g. local species pool, site area, depth) is strongly reduced. This also allowed for the analysis of different effects caused by the same disturbance, i.e. it was possible to separate processes in the execution as well as in the recovery phase. (2) The habitat changes resulting from large scale restoration measures are so pronounced and influential in structuring the species assemblage that the level of detail required from the ecological knowledge is limited. I.e. in this study data on morphology and life history were sufficient for interpretation and no data on physiology, behaviour and species interactions were needed. Understanding of the changes in species assemblages resulting from restoration measures would have been more complicated when the measures had induced a more gradual change in habitat or when the lakes would have had more time to recover.

Response of macroinvertebrates to restoration

This study shows that the macroinvertebrate assemblage is selectively impoverished by the way restoration measures are being carried out nowadays. Restoration measures erect multiple filters (Tonn 1990, Poff 1997) through which species have to pass in order to maintain their population. These filters can be separated in two categories, each posing restrictions on a different set of biological traits. The first set of filters is in operation during the execution phase, at the moment that restoration measures are taken. It is applied when the water table is lowered and animals are removed along with the accumulated organic matter and macrophytes. As a result, the abundance of all species seriously decreases. However, species that are able to swim are less susceptible to restoration measures than species with a low mobility in the water layer. The lower mortality of swimming species is probably the result of their ability to reach the relative safety of the small pools of waters that remain after lowering of the water table. High mortality may result in the complete disappearance of species. Especially species occurring in low densities have a high chance of being removed along with the organic matter entirely. These species often include relict populations of characteristic species, the very same species that the restoration efforts are meant to preserve.

Although the effects of a strongly reduced population size could not be determined in this study, it theoretically may decrease the persistence of the species in a number of ways. Isolated populations consisting of a small number of individuals have an increased vulnerability to inbreeding depression (Charlesworth & Charlesworth 1987), demographic factors (Menges 1991), such as mortality by chance (Reed et al. 2003), dispersal (Rohani et al. 1996) and the Allee-effect (Boukal & Berec 2002, Engen et al. 2003).

The second set of filters applies to species that have survived the execution phase and have to complete their life cycles under the newly created conditions (recovery phase). We hypothesized that species will experience problems completing their life cycles when they depend on specific conditions to be present in the lake. Our predictions were confirmed in 25 out of 39 cases. Species that require specific habitat features for ovipositing (aquatic or terrestrial vegetation), nutrients (animal food sources) and habitats (swards of vegetation) decline or disappear after restoration measures have been taken. Classes of biological traits are not randomly distributed (Table 2). I.e. biological traits that were expected to influence the performance of species in opposite ways coincided and clustered together in the ordination analysis. This may have been the reason why species with different classes for the biological traits respiration and flight capability did not react to restoration measures as predicted. Negative responses induced by delicate respiratory systems (e.g. lungs and gills in water snails) were compensated through asexual reproduction and detritivory. Positive responses resulting from flight ability were negated by food (carnivory) and parental care bottlenecks (ovipositing in vegetation).

Long term perspectives for macroinvertebrates

Due to the restrictions put on the performance of specific biological traits during the process of restoration, the abundance of many species declined and most characteristic species were not recorded again after restoration. It cannot be excluded that these species were still present in the lakes and have been missed during sampling as a result of their reduced numbers. And as many species depend on aquatic vegetation, they may recover in time as the vegetation recovers. However, due to wind action and restored nutrient limitation the lakes can remain in a pioneer stage for hundreds of years (Brouwer 2001)

and development of later successional vegetation and the recovery of accompanying fauna species may take a long time. The disappearance of species as a consequence of restoration efforts along this path has been recorded in the Netherlands for a number of rare and characteristic dragonflies, e.g. *Coenagrion hastulatum* Charpentier, 1985 and *Aeshna subarctica* Walker, 1908 (pers. comm. R Ketelaar).

Even when species are not able to pass through the multiple filters imposed on them by restoration measures, their survival on the long term is not necessarily endangered if they are able to recolonise the restored lakes. In fact the number of observed characteristic species increased relatively faster than the number of other species (Figure 6), indicating a good colonisation capacity and/or ability to increase their numbers through reproduction. However, shallow softwater lakes in the Netherlands have a long history of degradation and habitat fragmentation resulting from land reclamation, acidification, eutrophication and the loss of natural and anthropogenic dynamics (Arts & Leuven 1988). At present, there are no intact softwater lakes left and many characteristic species have become very rare and their remaining populations small (Leuven et al. 1987, Leuven 1988). Furthermore, in some characteristic macroinvertebrate species, most of the specimens have a poorly developed flight musculature, e.g. the water beetle *Hygrotus novemlineatus* (Stephens, 1829) (Jackson 1956). These species are unlikely to cover the large distances required to colonise the restored waters. Restoration efforts in fragmented landscapes should therefore not only focus on restoring ecosystem functions, but also on preserving remaining relict populations and (re)creating suitable habitats.

Management implications

The problem of declining and disappearing characteristic fauna species as a result of restoration measures most likely is not limited to softwater lakes. In many other ecosystems similar restoration measures are being taken (e.g. restoring meanders in streams, sod cutting of heather, rewetting of raised bogs, etc.). These measures are often carried out on a large scale and may result in strong disturbances and the (temporary) disappearance of advanced successional stages. Van Duinen et al. (2003) demonstrated that large scale rewetting measures in raised bog remnants benefit only a limited number of characteristic species. Degraded bog remnants still harboured many characteristic bog species. They attributed the limited species spectrum of treated locations to a decrease in habitat diversity resulting from the large scale at which the measures were taken. They argue that restoration measures should not only focus on restoring a single aspect of the ecosystem (in their case hummock-hollow vegetation types). The preservation and restoration of the whole array of habitats associated with an ecosystem must become the objective of restoration efforts, as many animal species depend on these habitats or on a combination of them (Verberk et al. 2001, 2002, Smits et al. 2002, Van Duinen et al. 2003). Their argumentation also holds true for the restoration of softwater lakes, which at the moment mainly focuses on restoring physico-chemical conditions for early pioneer communities dominated by isoetid plants.

What do the results of this study indicate for restoration management in shallow softwater lakes? Restoration measures are necessary in order to prevent the extinction of a large number of characteristic species. In fragmented landscapes, this goal is not reached the way measures are being carried out nowadays. Therefore, the measures have to be adjusted in order to ensure the survival of relict populations during the process of restoration. Adjustments of restoration measures should decrease the number of

individuals that are being removed along with the organic matter and should not lead to an environment in which species are unable to complete their life cycles. Even though there is no actual experience in optimising restoration measures with respect to the preservation of relict populations, there are several intuitively feasible alternatives. Temporary storage of removed organic matter on the shores of the lake facilitates the return to the water of species that are large and mobile, hereby reducing their initial mortality. By preserving parts of the original vegetation, refuges are created for less mobile species and it enables species that rely on vegetation to complete their life cycles. The best chances of survival for species will be provided by phasing the restoration measures in space and time. Verberk et al. (2001) and Van Duinen et al. (2003) also recommended phasing of restoration measures for raised bog remnants and complex landscapes. One part of the lake is restored, while the other part remains untreated until the characteristic species have colonised the restored part. It is important to divide the lake in compartments in order to prevent the redistribution of excess nutrients. In order to counteract habitat fragmentation, lakes can be created close to populations of characteristic species or on locations where they have been lost to land reclamation.

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References

- Arts GHP (2000) Natuurlijke levensgemeenschappen van de Nederlandse binnenwateren deel 13, Vennen. Achtergronddocument bij het "Handboek Natuurdoeltypen in Nederland". *Expertisecentrum LNV, Ministerie van Landbouw, Natuurbeheer en Visserij, Ede.*
- Arts GHP & Leuven RSEW (1988) Floristic changes in shallow softwaters in relation to underlying environmental factors. *Freshwater Biology* **20**: 97-111.
- Bloemendaal FHJL & Roelofs JGM (Eds.) (1988) Waterplanten en waterkwaliteit. *Uitgeverij KNNV, Utrecht.*
- Boukal DS & Berec L (2002) Single-species models of the Allee effect: Extinction boundaries, sex ratios and mate encounters. *Journal of Theoretical Biology* **218**: 375-394.
- Brouwer E (2001) Restoration of atlantic softwater lakes and perspectives for characteristic macrophytes. *Thesis, Radboud University, Nijmegen.*
- Brouwer E & Roelofs JGM (2001) Degraded softwater lakes: possibilities for restoration. *Restoration Ecology* **9**: 155-166.
- Charlesworth D & Charlesworth B (1987) Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology and Systematics* **18**: 237-368.
- Engen S, Lande R & Saether BE (2003) Demographic stochasticity and allee effects in populations with two sexes. *Ecology* **84**: 2378-2386.
- Foggo A, Rundle SD & Bilton DT (2003) The net result: evaluating species richness extrapolation techniques for littoral pond invertebrates. *Freshwater Biology* **48**: 1756-1764.

- Haines TA (1981) Acidic precipitation and its consequences for ecosystems: a review. *Transactions of the American Fisheries Society* **110**: 669-707.
- Henrikson L, Olofsson JB & Oscarson HG (1982) The impact of acidification on Chironomidae (Diptera) as indicated by subfossil stratification. *Hydrobiologia* **86**: 223-229.
- Hill MO (1979) TWINSPAN - a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. *Cornell University, Ithaca, New York*.
- Jackson DJ (1956) The capacity for flight of certain water beetles and its bearing on their origin on the western Scottish Isles. *Proceedings of the Linnean Society of London, London* **167**: 76-96.
- Juget J & Lafont M (1994) Theoretical habitat templates, species traits, and species richness: aquatic oligochaetes in the upper Rhône River and its floodplain. *Freshwater Biology* **31**: 327-340.
- Kerfoot WC (1982) A question of taste: crypsis and warning coloration in freshwater zooplankton communities. *Ecology* **63**: 538-554.
- Lamers LPM, Van Roozendaal SME & Roelofs JGM (1998) Acidification of freshwater wetlands: combined effects of non-airborne sulfur pollution and desiccation. *Water, Air, and Soil Pollution* **105**: 95-106.
- Lamers LPM, Smolders AJP & Roelofs JGM (2002) The restoration of fens in the Netherlands. *Hydrobiologia* **478**: 107-130.
- Leuven RSEW (1988) Impact of acidification on aquatic ecosystems in the Netherlands. *Thesis, Radboud University, Nijmegen*.
- Leuven RSEW, Van der Velde G, Vanhemelrijk JAM & Eeken RLE (1986) Impact of acidification on the distribution of aquatic insects in lentic softwaters. *Proceedings of the 3rd European Congress of Entomology, Dutch Entomological Society, Amsterdam*: 103-106.
- Leuven RSEW, Van der Velde JA, Vanhemelrijk JAM & Van der Velde G (1987) Impact of acidification on chironomid communities in poorly buffered waters in the Netherlands. *Entomologica Scandinavica Supplements* **29**: 269-280.
- Menges ES (1991) The application of minimum viable population theory to plants, in Falk D & Holsinger K (Eds.) *Genetics and Conservation of Rare Plants*. *Oxford University Press, New York*: 45-61.
- Nienhuis PH, Bakker JP, Grootjans AP, Gulati RD & De Jonge VN (2002) The state of the art of aquatic and semi-aquatic ecological restoration projects in the Netherlands. *Hydrobiologia* **478**: 219-233.
- Poff NL (1997) Landscape filters and species traits: towards a mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* **16**: 391-409.
- Ravera O (1986) The ecological aspects of acid deposition. *Experientia* **42**: 329-588.
- Reed DH, O'Grady JJ, Brook BW, Ballou JD & Frankham R (2003) Estimates of minimum viable population sizes for vertebrates and factors influencing those estimates. *Biological Conservation* **113**: 23-34.
- Resh VH, Hildrew AG, Statzner B & Townsend CR (1994) Theoretical habitat templates, species traits and species richness: a synthesis of long-term ecological research on the upper Rhône River in the context of concurrently developed theory. *Freshwater Biology* **31**: 539-554.
- Richoux P (1994) Theoretical habitat templates, species traits, and species richness: aquatic Coleoptera in the upper Rhône River and its floodplain. *Freshwater Biology* **31**: 377-395.
- Roelofs JGM (1983) Impact of acidification and eutrophication on macrophyte communities in softwaters in the Netherlands. I. Field observations. *Aquatic Botany* **17**: 139-155.
- Rohani P, May RM & Hassell MP (1996) Metapopulations and equilibrium stability: the effects of spatial structure. *Journal of Theoretical Biology* **181**: 97-109.
- Scarsbrook MR & Townsend CR (1993) Stream community structure in relation to spatial and temporal variation: a habitat template study of two contrasting New Zealand streams. *Freshwater Biology* **29**: 395-410.
- Smits MJA, Van Duinen GA, Bosman JG, Brock AMT, Javois J, Kuper JT, Peeters TMJ, Peeters MAJ & Esselink H (2002) Species richness in a species poor system: aquatic macroinvertebrates

- of Nigula Raba, an intact raised bog system in Estonia. *Proceedings of the international Peat Symposium, Pärnu*: 283-291.
- Southwood TRE (1977) Habitat, the templet for ecological strategies? *Journal of Animal Ecology* **46**: 337-365.
- Tachet H, Usseglio-Polatera P & Roux C (1994) Theoretical habitat templets, species traits, and species richness: Trichoptera in the upper Rhône River and its floodplain. *Freshwater Biology* **31**: 397-415.
- Ter Braak CJF & Šmilauer P (1998) CANOCO Reference Manual and User's Guide to Canoco for Windows: Software for Canonical Community Ordination (Version 4). *Microcomputer power, Ithaca, New York*.
- Tonn WM (1990) Climate change and fish communities: a conceptual framework. *Transactions of the American Fisheries Society* **119**: 337-352.
- Usseglio-Polatera P (1994) Theoretical habitat templets, species traits, and species richness: aquatic insects in the upper Rhône River and its floodplain. *Freshwater Biology* **31**: 417-437.
- Van der Hammen H, Claassen THL & Verdonschot PFM (1984) Handleiding voor hydrobiologische milieu-inventarisatie. *Interprovinciale Ambtelijke Werkgroep Milieu-inventarisatie, subwerkgroep Hydrobiologie, Haarlem*.
- Van Duinen GA, Brock AMT, Kuper JT, Leuven RSEW, Peeters TMJ, Roelofs JGM, Van der Velde G, Verberk WCEP & Esselink H (2003) Do restoration measures rehabilitate fauna diversity in raised bogs? A comparative study on aquatic macroinvertebrates. *Wetlands Ecology and Management* **11**: 447-459.
- Van Kleef H & Esselink H (2004a) Monitoring van abiotiek, vegetatie, dansmuggen en kokerjuffers in gerestaureerde zwakgebufferde oppervlaktewateren. Kolonisatie van diersoorten. *Expertisecentrum LNV, Ministerie van Landbouw, Natuur en Voedselkwaliteit, Ede*.
- Van Kleef H & Esselink H (2004b) Analyse van de effecten van herstelmaatregelen op watermacrofauna in zwakgebufferde oppervlaktewateren. Een vergelijkend onderzoek in vier vennen waar herstelmaatregelen zijn uitgevoerd. *Expertisecentrum LNV, Ministerie van Landbouw, Natuur en Voedselkwaliteit, Ede*.
- Van Kleef H & Esselink H (2005) Aquatic macroinvertebrates in deteriorated shallow softwater lakes undergoing restoration. Their abundances and biological traits. *Bargerveen Foundation, Department of Environmental Science, Radboud University, Nijmegen*.
- Verberk WCEP, Van Duinen GA, Peeters TMJ & Esselink H (2001) Importance of variation in watertypes for water beetle fauna (Coleoptera) in Korenburgerveen, a bog remnant in the Netherlands. *Proceedings Experimental and Applied Entomology, Dutch Entomological Society, Amsterdam* **12**: 121-128.
- Verberk WCEP, Brock AMT, Van Duinen GA, Van Es M, Kuper JT, Peeters TMJ, Smits MJA, Timan L & Esselink H (2002) Seasonal and spatial patterns in macroinvertebrate assemblages in a heterogeneous landscape. *Proceedings Experimental and Applied Entomology, Dutch Entomological Society, Amsterdam* **13**: 35-43.



Pumpkinseed sampling in a small stream in Limburg. The fishes are stunned by an electric pulse after which they can be caught. Foto: Wim Zweep.

Chapter 5

Pumpkinseed sunfish (*Lepomis gibbosus*) invasions facilitated by introductions and nature management strongly reduce macroinvertebrate abundance in isolated water bodies

Hein van Kleef, Gerard van der Velde, Rob Leuven & Hans Esselink

Abstract

The pumpkinseed sunfish, *Lepomis gibbosus*, originates from Eastern North America and was introduced to the Netherlands in 1902 as an aquarium and garden pond fish. At present the pumpkinseed is widely spread throughout the Netherlands and occurs in a variety of aquatic habitats. It is especially abundant in moorland pools, fishing ponds and urban waters. Strong population development of the pumpkinseed appears to be facilitated by nature management practices in existing ponds (the removal of accumulated organic matter and macrophytes) and by creating new ponds. These measures enhance suitable breeding habitats that are free of competitors and predators. Isolated waters harbouring pumpkinseed were more often situated close to human habitation and infrastructure than could be expected based on the distribution of randomly selected isolated waters, identifying introductions as an important dispersal mechanism. In order to minimize the chances of introductions, planning of nature management practices should be done at distances over 250 m from human habitation and 100 m from infrastructure. Macroinvertebrate abundance in pools populated by pumpkinseed was eighty three percent lower than in pools without pumpkinseed, probably due to opportunistic feeding and high pumpkinseed abundances. Currently there is little experience with pumpkinseed control. However, options to be explored include: decreasing depth of colonised waters by filling them with soil allowing them to occasionally dry up, introducing native competitors and predators and the use of biodegradable piscicides. In addition, limitation of the sale of pumpkinseed is required as well as public education on the consequences of introducing exotic species.

Introduction

The pumpkinseed sunfish, *Lepomis gibbosus* (Linnaeus, 1758), is native to the Atlantic Slope region of North America (Scott & Crossman 1973). At the end of the 19th century it was first imported in Europe for recreational fishery and as an aquarium and garden pond fish and now it is one of the most successfully introduced fish species (Holčik 1991, Garcia-Berthou & Moreno-Amich 2000). In the Netherlands, pumpkinseed have been bred in captivity since 1902 (Looijen 1948). Following its release, pumpkinseed were primarily restricted to interconnected running waters throughout the country (De Nie 1996), but were recorded from a few isolated waters (Leuven & Oyen 1987). Pumpkinseed abundance in running waters is generally low (Klaar et al. 2004, Hoogerwerf et al. 2005, This study). However, in recent years the species has been encountered with increasing frequency and in high abundance in isolated lentic waters and especially in moorland pools, that are subject to specific management aims.

Intact moorland pools are characterized by a sandy substrate, low alkalinity and low productivity due to carbon, phosphorus and nitrogen limitation. During the twentieth century many of these pools have been impacted by acidification and eutrophication (Arts & Leuven 1988, Leuven et al. 1992). Acidification initially enhanced dissolved CO₂ concentrations, thus removing carbon as a limiting factor for fast-growing plant species such as *Juncus bulbosus* L. and *Sphagnum* ssp. In many moorland pools primary production was further enhanced by agricultural run-off of phosphorus and deposition of airborne nitrogen. As ongoing acidification also decreased decomposition rates (Kelly et al. 1984, Leuven & Wolfs 1988), organic debris accumulated. These changes caused characteristic plant and animal species to decline or to disappear (Roelofs 1983, Leuven et al. 1986a,

1987, Arts & Leuven 1988, Arts et al. 1990). In order to counteract the effects of acidification and eutrophication in moorland pools (Brouwer & Roelofs 2001), management practices consisting of the removal of accumulated organic matter and macrophytes and the sod cutting of littoral shores have been implemented. This exposes bare mineral soils which facilitates the return of characteristic plant species.

Evidence of intentional release of non-native fish in Dutch moorland pools comes from repeated observations of common garden pond plants, such as *Ceratophyllum demersum* L. and *Azolla filiculoides* Lamk., in pools populated by pumpkinseed (unpublished data HH van Kleef). This indicates dumping of aquaria or garden pond contents, as these plant species cannot survive in these oligotrophic, low alkaline and often acidic waters. Humans have been demonstrated to be the main vector in the dispersal of non-native fish (Trombulac & Frissell 2000, Copp et al. 2005) and Copp et al. (2005) demonstrated that the likelihood of introduction is related to the accessibility of the pond. For the planning of nature management it is wise to select pools, that are least susceptible to introductions. Therefore, it is important to assess the accessibility and hereby the vulnerability of ponds to introductions.

The pumpkinseed is listed among the top ten introduced fish species with adverse ecological effects (Casal 2006). It has been reported to be responsible for the decline of other fish species (Welcomme 1988) as well as gastropods (Osenberg et al. 1992). Because of the importance of moorland pools for the conservation of native aquatic species, the aim of the present study was to assess the risk of pumpkinseed invasion and the ecological impact on native species in these waters. Our specific objectives were to: (1) test whether accessibility of Dutch isolated waters influenced the chance of pumpkinseed introductions; (2) examine if there was a relationship between pumpkinseed invasiveness and nature management practices and (3) assess the impact of pumpkinseed on fauna abundance.

Materials and methods

Distribution data

Distributional data of pumpkinseed were obtained from De Nie (1996), national and regional databases (i.e. Foundation RAVON, Dutch National Federation of Anglers and Natuurhistorisch Genootschap in Limburg), and by surveying biologists and nature managers. For each location identified, we documented whether the location was isolated or connected to other waters. For isolated sites data was obtained from terrain owners on management practices involved in habitat management and pumpkinseed control. Distinguished types of habitat management were: (1) removal of organic matter and macrophytes, (2) digging of pools, (3) sod cutting of shores and (4) no management. Isolated waters were further divided into moorland pools, meadow ponds, fishing and urban ponds and sand excavation pits. Pumpkinseed abundance was derived directly from the available databases or estimated based on the number of recorded specimens. Pumpkinseed abundance was divided into four categories (1 recorded specimen: rare, 2-4: frequent, 5 or more: abundant, number of fish not recorded: unknown). Twenty seven isolated waters were visited in 2007 in order to check the reported population status. These assessments were made during the breeding season (May and June) when territorial males guarding their nest are easily spotted (Figure 1). The census consisted of counting territorial male pumpkinseed along a 50 m stretch of shore. Data were converted into



Figure 1 Nests of male pumpkinseed sunfish (*Lepomis gibbosus*) on the shore of a dredged moorland pool.

categories: rare (1-5 territorial males), frequent (5-15 territorial males) and abundant (> 15 territorial males). Our census data revealed that abundance estimated from databases and other sources was accurate in 23 of 27 cases, whereas pumpkinseed abundance of four sites classified as “abundant” based on databases was classified as “rare” based on the 2007 census. For comparison of abundance in connected and isolated waters, we used all available data (databases, 2007 survey and other sources), whereas for the analyses of relationship between abundance and nature management, the confirmed data from the 2007 survey were used. Difference in pumpkinseed abundance between connected and isolated waters was tested with a χ^2 -test. A Kruskal-Wallis test was used to test for overall differences in abundance between different types of habitat management and χ^2 -tests were used to compare individual management types.

In order to assess the influence of accessibility of Dutch isolated waters on pumpkinseed introductions, the distance of colonised isolated waters to urban settlements as well as roads and paths was determined and compared with the distance to settlements and infrastructure of a random selection of 100 isolated waters, within a 10 km radius of the colonised waters. This 10 km radius was chosen to correct for the non-random distribution of isolated waters in the Netherlands and moorland pools, especially (Arts et al. 1989). Distances were measured from topographical maps (scale 1:25,000). For different distance intervals we calculated the percentage of water bodies falling into that interval. This was also done cumulative with increasing distance, in order to calculate the ratio between cumulative percentages of pumpkinseed waters and randomly selected water bodies. Differences in the distributions of isolated pumpkinseed waters and the randomly selected waters were tested on the cumulative number of water bodies using χ^2 -tests at 250 m from urban settlements and 100 m distance from roads or paths.

Environmental impact

To assess effects of pumpkinseed on fauna abundance, in May 2007 macroinvertebrates were sampled from eight pools, all of them heavily disturbed (dredged) or newly created. Four of these pools housed large populations of pumpkinseed (Kranenbroek-pool-1 (51°6'11.5" N, 5°54'57.5" E), Kranenbroek-pool-2 (51°6'11.5" N, 5°54'57.5" E), Haeselaarsbroek (51°4'27.9" N, 5°55'6.6" E), Uden-urban pond (51°40'29.8" N, 5°38'31.6" E)), whereas the other pools did not contain pumpkinseed (Nuenen-IJsbaan (51°29'7.6" N, 5°32'50.9" E), Banen (51°16'11.9" N, 5°47'56.2" E), Broekse Wiel-1 (51°43'46.1" N, 5°45'55.7" E), Broekse Wiel-2 (51°43'46.1" N, 5°45'55.7" E)). The pools were slightly acid to alkaline (pH between 5.2 and 9.6), oligotrophic (ortho-phosphate between 0.00 and 0.48 $\mu\text{mol l}^{-1}$ and total-N between 1.39 and 77.70 $\mu\text{mol l}^{-1}$) and their surface area ranged from 6.5 are to 2 ha. Pools without and with pumpkinseed did not differ in pH, alkalinity, NH_4^+ , NO_3^- and surface area (Mann-Whitney U tests). Ortho-phosphate was higher in pools without pumpkinseed (average 0.37 $\mu\text{mol l}^{-1}$) compared to pools with pumpkinseed (average 0.01 $\mu\text{mol l}^{-1}$), but still oligotrophic ($< 0.5 \mu\text{mol l}^{-1}$). Sampling was done using a 20 \times 30 cm pond net with 0.5 mm mesh size. At each site macroinvertebrates were sampled using a stratified random sampling procedure. Sampling effort per pool was 1.5 m². Samples were transported to the laboratory and stored at 4°C to minimize mortality. Samples were washed over three sieves with 2, 1, and 0.5 mm mesh sizes, respectively and sorted in white trays within two days after sample collection and preserved until identification. Macroinvertebrates were identified to the level of family in the case of Diptera or order in the case of other Insecta, Isopoda, Tricladida, Gastropoda, Hirudinea, Oligochaeta, Araneida and Acarina. Differences in densities of taxa at sites with and without pumpkinseed were tested with Mann-Whitney U tests.

In order to determine if observed differences in densities of taxa in sites with and without pumpkinseed could be explained by pumpkinseed predation, we examined the diet of pumpkinseed in a Dutch moorland pool. In autumn 2003, during an attempt to remove all the pumpkinseed from the moorland pool Rauwven (51°35'3.1" N, 5°37'43.0" E), 18 specimens from three different size classes (total length ranges 4.9-5.8, 8.8-9.7 and 11-13 cm) were collected. Their intestines were extracted and examined for remains of prey, which were identified to the level of family in the case of Diptera, order in the case of other Insecta and Arachnida or class in the case of Collembola.

Results

Pumpkinseed distribution, abundance and relation with human settlements and activities

The pumpkinseed is widely distributed in the Netherlands, especially in the southern part of the country (Figure 2). It has been recorded from 69 interconnected waters and 42 isolated water bodies (Table 1). In contrast to connected waters, pumpkinseed were more

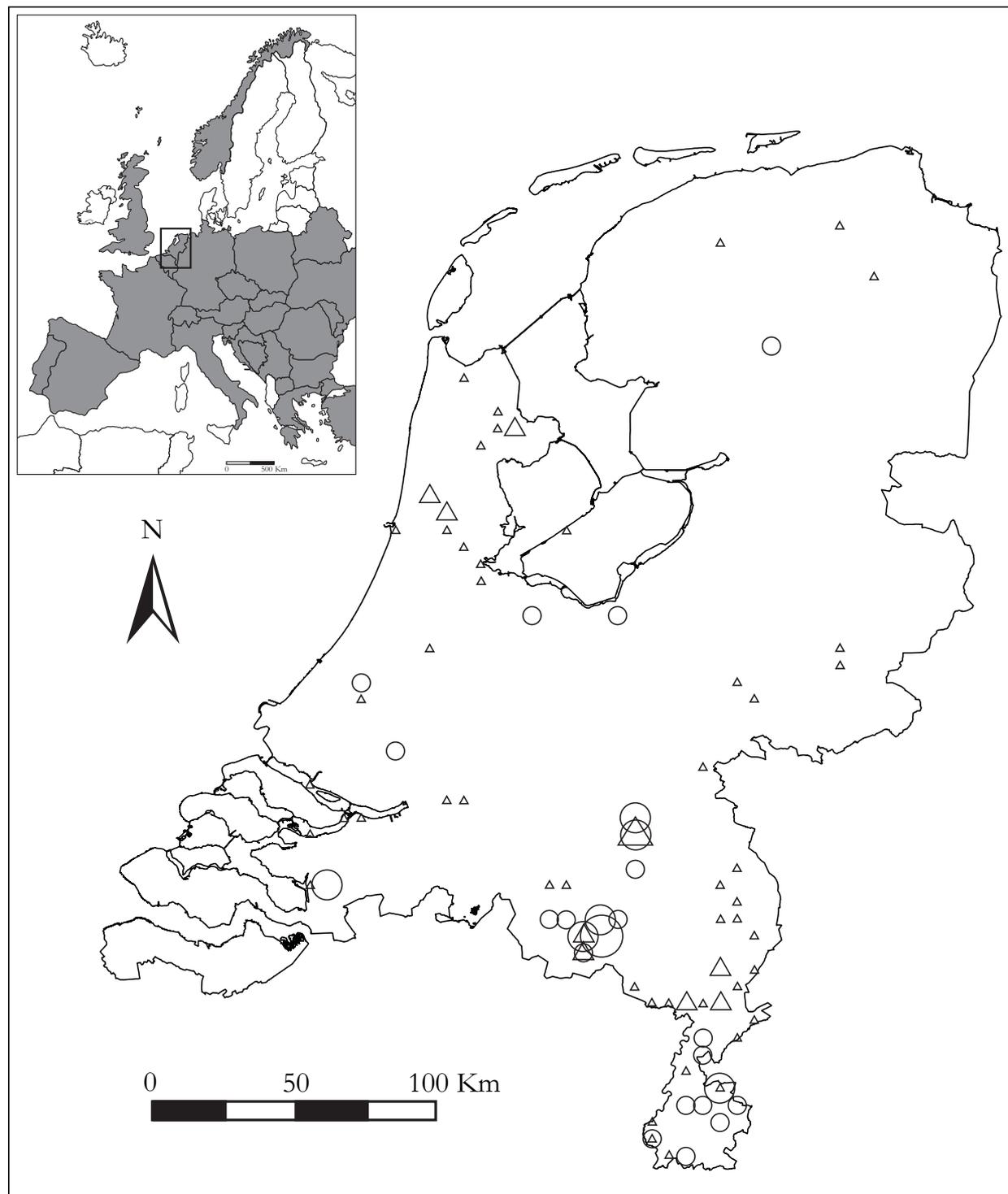


Figure 2 Distribution of the pumpkinseed in Europe by country based on Copp & Fox (2007) and its distribution in the Netherlands. Circles: isolated waters, triangles: connected waters; small symbols: 1 location, intermediate symbols: 2-4 locations and large symbols: 5 or more locations in squares of 10×10 km.

Table 1 Occurrence (%) and abundance of pumpkinseed in isolated and connected waters in the Netherlands.

	Connected waters (N = 69)	Isolated waters (N = 42)
Abundant	3%	45%
Frequent	13%	12%
Rare	61%	38%
Unknown	23%	5%

often abundant in isolated waters (χ^2 -test, $P < 0.0001$, Table 1). In a single moorland pool (0.3 ha surface area) over 5,000 specimens were caught in 4 h of seine netting. Although the species has become established in different types of waters, it is generally most abundant in moorland pools and fishing and urban ponds (Table 2). Eighty eight percent of the isolated waters with a high pumpkinseed abundance have been excavated (mainly urban ponds) or dredged (moorland pools), whereas only 22% of the waters with less rigorous (sod cutting) or no nature management had a high pumpkinseed abundance. Pumpkinseed abundance differed by type of management (Table 3, Kruskal-Wallis test, $P = 0.003$). In dredged pools pumpkinseed were more abundant, than under other types of management. Whereas, abundance in newly created pools was higher than in pools with less rigorous (sod cutting) and no nature management (Table 3).

Table 2 Occurrence (%) and abundance of pumpkinseed in different types of isolated waters in the Netherlands.

	Moorland pools (N = 17)	Fishing and urban ponds (N = 8)	Meadow ponds (N = 1)	Sand excavation pits (N = 1)
Abundant	71%	38%		100%
Frequent		50%		
Rare	29%	13%	100%	

Table 3 Occurrence (%) and abundance of pumpkinseed in isolated waters in relation to management practices

	Removal detritus and macrophytes ^a (N = 10)	Newly created ^b (N = 8)	Sod cutting of shores ^c (N = 4)	None ^c (N = 5)
Abundant	100%	50%	25%	20%
Frequent		50%		
Rare			75%	80%

Different letters indicate significant differences in pumpkinseed abundance (χ^2 -test, $P \leq 0.05$)

In isolated waters pumpkinseed were recorded up to 3,800 m from human habitation and 175 m from the nearest road or path. Thirty eight percent of the waters with pumpkinseed were located less than 250 m from settlements, whereas 69% of the pumpkinseed waters were located within 50 m for roads or paths. Isolated waters harbouring pumpkinseed were more often situated close to human habitation (distance less than 250 m, χ^2 -test, $P = 0.05$) and infrastructure (distance less than 100 m, χ^2 -test, $P = 0.05$) than could be expected based on the distribution of 100 randomly selected isolated waters (Figures 3a and 3b).

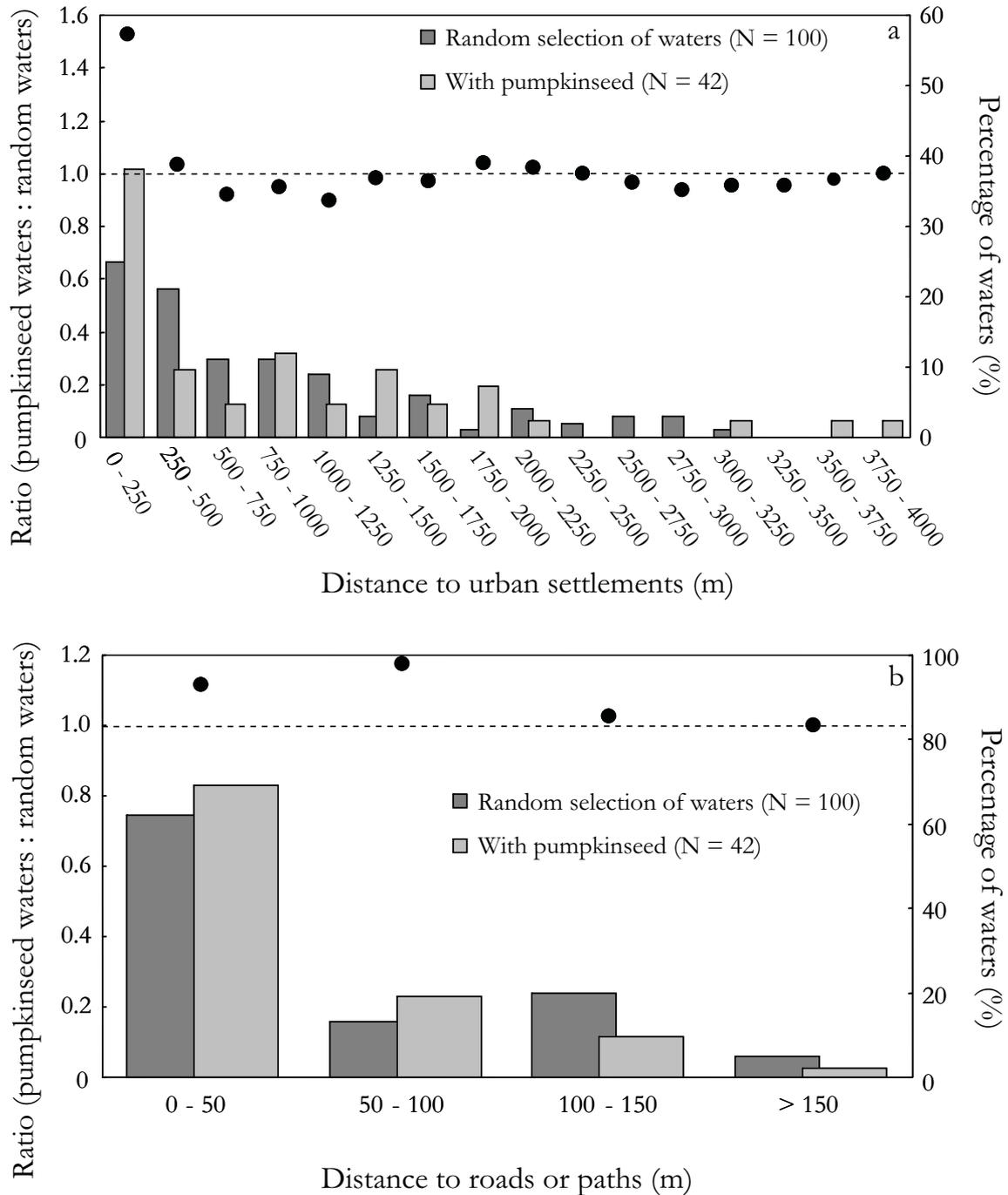


Figure 3 Distribution of randomly selected isolated waters and isolated waters with pumpkinseed in relation to distance to human settlements (a) and roads or paths (b). Bars: Percentage of waters in different distance intervals. Dots: ratio cumulative (with increasing distance) percentage of waters with pumpkinseed: cumulative percentage randomly selected waters. Dotted line: equal distribution of waters with pumpkinseed and randomly selected waters.

Pumpkinseed impacts

Average macroinvertebrate abundance in ponds with pumpkinseeds was 83% lower than in ponds without pumpkinseeds. The abundance of eight invertebrate taxa (Tricladida, Hirudinea, Oligochaeta, Odonata, Heteroptera, Chironomidae, Ceratopogonidae and Trichoptera) was significantly lower in pumpkinseed ponds (Mann-Whitney U-test, $P < 0.05$, Table 4), whereas no taxa were found to be more abundant. The abundance of

Table 4 Densities of aquatic macroinvertebrates (average number of individuals $\text{m}^{-2} \pm \text{SE}$) in moorland pools with and without pumpkinseed.

	Without pumpkinseed (N = 4)	With pumpkinseed (N = 4)
Tricladida *	13.2 \pm 6.1	0.0 \pm 0.0
Gastropoda	847.2 \pm 458.3	188.0 \pm 167.1
Hirudinea *	11.5 \pm 5.1	0.0 \pm 0.0
Oligochaeta *	170.7 \pm 58.2	5.0 \pm 1.5
Araneida	6.7 \pm 6.2	1.5 \pm 0.7
Acarina	107.2 \pm 38.4	98.5 \pm 13.3
Isopoda	34.5 \pm 19.5	1.3 \pm 1.3
Odonata *	40.3 \pm 6.7	5.4 \pm 4.2
Ephemeroptera	49.7 \pm 39.3	5.0 \pm 2.3
Heteroptera *	85.7 \pm 19.3	8.3 \pm 3.7
Megaloptera	1.2 \pm 1.2	0.0 \pm 0.0
Coleoptera	32.2 \pm 17.2	3.0 \pm 1.1
Diptera		
Chaoboridae	1.3 \pm 1.3	0.0 \pm 0.0
Culicidae	0.2 \pm 0.2	0.0 \pm 0.0
Chironomidae *	560.3 \pm 247.5	31.7 \pm 5.9
Ceratopogonidae *	44.0 \pm 8.0	4.2 \pm 1.5
Tabanidae	0.0 \pm 0.0	0.2 \pm 0.2
Trichoptera *	25.2 \pm 22.3	0.0 \pm 0.0
Lepidoptera	1.3 \pm 0.6	0.0 \pm 0.0
Total *	2032.2 \pm 327.2	352.1 \pm 8.6

* $P \leq 0.05$ (Mann-Whitney U-test)

water mites (Acarina) was similar in ponds with and without pumpkinseed. Eleven different types of prey were identified in pumpkinseed intestines collected in the Rauwven (Figure 4). In terms of prey numbers, chironomids and microfauna constituted the majority of the diet. As with many gape-limited predators dietary choice shifts to large prey as the predator increases in size. Consequently the amount of zooplankton in the diet decreases and chironomids and other macroinvertebrates in the diet become more important. Seven out of eleven prey types were recorded with abundances higher than 25 individuals per m^2 in ponds without pumpkinseed (Table 4), indicating a large overlap in diet and prey availability. The abundance of five of these taxa (Odonata, Heteroptera, Chironomidae, Ceratopogonidae and Trichoptera) was significantly lower in pumpkinseed ponds, making predation by pumpkinseed a plausible explanation for the apparent decrease of these taxa in the presence of pumpkinseed. No soft bodied prey (Tricladida, Hirudinea and Oligochaeta) were recorded in the diet, possibly due to rapid digestion without remains.

There is little experience in the Netherlands with pumpkinseed control. Three attempts (Schoapedobbe 52°57'10.57" N, 6°15'32.210" E; a meadow pond near Uden 51°41'18.45" N, 5°38'3.26" E and a pond near Echt 51°6'11.69" N, 5°54'6.08" E) were made by catching the fish using dip nets, electric fishing gear and seines. Only one of these attempts was successful. In the Rauwven pumpkinseed were successfully eradicated by draining the pools and subsequently catching and removing the fish with seines. The remaining mud, puddles and hard-to-catch fish were covered by a layer of sand in order to kill the last fishes and to change the permanent pool into a temporary one.

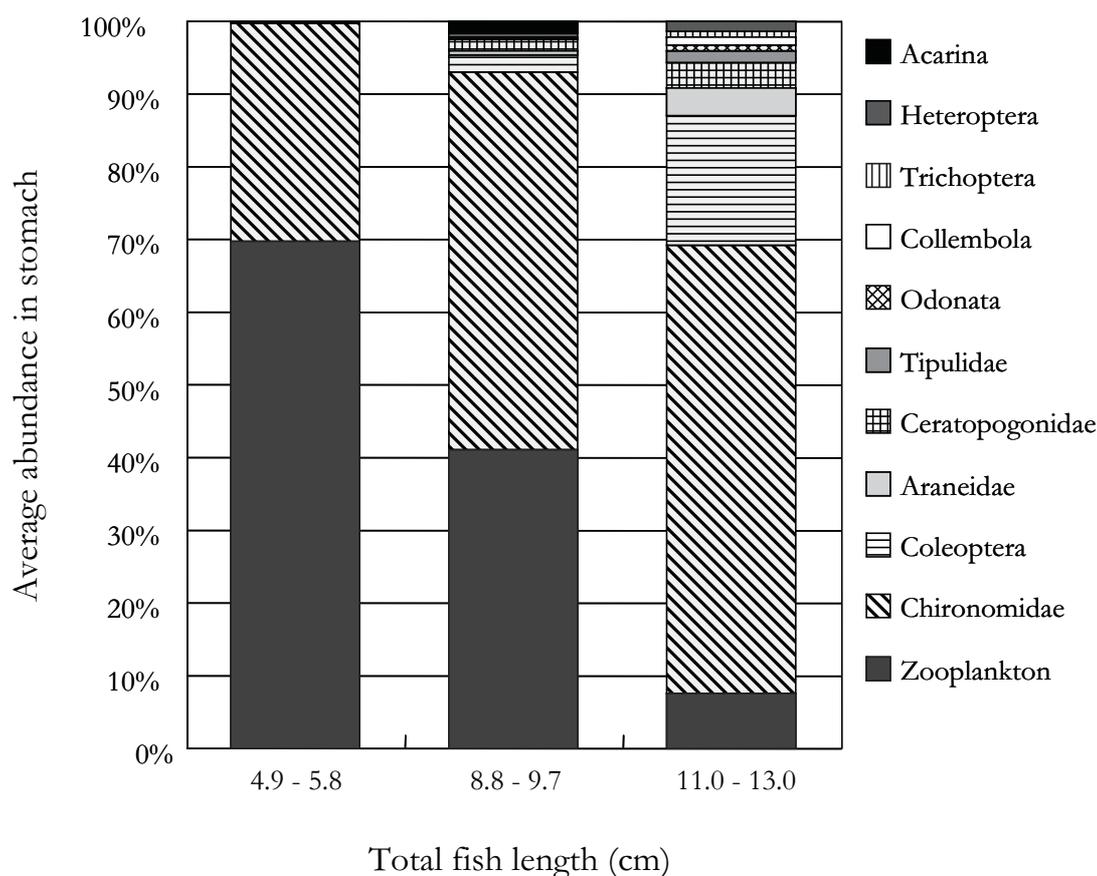


Figure 4 Average relative numbers of invertebrate taxa in pumpkinseed stomachs from three different length classes ($N = 6$ for each length class). Ranges of length classes are given.

Discussion

Triggers for pumpkinseed abundance

Although the pumpkinseed has been known to occur in the Netherlands since 1902 (Looijen 1948) and is nowadays widespread, its population densities are generally low. However, pumpkinseeds were found to be abundant in isolated waters which have been heavily disturbed by nature management practices (i.e. dredging) or which have been artificially created. Low pumpkinseed abundance in streams corresponds to reports from the UK, where reproduction only has been recorded in lentic waters from which non-reproducing stream populations are supplied (Klaar et al. 2004). In southern Europe, however, the species is also abundant in lotic waters (Godinho et al. 1997, Gutiérrez-Estrada et al. 2000). Copp & Fox (2007) demonstrated that pumpkinseed invasiveness at lower latitudes may be attributed to warmer climatic conditions resulting in a higher fecundity (i.e. rapid maturation and faster juvenile growth). Increased fecundity may also be partially responsible for the observed high abundance of pumpkinseed in Dutch isolated water bodies as these waters have extensive shallow sun-exposed shores. Pumpkinseeds in a Dutch dredged moorland pool matured at age 2 (GH Copp unpublished), which is comparable to populations from southern Europe (reviewed in Copp et al. 2002).

Favourable climatic conditions (i.e. rapid warming in spring and high temperatures in summer) are unlikely to be the only reason for pumpkinseed invasiveness in Dutch isolated waters, as high pumpkinseed abundance often coincided with specific management practices. These practices are actually likely to decrease the average water temperature as they expose mineral soils, which would increase water temperature less than the organic matter which covers soils of most undisturbed waters. High pumpkinseed abundance in dredged or newly created waters can possibly be attributed to an increased area of optimal spawning habitat (Figure 1). Although no studies have been performed on reproductive success on different spawning substrates, Danylchuk and Fox (1996) demonstrated a preference of female pumpkinseeds for nesting on firm substrates (sand or gravel) as opposed to soft substrates. In addition, severe disturbances (i.e. the removal of detritus and macrophytes) and the creation of new water bodies are likely to create conditions with few or no competitors and predators. Especially because nature managers strive to keep these waters free of fish, as they are known to have undesirable effects, such as bioturbation (Scheffer 1998), nutrient mobilisation (Carpenter & Kitchell 1993) and predation on larvae of amphibians (Smith et al. 1999). Fish diversity in moorland pools is further limited by acidification at the end of the 20th century when nearly 70% of the Dutch moorland pools acidified (Leuven et al. 1986b), strongly decreasing the number and abundance of fish species. Since 1980 deposition of acidifying substances has decreased resulting in a pH increase in many North European and Dutch moorland pools (Forsius et al. 2002, Van Dam & Mertens 2004) above levels toxic to fish (Baker & Schofield 1982).

Abundance, distribution and dispersal

Because pumpkinseed records in national and regional databases were gathered by volunteers and most records (56%) were older than ten years, the influence of temporal and methodological variation may be substantial. This is even more likely in shallow isolated waters such as moorland pools, as they may completely freeze in severe winters and dry up in dry summers. Furthermore, at the moment of discovery populations may have been in different stages of development (Williamson 1996). The census of pumpkinseed abundance in 2007, however, revealed that estimation of pumpkinseed abundance from databases and other sources led to an overestimation in only 4 of the 27 sites. Apparently, pumpkinseed population densities in isolated waters are relatively stable and data from the consulted databases is sufficiently accurate for the analysis of distribution and abundance patterns. Given the national scale of the study, a substantial number of pumpkinseed populations will have been overlooked. Nevertheless, most of our abundance data consist of records of small numbers of pumpkinseed rather than large populations and thus appear sufficiently detailed for analysing patterns in pumpkinseed abundance.

The importance of pumpkinseed introductions by human as a dispersal mechanism is illustrated by the fact that Dutch isolated waters with pumpkinseed were more often located close to human habitation and infrastructure than could be expected based on the distribution of randomly selected isolated waters (Figure 3). Copp et al. (2005) also found more occurrences of non-native species near roads and houses than expected. These findings also indicate that planning of nature management practices can best be done at distances over 250 m from human habitation and 100 m from roads and paths in order to minimize the chances of introductions. Further proof for voluntary introductions is provided by the occasional occurrence of common garden pond plants in Dutch waters

with pumpkinseeds. Egg dispersal by waterfowl is unlikely, as pumpkinseed reproduction does not coincide with bird migration peaks. Egg dispersal by animal vectors is further limited due to a short egg stage (i.e. as short as 3 days in warm waters, Scott & Crossman 1973) and loss of adhesiveness as they become covered in sand and dirt by the swimming activity of the male (pers. obs. MC van Riel).

Pumpkinseed impact

In Europe pumpkinseed are opportunistic predators (Godinho et al. 1997, Garcia-Berthou & Moreno-Amich 2000, Copp et al. 2002 and this study), feeding on the most frequent and abundant prey. Despite its invasive behaviour and opportunistic feeding, studies on the ecological impact of pumpkinseed are rare (Osenberg et al. 1992), speculative (Garcia-Berthou & Moreno-Amich 2000) or lack bibliography (Welcomme 1988). Introduced pumpkinseed have been reported to have a negative impact on native fish species (Welcomme 1988), dragonflies (Janssen 2000) and amphibians (Bosman 2003). We demonstrated that macroinvertebrate abundance in pools populated by large numbers of pumpkinseed was 83% lower than in pools without pumpkinseed. Of the abundant invertebrate taxa, only water mites (Acarina) appeared to be unaffected and comprised only a minor part of the diet, despite the fact that they are often larger than other prey such as zooplankton and chironomids. Lack of water mites in the pumpkinseed diet was also observed by Copp et al. (2002) and can be attributed to the distasteful secretions they shed to prevent predation by fish (Kerfoot 1982).

Pumpkinseed control

Currently there is little experience with pumpkinseed control. Promising is reducing the depth of colonised waters by filling them with soil in order to make them temporary. However, this method is not always feasible or desirable. Therefore other options need to be explored, such as introducing native competitors and predators and the use of biodegradable piscicides. Probably more important is reducing the number of introductions of pumpkinseeds. This requires limitation of the sale of the species and other measures to reduce introductions such as a growing public awareness of the ecological consequences of introducing invasive species, followed by an adequate control and enforcement of legislation concerning invasive species.

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References

- Arts GHP & Leuven RSEW (1988) Floristic changes in shallow soft waters in relation to underlying environmental factors. *Freshwater Biology* **20**: 97-111.
- Arts GHP, De Haan AJ, Siebum MB & Verheggen GM (1989) Extent and historical development of the decline of Dutch soft waters. *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen. Series C: Biological and Medical Sciences* **92**: 281-295.

- Arts GHP, Van der Velde G, Roelofs JGM & Van Swaay CAM (1990) Successional changes in the softwater macrophyte vegetation of (sub) Atlantic, sandy lowland regions during this century. *Freshwater Biology* **24**: 287-294.
- Baker JP & Schofield CL (1982) Aluminum toxicity to fish in acidic waters. *Water, Air, and Soil Pollution* **18**: 289-309.
- Bosman W (2003) Het Rauwven, een exotisch ven in het beekdal van de Aa. *RAVON* **15**: 33-36.
- Brouwer E & Roelofs JGM (2001) Degraded softwater lakes: possibilities for restoration. *Restoration Ecology* **9**: 155-166.
- Carpenter SR & Kitchell JF (eds.) (1993) The trophic cascade in lakes. *Cambridge University Press, Cambridge*.
- Casal CMV (2006) Global documentation of fish introductions: the growing crisis and recommendations for action. *Biological Invasions* **8**: 3-11.
- Copp GH & Fox MG (2007) Growth and life history traits of introduced pumpkinseed (*Lepomis gibbosus*) in Europe, and the relevance to its potential invasiveness, in Gherardi F (ed.) Biological invasions in inland waters: profiles, distribution and threats. *Springer, Dordrecht*: 289-306.
- Copp GH, Fox MG & Kováč V (2002) Growth, morphology and life history traits of a cool-water European population of pumpkinseed *Lepomis gibbosus*. *Archiv für Hydrobiologie* **155**: 585-614.
- Copp GH, Wesley KJ & Vilizzi L (2005) Pathways of ornamental and aquarium fish introductions into urban ponds of Epping Forest (London, England): the human vector. *Journal of Applied Ichthyology* **21**: 263-274.
- Danylchuk AJ & Fox MG (1996) Size and age-related variation in the seasonal timing of nesting activity, nest characteristics, and female choice of parental male pumpkinseed sunfish (*Lepomis gibbosus*). *Canadian Journal of Zoology* **74**: 1834-1840.
- De Nie HW (1996) Atlas van de Nederlandse zoetwatervissen. *Media Publishing, Doetinchem*.
- Forsius M, Vuorenmaa J, Mannio J & Syri S (2002) Recovery from acidification of Finnish lakes: regional patterns and relations to emission reduction policy. *Science of the Total Environment* **310**: 121-132.
- Garcia-Berthou E & Moreno-Amich R (2000) Food of introduced pumpkinseed sunfish: ontogenetic diet shift and seasonal variation. *Journal of Fish Biology* **57**: 29-40.
- Godinho FN, Ferreira MT & Cortes RV (1997) The environmental basis of diet variation in pumpkinseed sunfish, *Lepomis gibbosus*, and largemouth bass, *Micropterus salmoides*, along an Iberian river basin. *Environmental Biology of Fishes* **50**: 105-115.
- Gutiérrez-Estrada JC, Pulido-Calvo I & Prenda J (2000) Gonadosomatic index estimates of an introduced pumpkinseed (*Lepomis gibbosus*) population in a Mediterranean stream, using computational neural networks. *Aquatic Sciences* **62**: 350-363.
- Holčík J (1991) Fish introductions in Europe with particular reference to its central and eastern part. *Canadian Journal of Fisheries and Aquatic Sciences* **48** (supplement 1) :13-23.
- Hoogerwerf G, Voorn P & Ten Heggeler N (2005) Evaluatie van 4 vispassages in het beheergebied van het Waterschap De Dommel. *Natuurbalans-Limes Divergens BV, Nijmegen*.
- Janssen ICJM (2000) Monitoring van het Haeselaarsbroek in het brongebied van de Pepinusbeek. Ontwikkelingen in een natuurherstelproject in de Middenlimburgse gemeente Echt. Report 189. *Department of Environmental Science, Radboud University, Nijmegen*.
- Kelly CA, Rudd JWM, Furutani A & Schindler DW (1984) Effects of lake acidification on rates of organic-matter decomposition in sediments. *Limnology and Oceanography* **29**: 687-694.
- Kerfoot WC (1982) A question of taste: crypsis and warning coloration in freshwater zooplankton communities. *Ecology* **63**: 538-554
- Klaar M, Copp GH & Horsfield R (2004) Autumnal habitat use of non-native pumpkinseed *Lepomis gibbosus* and associations with native fish species in small English streams. *Folia Zoologica* **53**: 189-202.
- Leuven RSEW, Van der Velde G, Vanhemelrijk JAM & Eeken RLE (1986a) Impact of acidification on the distribution of aquatic insects in lentic softwaters. *Proceedings of the 3rd European Congress of Entomology, Dutch Entomological Society, Amsterdam*: 103-106.

- Leuven RSEW & Oyen FGF (1987) Impact of acidification and eutrophication on the distribution of fish species in shallow and lentic soft waters of the Netherlands – an historical perspective. *Journal of Fish Biology* **31**: 753-774.
- Leuven RSEW & Wolfs WJ (1988) Effects of water acidification on the decomposition of *Juncus bulbosus* L. *Aquatic Botany* **31**: 57-81.
- Leuven RSEW, Kersten HLM, Schuurkes JAAR, Roelofs JGM & Arts GHP (1986b) Evidence for recent acidification of lentic soft waters in the Netherlands. *Water, Air, and Soil Pollution* **30**: 387-392.
- Leuven RSEW, Van der Velden JA, Vanhemelrijk JAM & Van der Velde G (1987) Impact of acidification on chironomid communities in poorly buffered waters in the Netherlands. *Entomologica Scandinavica Supplements* **29**: 269-280.
- Leuven RSEW, Van der Velde G & Kersten HLM (1992) Interrelations between pH and other physico-chemical factors of Dutch soft waters. *Archiv für Hydrobiologie* **126**: 27-51.
- Looijen AJL (1948) De Nederlandsche Heidemaatschappij en haar bemoeiingen op visserij-gebied, in De Nederlandsche Heidemij 60 jaar. *Heidemij, Arnhem*.
- Osenberg CW, Mittelbach GG & Wainwright PC (1992) Two-stage life histories in fish: the interaction between juvenile competition and adult performance. *Ecology* **73**: 255-267.
- Roelofs JGM (1983) Impact of acidification and eutrophication on macrophytes communities in soft waters in the Netherlands. 1. Field observations. *Aquatic Botany* **17**: 139-155.
- Scheffer M (1998) Ecology of shallow lakes. *Chapman & Hall, London*.
- Scott WB & Crossman EJ (1973) Freshwater fishes of Canada. Bulletin 184. *Fisheries Research Board of Canada, Ottawa*.
- Smith GR, Rettig JE, Mittelbach GG, Valiulis JL & Schaack SR (1999) The effects of fish on assemblages of amphibians in ponds: a field experiment. *Freshwater Biology* **41**: 829-837.
- Trombulac SC & Frissell CA (2000) Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology* **14**: 18-30.
- Van Dam H & Mertens A (2004) Vennen in weer en wind: langetermijneffecten van verzuring en klimaatsverandering op chemie en kiezelwieren. *De Levende Natuur* **105**: 13-18.
- Welcomme RL (1988) International introductions of inland aquatic species. FAO fisheries technical paper no. 294. *Food and Agriculture Organization of the United Nations, Rome*.
- Williamson M (1996) Biological invasions. *Chapman Hall, London*.



Water from the stream “Tongelreep” supplies the Greveschutven with alkaline nutrient rich water for stimulating fish production. As a result a species rich gradient has developed in one of the more sheltered corners of the lake. Photo: Hein van Kleef.

Chapter 6

Anthropogenically impacted moorland pools as refugia for endangered macrophyte and macroinvertebrate species characteristic of gradients in bog landscapes

Hein van Kleef, Gert-Jan van Duinen, Wilco Verberk, Rob Leuven,
Gerard van der Velde & Hans Esselink

Submitted

Abstract

In intact raised bog landscapes transitions from ombrotrophic into minerotrophic conditions occur. These gradients are lost from many bogs due to peat harvesting and drainage and are difficult to restore. To determine which endangered species are characteristic of pristine raised bog gradients and their current status in degraded bogs, plants and macroinvertebrates were surveyed in Estonian intact raised bogs and Dutch degraded bog remnants. Dutch national distribution data were used to determine whether communities with these species occurred outside bog habitats. Water chemistry data were used to describe associated environmental conditions. Intact bog gradients were the preferred habitat for six endangered plant and fifteen macroinvertebrate species. In degraded bogs these species were scarce or not recorded. In intact bogs these species lived at sites where runoff from the bog massive came into contact with regional ground water resulting in a gradient in pH, alkalinity, Ca, Fe and ionic ratio. Analysis of Dutch national distribution data revealed aggregations of these endangered species in moorland pools. These pools contained water chemistry gradients similar to those found in pristine bogs, which occurred at sites where young seepage water, older groundwater and stream water came in contact. In the past, stream water has been used to increase pH and trophic status of moorland pools facilitating fisheries. Today, this practice offers a conservation strategy for the protection of endangered species for which no short-term alternatives are available.

Introduction

Intact bog landscapes are characterised by a bog massive, which is formed by peat mosses (*Sphagnum* spp.) that may cover extensive areas (Pons 1992, Couwenberg & Joosten 2005). These mosses act as ecosystem engineers, creating their own optimal environment (i.e. permanently wet, acid and nutrient poor conditions) (Van Breemen 1995, Rochefort 2000). Such conditions offer an extreme environment for aquatic biota (Peus 1923, Van Duinen et al. 2006, Verberk et al. 2006). These harsh conditions are offset at places where mineral soils protrude through the peat and at the edge of the bog massive, giving rise to lagg zones and transitional mires (Wheeler & Proctor 2000). Here, the contact of acid, nutrient poor runoff from the bog massive and seepage of alkaline, mineral rich groundwater results in water chemistry gradients (Bragazza & Gerdol 2002). Despite their much smaller extent, these transitional zones harbour similar numbers of species compared to the raised bog massive (Desrocher & Van Duinen 2006, Van Duinen et al. 2006). The diversity of the transitions can be attributed to a gradient of sequential different environmental conditions (niche partitioning) and mass effects (Shmida & Wilson 1985). The diversity of the raised bog massive is limited by extreme environmental conditions (i.e. acid and nutrient poor conditions).

The area covered by raised bogs has decreased considerably in many parts of the world and this decrease is still ongoing (Joosten & Clarke 2002). Exploitation of bogs (i.e. drainage, peat cutting and cultivation) started at the bogs' edges and gradually extended inwards (Verhoeven 1992). Consequently, the species rich gradients were lost first. Pressure on this element of the bog landscape further increased due to decreased groundwater quality and quantity as a result of agriculture and extraction of drinking water and to increased downward seepage in the bog massive itself due to drainage and peat cutting (Schouwenars 1993).

In many European bog remnants restoration measures are being taken to restore the environmental conditions and their populations of characteristic species. The primary target in most raised bog restoration projects is reformation of the bog massive by facilitation of *Sphagnum* growth. Consequently, restoration measures mainly focus on raising the water tables by retaining rainwater and reducing nutrient availability (Wheeler & Shaw 1995). However, species rich gradients in bog landscapes also depend on base-rich ground water and therefore require a functional regional hydrology. Yet groundwater systems are only occasionally being restored as this is difficult to achieve and often requires measures outside the bog remnants. Consequently, restoration of lagg zones, transitional mires and their characteristic communities is unlikely to be realised in the near future. Therefore, Van Duinen et al. (2003) emphasise the importance of conserving populations of these species in addition to bog ecosystem restoration by facilitating *Sphagnum* growth. This requires an overview of the endangered species belonging to these communities, insights in the perspectives for these species in raised bog remnants and other habitats, knowledge on their environmental requirements as well as management tools to ensure the viability and expansion of populations. More specifically, the following questions are addressed:

1. Which endangered species are characteristic of pristine raised bog gradients?
2. Do these species still occur in raised bog remnants?
3. Do communities with these species occur in other habitats?
4. Under what environmental conditions do these species occur in intact bog landscapes?
5. How are these conditions realised in other habitats?

Material and methods

For this study datasets on distribution of plants and macroinvertebrates were used from (I) intact raised bogs in Estonia, (II) Dutch raised bog remnants and (III) Dutch distribution data of a selection of endangered species.

Surveys of intact and degraded raised bogs

To identify endangered species characteristic of raised bog gradients, vegetation relevés were made and aquatic macroinvertebrates were sampled from 26 sites in intact raised bogs in Estonia in spring 2001 and autumn 2005. These sites were selected from different parts of the raised bog landscape: 15 sites in the bog massive and 11 from transitional mire and lagg. Species with a higher presence (i.e. the percentage of samples in which a species was recorded) in transitional mire and lagg than in the bog massive were considered as endangered if they were listed in Red Data Books as vulnerable, endangered, critically endangered or extinct. In the Netherlands such lists are available for higher plants (Van der Meijden et al. 2000), dragonflies (Wasscher et al. 1998), caddisflies (Verdonschot et al. 2003) and aquatic beetles (Drost et al. 1992).

In order to determine the status of the selected endangered species in bog remnants in the Netherlands, data on plant and macroinvertebrate species occurrence for 198 sites in bog remnants was analysed. These data were previously collected in spring and autumn in the period 1998 – 2007 in different raised bog remnants (Figure. 1, Korenburgerveen 45, Dwingelderveld 8, Bargerveen 43, Haaksbergerveen 10, Fochteloërveen 4, Wierdense Veld 36, Peel 46 and Tuspeel 6 sites) (Van Duinen et al. 2003, Verberk et al. 2006, Van Duinen 2008, Verberk 2008). Sampling methods for aquatic macroinvertebrates at

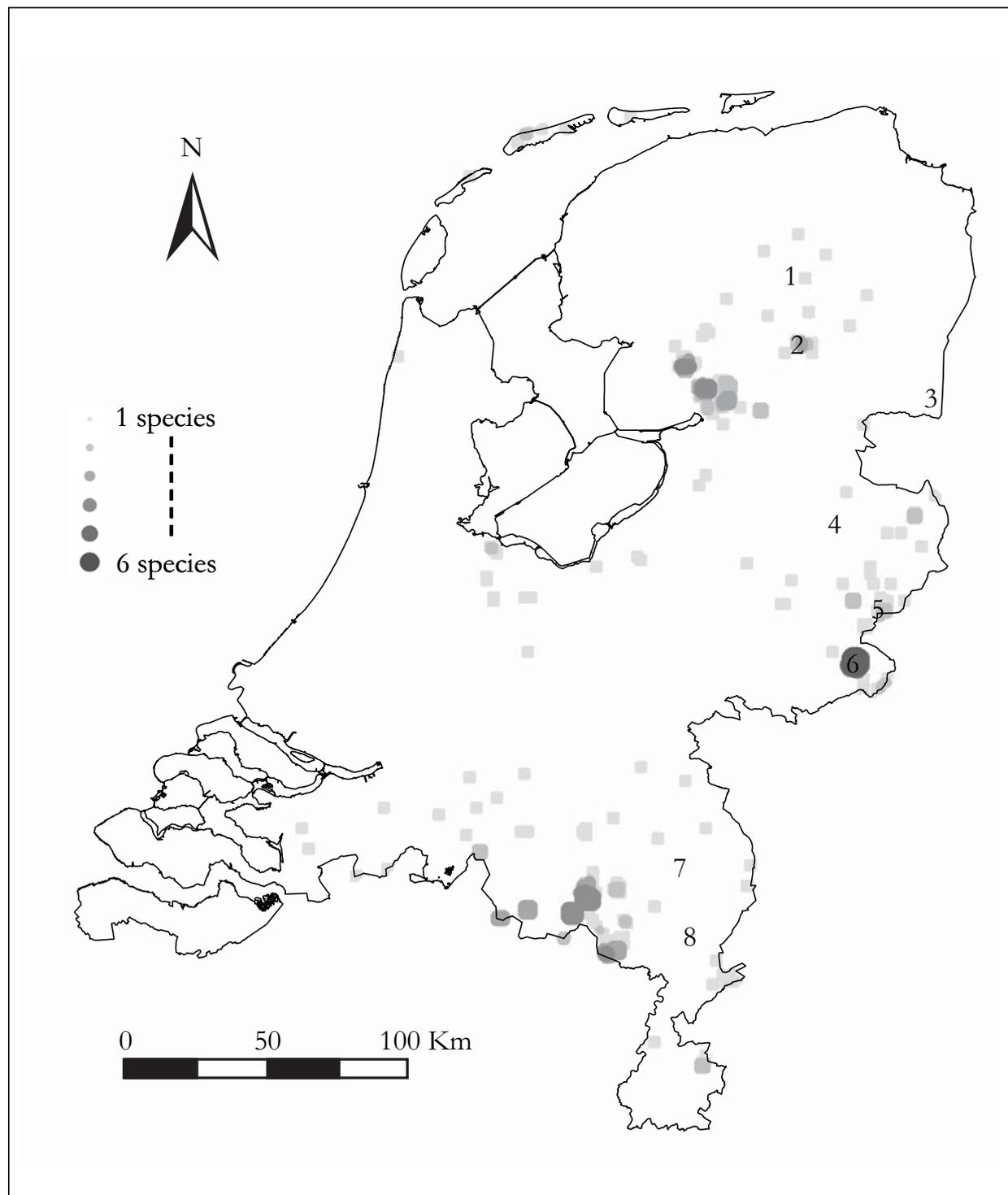


Figure 1 Number of endangered bog-gradient species per km², based on Dutch national databases in the period 1991-2006. The number of species corresponds to the total number in that square and directly adjacent squares. Increasing dot size and darkness correspond to a higher number of species. Numbers correspond to studied raised bog remnants. (1) Fochteloërveen, (2) Dwingelderveld, (3) Bargerveen, (4) Wierdense Veld, (5) Haaksbergerveen, (6) Korenburgerveen, (7) Peel and (8) Tuspeel.

Estonian and Dutch sites have been described in detail by Van Duinen et al. (2003, 2006) and Verberk et al. (2008). Vascular plants were censused within a radius of 5 m of the area sampled for invertebrates.

Dutch distribution data of endangered species

For vascular plants, dragonflies and caddisflies reliable data on their distribution in the Netherlands are available. These data were used to determine the status of endangered species outside bog remnants and to identify areas where environmental gradients similar to those in raised bog lagg zones and transitional mires still occur. For the period 1990-2006 data were provided by NGO's (i.e. FLORON, the Dutch Butterfly Conservation and European Invertebrate Survey) on a grid of 1×1 km. Since information on the distribution of aquatic beetles was scattered and without good coverage, their status outside bog remnants could not be determined. For the three taxonomic groups that were included, the species are likely to differ in the extent in which they are indicative for the whole or different parts of the gradient. In addition some species may not be restricted to these gradients and their occurrence is therefore less suitable to identify areas where environmental gradients similar to those in raised bog lagg zones and transitional mires still occur. To determine the indicative value of a species, we compared the observed co-occurrence of two species with the co-occurrence that would be expected when both species would be randomly distributed. The underlying rationale is that if both species are highly restricted to the same environmental gradient their weighted co-occurrence would be relatively high. Using weighted co-occurrences therefore more accurately identifies areas where the environmental gradients of interest are still present. Weighted co-occurrences were calculated for each species-couple:

$$\text{Weighted co-occurrence} = \text{OCO}_{AB} / \text{ECO}_{AB} \quad (\text{equation 1})$$

$$\text{and} \quad \text{ECO}_{AB} = \frac{\text{SQ}_A \times \text{SQ}_{\text{NL}}}{\text{SQ}_{\text{TOT}}} \times \frac{\text{SQ}_B \times \text{SQ}_{\text{NL}}}{\text{SQ}_{\text{TOT}}} \times \text{SQ}_{\text{TOT}} \quad (\text{equation 2})$$

where OCO_{AB} = observed co-occurrence, calculated as the number km-squares where species A and B co-occur. When the species was present in a directly adjacent square this was counted as a co-occurrence to allow for gradients to cross two km-squares; ECO_{AB} = expected co-occurrence when the species would be randomly distributed; SQ_A = number of km-squares where species A is recorded; SQ_B = number of km-squares where species B is recorded, SQ_{NL} = average number of km-squares surrounding each square (i.e. 3 by 3 km with adjustments for shoreline and borders = 8.805) and SQ_{TOT} = total number of km-squares in the Netherlands (= 36,913 km²). Equation 1 thus describes the ratio between the observed number of km-squares where two species co-occur and the expected number of co-occurrences under a random distribution. The species are most likely restricted to natural areas, which would automatically increase weighted co-occurrence. Twenty two percent of the surface area in the Netherlands consists of natural terrain and wetlands (CBS 2009). Therefore species occurring randomly within natural areas without any affinity with other selected species would be expected to have weighted co-occurrence of 4.5. For this reason, species with an average weighted co-occurrence of less than 5 were not used to identify aggregations of species as they are likely to have any affinity with the gradient community but rather are randomly distributed within natural areas.

Areas where environmental gradients similar to those in raised bog lagg zones and transitional mires still occur were identified from aggregations of endangered species (> 4 different endangered species in a km-square or any of the 8 directly adjacent squares). These areas were classified as raised bog remnant, moorland pool or fen.

Environmental conditions

To characterise the environmental conditions in raised bog lagg zones and transitional mires data on surface water chemistry from sampling sites in Estonian raised bogs were used (Van Duinen et al. 2006). To test if environmental conditions were similar in areas with aggregations of endangered species, surface water chemistry samples were collected from three such areas (Greveschutven (51°22'13" N, 5°30'42" E), Ringselven (51°19'46" N, 5°26'49" E) and Rijsven (51°13'42" N, 5°36'10" E)), where according to national databases aggregations of four or more endangered species have been recorded. Water samples were taken at sites where the occurrence of species aggregations was confirmed by the presence of selected plants, Trichoptera and Odonates (imagos and larvae). Samples were collected in iodated polyethylene bottles. The pH and alkalinity of water samples were measured within 24 h after collection. After filtering (Whatman GF/C filter) and adding 1 mg citric acid per 25 ml of water, samples were stored at -20 °C until further analysis. The following concentrations were determined colorimetrically; NO₃⁻ according to Kamphake et al. (1967) and NH₄⁺ according to Grasshoff & Johanssen (1972), using a Bran & Luebbe, TRAACS 800+, ortho-PO₄³⁻ according to Henriksen (1965), using a Technicon AA II system, and Cl⁻ according to O'Brien (1962), using a Technicon AA III system. Total concentrations Ca, Fe and S were measured by inductively coupled plasma emission spectrometry (Jarrell Ash IL Plasma-200). The ionic ratio, an index for the relative importance of groundwater in a water sample (Van Wirdum 1991), was calculated as $\frac{1}{2} [\text{Ca}] / (\frac{1}{2} [\text{Ca}] + [\text{Cl}])$.

Differences in water chemistry between the bog massive, lagg zone and transitional mires in Estonian bogs and Dutch refugia were tested with Mann-Whitney-U tests. Spearman rank correlations were used to describe the relationship between the ionic ratio and other parameters.

Results

Characteristic endangered species in intact and degraded bog landscapes

Twenty one endangered species were recorded more often in the transitional mire and lagg zone of Estonian bogs than in the bog massive (Table 1). In contrast, twelve endangered species were concentrated in the massive, confirming the importance of bog gradients as habitat for endangered species.

Despite the large number of sampling sites (N=198), only ten of the twenty-one endangered species characteristic of raised bog gradients were recorded in Dutch bog remnants (Table 1). In addition, each of those species was recorded with a relatively low frequency of occurrence, confirming the present-day scarcity of these gradient species in Dutch bog remnants.

Co-occurrence of endangered species in other habitats

Dutch national databases of vascular plants, dragonflies and caddisflies contained 711 recent (1991-2006) records of endangered species in 574 km-squares. *Carex lasiocarpa* (418 records) and *Somatochlora flavomaculata* (49 records) were most abundant and

Table 1 Occurrence of species listed on the Dutch red lists in the lagg zone, transitional mire and bog massive of Estonian bogs and their occurrence in Dutch bog remnants. Occurrences are based on vegetation relevés and aquatic invertebrate sampling and are presented as the percentage of occupied sites. Status NL: red list category. D: disappeared, CE: critically endangered, E: endangered, V: vulnerable. N = Number of sampling sites. Bold figures indicating the observed preference of species (i.e. a higher occurrence).

Species	Status NL	Occurrence in Estonia		Occurrence in Netherlands
		Lagg/ transitional mire N = 11	Bog massive N = 15	Bog remnants N = 198
Tracheobionta - Higher plants				
<i>Carex lasiocarpa</i> Ehrh.	V	27%	0%	0%
<i>Carex limosa</i> L.	D	45%	40%	0%
<i>Hammarbya paludosa</i> (L.) Kuntze	CE	18%	0%	0%
<i>Sparganium natans</i> L.	E	9%	0%	0%
<i>Utricularia intermedia</i> Hayne	V	18%	0%	0%
<i>Vaccinium uliginosum</i> L.	E	9%	0%	5%
<i>Andromeda polifolia</i> L.	V	64%	100%	8%
<i>Eriophorum vaginatum</i> L.	V	73%	100%	18%
<i>Oxycoccus palustris</i> Pers.	V	82%	100%	5%
<i>Scheuchzeria palustris</i> L.	CE	27%	73%	0%
Odonata - Dragonflies				
<i>Coenagrion hastulatum</i> Charpentier, 1985	CE	27%	0%	3%
<i>Somatochlora arctica</i> (Selys, 1871)	E	45%	13%	0%
<i>Somatochlora flavomaculata</i> (Vander Linden, 1825)	CE	18%	0%	0%
<i>Aeshna subarctica</i> Walker, 1908	E	36%	67%	2%
<i>Leucorrhinia albifrons</i> (Burmeister, 1839)	CE	9%	47%	0%
<i>Leucorrhinia dubia</i> (Vander Linden, 1825)	V	18%	67%	8%
Trichoptera - Caddisflies				
<i>Anabolia brevipennis</i> (Curtis, 1834)	V	9%	0%	0%
<i>Hagenella clathrata</i> (Kolenati, 1848)	V	27%	7%	5%
<i>Limnephilus griseus</i> (L., 1758)	CE	9%	0%	0%
<i>Limnephilus stigma</i> Curtis, 1834	E	27%	0%	2%
<i>Trichostegia minor</i> (Curtis, 1834)	V	45%	7%	10%
<i>Agrypnia obsoleta</i> Hagen, 1864	V	9%	40%	3%
Coleoptera - Beetles				
<i>Agabus affinis</i> (Paykull, 1798)	E	27%	7%	7%
<i>Agabus striolatus</i> (Gyllenhal, 1808)	E	18%	0%	2%
<i>Agabus unguicularis</i> (Thomson, 1867)	E	9%	0%	2%
<i>Graptodytes granularis</i> (L., 1767)	E	9%	0%	1%
<i>Helophorus laticollis</i> Thomson, 1853	D	9%	0%	0%
<i>Hydroporus glabriusculus</i> Aubé, 1838	CE	18%	0%	0%
<i>Rhantus grapii</i> (Gyllenhal, 1808)	E	36%	0%	3%
<i>Colymbetes paykulli</i> Erichson, 1837	CE	18%	40%	2%
<i>Dytiscus dimidiatus</i> Bergsträsser, 1778	E	27%	33%	1%
<i>Dytiscus lapponicus</i> Gyllenhal, 1808	CE	18%	53%	2%
<i>Laccophilus poecilus</i> Klug, 1834	CE	9%	53%	1%

Limnophilus griseus (5 records) and *Carex limosa* (1 record) were least recorded (Table 2). The species in table 2 are sorted by their average weighted co-occurrence, reflecting their present-day ability to represent other species characteristic of the bog gradient. *Hagenella clathrata* and *Trichostegia minor* often occurred together with other endangered species as reflected by their high average weighted co-occurrence (Table 2). These two species are most suitable to identify areas still harbouring gradient communities. Both *C. lasiocarpa* and *Hammarbya paludosa* had low weighted co-occurrences with other species and averages below 5, indicating a low affinity with the gradient community. For this reason the latter two species were not used to identify aggregations of endangered gradient species. The remaining species only had high weighted co-occurrences with part of the other species, indicating that they are indicative for a part of the gradient.

Table 2 Weighted co-occurrence of endangered species in the period 1991-2006 in the Netherlands based on national databases. The weighted co-occurrence describes the relation between the observed co-occurrence and the expected co-occurrence (see equation 1).

	<i>Hagenella clathrata</i>	<i>Trichostegia minor</i>	<i>Limnophilus stigma</i>	<i>Somatochlora arctica</i>	<i>Limnophilus griseus</i>	<i>Coenagrion bastulatum</i>	<i>Carex limosa</i>	<i>Anabolia brevipennis</i>	<i>Utricularia intermedia</i>	<i>Sparganium natans</i>	<i>Vaccinium uliginosum</i>	<i>Somatochlora flavomaculata</i>	<i>Carex lasiocarpa</i>	<i>Hammarbya paludosa</i>	Average	Number of records
<i>Hagenella clathrata</i>	X	32	21	50	66	15	0	0	11	7	45	18	5	0	21	13
<i>Trichostegia minor</i>	32	X	24	15	55	6	31	0	1	7	14	4	3	0	15	31
<i>Limnophilus stigma</i>	21	24	X	17	7	4	0	49	16	4	14	2	4	0	12	26
<i>Somatochlora arctica</i>	50	15	17	X	17	7	0	0	0	0	41	13	1	0	12	11
<i>Limnophilus griseus</i>	66	55	7	17	X	0	0	0	0	0	0	0	3	0	11	5
<i>Coenagrion bastulatum</i>	15	6	4	7	0	X	65	0	9	9	7	8	3	10	11	44
<i>Carex limosa</i>	0	31	0	0	0	65	X	0	0	36	0	0	10	0	11	1
<i>Anabolia brevipennis</i>	0	0	49	0	0	0	0	X	42	12	0	21	6	0	10	6
<i>Utricularia intermedia</i>	11	1	16	0	0	9	0	42	X	21	0	15	5	10	10	30
<i>Sparganium natans</i>	7	7	4	0	0	9	36	12	21	X	0	10	6	14	10	40
<i>Vaccinium uliginosum</i>	45	14	14	41	0	7	0	0	0	0	X	0	1	0	9	17
<i>Somatochlora flavomaculata</i>	18	4	2	13	0	8	0	21	15	10	0	X	3	1	7	49
<i>Carex lasiocarpa</i>	5	3	4	1	3	3	10	6	5	6	1	3	X	2	4	418
<i>Hammarbya paludosa</i>	0	0	0	0	0	10	0	0	10	14	0	1	2	X	3	2

Aggregations of endangered species (i.e. all species excluding *C. lasiocarpa* and *H. paludosa*) were scarce and concentrated in three areas (Figure 1). Aggregations of four or more species were recorded in only seven nature reserves since 1990 (Table 3), four moorland pools, two fens and one raised bog remnant. The conservation value of these reserves is high as all selected endangered species were recorded, with the exception of *L. griseus*. Many of these species (i.e. *C. limosa*, *Sparganium natans*, *Utricularia intermedia*, *Somatochlora arctica*, *S. flavomaculata* and *Anabolia brevipennis*) had not been recorded during censuses of vegetation and aquatic invertebrates in Dutch bog remnants (Table 1).

Most endangered species were recorded from the Korenburgerveen raised bog remnant (Table 3). The importance of the Korenburgerveen reserve for endangered species became also apparent from our own censuses of Dutch bog remnants as all recorded endangered gradient species (Table 1) were only encountered

Table 3 Recent (since 1990) occurrence (%) of endangered species in different types of nature reserves with four or more recorded species according to Dutch national databases.

Species	Raised bog remnant	Moorland pool	Fen
<i>Sparganium natans</i> *		75%	50%
<i>Coenagrion hastulatum</i>	100%	75%	
<i>Vaccinium uliginosum</i>	100%		
<i>Carex limosa</i> *		25%	
<i>Somatochlora arctica</i> *	100%		
<i>Somatochlora flavomaculata</i> *		75%	100%
<i>Trichostegia minor</i>	100%	75%	
<i>Hagenella clathrata</i>	100%	50%	
<i>Limnephilus stigma</i>	100%		100%
<i>Utricularia intermedia</i> *		50%	100%
<i>Anabolia brevipennis</i> *			100%
Number of reserves	1	4	2
Total number of species	6	7	5
Average number of species reserve ⁻¹	6.0	4.3	4.5

* species not recorded during censuses of vegetation and aquatic invertebrate in Dutch bog remnants (Table 1).

(*Vaccinium uliginosum*, *Coenagrion hastulatum*, *Graptodytes granularis*) or were most abundant (*H. clathrata*, *Limnephilus stigma*, *T. minor*, *Agabus affinis*, *Agabus striolatus*, *Agabus unguicularis* and *Rhantus grapii*) in the Korenburgerveen reserve.

Most species aggregations of four or more species were found in moorland pools. Cumulative species richness in the moorland pools exceeded those of fens and equalled the bog remnant and included both gradient indicator species *T. minor* and *H. clathrata* (Table 3), indicating that these pools function as refugia for endangered species characteristic of the complete bog gradient.

Environmental conditions in intact bog gradients

Groundwater influence was mostly present in the transitional mire and lagg of an intact raised bog but the chemical data indicate that the quantity was highly variable. The ionic ratio (see methods) varied from 0.07 at sites fed by runoff from the bog massive to 0.55 on locations influenced by groundwater seepage with an average of 0.27 (Table 4). The ionic ratio was positively correlated with pH, alkalinity, Ca and Fe, (Spearman rank correlations, $P < 0.05$, $N = 11$), indicating that these substances were also supplied by groundwater seepage in the raised bog gradients. Concentrations of Cl^- , ortho- PO_4^{3-} , NO_3^- , NH_4^+ and S did not vary with groundwater influence. Because the bog massive was

Table 4 Surface water chemistry (mean \pm SE) in different parts of Estonian raised bogs.

	Transitional mire and lagg N=11	Bog massive N=15
Ionic ratio	0.27 \pm 0.05 ^a	0.09 \pm 0.01 ^b
pH	4.9 \pm 0.3 ^a	4.1 \pm 0.1 ^b
Alkaliniteit (meq l ⁻¹)	0.15 \pm 0.05 ^a	0.01 \pm 0.00 ^b
Ca ($\mu\text{mol l}^{-1}$)	78.5 \pm 19.1 ^a	17.1 \pm 1.3 ^b
Cl ⁻ ($\mu\text{mol l}^{-1}$)	93.5 \pm 8.4	85.7 \pm 5.6
Fe ($\mu\text{mol l}^{-1}$)	13.0 \pm 3.9 ^a	2.9 \pm 0.2 ^b
NO_3^- ($\mu\text{mol l}^{-1}$)	1.95 \pm 0.18	1.63 \pm 0.16
NH_4^+ ($\mu\text{mol l}^{-1}$)	4.37 \pm 0.82	4.64 \pm 1.28
Ortho- PO_4 ($\mu\text{mol l}^{-1}$)	0.22 \pm 0.07	0.13 \pm 0.03
S ($\mu\text{mol l}^{-1}$)	16.6 \pm 1.7	17.6 \pm 1.0

Different letters (^a, ^b) indicate significant differences (Mann-Whitney-U tests; $P < 0.05$).

not subjected to groundwater input, ionic ratio, pH, alkalinity and concentrations of Ca and Fe were lower there than in the transitional mire and lagg (Table 4). Concentrations of ortho- PO_4^{3-} , NO_3^- , NH_4^+ and S were low throughout the bog landscape and did not differ between the different parts. The absence of groundwater seepage in the bog massive also resulted in a more uniform chemical environment than in the gradients (Table 4).

Not all species were equally distributed along the groundwater gradient in intact bog landscapes (Figure 2). *C. limosa*, *S. arctica*, *H. clathrata* and *T. minor* were recorded along nearly the entire gradient. For the latter two species this corresponded with their high average weighted co-occurrence in the Netherlands (Table 2) and confirmed their value as indicator species for the gradient community. Other species were recorded from part of the gradient only. *L. griseus*, *C. bastulatum*, and *V. uliginosum* were recorded at sites with a

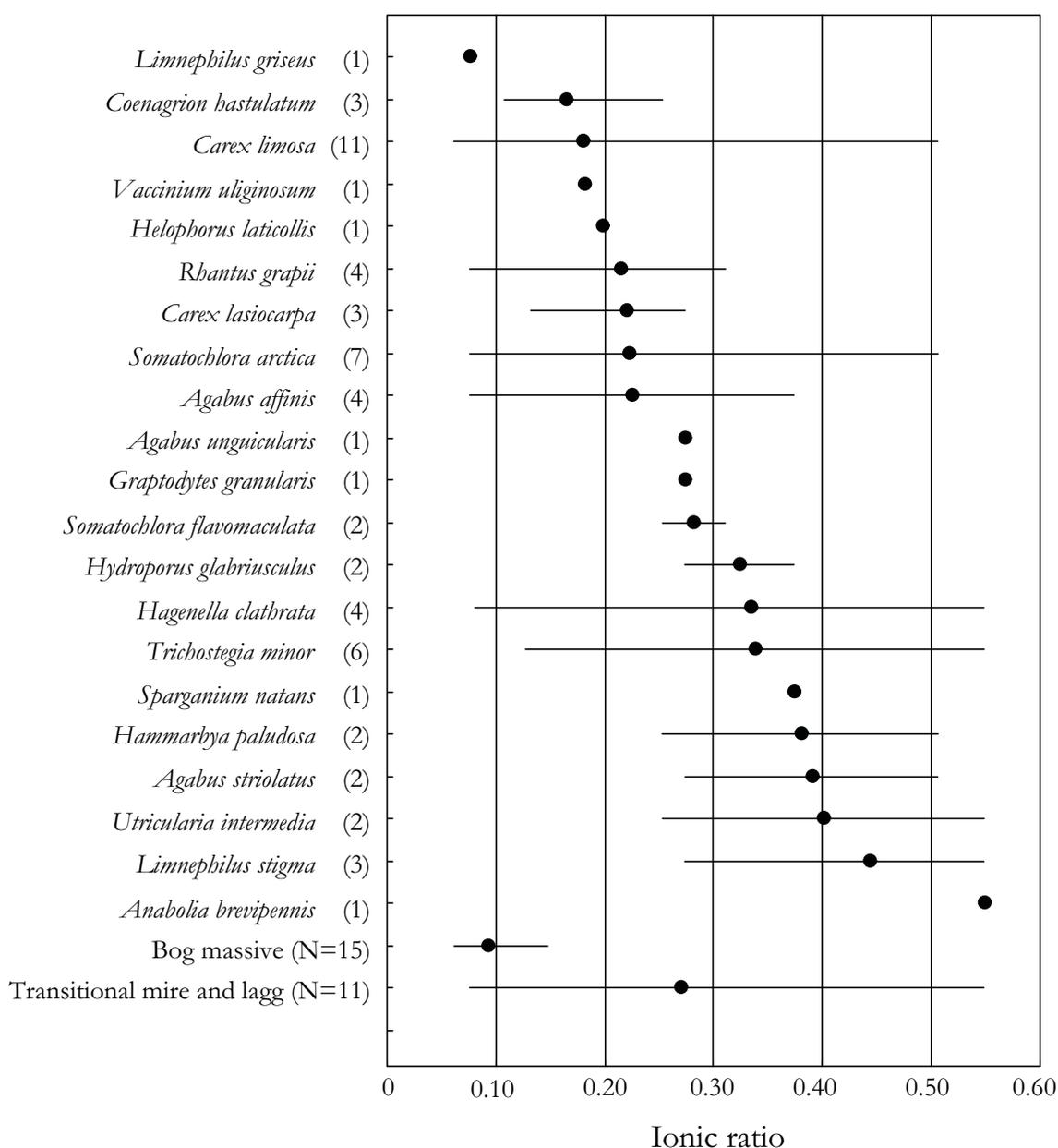


Figure 2 Minimum, mean and maximum ionic ratio of sampling sites in Estonian raised bogs harbouring endangered species. In brackets: number of sites where the species was recorded.

low ionic ratio, while *A. brevipennis*, *L. stigma* and *U. intermedia* were recorded at sites with a high mean ionic ratio. This corresponded with their distribution as species from the same part of the gradient often co-occurred (Table 2).

Environmental conditions in Dutch refugia for endangered species

Water chemistry was studied in three nature reserves with aggregations of selected endangered species (Table 5). In each of these moorland pools from shore to open water a gradient was recorded in pH, alkalinity and Ca (Table 5). With pH ranging between 3.8 and 7.7, alkalinity between 0.0 and 2.1 meq l⁻¹ and Ca between 44 and 1010 µmol l⁻¹ ranges of environmental conditions were similar to the gradient in transitional mire and lagg of an intact raised bog. Corresponding to the raised bog gradient, concentrations of ortho-PO₄³⁻, NO₃⁻, NH₄⁺ and S did not reveal clear patterns. Concentrations of NH₄⁺ and S were higher in the Dutch moorland pools than in the Estonian bog gradient (Mann-Whitney U test). Thus, reserves with aggregations of endangered species contain gradients similar to those found in transitional mires and lags of intact raised bogs.

The moorland pool gradients differed from those in the raised bogs in the absence of gradients in ionic ratio and Fe (Table 5). Each of the studied moorland pools received water from nearby streams, either through intentional water supplements through a series of lakes (Ringselven and Greveschutven) or periodic flooding (Rijsven). Water in the streams was alkaline (pH between 6.7 and 7.5 and alkalinity between 1.12 – 2.65 meq l⁻¹), rich in Ca (concentrations exceeding 1200 µmol l⁻¹) and responsible for the occurrence of a water chemistry gradient in the moorland pools. The streams were also rich in ortho-PO₄³⁻, NO₃⁻, S and Cl⁻ of agricultural origin, which resulted in elevated levels of the latter two in the pools. High concentrations of Ca and Cl⁻ in the stream water made the ionic

Table 5 Surface water chemistry in moorland pools and streams discharging on the pools.

	Sample code	Ionic ratio	pH	Alkalinity meq l ⁻¹	Ca µmol l ⁻¹	Cl ⁻ µmol l ⁻¹	Fe µmol l ⁻¹	NO ₃ ⁻ µmol l ⁻¹	NH ₄ ⁺ µmol l ⁻¹	o-PO ₄ ³⁻ µmol l ⁻¹	S µmol l ⁻¹
Ringselven											
Shore	RV1	0.09	3.9	0.00	51	261	6.2	3.2	6.6	0.03	73
	RV2	0.05	4.1	0.00	21	221	9.4	1.6	4.5	0.00	44
	RV3	0.05	4.3	0.01	24	221	4.0	4.7	3.6	0.63	41
	RV4	0.09	5.8	0.18	117	618	15.0	0.8	4.6	0.04	63
	RV5	0.09	5.7	0.22	124	649	25.1	1.2	6.8	0.00	57
	RV6	0.08	5.7	0.20	119	643	15.8	0.9	5.1	0.00	53
	RV7	0.07	5.5	0.16	102	660	14.6	0.7	4.6	0.07	60
	RV8	0.01	5.4	0.17	106	3506	21.8	4.4	12.0	0.99	51
Open water	RV9	0.36	7.7	2.07	1010	887	1.7	10.8	9.5	0.25	303
Stream	RV10	0.36	7.5	2.65	1258	1133	1.1	249.4	5.8	4.56	1488
Greveschutven											
Shore	GSV1	0.08	4.6	0.03	44	257	5.9	2.9	4.9	1.71	59
	GSV2	0.10	5.3	0.06	46	216	12.8	1.2	5.5	2.25	58
	GSV3	0.10	5.6	0.18	112	523	10.0	8.7	35.6	2.44	104
	GSV4	0.30	6.7	0.92	700	822	2.9	1.4	3.6	0.56	453
Open water	GSV5	0.24	7.1	1.44	765	1225	1.0	0.4	7.4	0.77	376
Stream	GSV6	0.38	7.4	1.41	1280	1044	1.8	40.3	8.3	0.42	573
Rijsven											
Shore	RIJ1	0.14	3.8	0.00	130	407	5.7	32.5	10.7	2.60	504
	RIJ2	0.12	5.2	0.11	177	623	12.0	10.9	9.2	0.74	346
Open water	RIJ3	0.10	6.1	0.29	218	971	2.7	9.9	8.6	0.29	359
Stream	RIJ4	0.20	6.7	1.12	1264	2457	1.9	365.0	0.4	3.52	1716

ratio ineffective to identify ground water influence in the pools. Seepage of older groundwater was indicated by elevated Fe concentrations recorded halfway from shore to open water (RV4-8, GSV2-3 and RIJ2, Table 5), whereas the absence of elevated Fe concentrations directly near the shore (RV1-3, GSV1 and RIJ1) together with low pH indicated seepage of young groundwater. Rapid mixing of different types of water was prevented by the extensive macrophyte vegetation (Figure 3) resulting in gradient lengths of 65 to 270 m. So, the moorland pool gradients had different origins than the bog gradients as the alkaline influence was provided by stream water supplements and the acid part of the gradient by groundwater seepage.

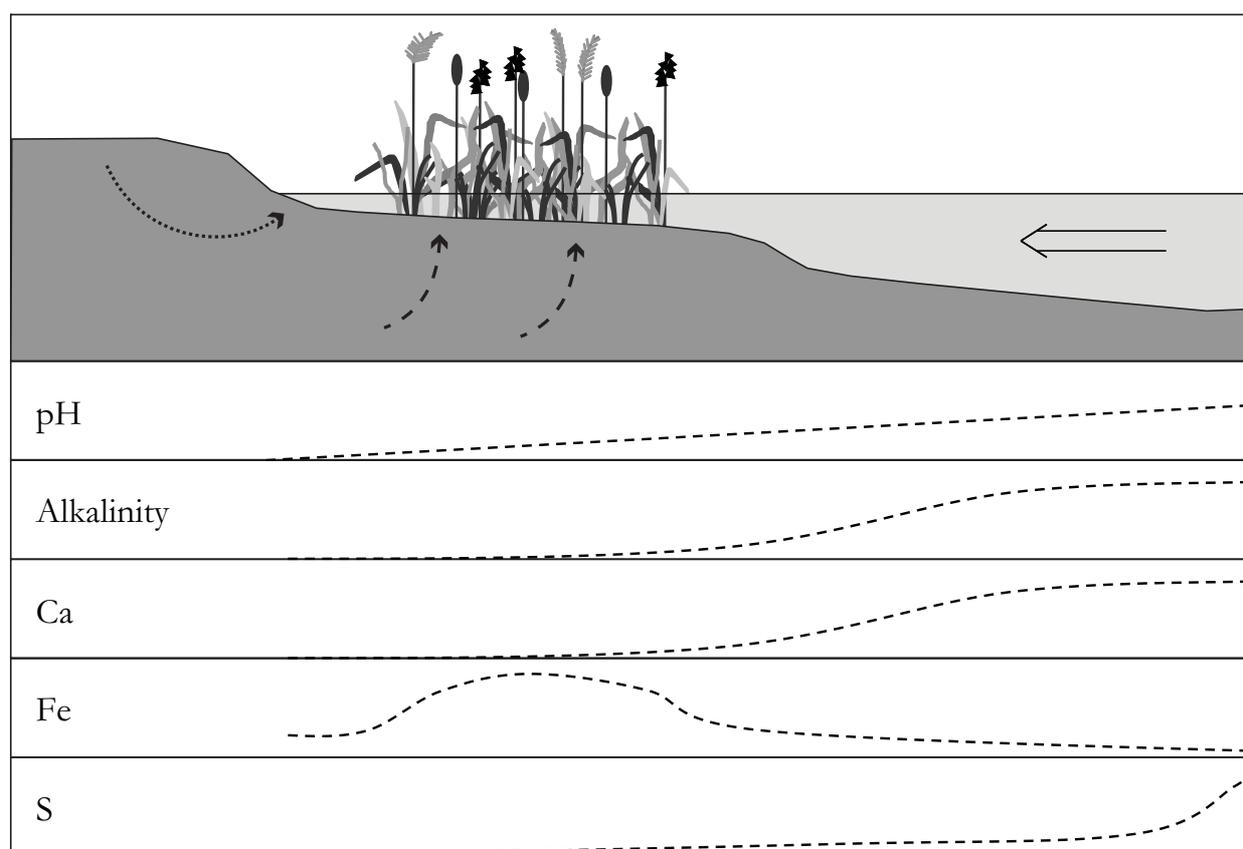


Figure 3 Schematic overview of the hydrology of a moorland pool gradient and idealised chemistry. Arrows: dotted = young groundwater, dashed = old groundwater, double = stream water.

Discussion

Gradient communities in intact and degraded raised bog landscapes

In the lagg zone and transitional mire of intact Estonian raised bog landscapes, mixing of alkaline ground water and acidic bog water resulted in water chemistry gradients: i.e. pH, alkalinity, Ca and Fe, similar to those reported by Bragazza & Gerdol (2002). Despite the fact that these gradients occupy only a small area, this study demonstrates them to be an important habitat for species which are nowadays endangered in the Netherlands (Table 1).

In degraded Dutch bog remnants these endangered species were only rarely recorded during extensive sampling (198 sites) and some were only recorded outside the bog remnants. The only exception was the Korenburgerveen reserve (Figure 1, Table 3),

which harboured populations of many of the endangered species (Verberk 2008). This area still encompasses a high diversity of water types and transitions between them, providing many different niches for aquatic macroinvertebrates (Verberk et al. 2008), which has resulted in a high species richness (Verberk et al. 2006). Extensive degradation, cultivation and restoration of Dutch bog remnants made it impossible to distinguish between transitional mire, lagg zones and ombrotrophic bog habitats. Therefore occurrence of gradient species in Dutch bog remnants was presented for all sites together (Table 1). This may have partially resulted in a relatively low recorded occurrence of gradient species in Dutch bog remnants. However, analysis of national distribution data confirmed that aggregations of endangered species are only found outside bog remnants with exception of the Korenburgerveen reserve.

Refugia of gradient communities in moorland pools

Analysis of national distribution data revealed that moorland pools provide important refugia for endangered species of bog gradients (Table 3). Key factors shaping their function as refugia were gradients in pH, alkalinity and Ca similar to the gradients in intact Estonian bog landscapes (Table 5). Water chemistry gradients in the pools appear to be the result of three types of water (Figure 3); i.e. young seepage water, older groundwater and stream water. Extensive macrophyte vegetation near the shore prevented rapid mixing of seepage and stream water and allowed for a gradual transition between the different water types.

Uncertainty of grid based distribution data

National distribution data of endangered species were used to identify refugia for endangered species from raised bog gradients. Donald & Fuller (1998) discussed the limitations of grid based distribution data. They mentioned two factors which may negatively affect data quality. Firstly, linking data on distribution and environmental conditions may be difficult when distribution data is coarse, i.e. available on a 1-km grid. This problem was circumvented by using grid data to identify important areas, which in turn were visited in order to determine the exact reproduction and growing sites of selected species and allow for collection of environmental data on the appropriate scale. Secondly, the accuracy of identification of areas of conservational interest is influenced by the intensity of coverage. In the Netherlands the collection of plant and macroinvertebrate distribution data is not standardised and many of the studied species are inconspicuous and easily overlooked. As a result the list of areas with species' aggregations is likely –and hopefully– not complete. Furthermore, several steps were taken to increase the likelihood of correctly identifying areas with high conservation value. The co-occurrence of multiple species was used to prevent biased distribution patterns of single species to determine the results. Additionally, a weighted co-occurrence was calculated and applied with a threshold in order to separate coincidental from nested co-occurrence. Although the list of areas may be incomplete, those areas identified as having high conservation value are likely to be correct since the pattern resulting from the intensive survey of raised bog remnants was consistent with that of the national distribution data: the near absence of aggregations of endangered species in bog remnants. In addition, since the environmental conditions are very specific such places are unlikely to be detected by chance and field measurements consistently verified the presence of these special conditions.

Management implications and additional research

The challenges for restoration of raised bog landscapes are considerable. It requires restoration of regional hydrology (Lamers et al. 1999) and in many places is hampered by elevated deposition of airborne nitrogen (Lamers et al. 2000). Even if these challenges are met, it still takes a long time for a hydrological functioning acrotelm (Belyea & Clymo 2001) and thus for species-rich gradients to develop. At present many of the species that are characteristic of raised bog gradients are very rare and endangered. Therefore, conservation of existing and especially development of new populations is required to ensure their short-term survival and their colonisation of restored raised bogs in the long-term. Man-made alkalinity gradients in moorland pools appear to be suitable refugia for these species. Up until the first half of the previous century, water inlet in moorland pools was frequent land use for local fisheries (Leuven & Oyen 1987, Arts et al. 1988) and these gradients were probably common. Eventually, the economic importance of this practice decreased and most pools regained their natural status. Alkalinisation and the associated eutrophication was considered undesirable for these pools and the inlet of stream waters was ceased on all but a few locations.

An important question when considering supplying moorland pools with stream water is therefore how durable such inlet of stream water is as a management tool. Wassen et al. (1990) and Boeye et al. (1996) reported similar plant communities occurring under the influence of both ground water and nutrient rich stream water in valleys. Navrátilová et al. (2006) also concluded that these species-rich gradients can persist under fluctuating supplies of alkaline, nutrient rich water. It thus appears possible to create stable alkalinity gradients. On the other hand, high alkalinity and S concentrations were observed in the moorland pools (Table 5) exceeding previously established thresholds for reduced mineralization (Roelofs 1991, Smolders & Roelofs 1993, Lamers et al. 1998, Lamers et al. 2002). High S concentrations can also mobilise phosphate from the sediment (Caraco et al. 1989, Smolders & Roelofs 1993, Lucassen et al. 2005a, Smolders et al. 2006) and cause severe acidification and metal toxicity during droughts (Vangenechten et al. 1981, Kemmers & Jansen 1988, Lamers et al. 1998). Therefore, the durability of the studied gradients in moorland pools remains questionable. Based on state-of-the-art knowledge on biogeochemical processes, we expect that maintaining moorland pool gradients requires alternating supplies of ground and stream water in order to prevent one type of water supply to gain the upper hand. In addition, some situations will require mitigation of the S supplements from streams by means of temporary desiccation. This will oxidise sulphide to sulphate which is soluble and can then be flushed from the system (Lucassen et al. 2005b). Temporary desiccation was historically also applied as part of the fishery management, when pools were drained in winter to harvest the fish. Lowering of the water table during winter will allow oxidization of the sediment, while groundwater seepage simultaneously prevents complete desiccation of the substrate. We expect that these permanently moist conditions combined with the low metabolic activity in winter ensure the survival of the gradient species during the oxidization process. On the other hand, lowering of the water table in summer will completely desiccate the sediment due to the absence of seepage and therefore is unlikely to be suitable for managing moorland pool gradients. Given the demonstrated potential of moorland pools to function as refugia for endangered species, future research should focus on the sustainability of these water chemistry gradients and how this function is affected by efforts to increase its durability such as temporary desiccation.

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References

- Arts GHP, Schaminée JHJ & Van den Munckhof PJJ (1988) Human impact on origin, deterioration and maintenance of Littorelletalia-communities. *Proceedings of the 5th symposium on synanthropic flora and vegetation, 1988. Martin, Czechoslovakia*: 11-18.
- Belyea LR & Clymo RS (2001) Feedback control of the rate of peat formation. *Proceedings of the Royal Society B-Biological Sciences* **268**: 1315-1321.
- Boeye D, Van Haesebroeck V, Verhagen B, Delbaere B, Hens M & Verheyen RF (1996) A local rich fen fed by calcareous seepage from an artificial river water infiltration system. *Vegetatio* **126**: 51-58.
- Bragazza L & Gerdol R (2002) Are nutrient availability and acidity-alkalinity gradients related in *Sphagnum*-dominated peatlands? *Journal of Vegetation Science* **13**: 473-482.
- Caraco NF, Cole JJ & Likens GE (1989) Evidence for sulphate-controlled phosphorus release from sediments of aquatic systems. *Nature* **341**: 156-158.
- CBS (2009) Retrieved October 23, 2009, from <http://www.cbs.nl/>.
- Couwenberg J & Joosten H (2005) Self-organization in raised bog patterning: the origin of microtope zonation and mesotope diversity. *Ecology* **93**: 1238-1248.
- Desrochers A & Van Duinen GA (2006) Peatland Fauna, in Wieder RK & Vitt DH (Eds.), *Boreal Peatland Ecosystems. Ecological Studies, Vol. 18. Springer-Verlag, New York*: 67-100.
- Donald PF & Fuller RJ (1998) Ornithological atlas data: a review of uses and limitations. *Bird Study* **45**: 129-145.
- Drost MBP, Cuppen HPJJ, Van Nieuwerkerken EJ & Schreijer M (Eds.) (1992) *De waterkevers van Nederland. Uitgeverij KNNV, Utrecht*.
- Grasshoff H & Johanssen H (1972) A new sensitive and direct method for the automatic determination of ammonia in sea water. *Journal du Conseil* **34**: 516-521.
- Henriksen A (1965) An automated method for determining low-level concentrations of phosphate in fresh and saline waters. *Analyst* **90**: 29-34.
- Joosten H & Clarke D (2002) Wise use of mires and peatlands - Background and principles including a framework for decision-making. *International Mire Conservation Group & International Peat Society, Greifswald*.
- Kamphake LH, Hannah SA & Cohen JM (1967) Automated analysis for nitrate by hydrazine reduction. *Water Research* **1**: 206.
- Kemmers RH & Jansen PC (1988) Hydrochemistry of rich fen and water management. *Agricultural Water Management* **14**: 399-411.

- Lamers LPM, Van Roozendaal SME & Roelofs JGM (1998) Acidification of freshwater wetlands: Combined effects of non-airborne sulphur pollution and desiccation. *Water, Air, and Soil Pollution* **105**: 95-106.
- Lamers LPM, Farhoush C, Van Groenendael JM & Roelofs JGM (1999) Calcareous groundwater raises bogs; the concept of ombrotrophy revisited. *Journal of Ecology* **87**: 639-648.
- Lamers LPM, Bobbink R & Roelofs JGM (2000) Natural nitrogen filter fails in polluted raised bogs. *Global Change Biology* **6**: 583-586.
- Lamers LPM, Falla SJ, Samborska EM, Van Dulken LAR, Van Hengstum G & Roelofs JGM (2002) Factors controlling the extent of eutrophication and toxicity in sulphate-polluted freshwater wetlands. *Limnology and Oceanography* **47**: 585-593.
- Leuven RSEW & Oyen FGF (1987) Impact of acidification and eutrophication on the distribution of fish species in shallow and lentic soft waters in the Netherlands: An historical perspective. *Journal of Fish Biology* **31**: 752-774.
- Lucassen ECHET, Smolders AJP & Roelofs JGM (2005a) Effects of temporary desiccation on the mobility of phosphorus and metals in sulphur-rich fens: differential responses of sediments and consequences for water table management. *Wetlands Ecology and Management* **13**: 135-148.
- Lucassen ECHET, Smolders AJP, Lamers LPM & Roelofs JGM (2005b) Water table fluctuations and groundwater supply are important in preventing phosphate-eutrophication in sulphate-rich fens: Consequences for wetland restoration. *Plant and Soil* **269**: 109-115.
- Navrátilová J, Navrátil J & Hájec M (2006) Relationships between environmental factors and vegetation in nutrient-enriched fens at fishpond margins. *Folia Geobotanica* **41**: 353-376.
- O'Brien JE (1962) Automatic analysis of chlorides in sewage. *Sewage Industries Wastes Engineering* **33**: 670-682.
- Peus F (1923) Die Tierwelt der Moore. *Handbuch der Moorkunde III*. Bornträger verlag, Berlin.
- Pons LV (1992) Holocene peat formation in the lower parts of the Netherlands, in Verhoeven JTA (Ed.). Fens and bogs in The Netherlands: Vegetation, History, Nutrient Dynamics and conservation. *Kluwer, Dordrecht*: 7-80.
- Rochefort L (2000) New frontiers in bryology and lichenology – *Sphagnum* – a keystone genus in habitat restoration. *Bryologist* **103**: 503-508.
- Roelofs JGM (1991) Inlet of alkaline river water into peaty lowlands: effects on water quality and *Stratiotes aloides* L. stands. *Aquatic Botany* **39**: 267-293.
- Schouwenaars JM (1993) Hydrological differences between bogs and bog-relicts and consequences for bog restoration. *Hydrobiologia* **265**: 217-214.
- Shmida A & Wilson MV (1985) Biological determinants of species diversity. *Journal of Biogeography* **12**: 1-20.
- Smolders A & Roelofs JGM (1993) Sulphate-mediated iron limitation and eutrophication in aquatic ecosystems. *Aquatic Botany* **46**: 247-253.
- Smolders AJP, Lamers LPM, Lucassen ECHET, Van der Velde G & Roelofs JGM (2006) Internal eutrophication: How it works and what to do about it – a review. *Chemistry and Ecology* **22**: 93-111.
- Van Breemen N (1995) How *Sphagnum* bogs down other plants. *Trends in Ecology and Evolution* **10**: 270-275.
- Van der Meijden R, Odé B, Groen CLG, Witte JPM & Bal D (2000) Bedreigde en kwetsbare vaatplanten in Nederland. Basisrapport met voorstel voor de Rode Lijst. *Gorteria* **26**: 85-208.
- Van Duinen GA, Brock AMT, Kuper JT, Leuven RSEW, Peeters TMJ, Roelofs JGM, Van der Velde G, Verberk WCEP & Esselink H (2003) Do restoration measures rehabilitate fauna diversity in raised bogs? A comparative study on aquatic macroinvertebrates. *Wetlands Ecology and Management* **11**: 447-459.
- Van Duinen GA, Timm T, Smolders AJP, Brock AMT, Verberk WCEP & Esselink H (2006) Differential response of aquatic oligochaete species to increased nutrient availability – a comparative study between Estonian and Dutch raised bogs. *Hydrobiologia* **564**: 143-155.

- Van Duinen GA (2008) Evaluatie van hoogveenherstel in Mariapeel & Deurnese Peel. Watermacrofauna. *Report Stichting Bargerveen, Nijmegen*.
- Vangenechten JHD, Bosmans F & Deckers H (1981) Effects of short-term changes in rain water supply on the ionic composition of acid moorland pools in the Campine of Antwerp (Belgium). *Hydrobiologia* **76**: 149-159.
- Van Wirdum G (1991) Vegetation and hydrology of floating rich-fens. *Thesis, University of Amsterdam, Amsterdam*.
- Verberk WCEP, Van Duinen GA, Brock AMT, Leuven RSEW, Siepel H, Verdonschot PFM, Van der Velde G & Esselink H (2006) Importance of landscape heterogeneity for the conservation of aquatic macroinvertebrate diversity in bog landscapes. *Journal of Nature Conservation* **14**: 78-90.
- Verberk WCEP, Siepel H & Esselink H (2008) Applying life-history strategies for freshwater macroinvertebrates to lentic waters. *Freshwater Biology* **53**: 1739-1753.
- Verberk WCEP (2008) Matching species to a changing landscape – Aquatic macroinvertebrates in a heterogeneous landscape. *Thesis, Radboud University, Nijmegen*.
- Verdonschot PFM, Higler LWG, Nijboer RC & Van den Hoek TH (2003) Naar een doelsoortenlijst van aquatische macrofauna in Nederland: Tricladida, Plecoptera, Ephemeroptera en Trichoptera. *Alterra rapport 858. Wageningen*.
- Verhoeven JTA (Ed.) (1992) Fens and bogs in the Netherlands: vegetation, history, Nutrient dynamics and conservation. *Kluwer, Dordrecht*.



Study area of this thesis. Photo: Hein van Kleef.

Chapter 7

Synthesis

Hein van Kleef

Moorland pool restoration: theory and practice

Moorland pools have undergone many changes in the course of centuries: natural dynamics have been replaced by human activities, pools were reclaimed for agriculture, human exploitation ceased, acidification, eutrophication and desiccation increased and subsequently decreased. Each of these changes has had profound effects on moorland pool biota, resulting in the most recent addition of human activities in these pools: ecological restoration.

In this thesis the effectiveness of moorland pool nature management in conserving and restoring communities of characteristic aquatic macroinvertebrates is assessed. Ideally, degraded nature is restored by eliminating environmental stressors. These stressors are conditions and processes resulting in degradation, but also include changes in natural dynamics inducing different succession trajectories. However, there are many examples of degraded ecosystems where natural recovery and even recovery aided by management is hampered by abiotic or biotic barriers (Suding et al. 2004 and the literature therein). Hobbs (2007) presented a framework that describes how an ecosystem passes through different states during the process of degradation and how recovery can be prevented by thresholds. Effectiveness of measures is highly dependent on the kind of abiotic and biotic problems preventing natural recovery of degraded moorland pools, the scale on which they operate and the extent in which they have been tackled. Figure 1 is an adapted version of Hobbs’ model of degradation and thresholds. It depicts the response of ecosystem structure to increasing and chronic environmental stress (pristine towards degraded) and restoration or recovery from decreasing environmental stress (degraded

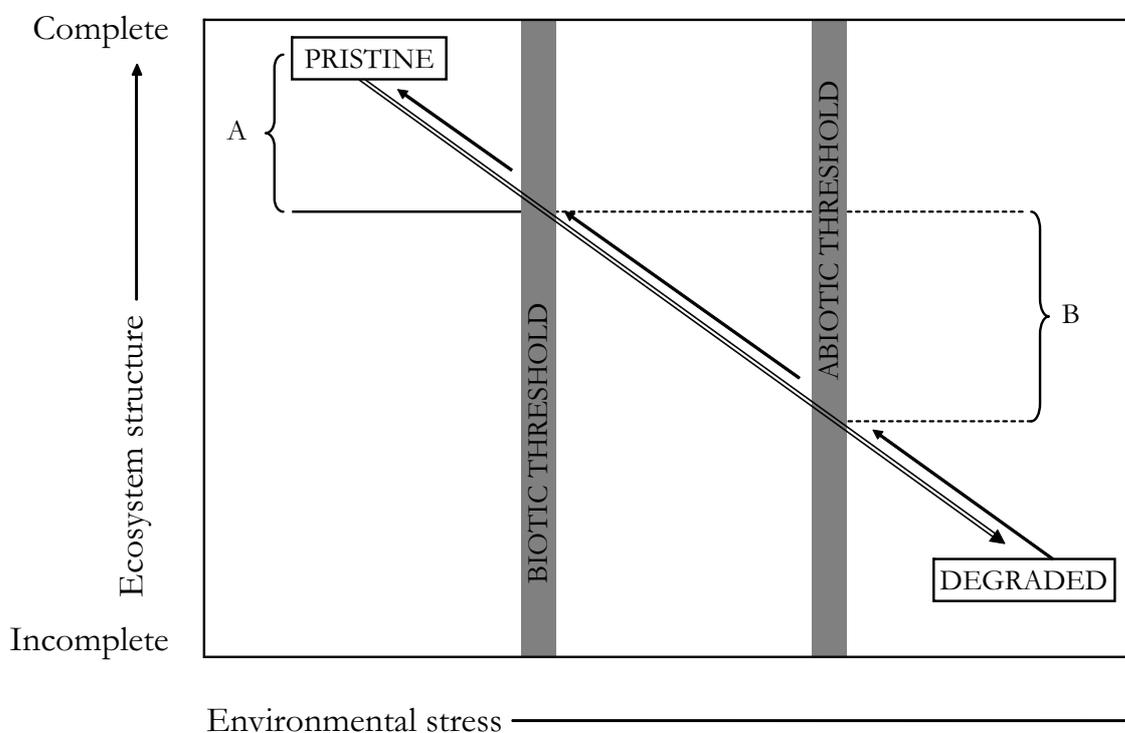


Figure 1 Schematic of ecosystem degradation and restoration adapted from Hobbs (2007). Boxes represent ecosystem states and arrows represent transitions between states. Double-lined arrow: degradation trajectory. Single-lined arrow: theoretic recovery trajectory. Barriers preventing transition from a degraded to a less degraded state are indicated by grey bars. A: potential recovery prevented by biotic threshold. B: potential recovery prevented by abiotic threshold.

towards pristine). During the process of degradation certain directional thresholds may be passed, which cannot be crossed from the other side and prevent completion of the recovery trajectory. It is important to note that the x-axis contains an environmental component (for example supply of nutrients) as well as a temporal component (for example to encompass cumulative effects and time limited biological processes).

A prominent assumption in the current practice of moorland pool restoration is that natural recovery is prevented by adverse abiotic conditions (Roelofs et al. 2002). The abiotic threshold in acidifying moorland pools is the result of transformation of bicarbonate into carbon dioxide, leaching of base cations and carbon from the catchment, increased primary production and decreased decomposition rate. Important processes for eutrophication are increased primary production and accumulation of nutrients in the catchment. These changes give rise to an abiotic threshold consisting of accumulated nutrients on the pool bottoms and deterioration of the catchments (i.e. loss of alkalinity, accumulation of nutrients) which prevents natural recovery (Roelofs et al. 2002).

Moorland pool restoration measures are thus devised to eliminate detrimental abiotic conditions and restore conditions suitable for the development of characteristic soft water vegetation, such as a variety of isoetids. Moorland pools are dredged to remove accumulated organic sediment and unwanted helophyte swards. Many pools are temporarily drained in order to increase accessibility and to facilitate dredging (Roelofs et al. 2002). Often this measure is combined with restoring alkalinity through the supply of calcareous, nutrient-poor water or catchment liming because acid deposition still exceeds critical loads and catchments no longer provide alkalinity (Brouwer et al. 2002, Brouwer & Roelofs 2002, Dorland et al. 2005). Removal of forest from the shores and catchment reduces input of allochthonous organic material and increases groundwater supply by reducing evapotranspiration. Occasionally groundwater influence is increased by removing drainage ditches, thus decreasing drainage.

In short, these measures focus on restoring pre-industrial abiotic state of the moorland pools. Pioneer conditions are created, allowing a natural succession trajectory and assuming that recovery is sufficient (i.e. complete, sustainable and fast) enough to balance the negative effects of degradation. Nevertheless, limited colonisation of restored pools has been demonstrated for characteristic macrophytes (Brouwer et al. 2002). Limited colonisation is a plausible result of the extensive reclamation (longer distances) and degradation of pools (smaller source populations) and constitutes a biotic threshold responsible for incomplete restoration of moorland pools (Figure 1). However, at present no additional measures are being taken to improve the regional species pool.

In the previous chapters the presence and functioning of these thresholds in moorland pool recovery have been explored. In this chapter, I discuss the implications for the management of moorland pools, the framework of restoration thresholds and restoration ecology in general.

Organic sediment, the abiotic threshold

Current practice of moorland pool restoration not only induces a significant disturbance of the ecosystem (see following paragraphs), it is also relatively expensive with costs up to €30,000 ha⁻¹. Therefore, natural recovery of degraded pools would be preferable. However, natural recovery from acidification and eutrophication is expected to be limited by accumulation of organic material in the pools as well as acidification and nutrient

accumulation of the catchment (Roelofs et al. 2002). Nevertheless, reduction of emissions of acidifying compounds has shown to lead to at least partial recovery from acidification in lakes in Northern Europe and America (Stoddard et al. 1999, Forsius et al. 2003, Davies et al. 2005, Skjelkvåle et al. 2005) as well as Dutch moorland pools (Van Dam 1996). Whether the continuing decline of acidifying deposition has resulted in a recovery of moorland pool water chemistry and chironomid assemblages has been studied in chapter 2 and 3, respectively.

The response of moorland pool water chemistry proved to be twofold (Chapter 2). On the one hand, water quality improved in terms of increased pH and alkalinity and decreased concentrations of nitrate- and ammonium-N, sulphur, aluminium, calcium and magnesium. On the other, turbidity more than doubled in the pools, which appeared to be the result of water coloration by organic acids. Increased concentrations of organic compounds have also been observed in streams and lakes (Evans et al. 2005, 2006, Vuorenmaa et al. 2006, Monteith et al. 2007). Various mechanisms for increased levels of organic compounds have been proposed: hydrological change, land-use change, N enrichment, atmospheric CO₂ enrichment, increased decomposition, reduced acidification and temperature change (Evans et al. 2005, 2006). Reduced acidity was positively correlated with increases in ortho-phosphate and turbidity, indicating that reduced acidification might have stimulated decomposition of organic material (Chapter 2). Bellemakers et al. (1994) also reported increased decomposition resulting from reduced acidity in moorland pools where lime was added. Increased turbidity was shown to correlate with a decrease in the abundance of chironomid species, that are vulnerable for low summer oxygen concentrations (Chapter 3). This indicates an increased mineralisation of organic sediments leading to high oxygen consumption and oxygen deficiency and supports our findings on changes in water chemistry.

The release of organic acids associated with reduced S-deposition has been regarded by Monteith et al. (2007) as a sign of natural recovery of lakes and streams. This may indeed be the case for the aquatic ecosystems studied by this author as they depend on large catchments with a natural store of organic material. Moorland pools on the other hand have small catchments where in pre-industrial times organic material was scarce. Therefore, water chemistry in the pools is largely determined by internal processes and rising organic acids concentrations at present indicate a trajectory of deterioration. It is unclear if moorland pools will be able to purge themselves from accumulated carbon through this mechanism. It is expected that increased water coloration and phosphate concentrations will persist until most of the readily degradable organic matter has been decomposed. It is apparent that the reduction of acidification has not yet halted the decline of characteristic species and actually appears to contribute to degradation as long as decomposable organic sediments remain present. Active management in the form of removal of organic sediments at present is the only option for a speedy recovery of moorland pools.

Contrary to dominant views, natural recovery of degraded moorland pools was not merely obstructed by the abiotic threshold. Reduction of the acidifying deposition actually appeared to trigger decomposition of accumulated organic material, resulting in a new ecosystem state with a different structure than encountered during the process of degradation (Figure 2). Analysis of changes in chironomid assemblages revealed that stimulated decomposition was associated with a further decrease in the abundance of characteristic species (Chapter 3). Van Dam (1996) on the other hand reported a recovery

of diatom communities as a result of decreased acidifying decomposition. The combination of all different structural components of moorland pool biota will determine whether “A” in Figure 2 is large or small.

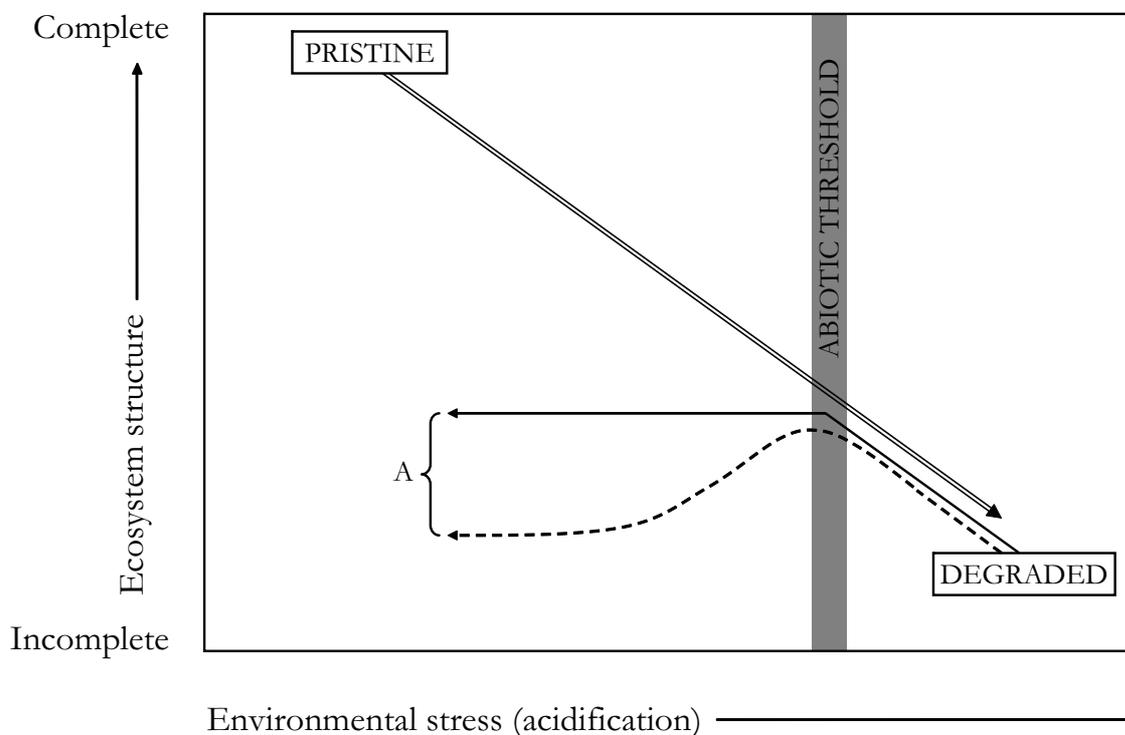


Figure 2 Schematic of moorland pool acidification and recovery. Boxes represent ecosystem states and arrows represent transitions between states. The abiotic barrier (i.e. layer of accumulated organic material and alkalinity depleted catchment) preventing transition from a degraded to a less degraded state is indicated by the grey bar. Double-lined arrow: acidification trajectory. Single-lined arrow: theoretic trajectory of recovery. Dotted-lined arrow: realised trajectory under reduced acidifying deposition. A: recovery prevented due to interaction between reduced environmental stress and abiotic threshold.

Also in other ecosystems (mainly lakes and streams) biotic recovery from acidification has been reported (Lancaster et al. 1996, Tipping et al. 2002, Hynynen & Meriläinen 2005, Monteith et al. 2005, Ormerod & Durance 2009). However, as in moorland pools, responses to reduced acidification differ between taxonomic groups, preventing complete recovery. Hypotheses explaining the response of biota assume direct linear or non-linear responses of assemblage structure to chemistry, time-lags due to limited dispersal or limited recovery resulting from species interactions (Monteith et al. 2005 and the literature therein). Chironomids in moorland pools did not appear to react directly to reduced acidification. Instead they seemed to be at least partly influenced by mineralisation of organic sediment. This is to be expected as they are mainly bottom-dwelling species. Natural recovery of chironomid assemblages is not expected to occur until the degradable organic matter has been decomposed. Hence, the response of chironomids in moorland pools can best be characterised as a non-linear response to reduced acidification.

Dealing with local and regional species pools

Reduced landscape connectivity and propagule availability are known to limit recovery of species in degraded communities (Bakker & Berendse 1999, Hanski & Ovaskainen 2002, Suding & Hobbs 2009). This also appears to be the case for characteristic soft water plants in restored moorland pools (Brouwer et al. 2002). Limited colonisation of restored moorland pools is attributed to strong reductions in the number of moorland pools increasing distances to potential source populations as well as smaller source populations due to degradation (Roelofs et al. 2002). Although many aquatic macroinvertebrates have mechanisms of dispersal to potentially cover expanses of land, that does not by definition imply that they are willing or able to cover large distances or will do so in large numbers (Bohonak & Jenkins 2003). Effectiveness of regional species pools as a source of propagules for recolonisation is expected to be further limited by increased abundance of competing species or predators at the restored sites due to higher abundance in adjacent waters (Morin 1984, Mouquet et al. 2003, Leps 2004, Price & Morin 2004).

A recent study (Brouwer et al. 2009) revealed no changes in abundance and richness of macroinvertebrate species characteristic of low alkaline moorland pools (Arts 2000) between 1983 and 2004–2007 in non-restored moorland pools. In restored moorland pools their abundance increased significantly (Figure 3) but the number of characteristic species did not, suggesting that recovery of moorland pool macroinvertebrate assemblages might be hampered by a damaged regional species pool. Limited effectiveness of regional species pools as a source of propagules for recolonisation, enhances the importance of local species pools (i.e. relict populations) for the recovery of ecosystem structure. The response of the local species pool to restoration measures has been studied in chapters 3 and 4.

Degraded moorland pools still harboured characteristic species (Chapter 3 and 4, Figure 3, Table 1). These species were having difficulties surviving the process of

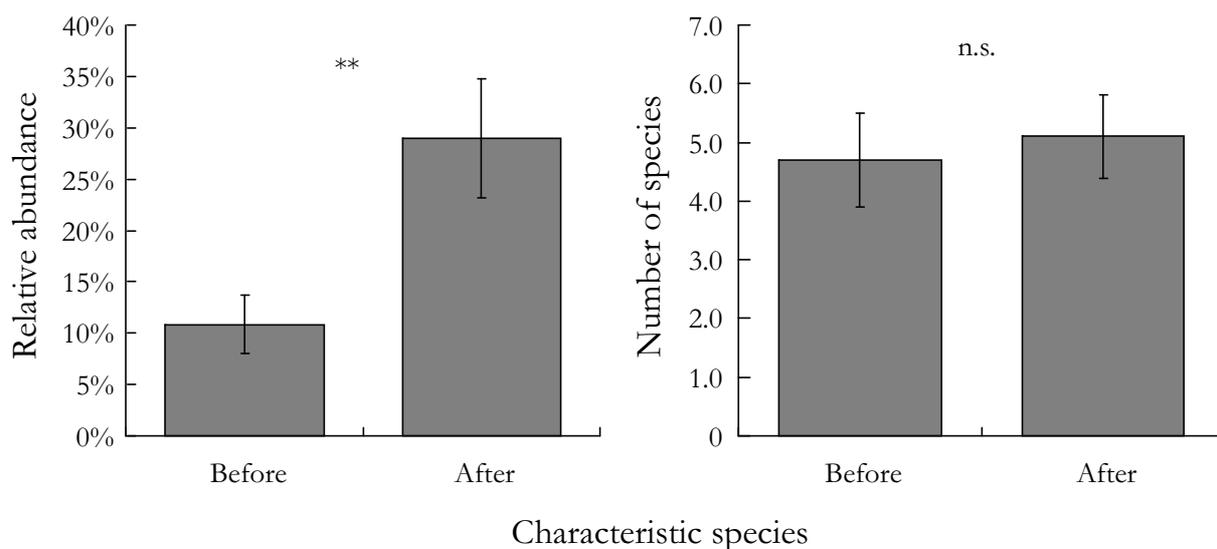


Figure 3 Average abundance and richness of characteristic macroinvertebrates (average \pm SE; Odonata, Trichoptera, Hemiptera and Chironomidae) in 1983 and 2004/2007 in ten moorland pools where restoration measures have been taken. Changes from 1983 to 2004/2007 were tested using Wilcoxon signed ranks test (**: $P < 0.01$ and n.s.: not significant). See Table 1 for presence of individual species.

Table 1 Changes in the presence (expressed as number of sites) of characteristic macroinvertebrates in restored (N=10) and non-restored moorland pools (N=9) from 1983 to 2004/2007. Species mentioned were recorded only before (-), before and after (=) or only after restoration measures were carried out (+).

	No restoration			Restoration		
	-	=	+	-	=	+
Hemiptera						
<i>Arctocorisa germari</i> (Fieber, 1848)	0	0	0	1	0	1
<i>Corixa dentipes</i> Thomson, 1869	2	0	0	5	0	0
<i>Cymatia bondsdorffii</i> (C R Sahlberg, 1819)	3	0	1	4	2	2
<i>Glaenocorisa propinqua</i> (Fieber, 1860)	0	0	0	1	0	0
<i>Notonecta obliqua</i> Thunberg, 1787	1	0	0	2	1	0
<i>Notonecta reuteri</i> Hungerford, 1928	0	0	0	2	0	0
<i>Notonecta viridis</i> Delcourt, 1909	2	0	1	3	1	2
<i>Sigara scotti</i> (Douglas & Scott, 1868)	1	0	2	2	2	4
Odonata						
<i>Coenagrion bastulatum/lunulatum</i>	0	0	0	2	0	0
<i>Lestes dryas</i> Kirby, 1890	0	0	0	2	0	0
Trichoptera						
<i>Agrypnia obsoleta</i> Hagen, 1864	0	0	0	1	0	1
<i>Agrypnia varia</i> (Fabricius, 1793)	1	1	1	2	0	3
<i>Holocentropus dubius</i> (Rambur, 1842)	0	0	0	1	0	2
<i>Trichostegia minor</i> (Curtis, 1834)	1	1	0	0	1	0
Chironomidae						
<i>Dicrotendipes</i> gr. <i>tritonus</i>	2	0	0	0	0	2
<i>Pagastiella orophila</i> (Edwards, 1929)	0	0	0	0	0	2
<i>Parakiefferiella</i> ssp.	0	0	0	0	0	1
<i>Polypedium uncinatum</i> (Goetghebuer, 1921)	0	9	0	1	6	2
<i>Psectrocladius psilopterus</i> Kieffer & Thienemann, 1906	0	2	3	1	2	5
<i>Pseudochironomus prasinatus</i> (Stæger, 1839)	0	3	2	0	1	8
<i>Telmatopelopia nemorum</i> (Goetghebuer, 1921)	3	0	1	1	0	0

restoration. One year after restoration only 13 % of the characteristic species present before measures were taken were recorded (Chapter 4). Ten to twenty years after restoration this percentage was still low (i.e. 34%, N=10, based on Brouwer et al. 2009), whereas in non-restored moorland pools (N=9) 50 percent of the characteristic species were re-encountered over the same period.

During the process of degradation altered environmental conditions have impacted the macroinvertebrate community. For part of the characteristic species the new conditions have acted as a filter, reducing their abundance and presence (Leuven et al. 1986, Poff 1997). Subsequently, restoration measures impose a new and completely different set of filters, reducing abundance and persistence of many of the remaining species. Responses of biological traits indicated that aquatic macroinvertebrates were negatively impacted by removal of specimens, food shortage and removal of macrophytes. As a result the local and regional species pools are likely to have been damaged and their effectiveness in supplying colonists reduced. Turnover of characteristic species in restored moorland pools was high because species that colonised tended to be different from those that were lost. The winners in moorland pool restoration primarily were midges, whereas damselflies and aquatic bugs were the losers (Table 1, Brouwer et al. 2009) and many characteristic species (mainly Trichoptera) have not yet been recorded in restored pools.

By reducing the local species pool, restoration measures are likely to damage the regional species pool, increasing this biological restoration threshold, thus limiting the recovery potential of present and future restoration projects (Figure 4). This, of course, was not the intention of the projects in question. Optimal restoration management reduces and negates past and present impact of environmental stress while simultaneously taking habitat requirements of the species present into account. Solutions to this problem are discussed in chapter 4. There, management options are given to increase species persistence: temporary storage of removed organic matter on the shores, preserving parts of the original vegetation and phasing the restoration measures in space and time.

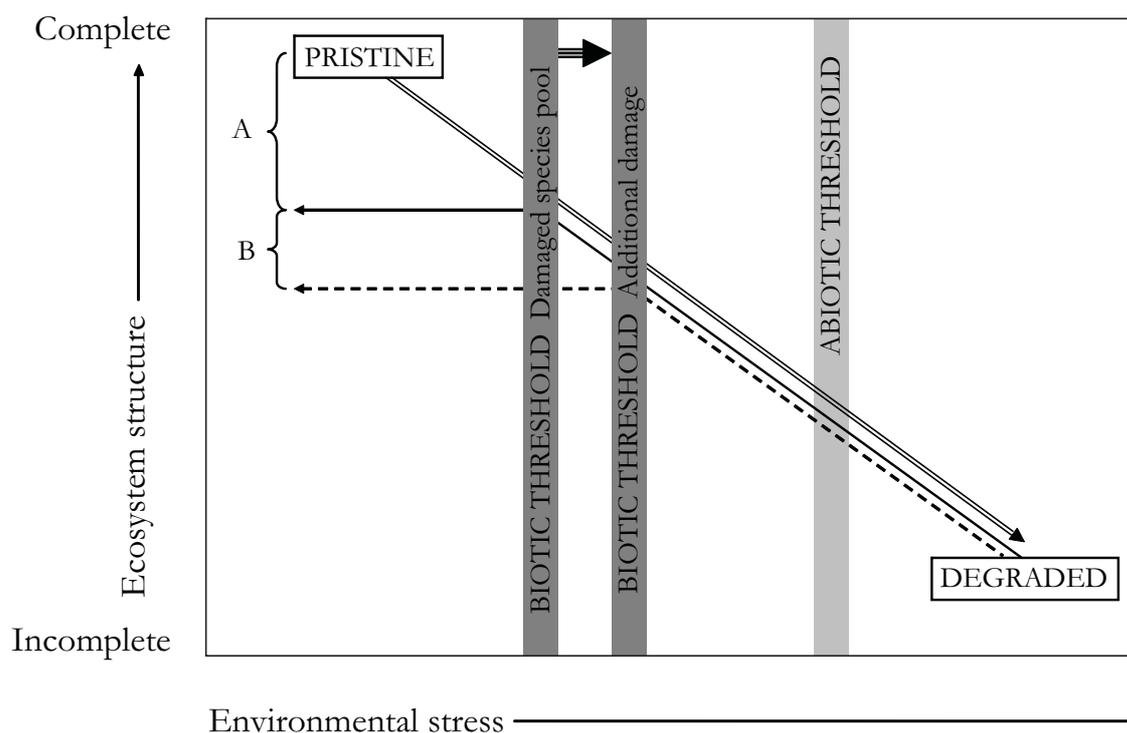


Figure 4 Schematic representation of moorland pool degradation and restoration. Boxes: ecosystem states. The abiotic barrier preventing natural recovery is indicated by the light grey bar and here has been negated by restoration. The dark grey bars represent degenerated species pool. Double-lined arrow: degradation trajectory. Single-lined arrow: theoretical restoration trajectory. Dotted-lined arrow: realised restoration trajectory. Triple-lined arrow: Shifting of the biotic threshold induced by large scale and intensive restoration measures. A: recovery prevented by damage to regional species pool. B: additional damage to species pool due to restoration.

Dispersal may be stimulated by increasing landscape connectivity through restoration of moorland pools on formerly reclaimed sites. Another solution would be to (re)introduce characteristic macroinvertebrates into restored moorland pools. Most animal relocations are performed with vertebrates (Fischer & Lindenmayer 2000). Invertebrate translocations are few and often performed with species that are easy to identify and collect, such as crickets (Berggren 2001) and butterflies (Wynhoff 2001). Many aquatic macroinvertebrate species however, do not fit this profile and require cumbersome optical equipment for identification, making directed collection of relocation specimens difficult. For the restoration of plant communities this issue has been solved by transferring hay from reference sites onto restoration sites (Kiehl &

Wagner 2006). Introducing preferred invertebrate species through transportation of unsorted plant and soil material containing the target species has to my knowledge not been performed before, but may be a cost effective way to cross colonisation thresholds.

Historically, a conservation approach was taken to halt the decline of biodiversity. Conservation biology is primarily concerned with halting the extirpation of local populations, by increasing the size of small populations and countering fragmentation by improving connectivity in cases where dispersal between subpopulations is deemed important. Ongoing reduction of our natural heritage initiated the development of and increased the importance of restoration ecology for long term preservation of biodiversity (Dobson et al. 1997, Young 2000). Over the last decades the conservation approach has gradually been replaced by a restoration mindset. The findings in this thesis demonstrate that both approaches should be applied simultaneously to optimally restore biodiversity, especially on sites that still harbour relict populations of characteristic species. Negative effects of restoration and nature management on characteristic fauna species have also been reported for raised bogs, heathland and grasslands (Van Duinen et al. 2003, Stuijzand et al. 2004 and the literature therein, Verberk et al. 2010). In these and likely various other ecosystems a more diverse approach to preserving biodiversity is required and can be achieved by integrating conservation and restoration measures (Noss et al. 2006).

This diversification also includes considering all the options for partial and complete recovery of biodiversity. Restoration ecology traditionally uses historical references for formulating restoration targets, irrespective of the time required to achieve these goals (Egan & Howell 2001, Noss et al. 2006). For some ecosystems, this philosophy is simply not realistic as continuing environmental stress (i.e. N-deposition, biological globalisation, climate change, fragmentation) limits the available time window. Chapter 6 describes a short-term alternative for developing and maintaining populations of threatened species. Although the species involved originate from hydrologically intact raised bog landscapes, they can be sustained by creating the necessary conditions through human intervention involving the inlet of alkaline water. Historical use of moorland pools for the cultivation of fish (i.e. inlet of alkaline, nutrient enriched water) can, in combination with ground water seepage, result in suitable habitat for these species and thus contribute to their persistence. Historical land use is known to create habitat for nowadays threatened species (Shea et al. 2004 and the literature therein), especially for species that depend on gradients and mesotrophic conditions. However, the mechanisms involved are still poorly understood, especially in relation to degradation processes, and knowledge of historical land use is still not optimally applied in the practice of ecological restoration. In short, restoring the required conditions can be achieved in other ways than restoring the natural habitat. Alternative creative solutions are possible, but their application requires a mechanistic understanding of how species are connected to these environmental conditions.

Invasion by non-native pumpkinseeds, an unforeseen threshold

In a number of isolated water bodies and moorland pools especially, the North American pumpkinseed sunfish has become dominant (Chapter 5). Aquatic macroinvertebrates appeared to be impacted by pumpkinseed dominance as macroinvertebrate abundance in pools populated by pumpkinseed was 83 percent lower than in pools without

pumpkinseed. The results indicate that pumpkinseed invasions are facilitated by introductions as well as nature management, such as dredging of moorland pools. So again, restoration itself triggers a threshold and decreases recovery potential (Figure 5). Preventing additional pumpkinseed introductions will slow the rate of spread of the species. However, eradication on a national scale has become impossible as the species has spread to a large part of the country. Even local eradication appears feasible only in small occupied systems. New solutions to this problem are urgently needed and require more research.

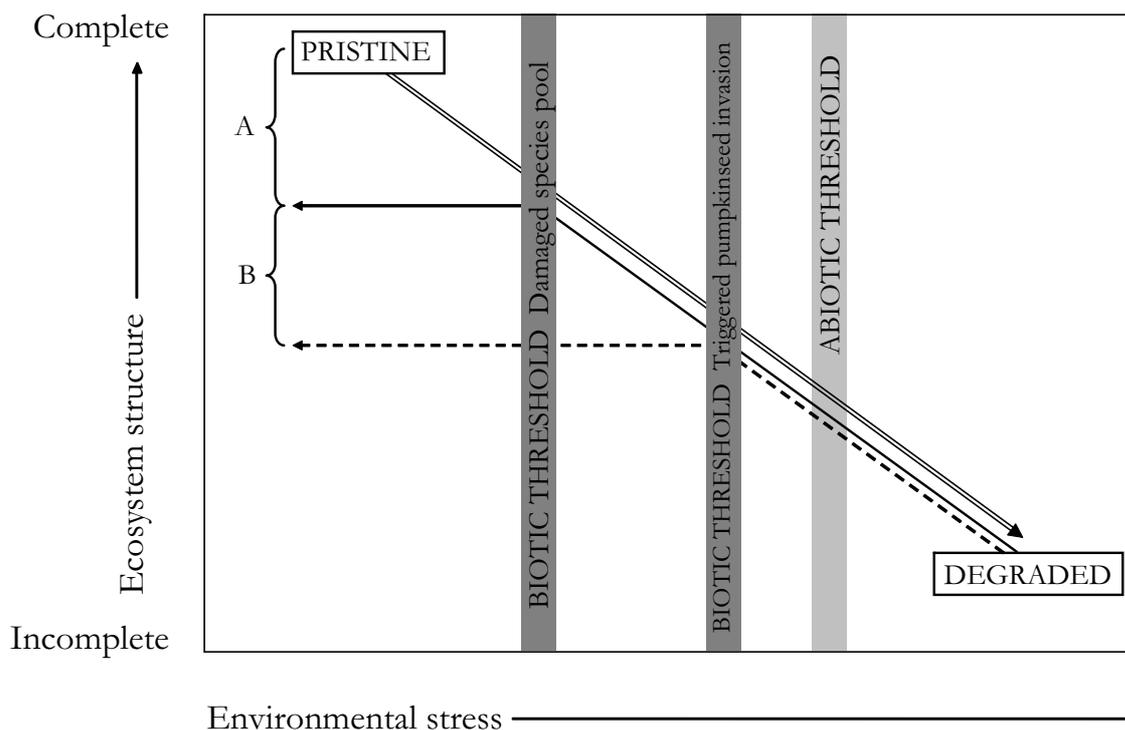


Figure 5 Schematic process moorland pool degradation and restoration. Boxes: ecosystem states. The abiotic barrier preventing natural recovery is indicated by the light grey bar and here has been negated by restoration. The dark grey bars represent biotic thresholds. Double-lined arrow: degradation trajectory. Solid-lined arrow: theoretical restoration trajectory. Dotted-lined arrow: realised restoration trajectory. A: recovery prevented by damage to regional species pool. B: recovery prevented due to triggered invasiveness of non-native pumpkinseed sunfish (*Lepomis gibbosus*).

The number of incursions by non-native species is rapidly increasing as global traffic is being intensified and migration barriers are reduced. This raises the question “What to do about invasion by non-natives?” Prevention is considered to be the most efficient and cost effective way to minimise the number of invasions (Leung et al. 2002). However, biotic globalisation is a fact and it will prove very difficult to prevent all species incursions through any of the increasing number of invasion pathways. In addition, rapid response is often difficult due to low detection rate of recent invaders (Hulme 2006). Eradication of invasive species is often nearly impossible after they have spread and become abundant. Ideally, natural ecosystems are managed in a way that non-native species cannot become abundant. Invasion theory has primarily focussed on the relation between biotic interactions and ecosystem invasiveness (Elton 1958, Tilman 1997, Levine & D’Antonio 1999). This diversity resistance hypothesis is still disputed as its applicability varies with

scale (Kennedy et al. 2002). Progress in understanding and managing invasiveness is mainly to be expected from the field of population biology (Sakai et al. 2001), because it helps identifying the mechanisms that allow non-native species to become dominant. Within this context, population biology of pumpkinseed is being studied within and outside of its native distribution (Fox 1994, Cucherousset et al. 2009) and is a promising way for identifying triggers of its invasiveness and to develop appropriate management actions. Similar research on other non-native species is needed to develop theory on ecosystem invasibility and translate this into appropriate action to increase ecosystem resistance against invasions.

Identifying thresholds using species traits

Studies on species occurrences and performance are valuable tools for evaluating management and monitoring ecosystem health. However, their value strongly increases when they can be used to identify the mechanisms responsible for observed differences and changes in species assemblages. Recent studies use biological traits to understand species occurrences and responses (Townsend & Hildrew 1994, Resh et al. 1994, Poff et al. 2006, McGill et al. 2006). Others approach this matter by using trait combinations with a similar adaptive function (Stearns 1976, Siepel 1994, Verberk et al. 2008). These trait combinations, called life history tactics, can be considered as an integrated evolutionary response to the environment.

In chapter 4, the response of individual traits was used to identify restoration induced bottlenecks for aquatic macroinvertebrates. Low mobility and abundance were associated with species declining during restoration, while vegetation dependence (i.e. for shelter and ovipositing) and carnivory were traits found in species that declined after restoration. Life history tactics were used in chapter 3 to relate changes in chironomid assemblages to environmental changes resulting from reduced acidification and restoration. Abundance of species adapted to low stress and low dynamic environments had increased in restored moorland pools. In non-restored pools they decreased, possibly due to increased decomposition of organic sediments and oxygen deficiency resulting from decreased acidification.

Trait based approaches thus present excellent opportunities to increase our understanding of the mechanisms shaping communities. Moreover, they are valuable conservation tools as they provide understanding in the causes for population decrease, restoration thresholds and allow us to anticipate and eventually prevent undesired ecological developments.

Priorities for moorland pool management and research

The research presented in this thesis was conducted in order to assess and suggest improvements of effectiveness of moorland pool management in restoring communities of characteristic aquatic macroinvertebrates. In the previous chapters it became apparent that a lot has been gained in terms of increased water quality and abundance of characteristic macroinvertebrates. However, there appeared to be room for improvement.

A high priority for the management of moorland pools lies in preventing the loss of species as a result of restoration. In chapter 4 options are presented for increasing species persistence. These modifications of moorland pool restoration are still theoretical and should be tested in field experiments. Colonisation of restored moorland pools appears

to be limited (Figure 3), probably due to habitat fragmentation and reduced connectivity. Nature development and restoration on reclaimed sites may be a way to overcome the colonisation threshold (Chapter 4) as well as translocation of characteristic species assemblages. As there is no or little experience with translocation of macroinvertebrate assemblages, practical guidelines and experimental translocations are needed.

In moorland pools historical land use for the cultivation of fish can result in suitable habitat for a number of threatened species (Chapter 6). This is probably also the case in other ecosystems with different types of land use. Research in the applicability of historical land use as a form of management may uncover a variety of unexploited opportunities for developing gradients and habitat for endangered species.

Invasions of non-native species pose a global threat to biodiversity. In restored moorland pools invasions of pumpkinseed sunfish can severely impact macroinvertebrate communities (Chapter 5). On the short term, management options should be developed and evaluated for pumpkinseed control. In addition, more general strategies are needed to prevent damage by invasive non-native species. Instead of constantly adapting management to new invasions, research efforts should focus on developing theory on ecosystem invasibility and its translation to management for increasing ecosystem resistance against invasions.

References

- Arts GHP (2000) Natuurlijke levensgemeenschappen van de Nederlandse binnenwateren deel 13, Vennen. Achtergronddocument bij het "Handboek Natuurdoeltypen in Nederland". *Expertisecentrum LNV, Ministerie van Landbouw, Natuurbeheer en Visserij, Ede.*
- Bakker JP & Berendse F (1999) Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends in Ecology and Evolution* **14**: 63-68.
- Bellemakers MJS, Maessen M & Roelofs JGM (1994) Effects of liming on water chemistry in shallow acidified pools in the Netherlands: enclosure experiments. *Water, Air, and Soil Pollution* **73**: 131-142.
- Berggren A (2001) Colonization success in Roesel's bush-cricket *Metrioptera roeseli*: The effects of propagule size. *Ecology* **82**: 274-280.
- Bohonak AJ & Jenkins DG (2003) Ecological and evolutionary significance of dispersal by freshwater invertebrates. *Ecology Letters* **8**: 783-796.
- Brouwer E, Bobbink R & Roelofs JGM (2002) Restoration of aquatic macrophyte vegetation in acidified and eutrophied softwater lakes: an overview. *Aquatic Botany* **73**: 405-431.
- Brouwer E & Roelofs JGM (2002) Oligotrophication of acidified, nitrogen-saturated softwater lakes after dredging and controlled supply of alkaline water. *Archiv für Hydrobiologie* **155**: 83-97.
- Brouwer E, Van Kleef H, Van Dam H, Loermans J, Arts GHP & Belgers D (2009) Effectiviteit van herstelbeheer in vennen en duinplassen op de middellange termijn. *Dienst Kennis, Ministerie van Landbouw, Natuurbeheer en Voedselkwaliteit, Ede.*
- Cucherousset J, Copp GH, Fox MG, Sterud E, Van Kleef HH, Verreycken H & Záhorská E (2009) Life-history traits and potential invasiveness of introduced pumpkinseed *Lepomis gibbosus* populations in northwestern Europe. *Biological Invasions* **11**: 2171-2180.
- Davies JJJ, Jenkins A, Monteith DT, Evans CD & Cooper DM (2005) Trends in surface water chemistry of acidified UK freshwaters, 1988-2002. *Environmental Pollution* **137**: 27-39.
- Dobson AP, Bradshaw AD & Baker AJM (1997) Hopes for the future: restoration ecology and conservation biology. *Science* **277**: 515-525.
- Dorland E, Van den Berg LJJ, Brouwer E, Roelofs JGM & Bobbink R (2005) Catchment liming to restore degraded, acidified heathlands and moorland pools. *Restoration Ecology* **13**: 302-311.

- Egan D & Howell EA (Eds) (2001) The historical ecology handbook: a restorationist's guide to reference ecosystems. *Island Press, Washington, D.C.*
- Elton CS (1958) The ecology of invasions by animals and plants. Methuen and Co. Ltd. London.
- Evans CD, Monteith DT & Cooper DM (2005) Long-term increases in surface water dissolved organic carbon: Observations, possible causes and environmental impacts. *Environmental Pollution* **137**: 55-71.
- Evans CD, Chapman PJ, Clark JM, Monteith DT & Cresser MS (2006) Alternative explanations for rising dissolved organic carbon export from organic soils. *Global Change Biology* **12**: 2044-2053.
- Fischer J & Lindenmayer DB (2000) An assessment of the published results of animal relocations. *Biological Conservation* **96**: 1-11.
- Forsius M, Vuorenmaa J, Mannio J & Syri S (2003) Recovery from acidification of Finnish lakes: regional patterns and relations to emission reduction policy. *Science of the Total Environment* **310**: 121-132.
- Fox MG (1994) Growth, density and interspecific influences on pumpkinseed life histories. *Ecology* **75**: 1157-1171.
- Hanski I & Ovaskainen O (2002) Extinction debt at extinction threshold. *Conservation Biology* **16**: 666-673.
- Hobbs RJ (2007) Setting Effective and realistic restoration goals: Key directions for research. *Restoration Ecology* **15**: 354-357.
- Hulme PE (2006) Beyond control: wider implications for the management of biological invasions. *Journal of Applied Ecology* **43**: 835-847.
- Hynynen J & Meriläinen JJ (2005) Recovery from acidification in boreal lakes inferred from macroinvertebrates and subfossil chironomids. *Hydrobiologia* **541**: 155-173.
- Kennedy TA, Naeem S, Howe KM, Knops JMH, Tilman D & Reich P (2002) Biodiversity as a barrier to ecological invasion. *Nature* **417**: 636-638.
- Kiehl K & Wagner C (2006) Effect of hay transfer on long-term establishment of vegetation and grasshoppers on former arable fields. *Restoration Ecology* **14**: 157-166.
- Lancaster J, Real M, Juggins S, Monteith DT, Flower RJ & Beaumont WRC (1996) Monitoring temporal changes in the biology of acid waters. *Freshwater Biology* **36**: 179-201.
- Leps J (2004) What do the biodiversity experiments tell us about consequences of plant species loss in the real world? *Basic and Applied Ecology* **6**: 529-534.
- Leung B, Lodge DM, Finnoff D, Shogren JF, Lewis M & Lamberti G (2002) An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. *Proceedings of the Royal Society, Series B* **269**: 2407-2413.
- Leuven RSEW, Van der Velde G, Vanhemelrijk JAM & Eeken RLE (1986) Impact of acidification on the distribution of aquatic insects in lentic softwaters. *Proceedings of the 3rd European Congress of Entomology, Dutch Entomological Society, Amsterdam*: 103-106.
- Levine JM & D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* **87**: 15-26.
- McGill BJ, Enquist BJ, Weiher E & Westoby M (2006) Rebuilding community ecology from functional traits. *Trends in Ecology and Evolution* **21**: 178-185.
- Monteith DT, Hildrew AG, Flower RJ, Raven PJ, Beaumont WRB, Collen P, Kreiser AM, Shilland EM & Winterbottom JH (2005) Biological responses to the chemical recovery of acidified fresh waters in the UK. *Environmental Pollution* **137**: 83-101.
- Monteith DT, Stoddard JL, Evans CD, De Wit HA, Forsius M, Høgåsen T, Wilander A, Skjelkvåle BL, Jeffries DS, Vuorenmaa J, Keller B, Kopáček J & Vesely J (2007) Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. *Nature* **450**: 537-541.
- Morin PJ (1984) Odonate guild composition – Experiments with colonization history and fish predation. *Ecology* **65**: 1866-1873.
- Mouquet N, Munguia P, Kneitel JM & Miller TE (2003) Community assembly time and the relationship between local and regional species richness. *Oikos* **103**: 618-626.

- Noss RF, Beier P, Covington WW, Grumbine RE, Lindenmayer DB, Prather JW, Schmiegelow F, Sisk TD & Vosick DJ (2006) Recommendations for integrating restoration ecology and conservation biology in ponderosa pine forests of the southwestern United States. *Restoration Ecology* **14**: 4-10.
- Ormerod SJ & Durance I (2009) Restoration and recovery from acidification in upland Welsh streams over 25 years. *Journal of Applied Ecology* **46**: 164-174.
- Poff NL (1997) Landscape filters and species traits: Towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society* **16**: 391-409.
- Poff NL, Olden JD, Vieira NKM, Finn DS, Simmons MP & Kondratieff BC (2006) Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. *Journal of the North American Benthological Society* **25**: 730-755.
- Price JE & Morin PJ (2004) Colonization history determines alternate community states in a food web of intraguild predators. *Ecology* **85**: 1017-1028.
- Resh VH, Hildrew AG, Statzner B & Townsend CR (1994) Theoretical habitat templates, species traits and species richness: a synthesis of long-term ecological research on the Upper Rhone River in the context of concurrently developed theory. *Freshwater Biology* **31**: 539-554.
- Roelofs JGM, Brouwer E & Bobbink R (2002) Restoration of aquatic macrophyte vegetation in acidified and eutrophicated shallow soft water wetlands in the Netherlands. *Hydrobiologia* **478**: 171-180.
- Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCauley DE, O'Neil P, Parker IM, Thompson JN & Weller SG (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics* **32**: 305-332.
- Shea K, Roxburgh SH & Rauschert ESJ (2004) Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. *Ecology Letters* **7**: 491-508.
- Siepel H (1994) Life-history tactics of soil microarthropods. *Biology and Fertility of Soils* **18**: 263-278.
- Skjelkvåle BL, Stoddard JL, Jeffries DS, Tørseth K, Høgåsen T, Bowman J, Mannio J, Monteith DT, Mosello R, Rogora M, Rzychon D, Vesely J, Wieting J, Wilander A & Worsztynowicz A (2005) Regional scale evidence for improvements in surface water chemistry 1990-2001. *Environmental Pollution* **137**: 165-176.
- Stearns SC (1976) Life-history tactics: A review of the ideas. *Quarterly Review of Biology* **51**: 3-47.
- Stoddard JL, Jeffries DS, Lükewille A, Clair TA, Dillon PJ, Driscoll CT, Forsius M, Johannessen M, Kahl JS, Kellogg JH, Kemp A, Mannio J, Monteith DT, Murdoch PS, Patrick S, Rebsdorf A, Skjelkvåle BL, Stainton MP, Traaen T, Van Dam H, Webster KE, Wieting J & Wilander A (1999) Regional trends in aquatic recovery from acidification in North America and Europe. *Nature* **40**: 575-578.
- Stuijzand SC, Van Turnhout CAM & Esselink H (2004) Gevolgen van verzuring, vermeting en verdroging en de invloed van beheer op heidefauna. 2. Basisdocument. *Dienst Kennis, Ministerie van Landbouw, Natuurbeheer en Voedselkwaliteit, Ede.*
- Suding KN, Gross KL & Houseman GR (2004) Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology and Evolution* **19**: 46-53.
- Suding KN & Hobbs RJ (2009) Threshold models in restoration and conservation: a developing framework. *Trends in Ecology and Evolution* **24**: 271-279.
- Tilman D (1997) Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* **78**: 81-92.
- Tipping E, Bass JAB, Hardie D, Haworth EY, Hurley MA & Wills G (2002) Biological responses to the reversal of acidification in surface waters of the English Lake District. *Environmental Pollution* **116**: 137-146.
- Townsend CR & Hildrew AG (1994) Species traits in relation to a habitat template for river systems. *Freshwater Biology* **31**: 265-275.

- Van Dam H (1996) Partial recovery of moorland pools from acidification: indications by chemistry and diatoms. *Netherlands Journal of Aquatic Ecology* **30**: 203-218.
- Van Duinen GA, Brock AMT, Kuper JT, Leuven RSEW, Peeters TMP, Roelofs JGM, Van der Velde G, Verberk WCEP & Esselink H (2003) Do restoration measures rehabilitate fauna diversity in raised bogs? A comparative study on aquatic macroinvertebrates. *Wetlands Ecology and Management* **11**: 447-459.
- Verberk WCEP, Sipel H & Esselink H (2008) Life-history strategies in freshwater macroinvertebrates. *Freshwater Biology* **53**: 1722-1738.
- Verberk WCEP, Leuven RSEW, Van Duinen GA & Esselink H (2010) Loss of environmental heterogeneity and aquatic macroinvertebrate diversity following large scale restoration management. *Basic and Applied Ecology* **11**: 440-449.
- Vuorenmaa J, Forsius M & Mannio J (2006) Increasing trends of total organic carbon concentrations in small forest lakes in Finland from 1987 to 2003. *Science of the Total Environment* **365**: 47-65.
- Wynhoff I (2001) At home on foreign meadows: the reintroduction of two *Maculinea* butterfly species. *Thesis, Wageningen University, Wageningen*.
- Young TP (2000) Restoration ecology and conservation biology. *Biological Conservation* **92**: 73-83.



*Good help and company make long field days sampling in the smelly muck much more enjoyable.
Photo: Hein van Kleef*

Summary

Present day landscapes are heavily influenced by human activities. Habitat destruction, fragmentation, eutrophication, acidification and desiccation are threatening the persistence of many species. This also takes place in moorland pools, which are relatively small and shallow water bodies and due to their oligotrophic and low alkaline nature are susceptible to eutrophication and acidification.

An introduction to the ecology of moorland pools is provided in **Chapter 1**. The environmental drivers and processes involved in the degradation of the pools are described. Efforts to prevent the loss of biodiversity from moorland pools use two different approaches. First, policy and management measures have been developed to reduce emissions of acidifying and eutrophying compounds and regulate drainage to reduce desiccation. Next, restoration measures have been developed to mitigate the effects of acidification, eutrophication and desiccation. Both approaches have yielded positive results for water quality, diatoms and higher plants. However, the effects on aquatic macroinvertebrates were largely unknown, resulting in the goal of this thesis: “*to assess effectiveness of moorland pool nature management in conserving and restoring communities of characteristic aquatic macroinvertebrates and to help nature managers to improve effectiveness of their practices by developing knowledge and tools*”. This requires knowledge on the thresholds preventing complete recovery.

Spontaneous recovery is preferable over active restoration. Since the 1980s atmospheric deposition of acidifying compounds has decreased considerably. In order to assess the possibility of spontaneous recovery of acidified moorland pools, water chemistry data from the 1980s and from recent years were compared. The results of this field study are described in **Chapter 2**. Partial recovery was observed: nitrate- and ammonium-N, sulphur and aluminium concentrations decreased, while pH and alkalinity increased. Calcium and magnesium concentrations decreased. These trends were supported by long term monitoring data (1978-2006) of four pools. Increased pH correlated with increases in ortho-phosphate and turbidity. Increased ortho-phosphate and turbidity are probably the result of stronger decomposition of organic sediments due to decreased acidification and may slow or even hamper recovery of moorland pool communities.

Long term biotic responses to reduced acidification and restoration management were examined in **Chapter 3**. This was done by studying changes in chironomid assemblages in non-restored moorland pools and in restored pools where organic sediments had been removed. Changes in chironomid assemblages were analysed by comparing data from 1983 and 2004 using species responses, multivariate analyses and life history tactics. In restored pools chironomid responses indicated a shift towards pre-acidification assemblages. Water chemistry improvement in non-restored moorland pools did not result in consistent changes in species abundance or community structure. In non-restored pools the change in abundance of the life history tactic, adapted to low stress and low dynamic environments, was negatively correlated with changes in turbidity suggesting increased periodic oxygen stress. Oxygen deficiency is hypothesised to be the result of the increased decomposition as described in chapter 2.

The short term effects of moorland pool restoration measures were assessed by studying the composition of macroinvertebrate assemblages in four degraded lakes undergoing restoration. The results of this study are described in **Chapter 4**. The degraded lakes still harboured species characteristic of moorland pools. However, many

of these species were not recorded after restoration. Biological traits were used to identify restoration induced bottlenecks for aquatic macroinvertebrates. Low mobility and abundance were associated with species declining during restoration, while vegetation dependence (i.e. for shelter and ovipositing) and carnivory were traits found in species that declined after restoration. Because recolonisation may be restricted, it is recommended to ensure the survival of relict populations when taking measures to restore degraded moorland pools. This may be achieved by temporary storage of removed organic matter on the shores, preserving parts of the original vegetation and phasing the restoration measures in space and time.

Biotic interactions and especially those involving exotics may prevent recovery of degraded ecosystems. A non-native species regularly recorded in moorland pools is the pumpkinseed sunfish *Lepomis gibbosus* (Linnaeus, 1758). This species appears to decimate macroinvertebrate populations as abundance of invertebrates in pools populated by pumpkinseed was eighty-three percent lower than in pools without pumpkinseed. Processes determining distribution and abundance of pumpkinseeds are examined in **Chapter 5**. High pumpkinseed abundance was correlated with nature management practices, such as dredging of pools and creating new ponds. Waters harbouring pumpkinseed were more often situated close to human habitation and infrastructure than could be expected based on the distribution of randomly selected isolated waters, indicating that intentional introductions are an important dispersal mechanism.

Restoration ecology traditionally uses local historical references for formulating restoration targets. However, this requirement limits the range of options available and it might be preferable to explore alternative conservation trajectories. **Chapter 6** describes a short-term alternative for developing and maintaining populations of threatened species. The six endangered plant and fifteen macroinvertebrate species involved originate from hydrologically intact raised bog landscapes. In intact bogs these species lived at sites where runoff from the bog massive came into contact with regional ground water resulting in a gradient in pH, alkalinity, calcium, iron and ionic ratio. In degraded bogs these species are nowadays scarce or not recorded. Analysis of Dutch national distribution data revealed aggregations of these endangered species in moorland pools. These pools contained water chemistry gradients similar to those found in pristine bogs, which occurred at sites where young seepage water, older groundwater and stream water came in contact. In the past, stream water has been used to increase pH and trophic status of moorland pools facilitating fisheries. Today, this practice offers a conservation strategy for the protection of endangered species for which no short-term alternatives are available.

The effectiveness of moorland pool management in conserving and restoring communities of characteristic aquatic macroinvertebrates and its implications for restoration theory and practice are discussed in **Chapter 7**. Additional data on long term responses of characteristic species to moorland pool restoration are presented. Effects of reduction of environmental stress (i.e. acid rain) and restoration measures are partially positive and to some extent resulted in additional loss of characteristic moorland pool macroinvertebrates. Research in this thesis demonstrates that the trajectory of restoration may not only be hampered by restoration thresholds, but that restoration efforts themselves may function as or induce thresholds. Therefore optimal management should not only focus on restoring damaged ecosystems, but take care not to lose endangered biodiversity elements in the process. Undesirable ecological developments resulting from

degradation and management can be identified and anticipated by using biological traits in the analysis of species performance. These trait-based approaches increase our understanding of the mechanisms shaping communities, making them valuable conservation tools.

The main conclusions of the research presented in this thesis are:

- Reduced emissions of acidifying compounds have led to a partial recovery of moorland pool water chemistry.
- Decreased acidification also appears to have led to increased decomposition of organic sediments, reducing abundance of sensitive chironomid species.
- Active management in the form of removal of organic sediments at present is the only option for a speedy recovery of acidified moorland pool biota.
- Dredging of moorland pools decreases persistence of the species through high mortality during restoration and temporary habitat unsuitability after restoration.
- Long-term responses of chironomids to moorland pool restoration indicate a development towards pre-acidification assemblages. Other macroinvertebrate taxa exhibit less resilience and require conservation during execution of restoration measures.
- Intensive nature management practices, such as dredging of pools and creating new ponds, may facilitate invasiveness of non-native pumpkinseed sunfish, reducing efficiency of management efforts.
- Stream water supply in moorland pools fed by groundwater seepage may result in water chemistry gradients and habitat of endangered species, which are characteristic for transitions in hydrologically intact raised bog landscapes.
- Analysis of species performance using biological traits increases our understanding of the mechanisms shaping communities. This makes trait-based approaches valuable conservation tools allowing identification, anticipation and prevention of undesirable ecological developments.

Recommendations for future research:

- Test suggested modifications of moorland pool restoration for improving persistence of characteristic species in field experiments.
- Develop and test practical guidelines for translocation of macroinvertebrate assemblages.
- Enhance knowledge and applicability of historical land use as a form of management for developing gradients and habitat for endangered species.
- Develop and evaluate management options for pumpkinseed control.
- Translate theory on ecosystem invasibility into practical management options for increasing ecosystem resistance against invasions.



*Many of the moorland pools in the nature reserve The Malpie are acidified by acid rain and nutrient enriched by a large colony of Black-headed gulls (*Larus ridibundus*). In 2010 restoration measures have been taken in the largest pool in this reserve. Photo: Hein van Kleef*

Samenvatting

Landschappen en ecosystemen worden sterk beïnvloed door menselijke activiteiten. Verlies, versnippering, vermesting, verzuring en verdroging van habitat bedreigen het voortbestaan van veel soorten. Dit is ook het geval in vennen, welke door hun voedselarme en zwak gebufferde karakter gevoelig zijn voor vermesting, verzuring en verdroging.

Een inleiding in de ecologie van vennen is gegeven in **Hoofdstuk 1**. De omgevingsfactoren en processen verantwoordelijk voor de aantasting van vennen worden hierin besproken. Via twee benaderingen is getracht het verlies van biodiversiteit in vennen een halt toe te roepen. Allereerst zijn brongerichte maatregelen genomen om de uitstoot van verzurende en vermestende stoffen te verminderen en wordt wateronttrekking gereguleerd om verdroging terug te brengen. Daarnaast zijn effectgerichte herstelmaatregelen toegepast om lokaal de effecten van verzuring, vermesting en verdroging te niet te doen. Beide soorten maatregelen hebben positieve gevolgen gehad voor waterkwaliteit, kiezelwieren en planten. De effecten op watermacrofauna daarentegen waren grotendeels onbekend. Het doel van deze studie is daarom: *“het bepalen van de effectiviteit van venbeheer voor het behoud en herstel van karakteristieke macrofaunagemeenschappen en het ontwikkelen van nieuwe kennis en methodieken om het rendement ervan te vergroten”*. Hiervoor is kennis nodig van de drempels die volledig natuurherstel van vennen in de weg staan.

Spontaan herstel heeft de voorkeur boven actief herstelbeheer. Sinds de tachtiger jaren van de vorige eeuw is de atmosferische depositie van verzurende stoffen sterk afgenomen. Mogelijk optredend autonoom herstel van verzuurde vennen is onderzocht door waterkwaliteitsgegevens uit deze periode te vergelijken met recente data. De resultaten van deze veldstudie zijn beschreven in **Hoofdstuk 2**. Een gedeeltelijk herstel is waargenomen: nitraat, ammonium, sulfaat en aluminium concentraties zijn afgenomen en de pH en alkaliniteit zijn toegenomen. Concentraties calcium en magnesium zijn gedaald. Deze trends worden ondersteund door meerjarige (1978-2006) monitoringgegevens van vier vennen. Toegenomen pH gaat gepaard met toenames in ortho-fosfaat concentraties en turbiditeit, welke waarschijnlijk veroorzaakt worden doordat de remmende werking van verzuring op de afbraak van organisch sediment afgenomen is. Dit proces beperkt het herstel van karakteristieke levensgemeenschappen in vennen.

Lange termijn effecten van verminderde verzuring en herstelmaatregelen op fauna zijn onderzocht door dansmuggengemeenschappen in 1983 te vergelijken met die in 2004 in vennen waarin wel en geen effectgerichte herstelmaatregelen zijn uitgevoerd (**Hoofdstuk 3**). De veranderingen zijn geanalyseerd met behulp van de respons van individuele soorten, multivariate analyses en overlevingsstrategieën. In ‘herstelde’ vennen indiceerden de veranderingen in de dansmuggengemeenschap een verschuiving in de richting van de periode voorafgaand aan de grootschalige verzuring. Verbetering van de waterkwaliteit in ‘niet-herstelde’ vennen resulteerde niet in consistente veranderingen in de abundantie van soorten of opbouw van de gemeenschap. In ‘niet-herstelde’ vennen is de abundantieverandering van soorten met een overlevingsstrategie, die aangepast is aan lage stress en weinig dynamiek, negatief gecorreleerd met de verandering in turbiditeit. Dit is een indicatie dat deze soorten onder zuurstofstress hebben geleden, welke mogelijk het gevolg is van de toegenomen afbraak van organisch sediment door waterkwaliteitsveranderingen zoals beschreven in hoofdstuk 2.

De korte termijn effecten van venherstel op de samenstelling van macrofaunagemeenschappen zijn bepaald in vier gedegradeerde vennen waarin

herstelmaatregelen werden genomen (**Hoofdstuk 4**). De aangetaste vennen herbergden nog karakteristieke soorten. Veel van deze soorten zijn echter na herstel niet meer waargenomen. Biologische eigenschappen zijn gebruikt om na te gaan welke bottlenecks aquatische ongewervelden ondervinden als gevolg van herstelmaatregelen. Een lage mobiliteit en abundantie zijn eigenschappen van soorten die afnamen tijdens uitvoering van herstelmaatregelen. Afhankelijkheid van vegetatie (bijvoorbeeld voor schuilgelegenheid en eiafzet) en een dierlijk dieet zijn eigenschappen van soorten die achteruitgingen na herstel. Aangezien herkolonisatie mogelijk beperkt is door de afwezigheid van bronpopulaties in de directe omgeving, wordt aangeraden om bij herstel van vennen de overleving van relictpopulaties veilig te stellen. Dit kan worden bereikt door het tijdelijk op de oevers opslaan van verwijderd organisch materiaal, het sparen van delen van de oorspronkelijke vegetatie en door het faseren van maatregelen in tijd en ruimte.

Biotische interacties, zoals interacties tussen inheemse en uitheemse soorten, kunnen herstel van aangetaste ecosystemen belemmeren. Een exotische soort die regelmatig in vennen wordt waargenomen is de Amerikaanse zonnebaars *Lepomis gibbosus* (Linnaeus, 1758). Deze soort lijkt populaties van inheemse watermacrofauna te decimeren, aangezien de dichtheid van ongewervelden in vennen met zonnebaars drieëntachtig procent lager was dan in vergelijkbare wateren zonder zonnebaars. De processen van invloed op de verspreiding en abundantie van de zonnebaars zijn onderzocht in **Hoofdstuk 5**. Een hoge abundantie van deze vis was gecorreleerd met natuurbeheermaatregelen, zoals het baggeren van vennen en de aanleg van nieuwe poelen. Wateren met zonnebaars lagen vaker in de buurt van menselijke bewoning en infrastructuur dan op basis van toeval verwacht mag worden. Dit indiceert dat opzettelijk uitzetten van deze soort een belangrijk dispersiemechanisme is.

Voor het formuleren van doelen voor herstelbeheer is het gangbaar om gebruik te maken van lokale historische referentiebeelden. Deze insteek beperkt echter het scala aan beschikbare opties, terwijl het voordelen kan hebben om alternatieve wegen van natuurbeheer te overwegen. **Hoofdstuk 6** beschrijft een korte termijn alternatief voor de ontwikkeling en behoud van populaties van enkele bedreigde soorten. De soorten in kwestie zijn zes plantensoorten en vijftien soorten ongewervelden, welke van oorsprong voorkomen in hydrologisch intacte hoogveenlandschappen. In intacte venen leven deze soorten op locaties waar afstromend water uit het veen in contact komt met regionaal grondwater, wat resulteert in een gradiënt in pH, alkaliniteit, calcium, ijzer en de ionenratio. In aangetaste hoogvenen worden de onderzochte soorten tegenwoordig niet of nauwelijks meer waargenomen. Analyse van Nederlandse verspreidingsdata liet zien dat in sommige vennen aggregaties van deze soorten voorkomen. Deze vennen bevatten gradiënten in waterchemie welke vergelijkbaar zijn met de gradiënten in intacte hoogvenen. In vennen zijn deze gradiënten ontstaan op plaatsen waar jonge kwel, oud grondwater en beekwater met elkaar in contact komen. In het verleden werd beekwater gebruikt om de pH en voedselrijkdom van vennen te verhogen ten behoeve van de kweek van vis. Tegenwoordig biedt deze vorm van landgebruik een nieuwe strategie voor het behoud van deze soorten, waarvoor geen korte termijn alternatieven beschikbaar zijn.

De effectiviteit van venbeheer voor het behoud en herstel van karakteristieke macrofaunagemeenschappen en de implicaties daarvan voor de theorie en praktijk van restauratie ecologie worden besproken in **Hoofdstuk 7**. Aanvullende data van lange termijn effecten van venherstel op karakteristieke soorten worden gepresenteerd. De

effecten van verminderde omgevingsstress (in de vorm van zure regen) en herstelmaatregelen zijn deels positief gebleken, maar hebben ook geleid tot een aanvullend verlies van karakteristieke macrofauna. Het onderzoek in dit proefschrift laat zien dat herstel niet alleen belemmerd kan worden door biotische en abiotische drempels, maar dat herstelwerkzaamheden zelf drempels kunnen zijn of opwerpen. Een optimaal beheer zou daarom niet alleen gericht moeten zijn op het herstel van aangetaste ecosystemen, maar ook op het behoud van nog aanwezige bedreigde biodiversiteit. Analyse van de respons van soorten met bepaalde combinaties van biologische eigenschappen kan worden gebruikt voor het identificeren en anticiperen op ongewenste ecologische ontwikkelingen. Deze methodieken, die gebruik maken van soorteigenschappen, vergroten onze grip op de mechanismen betrokken bij de vorming van levensgemeenschappen en zijn daarom belangrijke hulpmiddelen bij het natuurbeheer.

De belangrijkste conclusies van dit proefschrift zijn:

- Verminderde uitstoot van verzurende stoffen heeft in vennen geleid tot een gedeeltelijk herstel van de waterkwaliteit.
- Verminderde verzuring lijkt ook te hebben geleid tot een verhoogde afbraak van organisch sediment, leidend tot een afname van gevoelige dansmugsoorten.
- Actief beheer in de vorm van verwijderen van organische sedimenten is momenteel de enige optie voor een spoedig herstel van biota in verzuurde vennen.
- Baggeren van vennen vermindert de overleving van soorten door een hoge sterfte tijdens uitvoering van maatregelen en tijdelijke ongeschiktheid van habitat na uitvoering.
- De lange termijn respons van dansmuggen op herstelmaatregelen indiceert een ontwikkeling in de richting van de periode voorafgaand aan de grootschalige verzuring. Andere soorten aquatische macrofauna vertonen minder veerkracht en dienen behouden te worden tijdens en na uitvoering van herstelmaatregelen.
- Intensieve natuurbeheermaatregelen, zoals het baggeren van vennen en de aanleg van nieuwe poelen, kunnen invasies van de uitheemse zonnebaars faciliteren en zodoende leiden tot het niet behalen van beheersdoelen.
- Inlaat van beekwater kan onder bepaalde omstandigheden in grondwatergevoede vennen leiden tot gradiënten in de waterchemie en habitat voor bedreigde soorten, die karakteristiek zijn voor overgangen in hydrologisch intacte hoogveenlandschappen.
- Door bij de analyse van de respons van soorten gebruik te maken van biologische eigenschappen wordt onze kennis van de mechanismen betrokken bij de vorming van levensgemeenschappen vergroot. Daardoor zijn methodieken, die gebruik maken van biologische eigenschappen, een waardevol hulpmiddel bij het identificeren en voorkomen van ongewenste ecologische ontwikkelingen.

Aanbevelingen voor toekomstig onderzoek:

- Met behulp van veldexperimenten testen of de voorgestelde aanpassingen van maatregelen voor venherstel bijdragen aan een verhoogde overleving van karakteristieke soorten.
- Ontwikkelen en testen van praktische richtlijnen voor translocatie van levensgemeenschappen van ongewervelden.
- Vergroten van de kennis en toepasbaarheid van historisch landgebruik als een vorm

van natuurbeheer voor de ontwikkeling van gradiënten en habitat voor bedreigde soorten.

- Ontwikkelen en evalueren van beheersopties voor de controle van zonnebaarspopulaties.
- Vertalen van wetenschappelijke theorieën over ecosysteem invasibiliteit naar praktische natuurbeheermaatregelen voor het vergroten van de resistentie van ecosystemen tegen invasies van uitheemse soorten.



*Almost 20 years after restoration this moorland pool not only harbours an enormous population of water lobelia, but also the very rare water beetle *Hygrotus novemlineatus* and the midge *Pagastiella orophila*. Photo: Hein van Kleef*

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Imago of Laccophilus poecilus refreshing its oxygen supply. Photo: Rene Krekels.

Curriculum vitae

Henricus Hubertus (Hein) van Kleef, werd geboren op 20 juli 1974 in Eindhoven. Mijn interesse in de biologie werd gewekt in 1986 toen ik lid werd van de Jeugdbond voor Natuur- en Milieustudie. Hier begon ik met vogels kijken en werd al snel bevangen door de schoonheid van de overige aspecten van de natuur. Na de afronding van het Atheneum aan het Anton van Duinkerken College in Veldhoven, begon ik in 1992 met de studie biologie aan de Katholieke Universiteit Nijmegen. Vanwege mijn grote fascinatie met het onderwaterleven lag de keuze voor een aquatisch ecologische hoofdvakstage voor de hand. In deze stage onderzocht ik de effecten van venherstel op watermacrofauna. Ook de tweede onderzoeksstage aan de Wageningen Universiteit stond in het teken van natuurbeheer, echter deze keer betrof het de effecten van diverse wijzen van dijkverzwaring op vegetatie. Tijdens de laatste onderzoekstage keerde ik terug naar mijn “roots” en deed onderzoek naar roofvogels met behulp van radiotelemetrie in het Spaanse nationale park Coto Doñana. Mijn fascinatie voor vogels is altijd aanwezig gebleven en in 1996, 1999 en 2005 heb ik ornithologische expedities opgezet en uitgevoerd in Albanese wetlands en de Russische toendra via de Werkgroep Internationaal Wad- en Watervogelonderzoek (WIWO). Verder heb ik jarenlang broedvogelinventarisaties uitgevoerd in de Ooijpolder, één van de meest soortenrijke gebieden in Nederland.

Na mijn afstuderen in 1997 heb ik tijdelijk freelance inventarisatiewerk verricht voor enkele adviesbureaus, waarna ik bij de Stichting Bargerveen onderzoek ben gaan doen naar de faunistische aspecten van het Nederlandse vennenbeheer. Tijdens deze periode was ik gastmedewerker bij afdeling Milieukunde van de Radboud Universiteit. Mijn onderzoek richtte zich op de effecten van verminderde verzurende depositie op waterkwaliteit en dansmuggen, het belang van vennen als habitat voor sterk bedreigde soorten en ongewenste neveneffecten van venherstel op watermacrofauna. De bevindingen hiervan staan in dit proefschrift beschreven en zijn tijdens diverse (inter)nationale congressen en symposia gepresenteerd.

Naast mijn onderzoekstaken verzorgde ik hoorcolleges, cursussen en practica voor universitaire studenten en begeleide een groot aantal tijdens hun stages. In 2007 heb ik een bijdrage geleverd aan de organisatie van de 15^{de} Internationale Conferentie over Aquatische Invasieve Soorten (ICAIS). Verder ben ik veel betrokken geweest bij het beheer en herstel van Nederlandse en Belgische ecosystemen. Dit gebeurde in de vorm onderzoeksopdrachten, maar vooral ook via lidmaatschappen van de werkgroep Exoten van de WEW/NecoV en de nationale deskundigenteams zwakgebufferde oppervlaktewateren, fauna, beekdallandschap, nat zandlandschap en laagveen- en zeekleilandschap in het kader van Ontwikkeling + Beheer Natuurkwaliteit (O+BN, voormalig OBN). De achteruitgang van de globale biodiversiteit baart mij grote zorgen. Daarom wil ik ook in de toekomst graag verder met praktijkgericht ecologisch onderzoek in de hoop in de loop der jaren mijn steentje bij te dragen aan het omkeren van de biodiversiteitscrisis.

Publications in peer-reviewed journals

- Van Kleef HH, Brouwer E, Leuven RSEW, Van Dam H, De Vries-Brock A, Van der Velde G & Esselink H (2010) Effects of reduced nitrogen and sulphur deposition on the water chemistry of moorland pools. *Environmental Pollution* **158**: 2679-2685.
- Cucherousset J, Copp GH, Fox MG, Sterud E, Van Kleef HH, Verreycken H & Záhorská E (2009) Life-history traits and potential invasiveness of introduced pumpkinseed *Lepomis gibbosus* populations in northwestern Europe. *Biological Invasions* **11**: 2171-2180.
- Van Kleef H, Van der Velde G, Leuven RSEW & Esselink H (2008) Pumpkinseed sunfish (*Lepomis gibbosus*) invasions facilitated by introductions and nature management strongly reduce macroinvertebrate abundance in isolated water bodies. *Biological Invasions* **10**: 1481-1490.
- Kharitonov SP, Volkov AE, Willems F, Van Kleef H, Klaassen RHG, Nowak DJ, Nowak AI & Bublichenko AG (2008) Brent goose colonies near Snowy owls: Internest distances in relation to abundance of lemmings and Arctic foxes. *Biological Bulletin* **35**: 270-278.
- Van Kleef HH, Willems F, Volkov AE, Smeets JJHR, Nowak D & Nowak A (2007) Dark-bellied brent geese *Branta b. bernicla* breeding near snowy owl *Nyctea scandiaca* nests lay more and larger eggs. *Journal of Avian Biology* **38**: 1-6.
- Van Kleef HH, Verberk WCEP, Leuven RSEW, Esselink H, Van der Velde G & Van Duinen GA (2006) Biological traits successfully predict the effects of restoration management on macroinvertebrates in shallow softwater lakes. *Hydrobiologia* **565**: 201-216.
- Van Duinen GA, Zhuge Y, Verberk WCEP, Brock AMT, Van Kleef HH, Leuven RSEW, Van der Velde G & Esselink H (2006) Effects of rewetting measures in Dutch raised bog remnants on assemblages of aquatic Rotifera and microcrustaceans. *Hydrobiologia* **565**: 187-200.
- Verberk WCEP, Van Kleef HH, Dijkman M, Van Hoek P, Spierenburg P & Esselink H (2005) Seasonal changes on two different spatial scales: response of aquatic invertebrates to water body and microhabitat. *Insect Science* **12**: 263-280.
- Volkov AE, Khomenko S, Van Kleef H & Willems F (1999) Breeding of Brent Geese at Meduza Bay, Taimyr, and relation with lemming predators. *Casarca* **5**: 63-75.
- Van Kleef H & Bustamante J (1999) First recorded polygynous mating in the Red kite (*Milvus milvus*). *Journal of Raptor Research* **33**: 254-257.

Publications in Symposium Proceedings and national journals

- Kivit H, Cromsigt J & Van Kleef H (2007) Op zoek naar de rol van de Wisent. Het wisentonderzoek in het Kraansvlak. *Nieuwe Wildernis* **11**: 17-20.
- Wiggers R, Van den Hoek T, Van Maanen B, Higler B & Van Kleef H (2006) Some rare and new caddis flies recorded for the Netherlands (Trichoptera). *Nederlandse Faunistische Mededelingen* **25**: 53-68.
- Felix R & Van Kleef H (2004) Zingende Boomkrekels: Mediterrane sferen in het Nederlandse rivierengebied. *Twirre natuur in Fryslân* **15**: 117.
- Felix R & Van Kleef H (2004) Boomkrekels *Oecanthus pellucens* bij Lobith het land in (Orthoptera: Gryllidae). *Nederlandse Faunistische Mededelingen* **21**: 1-6.
- Van Kleef HH, Leuven RSEW, Esselink H, Felix RPWH, & Van der Velde G (2001) Herstelbeheer in vennen: macrofauna in gevaar? *De Levende Natuur* **102**: 171-172.

- Van Duinen GA, Van Kleef HH, Kuper JT, Lomans SA, Peeters TMJ, Scarse D, Roelofs JGM & Esselink H (2000) Does restoration of peatlands imply restoration of peatland dragonfly fauna? *Proceedings of Québec 2000: 11th International Peat Congress*: 764-770.
- Van Duinen GA, De Bruijn L, Hanzen D, Van Kleef HH, Kuper JT, Scarse D & Esselink H (2000) Do restoration measures help to restore dragonfly communities in raised bog remnants? *Proceedings of the Section Experimental and Applied Entomology of the Netherlands Entomological Society (NEV)* **11**: 151-158.

Book chapters

- Van Duinen GJ, Van Kleef HH, Nijssen M, Van Turnhout C, Verberk W, Holtland J & Esselink H (2004) Schaal en intensiteit van herstelmaatregelen: hoe reageert de fauna? In: Van Duinen GJ, Bobbink R, Van Dam C, Esselink H, Hendriks R, Klein M, Kooijman A, Roelofs J & Siebel H (Eds.) *Duurzaam natuurherstel voor behoud van biodiversiteit – 15 jaar herstelmaatregelen in het kader van het overlevingsplan bos en natuur*. *Directie Kennis-LNV, Ede*: 189-240.

Reports

- Lamers L, Sarneel J, Geurts J, Pires MD, Remke E, Van Kleef H, Christianen M, Bakker L, Mulderij G, Schouwenaars J, Klinge M, Jaarsma N, Van der Wielen S, Verhoeven J, Verberk W, Esselink H, Ibelings B, Van Donk E & Roelofs J (2010) Onderzoek ten behoeve van het herstel en beheer van Nederlandse laagveenwateren Eindrapportage 2006-2009 (Fase 2). *Dienst Kennis, Ministerie van Landbouw, Natuurbeheer en Voedselkwaliteit, Ede*.
- Brouwer E, Van Kleef H, Van Dam H, Loermans J, Arts GHP & Belgers D (2009) Effectiviteit van herstelbeheer in vennen en duinplassen op de middellange termijn. *Dienst Kennis, Ministerie van Landbouw, Natuurbeheer en Voedselkwaliteit, Ede*.
- Aggenbach CJS, Groenendijk D, Kemmers RH, Van Kleef HH, Smolders AJP, Verberk WCEP & Verdonschot PFM (2009) Preadvies Beekdallandschappen. Knelpunten, kennislacunes en kennisvragen voor natuurherstel in beekdalen. *Dienst Kennis, Ministerie van Landbouw, Natuurbeheer en Voedselkwaliteit, Ede*.
- Vanderhaege F, Brouwer E, Van Kleef H, Van den Broeck S & Vercoutere B (2008) Expertenadvies prioritair venherstel Turnhouts Vennengebied-West. Bestek N4TV02/venherstel. *Royal Haskoning, België*.
- Van Kleef H & Brouwer E (2008) OBN-vooronderzoek naar de mogelijkheden voor natuurherstel in de Broekse Wielen. *Stichting Bargerveen, Nijmegen*.
- Brouwer E & van Kleef H (2008) Natuurwaarden in het Taamven en mogelijkheden voor herstel. *Onderzoekcentrum B-Ware, Nijmegen*.
- Van Kleef H (2008) Fauna-inventarisatie in het Buitengoor (Mol, België). *Stichting Bargerveen, Nijmegen*.
- Brouwer E, Van Kleef H, Arts G & Van Dam H (2006) Digitale sleutel voor het bepalen van herstelmaatregelen in vennen. *Onderzoekcentrum B-Ware, Nijmegen*.
- Van Kleef H, Brouwer E & Esselink H (2006) OBN-vooronderzoek naar de mogelijkheden voor natuurherstel in de Malpievennen. *Stichting Bargerveen, Nijmegen*.
- Van Kleef HH & Esselink H (2006) Herstel van sprengen op de Utrechtse Heuvelrug – Advisering ten behoeve van het behoud en herstel van faunadiversiteit. *Stichting Bargerveen, Nijmegen*.

-
- Van Kleef HH & Esselink H (2006) De entomofauna van het Greveschutven, Valkenswaard – Onderzoek ten behoeve van het behoud en herstel van het Greveschutven. *Stichting Bargerveen, Nijmegen*.
- Van Kleef HH & Esselink H (2005) Watermacrofauna-monitoring ten behoeve van herstel en behoud van het Weerterbos. Een evaluatie van herstelmaatregelen in het kader van het Overlevingsplan Bos en Natuur. *Directie Kennis-LNV, Ede*.
- Van Kleef HH & Esselink H (2005) Monitoring van abiotiek, vegetatie, dansmuggen en kokerjuffers in gerestaureerde zwakgebufferde oppervlaktewateren – Kolonisatie van diersoorten. *Directie Kennis-LNV, Ede*.
- Van Kleef HH & Esselink H (2005) Analyse van de effecten van herstelmaatregelen op watermacrofauna in zwakgebufferde oppervlaktewateren – Een vergelijkend onderzoek in vier vennen waar herstelmaatregelen zijn uitgevoerd. *Directie Kennis-LNV, Ede*.
- Van Dam H, Spier J, Gotjé W, Arts GHP, Van Delft JJCW, Ketelaar RR & Van Kleef HH (2004) Vooronderzoek ontwikkeling STOWA-beoordelingssysteem vennen. *STOWA, Utrecht*.
- Willems F, Van Turnhout C, Van Kleef H & Felix R (2002) Breeding birds of Medusa Bay, Taimyr, Russia. Methods for biological monitoring in the Arctic with results of 1998 and 1999. *Foundation WIWO, Zeist*.
- Sierdsema H, Van Kleunen A, Bouwman J, Spikmans F, Kroese B, Smit JT, Van Kleef HH & Lemaire AJJ (2002) Beleidsmonitoring OBN-Fauna 2002. *Vereniging Onderzoek Flora en Fauna, Nijmegen*.
- De Nobel WT, Bouwman JH, Van Kleef HH & Lemaire AJJ (2001) Beleidsmonitoring OBN-fauna 2001. *Vereniging Onderzoek Flora en Fauna, Nijmegen*.

Verschenen in de serie '*Mechanisms and constraints in biodiversity conservation and restoration*'

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Het samenwerkingsverband tussen Natuurplaza en de Radboud Universiteit Nijmegen (IWWR) ontwikkelt, bundelt en verspreidt kennis op het gebied van herstel en behoud van biodiversiteit en ecosystemen.

In Natuurplaza participeren:

- Stichting Bargerveen
- Vereniging SOVON vogelonderzoek Nederland
- Stichting reptielen, amfibieën en vissenonderzoek Nederland (RAVON)
- Stichting floristisch onderzoek Nederland (FLORON)
- Zoogdiervereniging
- Vereniging onderzoek flora en fauna (VOFF)

Deze combinatie van organisaties verbindt het verspreidingsonderzoek met het wetenschappelijk onderzoek. De koppeling van veldwaarnemingen in ruimte en tijd met ecologische lab-, veld- en beheerexperimenten resulteert in innovatieve kennis. De Natuurplaza partners hebben een breed en actief netwerk van vrijwilligers. Hierdoor is er een continue vernieuwing, ontwikkeling en doorstroom van kennis, waardoor maatschappelijke vraagstukken snel en adequaat aangepakt kunnen worden.

Stichting Bargerveen heeft als doel het ontwikkelen van kennis voor systeemgericht natuurherstel met focus op fauna en het (inter)nationaal verspreiden van kennis. Daarnaast is het bijdragen aan de opleiding van studenten en junior onderzoekers een belangrijke doelstelling. De onderzoeksvragen die de stichting beantwoordt komen voort uit de problemen waar beheerders of beleidsmakers tegenaan lopen. Veel thema's zijn gerelateerd aan de effectiviteit van de beheersmaatregelen, alsmede aan de VER-thema's, zoals verzuring, vermessing en verdroging. Het onderzoek wordt uitgevoerd in binnen- en buitenland en in een scala van landschappen, waaronder de kustduinen, stuifzanden, kalkgraslanden, laagveenwateren, hoogvenen, heide en vennen.

Stichting Bargerveen is met de andere Natuurplaza partners gehuisvest binnen de Radboud Universiteit Nijmegen en werkt nauw samen met de afdelingen dierecologie en -ecofysiologie, milieukunde, aquatische ecologie en milieubiologie van de RU Nijmegen.



Radboud Universiteit Nijmegen



