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Diatom diversity and habitat heterogeneity in lowland wetlands in south-western New Zealand

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If we reduce nature to what we understand, we would not be able to survive.

Wenn wir die Natur auf das reduzieren, was wir verstanden haben, sind wir nicht überlebensfähig.

Hans-Peter Dürr (*1929), dt. Physiker, 1987 Alternativer Nobelpreisträger

Contents

Preface

The present thesis is integrated in a project focussing on 'biodiversity in New Zealand freshwater ecosystems', which has been initiated by the National Institute of Water and Atmospheric Research in Christchurch.
Conservation in New Zealand is currently failing to halt the ongoing decline in the country's indigenous biodiversity, which is the decisive aim of the recently established New Zealand biodiversity strategy (2001). Among the threatened ecosystems, wetlands have undergone some of the most dramatic changes since colonisation. These habitats have been reduced by over 90 % of their pre-European area of 700.000 to 1.000.000 ha. Protected areas in fertile lowlands tend to be small, fragmented, isolated, extensively modified, and often poorly managed.

This thesis addresses the following limitations of current knowledge and research needs with respect to habitat heterogeneity and benthic diatom diversity in south-western New Zealand lowland wetlands:

1. The high degree of endemism among New Zealand's indigenous fauna and flora and the likelihood that, over the next several decades, a significant part of the country's biota may be at risk of extinction from habitat destruction and exotic species introduction, raises the importance of identifying and classifying indigenous biota.

2. Serious gaps in research are concerned with the influence of land-use on aquatic and wetland ecosystem studies, the influence of biodiversity on ecosystem stability and health, and the depiction and classification of indigenous systems.

3. First principles of ecology are fundamental to the development of good predictions; yet little research has been done in wetlands relating algal diversity and benthic primary production to elements of wetland ecology. Basic investigations to improve the understanding of the role of algae in wetlands will allow for more effective use of algal assessments and more successful management of wetlands.

4. Precise characterisation of reference conditions in wetlands is necessary for a sensitive detection of impairment. Precision, in turn, will be increased by improved means of wetland classification, sampling of multiple reference sites for each wetland class, and selection of suitable metrics.

5. Investigations on the scale of biological resolution involved, such as genus versus species level metrics or relative abundances versus presence/absence data are rare, though increased time and cost-efficiency in wetland monitoring and management could be achieved.

The manuscript is subdivided into four units, of which two sections have been submitted to international peer-reviewed scientific journals at the time of completion. Parts of the chapter on "Hydrochemistry and algal primary production in New Zealand lowland wetlands" are currently under review in *WETLANDS*. A modified section of chapter 4, "A synopsis of cosmopolitan, rare, and new *Frustulia* species (Bacillariophyceae) from ombrotrophic peat bogs and minerotrophic swamps in New Zealand" was handed in to *NOVA HEDWIGIA*. An electronic version of this manuscript will be available at the library website of the Technical University of Munich (http://www.tu-muenchen.de) once the evaluation process of the thesis is completed.

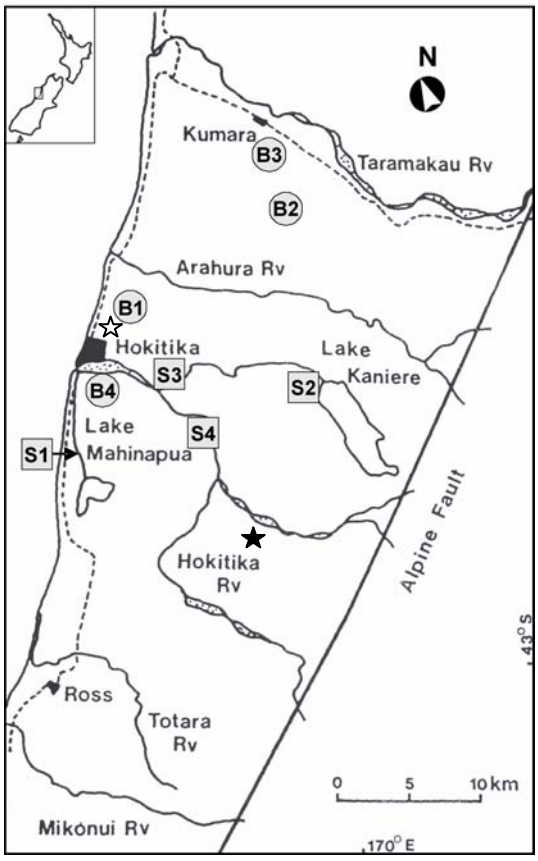
T. Beier

1 Area

The study area comprises eight wetlands situated in the south-western part of New Zealand. The description of the terrain covers a short overview of the region, followed by a detailed description of the studied wetlands. In addition to geography, climate, geology, and vegetation, the history, development, and ecological characteristics of the investigated sites are addressed.

1.1 Overview

The study sites are located in the Whataroa Ecological Region on the West Coast of New Zealand's southern island. Wetlands included in this study are scattered around the town Hokitika (Figure 1.1), about 2 km to 10 km inland from the coast. The area is part of the Westland terraces domain (Leathwick et al. 2003), which exhibits a high degree of environmental homogeneity within the south-western and southern lowlands. The northern boundary of the Hokitika Ecological District (McEwen 1987) is defined by the Taramakau River, while its southern limit constitutes the Mikonui River. The area extends from the Tasman Sea in the west to the alpine fault at the western edge of the Southern Alps, covering ca. 102 300 ha.



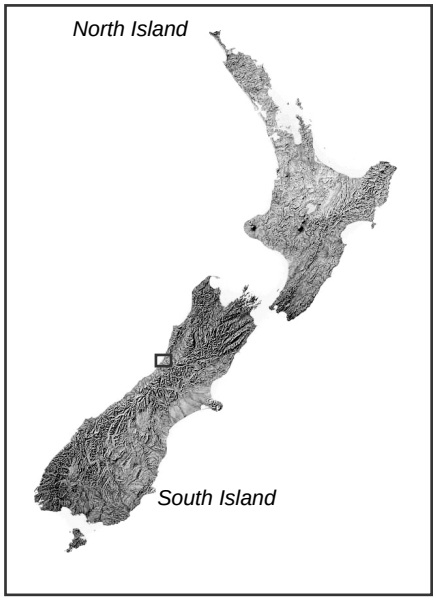
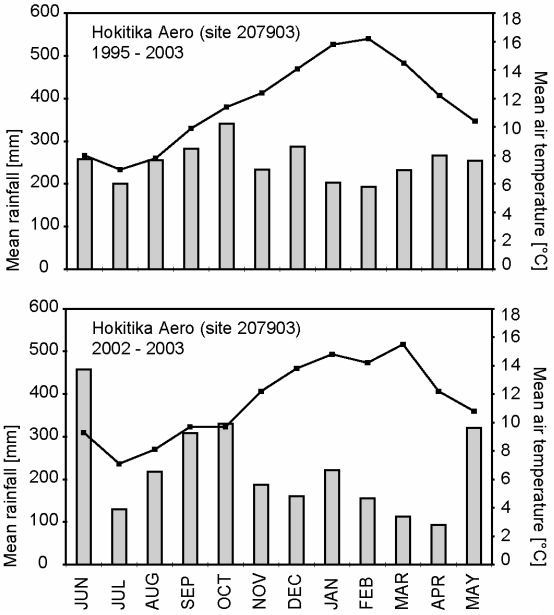
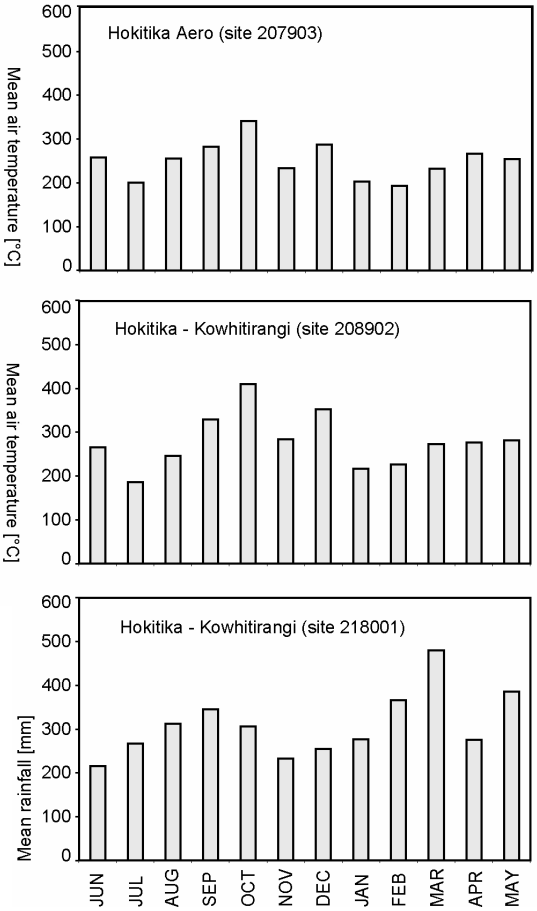


Figure 1.1. Map of the studied bogs (○) and swamps (□), (for GPS coordinates cp. Appendix, Part B). B1 = Keogans Rd., B2 = Stafford Loop Rd., B3 = Kumara; B4 = Arthurstown Rd., S1 = Mahinapua Swamp, S2 = Lake Kaniere; S3 = Tucker Flat; S4 = Back Creek Swamp. Climate stations: Hokitika airport (☆), Kowhitirangi (★).



▲ Figure 1.2. Comparison of mean monthly rainfall and mean monthly air temperatures from 1995 to 2003 with the study period from June 2002 to May 2003.



▶ Figure 1.3. Spatial heterogeneity in distribution of rainfall; localities cp. Figure? (1995-2002).

1.1.1 Climate

The Hokitika Ecological District features a superhumid mesothermal climate with annual rainfall between 2500 mm and 4000 mm. Precipitation is distributed evenly both temporally and spatially, with a slight winter minimum and a gradual increase towards the Southern Alps. However, the study period from June 2002 to May 2003 was characterised by paricularly low precipitation rates during late summer and fall (Figure 1.2). The comparison between climate stations at Hokitika and Kowhitirangi (Figure 1.3) demonstrates that local variation of precipitation in the study area is marginal. In the long term, mean monthly rainfall varies between 200 mm and 400 mm, with only few peaks above that mark.

The inter-annual average of the air temperatures at Hokitika indicates a mild climate with a February mean of 16 °C and a July mean of 7 °C (cp. Hessel 1982). This trend is also reflected by the mean 10 cm earth temperature (Figure 1.4C), which ranges from 5 °C in July to 17 °C in January. Due to the moderating influence of the Tasman Sea, the Westland Terraces are less prone to frost than inland regions (Leathwick et al. 2003), yet ground frost occurs at up to 15 days per month in winter (Figure 1.4D).

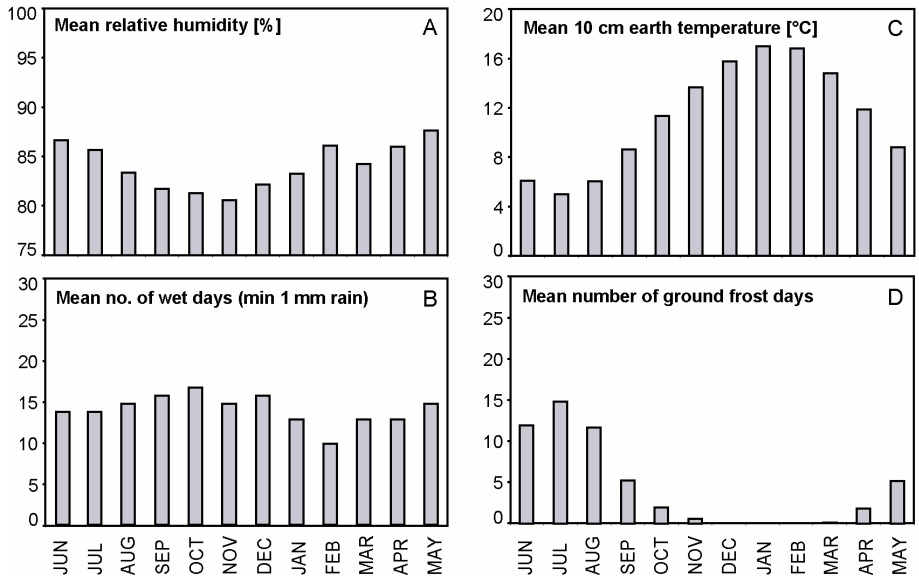


Figure 1.4. Disposition of mean relative humidity (A), mean number of wet days (B), mean 10 cm earth temperature (C), and mean number of ground frost days (D) in the study period from June 2002 to May 2003.

1.1.2 Geology and vegetation

Between Hokitika and Greymouth, successive advances of the Taramakau glacier reached to within a few kilometres of the present coast (Figure 1.5). Hence, glacial deposition and post-glacial dissection and deposition by rivers have shaped a landscape dominated by alluvial valleys and plains, and morainic hills and terraces (Moar and Suggate 1996). Isolated hills and blocks of hill country are moderately to heavily dissected and surrounded by recent fans. On the main terraces, poorly drained gley soils have developed from loess, moraine, and outwash gravels with small patches of poorly drained organic soils interspersed. In river valleys and adjacent low terraces, well to poorly drained mineral soils derived from greywacke, granite, and schist can be found (Mew 1980). Wetlands occur on various terrains, possessing a large variety of substrates from peaty silt to wet, untextured peat. Soils in the Hokitika Ecological District are generally infertile due to subsurface conditions and leaching by high rainfall.

Wetland vegetation patterns in the western South Island lowland vary depending on geologic subsurface and soil chemistry. Typical plants of nutrient poor bogs are *Carex gaudichaudiana*, *Baumea rubiginosa*, or *Baumea teretifolia* on slightly drier ground, and *Gleichenia dicarpa* and *Empodisma minus* in wet areas (Wardle 1991). *Sphagnum* spp. may form isolated hummocks and reaches continuous cover in some palustrine wetlands (Fife 1996). The term ‘pakihi’ describes a bog vegetation type that commonly occurs at the West Coast and is often dominated by *Leptospermum scoparium* and shorter sedge-

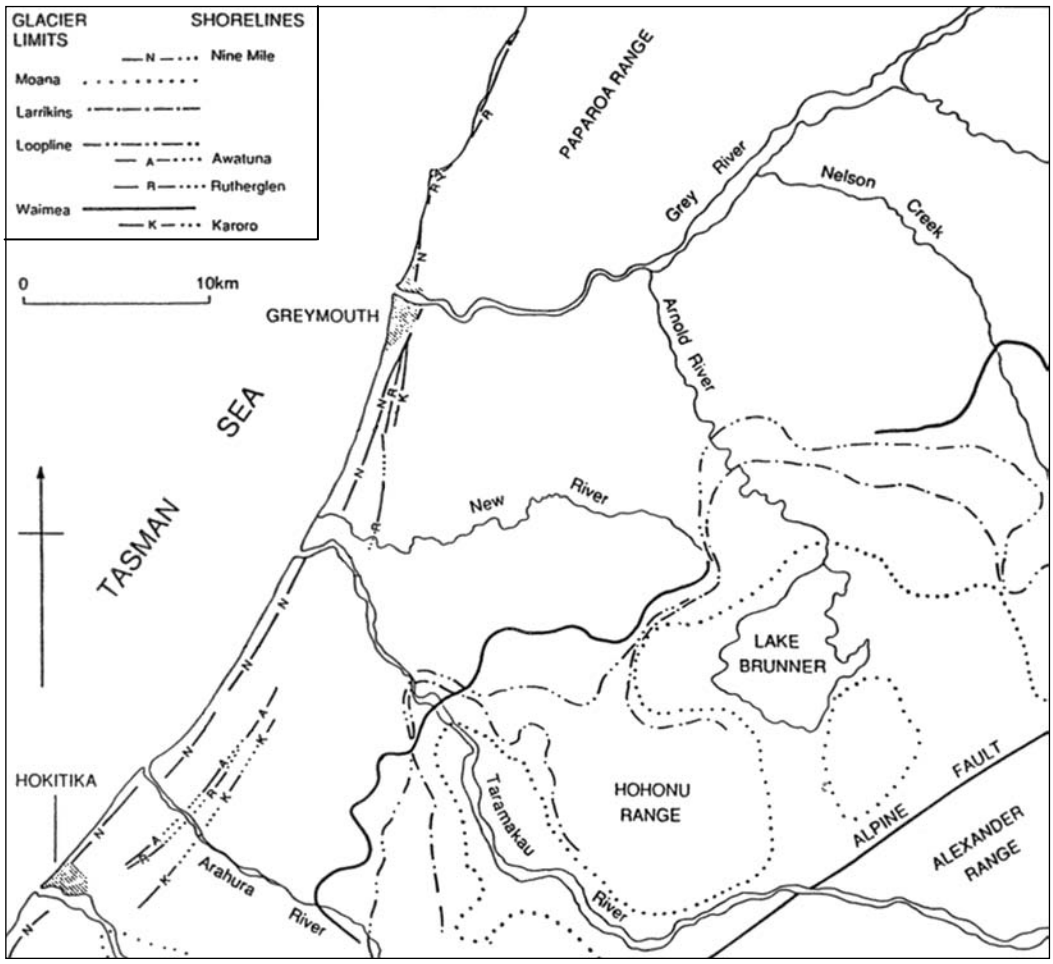


Figure 1.5. Greymouth-Hokitika area, with Quaternary ice limits and shorelines (modified, Moar and Suggate 1996).

fern- restiad communities comprising *Baumea* spp., *Gleichenia* spp., and *Empodisma* spp. (Burrows et al. 1979). In general, bog vegetation is adapted to ombrotrophy and highly acidic conditions, the pH typically being lower than 4.8 (Johnson and Gerbeaux 2004). The second group of wetland ecosystems incorporated in this survey is referred to as swamps. Johnson and Gerbeaux (2004) specify pH values of 4.8 to 6.3 for this wetland type, its predominant water source being surface and groundwater. Swamps often occur on alluvial surfaces and are dominated by *Phormium tenax*, *Carex secta*, *Dacrycarpus dacrydiodides*, *Typha orientalis*, and various shrubs, e.g. *Coprosma* spp.

1.1.3 Landuse

Historical records indicate that prior to the discovery of gold in the 1860s, humans had only limited impact on the Hokitika Ecological District (Harrop 1923; Peat 1987). The rapid increase in population size and development of European settlements during the

1864 to 1867 gold rush marked the beginning of an era during which most of the district's natural resources were drastically modified (Harrop 1923; May 1962). The timber industry developed and grew rapidly, spurred by the great demand within the mining community. By the late 19th century, the gold mining industry was in decline and forestry became the main economic activity. Agricultural activities developed at a slower pace, with pastures being established within areas of cleared forest (Peat 1987). Heavy fertilizer applications have been used to convert some pakihi areas to farms or plantation forest. Early this century, large areas on the fertile coastal and alluvial terraces were cleared of vegetation and drained for pastoral development. Since then, dairy farming has been the main agricultural activity, though deer farming has also become increasingly popular in the West Coast region. To date, areas under pasture range from clover and exotic grass pastures to rougher grasslands with a high cover of rushes, exotic weeds, and shrubs (Awimbo 1996). The *Sphagnum* exporting industry has also contributed to the decline of wetland areas in the last decades. In 1990, over 1000 t of *Sphagnum* were commercially harvested and exported to Japanese orchid nurseries (Buxton 1996).

1.2 Wetlands

The wetlands studied in the present thesis are categorised into two wetland types: bogs and swamps. According to the New Zealand wetland classification (Johnson and Gerbeaux 2004), a specific combination of features such as water origin, periodicity, substrate, nutrient status, pH, and vegetation characterise certain wetland types (Tables 1.1 and 1.2). However, a clear separation of pakihi and bog sites is problematic as denoted in the current classification framework. Since transitions between both types were commonly observed in the study region, these classes were combined and are referred to as pakihi bogs or simply as bogs in this study. That type of wetland is also termed 'ombrotrophic', as it is exclusively fed by rainwater. Fens can be distinguished by landform and vegetation patterns (Table 1.2), even though they possess hydrological,

Table 1.1. Water regime, substrate type, nutrient status and pH range of New Zealand wetland classes

Wetland class	Water origin (predominant)	Water flow	Water table	Water fluctuation	Periodicity	Substrate	Nutrient status	pH
Bog	rain only	almost nil	near surface	slight	wetness permanent	peat	low or very low	3-4.8
Fen	rain + groundwater	slow to moderate	near surface	slight to moderate	wetness near-permanent	mainly peat	low to moderate	4-6
Pakihi and gumland	mainly rain	almost nil	below surface	slight to moderate	wetness near-permanent, prone to temporary drought	mineral or peat	very low to low	4.1-5
Swamp	mainly surface water + groundwater	moderate	above surface in places	moderate to high	wetness permanent	peat and/or mineral	moderate to high	4.8-6.3

Table 1.2. Landforms, vegetation and key indicator plants associated with wetland classes in New Zealand

Wetland class	Predominant landforms	Common vegetation structural classes	Some key indicator plants
Bog	Usually almost level ground, including hill crests, basins, terraces	Wide range including moss, lichen, cushion, sedge, grass, restiad, fern, shrub, and forest types	Sphagnum, Oreobolus, Baumea tenax, Sporandanthus, Empodisma, Dracophyllum, Epacris, Leptospermum, Halocarpus
Fen	Slight slopes of bog margins, swamp perimeters, hillside toe slopes, alluvial fans	Usually sedge, restiad, rush, fern, tall herb, or scrub types	Schoenus pauciflorus, S. brevifolius, Empodisma, Chionochloa rubra, Hebe odora, Baumea teretifolia, Leptospermum
Pakihi and gumland	Level to rolling or sloping land having impervious soils, including formerly forested land	Mixtures of heaths and other small-leaved woody plants with restiads, ferns, sedges, lichens, mosses	Empodisma, Baumea temax, Gleichenia, Schoenus, Leptospermum, Dracophyllum, Nothofagus, Dacrydium
Swamp	Mainly on valley floors, plains, deltas	Usually sedge, rush, reed, tall herb, and scrub types, often intermingled, and including forest	Phormium, Carex, Soprosma, Gahnia, Typha, Cordyline, Dacrycarpus, Laurelia, Syzygium

hydrochemical, and substrate features that overlap with bogs and swamps. Henceforth, the term ‘minerotrophic wetland’ thus refers to swamps, designating that this wetland type receives a combination of rain and mineral water from varying sources.

A detailed description of the wetland ecosystems studied follows in chapters 1.2.1 to 1.2.5. High resolution aerial photographs of the study region (Land information New Zealand 2005), photographs of the wetlands, and GPS coordinates of the wetland sites are enclosed in the Appendix (Part B). For most of the bogs, only little information was obtainable due to the small size and hidden location. Pakihi sites thus were combined in one group and contrasted against the forested bog at Kumara. On the other hand, swamps received more attention in the past, and background information on the history, development, and ecological characteristics was available for all of the respective sites.

1.2.1 Pakihi bogs (B1, B2, and B4)

Pakihi is a Maori word meaning open grass country or barren land (Burrows et al. 1979). On surfaces up to about 1000 m, extensive tracts of such country occur in many parts of the northwest and west of the South Island, totalling over 300 000 ha. Pakihi is also used as a term for vegetation of such areas, which are often dominated by *Leptospermum scoparium*, sedges (*Baumea* spp.), ferns (*Gleichenia* spp.), and restiads (*Empodisma* spp.). The soils are always strongly gleyed and usually very infertile with no peat or a thin to deep peat cover over mineral soil. Landforms range from terrace surfaces, which originally were glacial outwash, to moraines, raised marine sediments, including beach gravels, dunes, estuarine deposits, dissected hill country, and plateaux formed on hard bedrock.

Three of the bogs studied, i.e. the sites at Keogan's Road (B1), Stafford Loop Road (B2), and Arthurstown Road (B4), belong to the pakihi type, though each wetland exhibits a distinct combination of features. Bog B1 is dominated by *Sphagnum* spp. and *Empodisma minus*, lacking taller sedges and scrubs, while bog B4 is in a transitional state from degenerating wetland forest to open pakihi, and *Gleichenia dicarpa* occurs more frequently (cp. photographs in Appendix, Part B). Most closely related to the genuine pakihi type is wetland B2, in which *Empodisma minor*, *Baumea tenax*, and *Gleichenia dicarpa* predominate, while *Sphagnum* spp. recedes.

Changing peculiarities in the composition of vegetation in this type of wetland are affiliated to the way of formation of pakihi bogs.
There is evidence from Westland that pakihi vegetation formed a kind of treeless and possibly shrubless moorland during the last glaciation. A pollen diagram, believed to demonstrate the transition from interglacial to glacial conditions, shows a clear sequence in which forest species were replaced by pakihi species (Dickson 1972). On fresh alluvial surfaces such as glacial outwash or moraines, pakihi probably originated following a sequence of vegetation development from scrub via mixed broadleaved angiosperm forest to gymnosperm forest. Under local conditions of excessive water logging and excessive nutrient impoverishment, forest degeneration gave rise to a semi-pakihi or bog forest community. Further degeneration on the wettest sites finally might have lead to the development of *Leptospermum*-sedge-fern-restiad communities, which are underlain by shallow peat (Burrows et al. 1979).
Another way in which pakihi might have originated naturally is that wet areas such as mesotrophic or eutrophic shallow lakes, which have formed at the close of glaciation, gradually accumulated peat. Eventually, oligotrophic conditions prevailed, but the peat was too wet for colonisation by forest which surrounded the site.
Present-day disturbance of the predominant forest on gley soils also gives rise to open pakihi. On the slightly more fertile and better-drained sites, dense *Leptospermum* spp. stands develop, and often there are indications of return to forest. On wetter and the most infertile sites the predominant plants are species of *Baumea*, *Empodisma minus*, and *Gleichenia* spp. Common causes for the development and maintenance of induced pakihi are burning and logging.
Irrespective of the cause and the time at which induced pakihi originated, the resultant vegetation is generally very similar. However, temporal, local and regional spatial differences occur depending on the stage of vegetation maturity which each site has reached, drainage variation, and the overall distribution pattern of plant species (Burrows et al. 1979).

1.2.2 Kumara forested bog (B3)

This wetland has developed on an outwash aggradational gravel terrace, approximately 1.5 km seaward of the Waimea glacier terminal moraine (cp. Figure 1.5). The peat bog is situated below a small freshwater reservoir and framed by timber plantation on its eastern margin. Originally, vegetation was dominated by *Dacrydium cupressinum* (Moar and Suggate 1996), while its clearance might have triggered the development of the present bog pools. In contrast to the previously described pakihi bogs, vegetation is dominated by sedges and *Sphagnum* spp., whereas *Gleichenia dicarpa*, *Baumea* spp., and *Empodisma* spp. occur only sporadically.

1.2.3 Mahinapua Swamp (S1)

Mahinapua Swamp is a minerotrophic wetland, about 2 km inland (15 m a.s.l) and adjacent to Mahinapua Creek, occupying an area of ca. 25 ha (Figure 1.1). Old glacial outwash gravel terraces extend into the northern and southern ends of the area (Moar and Suggate 1996), which have been separated by the past down cutting of Mahinapua Creek and its tributaries, Cowan and Sandstone Creeks. From the centre of the section, an extensive, irregular depression in the moraine opens out to the west and drains into Mahinapua Creek. This depression has been shut off from the sea by a series of linear sand dunes and is not exposed to tidal influence.
The area around Mahinapua Swamp was extensively logged and burnt of its tall podocarp forest between 1885 and 1952, although the wetland itself has been relatively unmodified. Sandstone Creek and Cowan Creek and their floodplains bisect the rural part from east to west to meet with Mahinapua Creek. That section of the wetland displays landforms ranging from an inundated delta-like environment to swampland, which would once have supported a tall kahikatea (*Dacrycarpus dacrydioides*) swamp forest. At present, 2-4 m high flax stands (*Phormium tenax*), *Carex gaudichaudiana*, *Coprosma* spp. (*C. tenuicaulis*, *C. rotundifolia*), and occasional cabbage trees (*Cordyline australis*) are scattered across the open water areas. In places of slightly higher and hence drier ground fringing the wet areas, a transition to dense, regenerating broadleaf forest can be observed.

1.2.4 Lake Kaniere (S2)

Adjacent to the north-western tip of dystrophic Lake Kaniere (150 m a.s.l, cp. Scott 1996), this remnant kahikatea (*Dacrycarpus dacrydioides*) swamp occupies a small area accessible by boardwalk. The wetland is located at the margin of a tall podocarp forest and is characterised by loose stands of *Phormium tenax* and *Cyperaceae*. Open water areas exhibit dense patches of submersed macrophytes. Bedrock and soils were formed at the end of the last glaciation, and, according to Mew (1980), the swamp covers gley

podzol soils that have developed from loess and glacial outwash alluvium comprising granite, greywacke and schist. Water level fluctuates with lake water depth, indicating a connection of hydrologic regimes through lateral water flow.

1.2.5 Tucker Flat (S3)

The minerotrophic swamp near the Kaniere township covers an old mining area and is surrounded by developed and semi-developed farmland. Much of the wetland is fenced off, although some stock still graze drier areas. The swamp complex is characterised by large areas of open water, which are connected by channels at the base of a scrub and bush covered hill. Vegetation is dominated by flax (*Phormium tenax*) and various sedges and herbs that form floating meadows at the margins of open water bodies.

1.2.6 Back Creek Swamp (S4)

Back Creek Swamp is situated at about 20 m a.s.l. on the true left bank of the Hokitika River. The wetland is an important wildlife habitat ranked of high value by the New Zealand Wildlife Service, due to its large extent and complexity, and the diverse native plant community.

The main catchment consists of higher terraced land to the southwest, which is discharged by a number of small streams flowing down a forested escarpment into Back Creek Swamp. The wetland itself is drained by Back Creek, which meanders through farmed freehold land before entering the Hokitika River in the north, and by a small stream at the southern end of the swamp that flows directly into the Hokitika River. Water levels within the wetland are known to vary according to rainfall, from periods when little standing water is present to times when up to 20 cm cover areas of rushland, shrubland, and forest. According to Eastwood (1998), there is no evidence that the river contributes flood water into the wetland area.

The swamp has developed on an alluvial river flat at the base of a glacial terrace. Parent material consists of schist, greywacke, and granite alluvium. Material size includes gravel, sand, and silt, which gave rise to silty and fine sandy loam soils formed under indigenous forest. A complex of imperfectly drained and moderately to strongly gleyed soils of medium to low nutrient status characterise the area at present.

Vegetation communities have been modified by logging and possibly by burning, drainage, and introduced weeds and mammals. Current vegetation patterns include areas of almost pure rush and reedland (*Baumea rubiginosa*, *Carex gaudichaudiana*) at the northern and southern ends of the reserve, through various proportions of mixed rushland/shrubland, to kahikatea dominated forest. Some almost pure stands of raupo (*Typha orientalis*) occur mainly on the western side and southern end of the wetland. Flax (*Phormium tenax*) occurs mostly in mixture with other species and is densest in parts of

the north-western end of the wetland. Some moderately dense areas of gorse (*Ulex europaeus*) occur amongst *Coprosma* spp. shrubland along the eastern side of the reserve, along kahikatea forest fringes, and around the wetland margins. In open water, the threatened *Myriophyllum robustum* forms loose stands.

Gold mining activity about a century ago has induced erosion and contributed to the deposition of a gravel fan at the base of the escarpment on the south-west boundary, which is currently relatively stable and covered in regenerating vegetation. Recently developed dairy pasture that has been drained adjoins the wetland immediately to the north-west. A narrow strip of developed pasture also borders much of the eastern boundary between the swamp and the river. An area of 205 ha, which comprises the core of the wetland, was gazetted in 1982 as Wildlife Management Reserve. An additional 288 ha of mainly surrounding catchment was gazetted as Wildlife Management Reserve Extension in 1997. Both areas are public land that is managed by the Department of Conservation.

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2 Hydrochemistry and primary production in New Zealand lowland wetlands

2.1 Abstract

Currently there are no comprehensive data on the hydrochemical features determining New Zealand wetland classes and their connection with algal primary production. Therefore, environmental variables and algal biomass in pristine New Zealand lowland bogs and swamps were quantified in this study. Alkalinity, pH, calcium, and silica were significantly higher in the swamp wetland class, whereas gilvin absorbance (g_{440}) was lower. Ion supply and primary production in bogs were controlled by high precipitation and wet deposition of sea salt aerosols, while in swamps the influence of groundwater dominated over precipitation effects. Benthic algae in both wetland types were affected by nutrient release from sediment or macrophytes, yet substrate effects were more pronounced under ombrotrophic conditions. While suspended tychoplankton reflected benthic biomass in bog pools, swamps exhibited a distinct phytoplankton community. Periphyton grown on artificial substrate provided reliable means for the comparison of wetlands, but underestimated absolute chlorophyll-*a* concentrations.

2.2 Introduction

In New Zealand, wetland ecosystems have been studied primarily with respect to vegetation patterns (Burrows and Dobson 1972, Burrows et al. 1979, Dobson 1979, Mark et al. 1979, Williams et al. 1990, Agnew et al. 1993, McQueen and Bastow 2000, Walker et al. 2001, Dickinson et al. 2002, Clarkson et al. 2004). However, the knowledge about hydrochemical features determining New Zealand lowland wetland types is sparse, and to date no results have been published in terms of algal primary production in these ecosystems. The lack of information of that environmental component thus limits our understanding of the functional relationships and processes operating within New Zealand wetlands. In a recently published classification framework, Johnson and Gerbeaux (2004) addressed this problem, but even though their approach allows for the identification of wetland classes on the basis of water regime, substrate, nutrient status, and pH, it does not account for the fundamental hydrochemical constitution of wetlands. In fact, there is a great demand for studies dealing with hydrochemistry and primary production to fill that gap and substantiate the existing knowledge about the wide variety of wetland types in New Zealand.

In this chapter, the basic abiotic parameters that separate lowland bogs and swamps in south-western New Zealand are outlined and quantified. It is discussed to what extent these observations correspond to internationally applied wetland classification criteria (e.g. Scott and Jones 1995, Zogg and Barnes 1995, Masing et al. 2000, Wheeler and Proctor 2000). The relative proportions of planktonic, epiphytic and epipelic biomass

estimates and their relation to environmental variables in each wetland class are also compared. Periphyton grown on polyethylene slides allowed for the standardisation of substrate characteristics across different sampling sites, providing reference for the biomass estimates from natural substrata.

2.3 Material and Methods

2.3.1 Site selection and site preparation

Criteria for the pre-selection of wetlands were vegetation patterns as an indicative measure of trophic state (cp. Burrows et al. 1979, Dobson 1979, Wardle 1991, Fife 1996, Johnson and Gerbeaux 2004) and pH measurements. Four pristine lowland bogs and four swamps were thus chosen to represent the two wetland types (cp. Figure 1.1). In total, 44 sites were selected, with five to eight plots established in each wetland.
In September 2002, posts with vertically orientated, exchangeable polyethylene slides were set up at all sites to provide a neutral substrate for periphyton colonization. The slides were exposed for twelve weeks before retrieval in December 2002 and March 2003. Tape measures were attached to the posts for recording water level fluctuations. At shallow sites, small wells (30 cm perforated PVC tubes, 5 cm in diameter) were installed that allowed for the withdrawal of water without disturbing the sediment. Onset® data loggers were deployed in both wetland types to obtain a continuous water temperature record (logging interval 30 minutes).

2.3.2 Water chemistry

In December 2002 and in March 2003, water samples were collected from each sampling site and stored in acid washed polyethylene bottles at 4 °C in the dark. Aliquots were filtered within 24 hours and subsequently preserved at -20 °C or temporarily kept at 4 °C until further analysis, depending on the requirements of the respective methods.
Total phosphorus (NIWA Hamilton Inorganic Chemistry Laboratories 1996), alkalinity (Clescerl et al. 2000), and gilvin absorbance g_{440} (Davies-Colley et al. 1993) as a proxy for dissolved organic matter were measured in the NIWA laboratory in Christchurch. The determination of ammonium and nitrate was carried out with a Technicon Auto-Analyser following the methods described in Downes (2001). Silica and soluble reactive phosphorus (SRP) were measured according to the methods suggested in Wetzel and Likens (2000). Colorimetric determinations were performed using a Jasco 7850 UV-VIS Spectrophotometer. Samples for the analysis of calcium, magnesium, potassium, sodium, chloride, and sulphate were sent to the Landcare Research Laboratory in Palmerston North. Cations and anions were determined using a Varian FS-220 fast sequential Atomic Absorption Spectrophotometer and a Lachat IC 5000 Ion Chromatograph, respectively (Clescerl et al. 2000). Sulphate deficit is calculated by assuming that all chloride in the

water is marine, and subtracting chloride multiplied by 0.105 (the ratio of sulphate to chloride in seawater) from the total sulphate concentration (Gorham et al. 1985). Sodium surplus is the difference between the expected amount of sodium ions as if solely introduced by sea spray (sodium : chloride = 0.86) and the actual concentrations in the water. The anion deficit is calculated by subtracting the sum of measured anions (SO_4^{2-}, Cl^-, PO_4^{3-}, NO_3^-, SiO_3^{2-}) from the sum of measured cations (Ca^{2+}, Mg^{2+}, K^+, Na^+, NH_4^+, H^+).
Every three weeks, from September 2002 until March 2003, water temperature, pH, and conductivity were recorded on site with a TPS WP81 conductivity/pH meter. Conductivity values were corrected for the contribution of H^+ ions according to Sjörs (1950) and expressed as corrected or specific conductivity. Water level was also measured every three weeks to obtain a representative long-term record (cp. Shaffer et al. 2000). Amplitude and frequency of water level fluctuations at each site were related to mean water depth, thus the intensity of relative water level fluctuation ($\Delta\phi$) is calculated as

$$\Delta\phi = \sum_{i=1}^{n} (a_i)^2 \Big/ \gamma + \sum_{i=1}^{n} (b_i)^2 \Big/ \gamma \qquad \text{(equation 2.1)}$$

where $a_i = \gamma - x_i$, the difference between mean water depth (γ) and the water level (x_i; $i = 1, \ldots, n$) measured at date i, and $b_i = x_i - x_j$, the absolute difference between water levels ($x_{ij;}$ $i,j = 1, \ldots, n$) measured at date i and the following date j.
At the end of the sampling period, the water temperature loggers were recovered and read out with an Optic Base Station™.

2.3.3 Biomass

Within five hours after sampling in early and late summer, a measured amount of water was filtered on glass fiber filters for subsequent determination of planktonic chlorophyll-*a*. To estimate benthic primary production, macrophytes, sediment, and artificial substrata were collected (cp. table 3.1). For the measurement of epiphytic chlorophyll-*a*, algae were removed from plant fragments and rinsed on glass fiber filters. Dry weight of the plain macrophyte leaves and stems was determined for the calculation of chlorophyll-*a* per surface area. All filters, polyethylene slides, and sediment samples were temporarily kept at -20 °C during field trips and subsequently transferred into a -80 °C freezer for long-term storage. Chlorophyll-*a* from plankton and sediment samples was extracted with acetone according to the method suggested by Marker (1972) and measured with a Perkin-Elmer LS-55 Flourometer at 431 nm and 670 nm. The determination of epiphytic chlorophyll-*a* followed the method described in Biggs and Kilroy (2000), slightly adjusting it for periphyton grown on artificial substrates. Hence, instead of extracting pigment from filtered algal material, the polyethylene slides were placed in sufficiently large sampling containers and boiled in 5 ml of 90 % ethanol.

Epiphytic and periphytic chlorophyll-*a* concentrations were measured at 663 nm and 750 nm, using a Jasco 7850 UV-VIS Spectrophotometer. Corrections for phaeophytin were made for all chlorophyll-*a* measurements.

2.3.4 Numerical methods

2.3.4.1 Relating similarity and dissimilarity matrices (RELATE)

Even though classical multivariate testing for seasonal differences is not justified, given only two sampling occasions and, therefore, lack of the required temporal replication across sites (cp. Hurlbert 1984), this non-parametric approach (PRIMER v5) provides a sensible measure of seasonal variation in abiotic and biotic data.

Similar to the well-known ***Mantel test*** (Mantel 1967), the ***RELATE*** routine measures how closely related two sets of multivariate data are, by calculating a rank correlation coefficient between all the elements of their respective similarity or dissimilarity matrices (Clarke and Warwick 2001). Thus, if the among-sample relationships are the same, then the rank correlation $R = 1$, a perfect match. Normalised ***Euclidean distance*** matrices (cp. equation 2.4) were created for both environmental data sets from December 2002 and March 2003 (including 20 environmental variables across 36 sites; missing values omitted), which were subsequently related by means of ***Spearman rank correlations*** in the following form:

$$\rho_s = 1 - \frac{6}{N\left(N^2 - 1\right)} \sum_{i=1}^{N} \left(r_i - s_i\right)^2 \qquad \text{(equation 2.2)}$$

where $N = n(n\text{-}1)/2$ and n is the number of samples, and $\{r_i;\ i = 1, \ldots, N\}$ and $\{s_i;\ i = 1, \ldots, N\}$ are the elements of the respective rank similarity matrices.

The same procedure applies to biotic data (analysis included 199 variables across 107 samples; missing values omitted), though rank correlations in this case were based on ***Bray-Curtis similarities*** between the square root transformed relative abundances of species i and l:

$$S_{il}^{'} = 100\left\{1 - \frac{\sum_{j=1}^{n} \left| y_{ij} - y_{lj} \right|}{\sum_{j=1}^{n} \left(y_{ij} + y_{lj} \right)}\right\} \qquad \text{(equation 2.3)}$$

It is anticipated that, prior to subsequent analysis of the data, all environmental variables and the relative abundances of diatom species were averaged across sampling dates to avoid confounding due to temporal non-independence of the data. In fact, this method provided evidence that the averaging process causes no loss of information in the analysis of different spatial levels (cp. chapter 2.4.1), which is the focus of this study.

2.3.4.2 Descriptive statistics

Descriptive statistics of the environmental variables were calculated with SPSS v11.5 (cp. Appendix, Part B) and illustrated by ***box and whiskers plots***. The graphs summarise the most important statistical parameters, showing the median (black bar), the 25th and 75th percentiles (lower and upper hinges of the "box"), and the minimum and maximum observed values that are not statistically outlying ("whiskers"). Open circles indicate outliers that are 1.5 to 3 box lengths apart from the median.

2.3.4.3 Data transformations

Water chemistry variables and biomass data were transformed prior to multivariate statistical analysis, because standardisation and ordination (see below), operate most effectively when the data are as near as possible to multivariate normality. Pairwise scatter plots of the environmental variables (cp. Appendix, Part B) should then show roughly linear relationships and a symmetric distribution of points. ***Draftsman plots*** (PRIMER v5) revealed that $\boldsymbol{log_e}$ transformations were appropriate for nitrogen and phosphorus concentrations, while ***square root*** transformations were adequate for all other ions, corrected conductivity, water level, water depth, water temperature, alkalinity, and chlorophyll-*a* concentrations. Due to explorative analysis, gilvin absorbance g_{440} and pH data did not require any transformation.
Justification for the correct choice of transformations was obtained by a combination of ***Kolmogorov-Smirnov*** and ***Shapiro-Wilkes*** tests (SPSS v11.5). Accordingly, significance values of $p \geq 0.05$ indicated that the distribution of the data did not differ significantly from a normal distribution (cp. Appendix, Part B). Minor deviations were screened, but repeated tests with other transformations did not result in any improvement.

2.3.4.4 Principal Components Analysis (PCA)

Principal components analysis (***PCA***; PRIMER v5) is an ordination method that was used to detect patterns in the distribution of environmental variables between wetlands and wetland types. The number of abiotic variables included in the ordination was limited to 25 parameters (cp. Appendix, Part B) to avoid distorting effects by redundant information. Data were transformed (see chapter 2.3.4.3) and standardised before analysis.
PCA is a projection of sample points from the multidimensional variable space onto a 'best-fitting' plane or other low-dimensional solution. For the purpose of this study, principal components were restricted to two dimensions, which per definition capture as much of the variability in the original data as possible. The extent to which the 2-dimensional picture is a good reflection of the relationship between samples is summarised by the '% variation explained', which constitutes a ratio of eigenvalues. PC axes reflect the

sum of contributions from each of the environmental parameters and represent simple linear combinations of the abiotic variables, their coefficients termed eigenvectors. Dissimilarity between two samples *j* and *k* is defined as their ***Euclidean distance*** (*d*) apart in the multidimensional space:

$$d_{jk} = \sqrt{\sum_{i=1}^{p} \left(y_{ij} - y_{ik} \right)^2} \qquad \text{(equation 2.4)}$$

3.3.4.5 Analysis of Similarities (ANOSIM)

The results obtained by PCA were reassessed and quantified by ***analysis of similarities*** (***ANOSIM***; PRIMER v5). This method was also used for the quantification of differences in the taxonomic composition of benthic diatom communities from the studied wetlands (cp. chapter 3).

ANOSIM is a generally applicable non-parametric permutation procedure (*Monte Carlo tests*, Hope 1968), based on the rank similarity matrix underlying the ordination or classification of samples (Clarke and Warwick 2001). The method has been chosen to test for differences between wetlands, because the assumptions implicit to the ***analysis of variance*** (***ANOVA***) are not met with the present data (cp. Underwood 2002). The analysis of similarities, however, is neither restricted to a balanced number of replicates nor does it require equal variance within groups.

The ***one-way ANOSIM*** layout is restricted to tests involving a single spatial level. The test statistic in this case contrasts differences between groups of samples with differences among replicates within sample groups. If $\bar{r}_W$ is defined as the average of all rank similarities among replicates within samples, and $\bar{r}_B$ is the average of rank similarities arising from all pairs of replicates between different groups of samples, then

$$R = \frac{\left(\bar{r}_B - \bar{r}_W \right)}{\frac{1}{2} M} \qquad \text{(equation 2.5)}$$

where $M = n(n-1)/2$ and n is the total number of samples under consideration. $R = 1$ only if all replicates within sites are more similar to each other than any replicates from different sites. If R is approximately zero, similarities between and within sites will be the same on average.

The ***2-way nested ANOSIM*** layout is appropriate where two levels of spatial replication are involved. In this study, wetlands were grouped *a priori* as representative elements of two superior categories (wetland classes) but there were also replicate samples taken within wetlands. Thus, the ANOSIM 2-way nested test compares differences between wetland types against variation among wetlands of a specific type.

2.3.4.6 Bivariate correlations between environmental variables

For assessing the strength and direction of the association between pairs of environmental variables (samples *j* and *k*), ***Pearson correlation coefficients*** were calculated:

$$r_{jk} = \frac{\sum_i \left(y_{ij} - \bar{y}_{\cdot j}\right)\left(y_{ik} - \bar{y}_{\cdot k}\right)}{\sqrt{\sum_i \left(y_{ij} - \bar{y}_{\cdot j}\right)^2 \sum_i \left(y_{ik} - \bar{y}_{\cdot k}\right)^2}} \qquad \text{(equation 2.6)}$$

where $\bar{y}_{\cdot j}$ is defined as the mean over all values for the *j*th sample and $\bar{y}_{\cdot k}$ .as the mean over all values for the *k*th sample. Coefficients vary in the range of -1 to +1, with positive linear correlations (*r* near +1) if high counts in one sample match high counts in the other, and negative linear correlations (*r* near -1) if high counts in one sample match low values in the other. The approach requires transformation of the data to approximate normality (cp. chapter 2.3.4.3).

2.3.4.7 Pairwise comparisons between variables and samples

Even though the environmental data have been shown to be normally distributed after transformation, it can not be assumed that variances are equally distributed across the measured parameters. Thus, to avoid erroneous rejection of the null hypothesis due to increased ***Type I error***, non-parametric numerical procedures were chosen for pairwise significance tests between variables and samples.

The ***Wilcoxon*** signed-ranks method tests the null hypothesis that two related medians are the same. This procedure allows testing for differences between paired scores of two related samples when the assumptions required by the paired-samples t test are not met. Ranks are based on the absolute value of the difference between the two test variables. In this study, the test was used to analyse if periphyton biomass on artificial substrates underestimated epiphytic chlorophyll-*a* concentrations in a consistent manner (2-sided significance level p = 0.05). The procedure was repeated with a confidence interval of 95 % defined by Monte-Carlo permutation tests.

The non-parametric ***Mann-Whitney U Test*** was applied to verify differences between the two wetland types by analysing differences in the absolute values of the environmental variables measured. The test is based on the null hypothesis that two independent samples come from the same population and does not assume normality or equal variances in the data.

2.3.4.8 Bonferroni adjustment

Repeated significance tests on the same set of variables or samples will raise ***Type I error***, i.e. the probability of erroneously rejecting a true null hypothesis will increase.

Therefore all significance levels obtained through multiple pairwise comparisons (e.g. by applying ANOSIM and Pearson correlations) were corrected by adopting the adjusted ***Bonferroni*** method suggested by Holm (1979).

2.4 Results

2.4.1 Seasonal variation

The comparison of environmental data sets from December 2002 and March 2003 by relating their respective dissimilarity matrices (cp. chapter 2.3.4.1) yielded a significant correlation between both groups of variables ($R = 0.569$, $p = 0.001$), indicating only small seasonal differences in the abiotic data. Considered the large number of parameters included in the analysis and the lack of replication at each sampling occasion, one would expect a noticeable deviation from the maximum value of $R = 1$, even if there were only small differences between single pairs of elements.

A cross-check by means of PCA ordinations for both early and late summer data sets also points to the fact that seasonal variation is of minor importance. In either ordination (figure 2.1), sites were arranged the same way, regardless of sampling date. Therefore, it is concluded that, by averaging the measured environmental variables across sampling dates to eliminate dependence of the data, no indispensable information is lost in the analysis of different spatial levels. Furthermore, the mean of the population is more likely correctly represented by the sample mean, as abiotic point measurements entail larger deviations than biological data such as diatom community composition, which integrate over a time period of several days or weeks (cp. chapter 4).

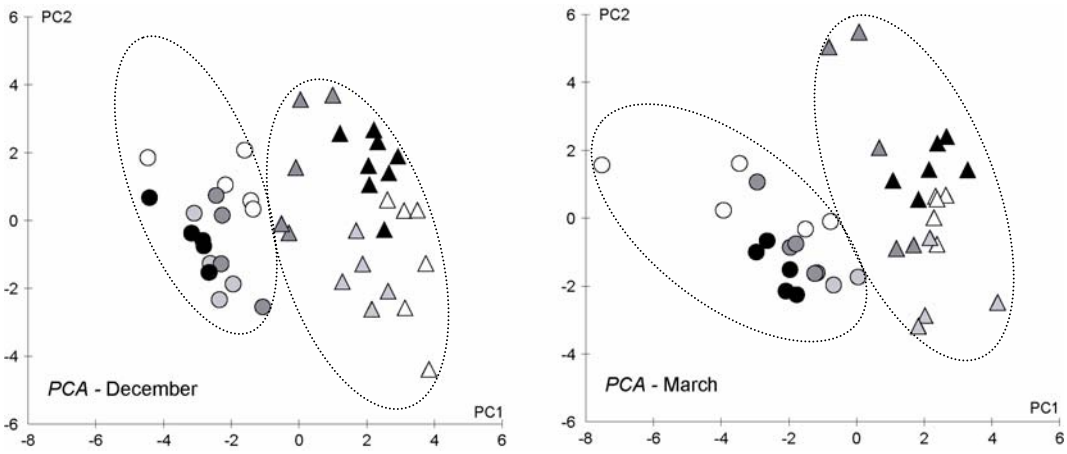

Figure 2.1. PCA ordinations of environmental data from bogs (△) and swamps (○), collected in December 2002 (left) and March 2003 (right). B1 (△); B2 (▲); B3 (▲); B4 (▲); S1 (○); S2 (●); S3 (●); S4 (●).

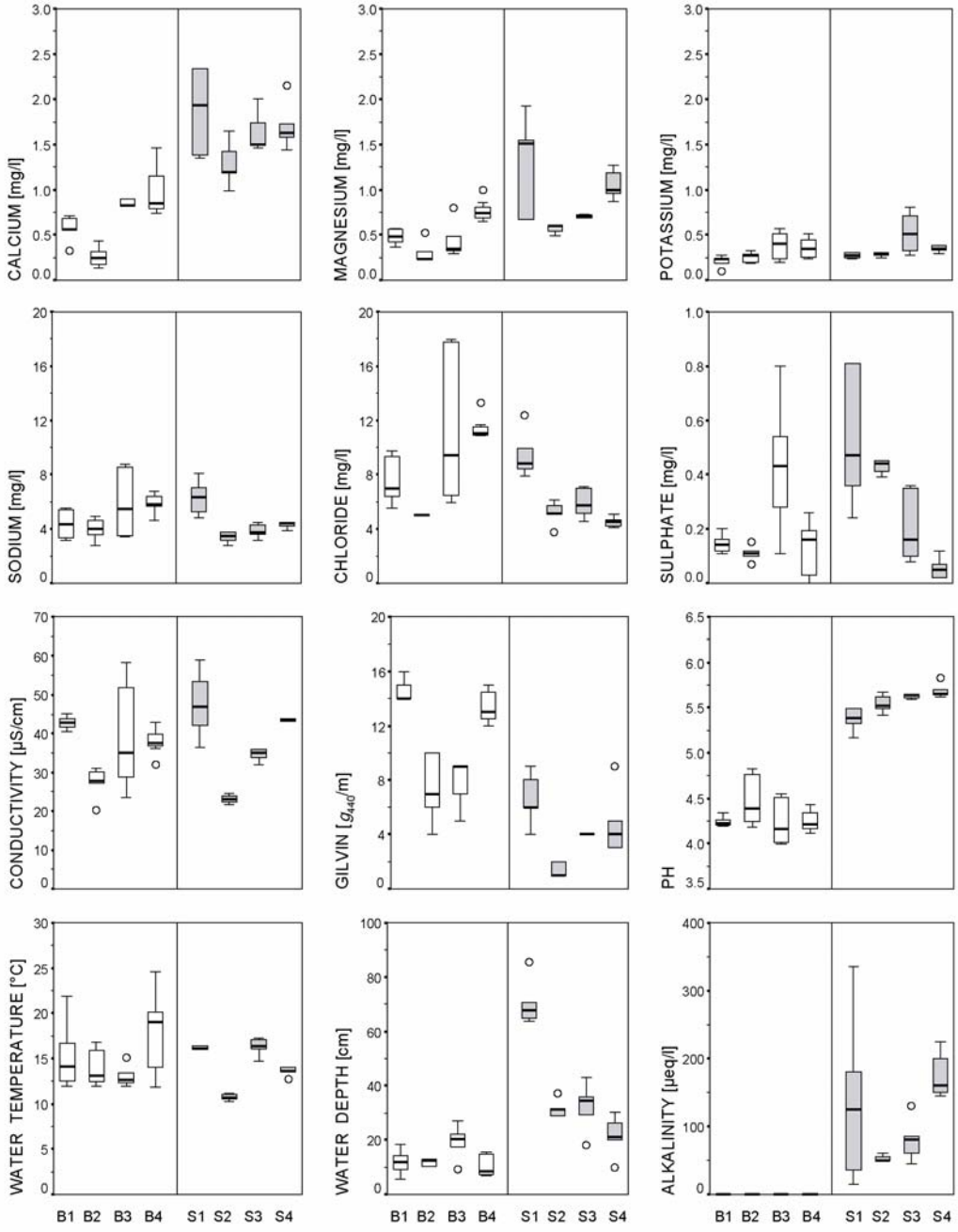

Figure 2.2a. Box and whiskers plots of environmental variables. Number of replicate sites in bogs (white bars): n = 6 (B1), 5 (B2), 5 (B3), 8 (B4); number of replicate sites in swamps (filled bars): n = 5 (S1, S2, S3, S4).

2.4.2 Descriptive statistics

The box and whiskers plots of water chemistry and biomass parameters (figures 2.2a and 2.2b) illustrate that there is considerable variation within wetlands and wetland types (cp. table 2.1). Differences that were constant for all wetlands could be detected in variation

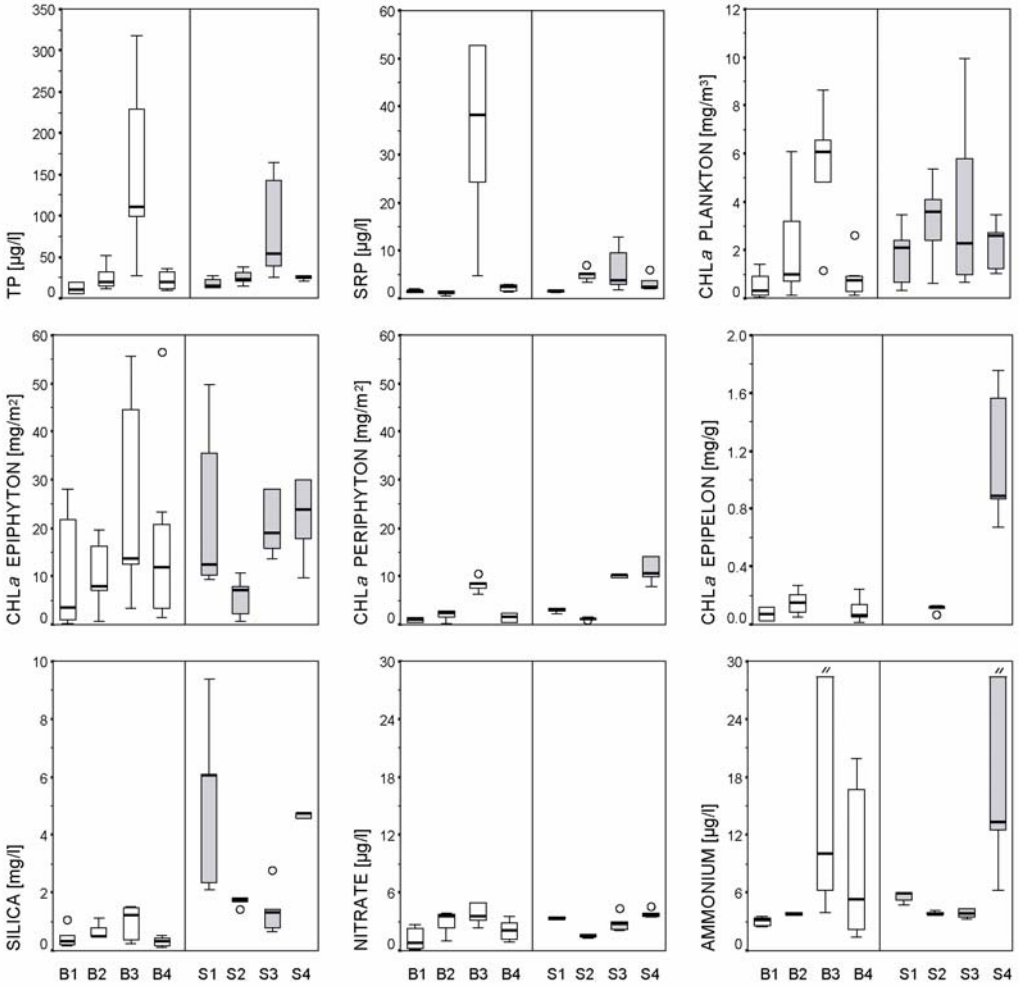

Figure 2.2b. Box and whiskers plots of environmental variables (continued). Number of replicate sites in bogs (white bars): n = 6 (B1), 5 (B2), 5 (B3), 8 (B4); number of replicate sites in swamps (filled bars): n = 5 (S1, S2, S3, S4). B1: n = 2 for epipelic chlorophyll-*a*. B4: n = 4 for chl-*a* epiphyton, n = 6 for chl-*a* epipelon; periphyton refers to benthic algae on artificial substrata.

and absolute biomass between epiphytic assemblages and periphytic algal communities that developed on artificial substrate. Primary production on polyethylene slides was significantly lower than epiphyton biomass ($p < 0.05$), but similar among sites of each wetland, while epiphytic chlorophyll-*a* concentrations greatly varied between sites.

Water temperature fluctuations followed the same trend in all wetlands provided with data loggers (figure 2.3). After a continuous increase from mid August, the temperature baseline stabilises in November 2002 and keeps at approximately the same level until March 2003. Within the bog wetland class, water temperature fluctuations at B2 were most distinct, the daily means rising as high as 20 °C in mid and late summer. The data for this wetland were derived from an unshaded, relatively shallow site (mean depth = 12 cm), which is fully exposed to solar radiation and prone to temporary drought.

Table 2.1. Mean values and standard errors of the means (in parentheses) for the environmental variables measured. Sediment samples for chlorophyll-*a* analysis were not available for wetlands B3, S1 and S3

	B1	B2	B3	B4	Mean	S1	S2	S3	S4	Mean
Sites (n)	*6*	*5*	*5*	*8*	*24*	*5*	*5*	*5*	*5*	*20*
Ca^{2+} [mg/l]	0.57 (0.05)	0.26 (0.05)	0.94 (0.10)	0.97 (0.09)	0.72 (0.07)	2.33 (0.61)	1.29 (0.11)	1.64 (0.10)	1.71 (0.12)	1.74 (0.17)
Mg^{2+} [mg/l]	0.48 (0.03)	0.31 (0.05)	0.45 (0.09)	0.77 (0.04)	0.54 (0.04)	1.26 (0.25)	0.57 (0.02)	0.69 (0.03)	1.06 (0.07)	0.89 (0.09)
K^{+} [mg/l]	0.21 (0.03)	0.26 (0.03)	0.38 (0.07)	0.36 (0.04)	0.31 (0.02)	0.43 (0.16)	0.31 (0.03)	0.53 (0.10)	0.39 (0.05)	0.42 (0.12)
Na^{+} [mg/l]	4.35 (0.41)	3.98 (0.38)	5.93 (1.17)	5.88 (0.24)	5.11 (0.32)	6.29 (0.60)	3.92 (0.65)	3.86 (0.24)	4.31 (0.11)	4.59 (0.31)
Cl^{-} [mg/l]	7.50 (0.70)	4.86 (0.13)	11.51 (2.66)	11.08 (0.46)	8.98 (0.78)	9.50 (0.80)	5.18 (0.40)	5.89 (0.51)	4.51 (0.17)	6.27 (0.50)
SO_4^{2-} [mg/l]	0.15 (0.01)	0.11 (0.01)	0.43 (0.12)	0.13 (0.03)	0.19 (0.04)	0.69 (0.24)	0.75 (0.33)	0.21 (0.06)	0.06 (0.02)	0.43 (0.12)
Sea distance [km]	2.39 (0.01)	10.55 (0.02)	8.67 (0.03)	2.39 (0.01)	5.40 (0.75)	1.82 (0.08)	8.88 (0.00)	6.32 (0.01)	9.55 (0.01)	6.64 (0.70)
Sulphate deficit [mg/l]	0.92 (0.09)	0.58 (0.02)	1.21 (0.32)	1.45 (0.09)	1.08 (0.10)	0.67 (0.25)	-0.02 (0.34)	0.63 (0.12)	0.59 (0.02)	0.47 (0.12)
Sodium surplus [mg/l]	0.17 (0.10)	1.27 (0.33)	-0.48 (0.35)	-0.30 (0.19)	0.11 (0.17)	1.00 (0.25)	1.03 (0.65)	0.58 (0.14)	1.79 (0.10)	1.10 (0.19)
Total ions [meq/l]	0.55 (0.04)	0.42 (0.02)	0.80 (0.16)	0.76 (0.03)	0.64 (0.05)	0.93 (0.12)	0.50 (0.04)	0.54 (0.02)	0.63 (0.03)	0.65 (0.05)
Sum cations [meq/l]	0.32 (0.02)	0.26 (0.02)	0.42 (0.07)	0.44 (0.01)	0.37 (0.02)	0.51 (0.07)	0.29 (0.03)	0.32 (0.01)	0.38 (0.02)	0.38 (0.03)
Anion deficit [meq/l]	0.09 (0.01)	0.09 (0.02)	0.05 (0.01)	0.11 (0.01)	0.09 (0.01)	0.09 (0.05)	0.08 (0.02)	0.11 (0.01)	0.12 (0.02)	0.10 (0.01)
K [meq/l] : Na [meq/l]	0.03 (0.00)	0.04 (0.00)	0.04 (0.00)	0.04 (0.00)	0.04 (0.00)	0.04 (0.01)	0.05 (0.00)	0.08 (0.01)	0.05 (0.01)	0.05 (0.01)
Ca [meq/l] : Mg [meq/l]	0.7 (0.0)	0.6 (0.1)	1.5 (0.4)	0.8 (0.0)	0.9 (0.1)	1.2 (0.1)	1.4 (0.2)	1.6 (0.1)	1.0 (0.0)	1.3 (0.1)
Conductivity [µS/cm]	42.8 (0.6)	27.3 (1.9)	39.5 (6.7)	37.9 (1.2)	37.3 (1.8)	47.6 (4.0)	23.2 (0.5)	37.0 (2.9)	42.0 (2.2)	37.4 (2.4)
Gilvin [g_{440}/m]	13.830(0.833)	7.400 (1.166)	7.800 (0.800)	13.370 (0.420)	11.080 (0.712)	6.600 (0.872)	1.400 (0.245)	4.800 (0.800)	4.800 (1.114)	4.400 (0.573)
pH	4.24 (0.02)	4.48 (0.13)	4.24 (0.12)	4.24 (0.04)	4.29 (0.04)	5.50 (0.17)	5.54 (0.05)	5.66 (0.04)	5.69 (0.04)	5.60 (0.05)
Alkalinity [µeq/l]	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	138 (58)	53 (2)	80 (14)	176 (16)	112 (18)
Water Depth [cm]	11.8 (1.8)	13.8 (2.4)	19.2 (3.0)	10.4 (1.4)	13.3 (1.2)	70.5 (4.0)	29.8 (2.7)	32.2 (4.2)	21.6 (3.4)	38.5 (4.6)
Temperature $_{aqua}$ [°C]	15.2 (1.5)	14.0 (1.0)	13.1 (0.6)	17.8 (1.5)	15.4 (0.8)	16.2 (0.7)	10.8 (0.2)	16.3 (0.5)	14.1 (0.6)	14.3 (0.6)
TP [µg/l]	12 (3)	26 (7)	157 (52)	21 (4)	48 (15)	18 (3)	26 (4)	85 (29)	28 (4)	39 (9)
SRP [µg/l]	1 (0)	1 (0)	57 (28)	4 (2)	14 (7)	2 (0)	5 (1)	6 (2)	3 (1)	4 (1)
NO_3^{-}-N [µg/l]	1 (0)	3 (1)	5 (2)	2 (0)	3 (0)	4 (1)	2 (0)	3 (0)	4 (0)	3 (0)
NH_4^{+}-N [µg/l]	3 (0)	6 (3)	48 (30)	9 (3)	15 (7)	7 (1)	4 (0)	24 (21)	53 (31)	22 (10)
SiO_2 [mg/l]	0.43 (0.14)	0.67 (0.13)	0.96 (0.28)	0.31 (0.06)	0.55 (0.09)	5.19 (1.35)	1.84 (0.20)	1.39 (0.37)	4.89 (0.53)	3.33 (0.53)
Chl-*a* plankton [mg/m^3]	0.52 (0.22)	2.21 (1.10)	5.44 (1.24)	0.84 (0.28)	2.00 (0.51)	1.79 (0.58)	3.22 (0.80)	3.94 (1.76)	2.21 (0.47)	2.79 (0.51)
Chl-*a* epiphyton [mg/m^2]	9.68 (4.92)	10.25 (3.42)	25.91±10.22	16.78 (7.31)	15.49 (3.50)	23.44 (8.16)	5.69 (1.90)	40.33 (21.37)	72.32 (52.13)	35.45 (14.23)
Chl-*a* periphyton [mg/m^2]	0.94 (0.18)	2.95 (1.31)	8.30 (0.69)	3.22 (1.95)	3.65 (0.87)	6.42 (3.57)	1.13 (0.13)	18.05 (8.94)	14.10 (3.65)	9.93 (2.80)
Chl-*a* epipelon [mg/g]	74.02 (44.84)	153.56 (39.35)	-	101.58 (40.43)	118.64 (24.50)	-	112.37 (11.34)	-	1149.77 (214.24)	631.07 (200.31)

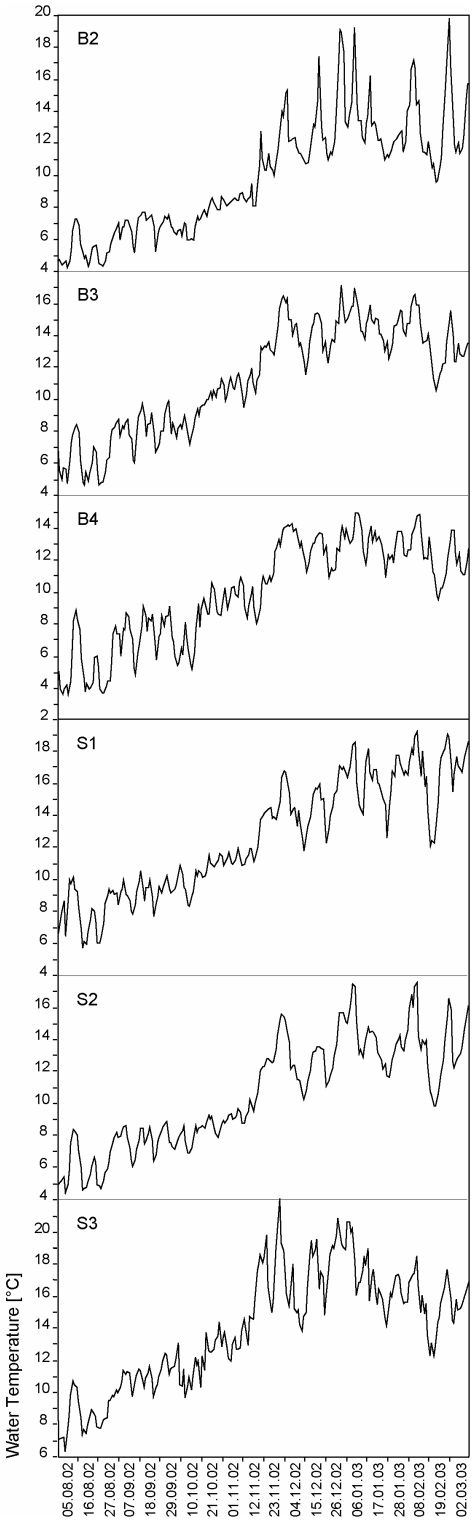

Figure 2.3. Water temperature fluctuations in bogs and swamps; each wetland type is represented by three sites. Daily means were derived from half-hourly readings over a period of six months (08.05.02-11.03.03).

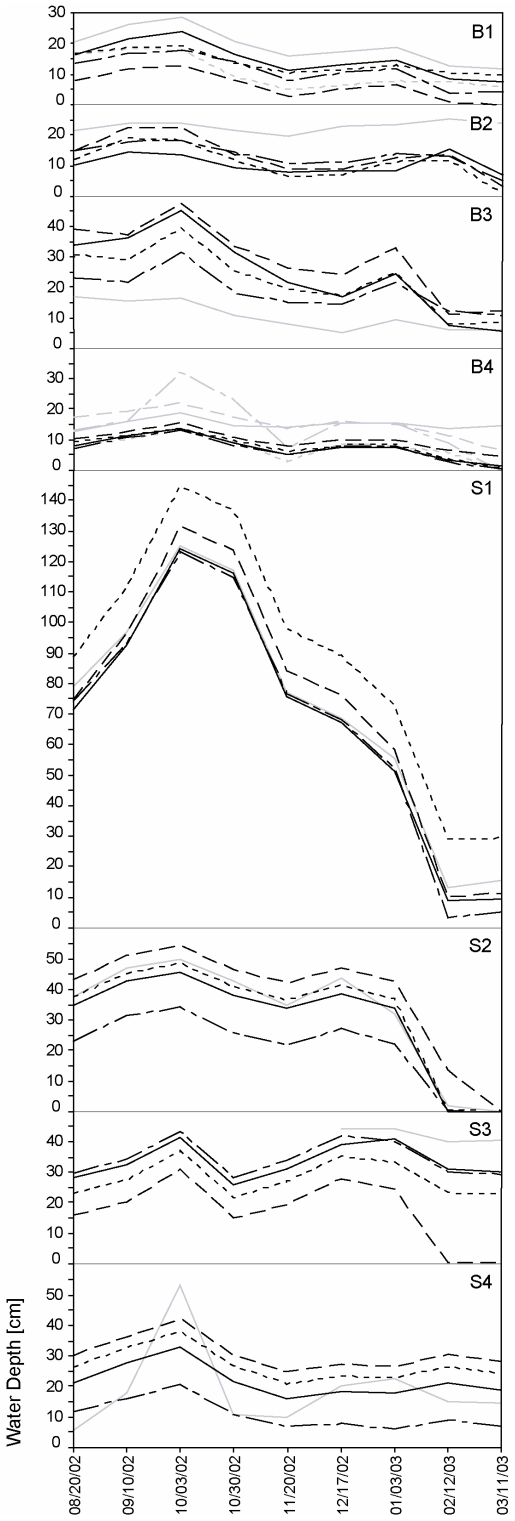

Figure 2.4. Water level fluctuations in bogs and swamps. Site signature: 1 ___ 2 _ _ 3 - - - - 4 __ . 5 ___ 6 _ _ _ 7 _ _ 8 ___ . At site S3-5 no data could be obtained until December 2002 due to destruction of equipment.

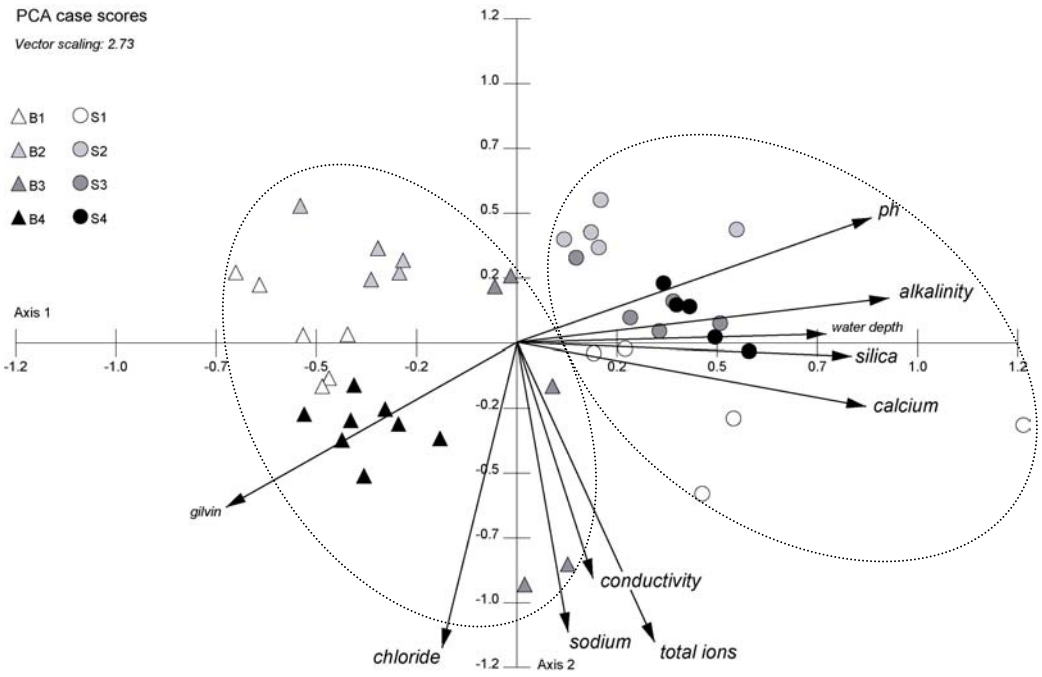

Figure 2.5. PCA ordination including bogs (△) and swamps (○). Arrows (eigenvectors > 0.25) indicate the direction of maximum change for the environmental variables.

At Tucker Flat (S3), a wetland that covers an old gold mining area, water temperatures fluctuated at a notedly higher frequency in comparison to other swamp sites.

Large differences between wetlands could be detected with respect to water level fluctuations in the period of August 2002 to March 2003 (figure 2.4). The highest variation was measured at Mahinapua Swamp, where water depth likewise fluctuated within amplitude of 130 cm at all plots, while only minor fluctuations were recorded at the bogs B1, B2 and B4. Sites B4-8 and S4-5 receive some drainage water from surrounding wetland area, therefore being characterised by more intense fluctuations compared to other plots within the same wetland. At Kumara (B3), water level fluctuations were more pronounced and resemble those measured in swamps S2 and S3.

2.4.3 Principal components analysis (PCA)

In the ordination of environmental variables including data from all wetlands (figure 2.5), 50 % of the variation is explained by the first two axes. PC axis 1 differentiates between wetland types, accounting for 30 % of the variance in the data. The most important environmental variables in the delineation of wetland classes were alkalinity, pH, calcium, and silica concentrations. These variables proved to be consistently higher in the swamps ($p \leq 0.001$). In contrast, the bogs are characterised by significantly higher humic matter concentrations as indicated by gilvin absorbance coefficients ($p \leq 0.001$). PC axis 2

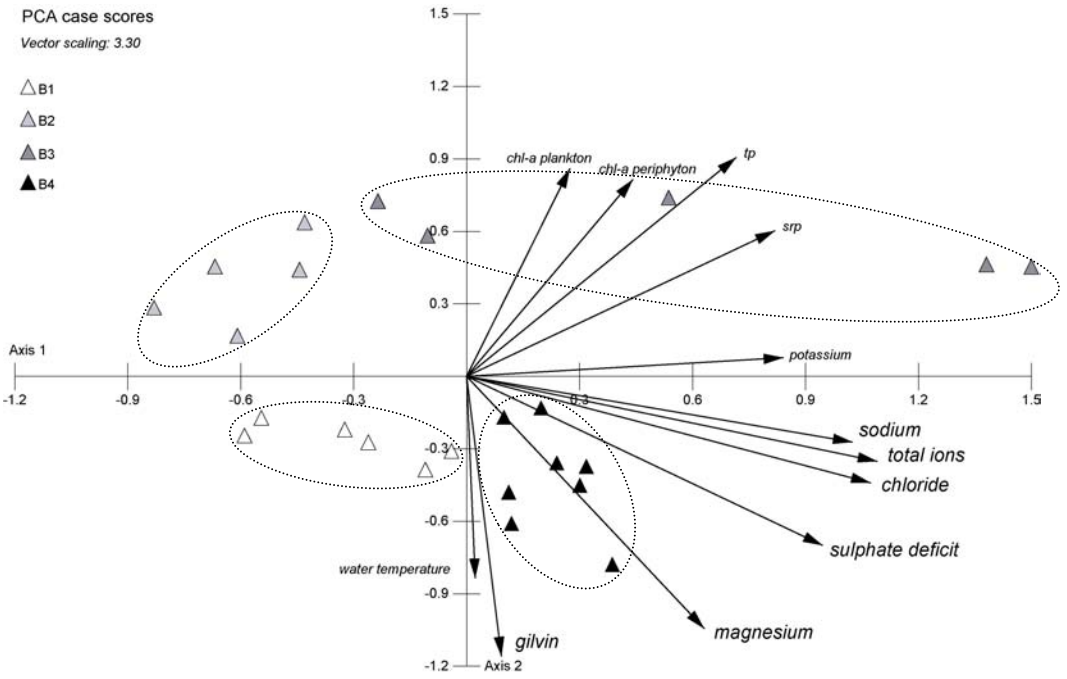

Figure 2.6. PCA ordination of bog sites. Arrows (eigenvectors > 0.25) indicate the direction of maximum change for the environmental variables; chl-*a* periphyton refers to benthic algae on artificial substrata.

explains 20 % of the variance in the data, representing a gradient in the supply of ions and nutrients by either rainfall or surface and groundwater. Sites are arranged according to sodium and chloride concentrations in conjunction with the total sum of ions and corrected conductivity values.

Important environmental variables separating the bogs along PC axis 1 are sodium and chloride concentrations, which constitute the majority of ions in these ecosystems, as well as sulphate deficit along PC axis 1. Gilvin and magnesium concentrations separate the bog sites along PC axis 2 (figure 2.6). The variation in the data explained by the first two ordination axes is 34 % and 23 % respectively. Wetlands B1 and B4 are strongly coloured, the gilvin absorption coefficients (g_{440}) indicating high organic matter content in the bog water (cp. table 2.1). In contrast, wetlands B2 and B3 are characterized by lower amounts of humic matter ($p \leq 0.01$), which are accompanied by low magnesium content. The lowest sodium and chloride concentrations and minor sulphate deficits were measured at the bog B2, followed by wetlands B1 and B4. While these bogs form homogenous groups of samples, B3 sites span a wide gradient across PC axis 1. This wetland is characterized by intensive algal primary production and high amounts of TP and SRP compared to the other ombrotrophic wetlands.

In the ordination of swamps, the percentage of the variation explained by the first two PC axes adds up to 54 % (figure 2.7). PC axis 1 accounts for 34 % of the variation in the

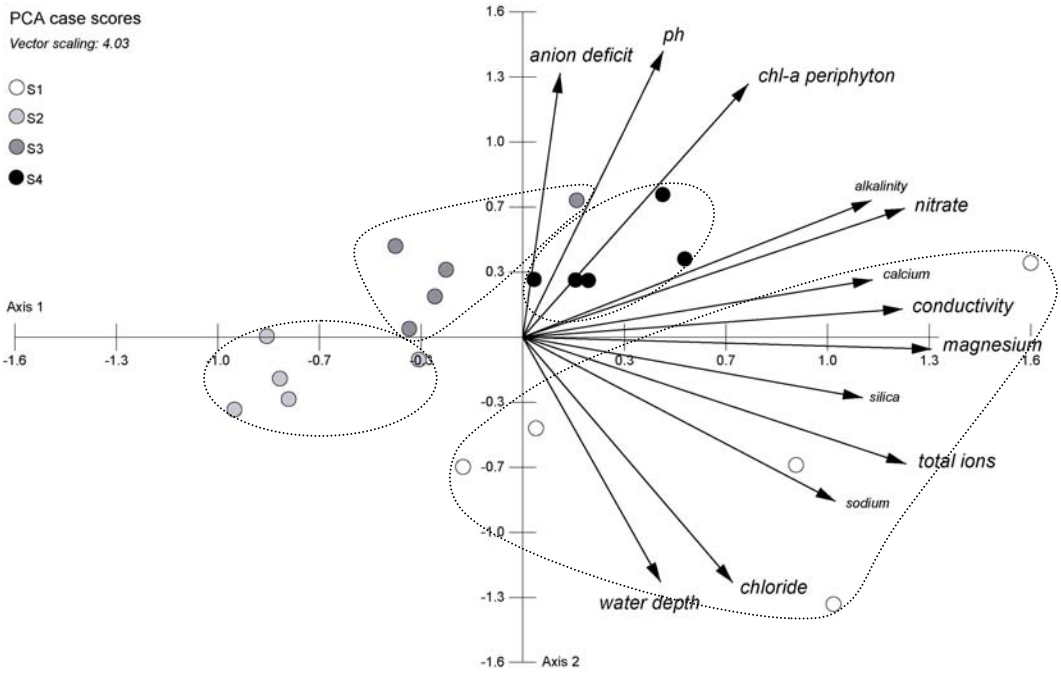

Fig. 2.7. PCA ordination of swamp sites. Arrows (eigenvectors > 0.25) indicate the direction of maximum change for the environmental variables; chl-*a* periphyton refers to benthic algae on artificial substrata.

data, representing a gradient in ion and nutrient availability. Positively correlated with this axis are magnesium and nitrate concentrations, the total sum of ions and corrected conductivity. The highest values for these parameters were found in wetland S1, whereas S2 gave the lowest readings (cp. table 2.1). PC axis 2, which is associated with anion deficit, pH, periphyton (as) biomass, chloride, and water depth, explains 20 % of the variation in the distribution of samples. S1 depicts the lower end of the gradient along PC axis 2, exhibiting a high degree of within wetland variation. Wetlands S3 and S4 are shallow and feature small amounts of chloride in contrast to a large anion deficit and high biomass and pH values, whereas wetland S2 takes in an intermediate position.

2.4.5 Analysis of similarities (ANOSIM)

The analysis of similarities (ANOSIM) affirms that the differences between wetland types, as illustrated by principal components analysis, are significant (R = 0.604, $p \leq 0.05$). Based on the (rank) similarity matrix underlying the ordination of samples (Clarke and Warwick 2001), this non-parametric permutation procedure (Monte Carlo tests, Hope 1968) accounts for the variability between wetlands grouped *a priori* to the respective wetland classes.

The one-way ANOSIM test (table 2.2) shows that swamps and bogs are generally well separated ($R \geq 0.7$; $p \leq 0.05$), although B3 occupies an intermediate position. The largest

differences within the swamp wetland class occur between S2 and S4 ($R = 0.8$; $p \leq 0.05$). The remaining combinations within the swamp type show that the environmental characteristics of these wetlands overlap to a larger degree ($R \leq 0.5$; $p \leq 0.05$). Bogs also constitute a heterogeneous group of wetlands, where sites at B1 and B4 ($R = 0.4$; $p \leq 0.05$) share a substantial band of common features and form a cluster which is distinctly separated from bogs B2 and B3 ($R > 0.7$; $p \leq 0.05$).

2.5 Discussion

2.5.1 Delineation of wetland types

A large variety of studies suggest environmental parameters that can be implemented within the framework of wetland delineation (e.g. Scott and Jones 1995, Zogg and Barnes 1995, Masing et al. 2000, Wheeler and Proctor 2000). However, it is questionable if these variables can be superimposed unmodified on wetlands that occur in different regions of the world. Therefore, the environmental variables that differentiate between wetland classes in the south-western lowlands of New Zealand are discussed with respect to internationally applied criteria.

2.5.1.1 Acidity and alkalinity

A pH of less than 4.0 is commonly assumed to indicate ombrotrophic conditions in mires (Lötschert and Gies 1973, Verhoeven 1986, Andreas and Bryan 1990, McQueen and Bastow 2000, Walker et al. 2001), but this does not necessarily apply to oceanic bogs. Bellamy and Bellamy (1966) and Daniels (1978) demonstrated that there is a marked decrease in the pH of ombrotrophic peatlands from coastal to continental areas. In oceanic bogs studied by Vitt et al. (1990), pH has been shown to vary from 4.1 to 4.8, which is less acidic than typically observed in continental regions of North America (Glaser et al. 1981, Andreas and Bryan 1990). Hence, the pH measured in New Zealand lowland bogs is characteristic of ombrotrophic oceanic wetlands. Alkalinity equalled zero, which is also typical for wetlands that depend on ion supply by rainwater (Andreas and Bryan 1990, van Dam and Buskens 1993, Vitt et al. 1995). Indirect effects of precipitation on pH (Table 3) may be due to adsorption and cation exchange on peat and peat forming plants (Newbould and Gorham 1956, Gorham and Cragg 1960, Sparling 1966, Brehm 1971, Clymo 1984, Göttlich 1990, Agnew et al. 1993). Anion deficit, gilvin absorbance, and pH were not significantly correlated (q.v. Ramaut 1955, Kilham 1982, Clymo 1984, McKnight et al. 1985, Gorham et al. 1985), which indicates that organic acids have only a marginal effect on hydrogen ion concentration in the studied bogs.
The average pH of 5.5 to 5.7 measured in New Zealand lowland swamps clearly separates this group of wetlands from the bog wetland class. However, the pH is low in comparison with other minerotrophic mires (c.p. Toetz 1995, Zogg and Barnes 1995) and can be

Table 2.2. Test statistics (*R*-values) for the one-way ANOSIM between wetlands (min 126, max 999 permutations). 2-sided significance level (after bonferroni correction): $p \leq 0.05$

	Bogs			Swamps			
	B2	B3	B4	S1	S2	S3	S4
B1	0.747	0.789	0.357	0.728	0.976	0.981	1.000
B2		0.640	0.988	0.772	0.776	0.952	1.000
B3			0.788	0.512	0.516	0.424	0.700
B4				0.811	0.995	0.982	1.000
S1					0.516	0.420	0.540
S2						0.540	0.780
S3							0.496

Table 2.3. Linear Pearson correlation coefficients for selected pairs of environmental variables; 2-sided significance level (after bonferroni correction): $p \leq 0.05$.

	Bogs	Swamps
TP – SRP	0.790	ns
TP – K^+	0.695	ns
TP – Chl-*a* plankton	0.694	ns
TP – Chl-*a* periphyton (as)	0.635	ns
NO_3^--N – Chl-*a* epipelon	ns	0.928
NO_3^--N – Chl-*a* periphyton (as)	0.593	0.741
NO_3^--N – Alkalinity	ns	0.814
NH_4^+-N – SO_4^{2-}	0.714	ns
SiO_2 – Chl-*a* epipelon	ns	0.872
SiO_2 – Alkalinity	ns	0.751
SiO_2 – Mg^{2+}	ns	0.824
Chl-*a* periphyton (as) – Chl-*a* plankton	0.572	ns
Chl-*a* periphyton (as) – Chl-*a* epiphyton	ns	0.771
Chl-*a* periphyton (as) – Chl-*a* epipelon	ns	0.939
Chl-*a* epipelon – Water temperature	ns	0.884
Ca^{2+} – Mg^{2+}	0.643	0.796
Ca^{2+} – Alkalinity	ns	0.770
Ca^{2+} – Cl^-	0.655	ns
Na^+ – Cl^-	0.920	0.762
Na^+ – K^+	0.771	ns
Na^+ – Total ions	0.960	0.912
Na^+ – SO_4^{2-}-deficit	0.874	ns
Mg^{2+} – Alkalinity	ns	0.847
Mg^{2+} – Na^+	0.663	0.704
Mg^{2+} – Gilvin	0.581	ns
Conductivity – Gilvin	ns	0.618
Conductivity – SO_4^{2-}-deficit	0.704	ns
Conductivity – Cl^-	0.701	ns
Conductivity – Alkalinity	ns	0.691
Conductivity – Chl-*a* epipelon	ns	0.896
pH – Alkalinity	ns	0.629
pH – Anion deficit	ns	0.807
pH – Total ions	-0.626	ns

attributed to the poor buffering capacity of the water, which corresponds to alkalinity values reported for other wetlands of this type (Zogg and Barnes 1995, Muñoz et al. 2003). Even though the correlation between anion deficit and pH ($r = 0.807$; $p < 0.01$) is evidence of the role that bicarbonate has in the regulation of acidity in the studied swamps, the low calcium levels and abundant rain on the West Coast also contribute to the low pH. In the south-western lowlands, a few kilometers north of our study area, a pH of 5.0 to 5.9 has been measured in rainwater (Verhoeven et al. 1987). Nichol et al. (1997) and Kieber et al. (2002) report even lower precipitation pH values for other coastal sites in New Zealand.

2.5.1.2 Calcium

Calcium concentrations higher than 2 mg/l are commonly considered to be characteristic of minerotrophic wetlands (Gorham and Pearsall 1956, Vitt and Slack 1975, Glaser et al. 1981, Glaser 1983, Eurola and Holappa 1985). Among the studied swamps, only Mahinapua Swamp featured a higher average calcium concentration, although all sites are connected to minerotrophic water sources. This discrepancy between the expected and the measured amount of calcium might be due to the limited base content of bedrock in the surrounding area (Mew 1980, Gray and Murphy 2002) and dilution of surface and pool water by the high precipitation. In this context, Bragazza and Gerdol (1999) demonstrated that calcium concentrations in mire waters were distinctly lower under wet conditions.
Calcium concentrations of less than 1 mg/l are regarded as indication of ombrotrophic conditions (Damman 1986, Pfadenhauer 1997, Muñoz et al. 2003), therefore the ombrotrophic bogs studied can be separated from calcium poor swamps. As opposed to minerotrophic wetlands, calcium in ombrotrophic wetland ecosystems is solely introduced by precipitation and percolating water. The calcium oxide fraction in weakly mineralized peat amounts to a mere 2 % (Göttlich 1990) and Ca^{2+} is not easily leached. In contrast to other alkali ions, this element is preferably bound to peat colloids and cation exchange sites on peat building plant species like *Sphagnum* spp. and *Empodisma* spp. (Clymo 1963, Brehm 1970, 1975, Boatman et al. 1975, Damman 1978, 1986, Breuer and Melzer 1990, Vitt et al. 1995). The average calcium concentrations in lowland bogs at the New Zealand West Coast concordantly are low, varying between 0.26 mg/l and 0.97 mg/l, a range that is comparable to results reported by Dickinson et al. (2002) for New Zealand patterned mires. Calcium complexation by humic and fulvic acids might also occur in the bogs we studied. However, complex formation has been shown to decline with decreasing pH (Ouatmane et al. 1999) and calcium concentrations are not likely affected by this process to a large extent.

2.5.1.3 Silica

The silica content measured in the studied swamps is comparable to that observed in shallow temperate lakes (e.g. Gibson 1986, 1988, Bennion and Smith 2000). In agreement with Gorham et al. (1985), SiO_2 concentrations were consistently higher in minerotrophic wetlands where silicon is supplied along with other nutrients by groundwater and surface runoff (table 2.3). The geologic subsurface in the study area comprises highly siliceous minerals, the majority of them containing more than 62 % silica (Gray and Murphy 2002). Hence, the amount of silica measured in New Zealand swamps is higher than silica concentrations observed by Muñoz et al. (2003), who investigated an alpine mire complex overlying gneiss and granodiorite bedrock. Silty peat, the predominating substrate in the studied minerotrophic wetlands, encloses up to 45 % SiO_2 (Göttlich 1990) and can also be a significant silicon source.
In contrast, the chemical analysis of peat samples from a raised bog revealed that silica accounts for only 10 % of the enclosed mineral components (Göttlich 1990). Accordingly, the average silica concentrations in New Zealand ombrotrophic bogs are low, ranging from 0.31 mg/l to 0.96 mg/l. Contribution of silica through silicon release from the sediment is expected to be marginal, since dissolution of diatom frustules subsides with decreasing pH (Bailey-Watts 1976).

2.5.1.4 Water colour

Ombrotrophic wetlands are generally characterized by low decomposition rates and peat accumulation, the surface and pool water being highly coloured by large amounts of dissolved humic substances. This could also be observed in ombrotrophic wetlands in the Hokitika Ecological District, which feature gilvin absorbance coefficients (g_{440}) between 7.392 and 13.767. In comparison with the studied lowland bogs, New Zealand low-alpine patterned mires contain less humic matter (Dickinson et al. 2002). Overall, water colour in the coastal bogs studied in south-western New Zealand appears to be higher than commonly reported for wetlands in the northern hemisphere (cp. Glaser et al. 1981, Muñoz et al. 2003). Only Klavins et al. (2003) found equally large amounts of humic substance for some bog lakes in Latvia.
The range of yellow substance in lowland swamps on the West Coast varies between g_{440} 1.492 and g_{440} 6.593, which coincides with values found in other New Zealand wetlands (Mark Schallenberg, NIWA, unpublished data). Fallu et al. (2002) reported similar colour values for lakes in a wetland forest. Our results are also in line with the observations of Glaser et al. (1981) and Muñoz et al. (2003), who found that highly acidic bogs are more intensely coloured than wetlands with only slightly acidic pH.

2.5.2 Variability within wetland types

Water chemistry may vary within a wetland, largely arising from the pattern of water flow. As water passes through peat, it is filtered and depleted in minerals. Variation between sampling sites will, therefore, decrease with primary ion levels in the water (Karlin and Bliss 1984, Bennion and Smith 2000). Damman (1986) presumes that lateral water movement through the acrotelm is the most important process in the relocation and removal of elements in wetlands. In minerotrophic wetland ecosystems with a large catchment, there may be a variety of water sources that influence hydrochemical characteristics and algal biomass, e.g. groundwater, stream overflow, drainage water, and surface runoff.

Variation in water chemistry and algal primary production was generally low within the investigated bogs and swamps (figures 2.6 and 2.7), even though a wide variety of habitats was sampled in each wetland. Exceptions are the bog at Kumara (B3) and Mahinapua Swamp (S1). The latter is a large wetland that is partly connected to Mahinapua Creek and fed by two of its tributaries, Cowan Creek and Sandstone Creek. The north-western margin of the swamp is surrounded by deer farming land. In a narrow section, cattle have direct access to the riparian zone. As sampling sites are distributed across all subdivisions of this wetland, the large variability of environmental parameters most likely indicates discontinuity of the hydrologic system associated with an apparent nutrient gradient. In contrast, the bog sites at Kumara do not exhibit any obvious differences with regard to nutrient supply. However, the two outliers in the PCA ordination (figure 2.6) represent samples from a temporarily flowing channel and an adjacent pool, which might receive some minerotrophic inflow.

2.5.3 Algal primary production in bogs

In the bogs studied, algal primary production largely depends on nutrient supply by rain and lateral water flow. Nitrate concentrations in the pool water were near or below the detection limit at most sites and might restrict algal growth as indicated by positive correlations with plankton and periphyton (as) biomass (cp. table 2.3). While epipelon and epiphyton communities can exploit nutrients from both the overlying water and the substrate, phytoplankton and periphyton on hard and chemically inert surfaces only have direct access to nutrients in the water column. This might explain why neither epipelon nor epiphyton chlorophyll-*a* concentrations are correlated to plankton and periphyton (as) biomass, even though the trend across sites is strikingly uniform for all biomass estimates (cp. Björk-Ramberg and Ånell 1985, Vadeboncoeur and Logde 2000). In fact, plankton chlorophyll-*a* measurements might not reflect a taxonomically distinct phytoplankton community, but represent a dilute suspension of benthic algae (*tychoplankton*, Round 1985). Similarly, much of what has been assumed phytoplankton in a large freshwater

wetland bordering Lake Manitoba was derived from the detachment and suspension of benthic forms (Ganf 1973, in Goldsborough and Robinson 1996). Accordingly, wind-induced resuspension of sedimentary particulate phosphorus has been shown to frequently occur in shallow water bodies (Bennion and Smith 2000, Søndergaard et al. 2003), especially at low submerged macrophyte densities. These conditions are met in the bog pools, and correspondingly, TP levels are high in comparison to the studied swamps. Positive correlations between total phosphorus, plankton biomass and periphyton (as) chlorophyll-*a* concentrations further support the assumption that benthic microorganisms get dispersed by wind-induced mixing.

The availability of nutrients for algal primary production is also controlled by microbial metabolism and decomposition processes. Sulphur metabolising bacteria are known to be active in the anaerobic zone of bogs (Benda 1957, Burgeff 1961, Clymo 1965, 1984, Dodds 2003), where sulphate is reduced to H_2S and sulphide. Gorham et al. (1985) describe that in many oceanic bog sites, especially those most affected by seaspray, excess sulphate was a distinctly negative quantity. The authors conclude that, where sulphate supply is high, sulphate reducing bacteria may be unusually active and lower the concentration of sulphate below that expected from sea spray. This has also been observed in ombrotrophic bogs at the superhumid south-western coast of New Zealand, where sulphate deficit is strongly correlated with sodium supply (cp. table 2.3). The assumption that algae and bacteria compete for nutrients is further supported by Holmer and Storkholm (2001), who state that desulphurication and sulphur cycling may become a relevant part of sediment processes if nitrate concentrations are low but supply of biodegradable organic matter and sulphate levels are sufficient. Dodds (2003) proposed that microorganisms might also indirectly affect the release of phosphorus from sediment by reducing sulphate to sulphide, which competes with phosphate for metal binding places. In this study, however, neither such relationship nor any correlation between the concentrations of phosphorus and humic matter, which is known to form chelat complexes with metal ions (Outmane et al. 1999), could be detected.

2.5.4 Algal primary production in swamps

Plankton biomass in New Zealand lowland swamps is similar to chlorophyll-*a* concentrations determined in other minerotrophic wetlands (e.g. Lougheed et al. 2001, Munoz et al. 2003). McNair and Chow-Fraser (2003) demonstrated that plankton chlorophyll-*a* concentrations within the observed range of 1.8 mg/m^3 to 3.9 mg/m^3 are characteristic of largely undisturbed, pristine wetlands. Periphyton (as) and epiphyton biomass are also within the range of unimpaired minerotrophic wetland ecosystems (Goldsborough and Robinson 1996, McNair and Chow-Fraser 2003). Strong positive correlations between chlorophyll-*a* concentrations, corrected conductivity, alkalinity, nitrate and ammonium (table 2.3) imply that epipelic algae in particular benefit from

nutrients supplied by groundwater infiltrating the sediment. Net removal of nutrients into a photosynthetically active epipelic biofilm has also been observed by Woodruff et al. (1999) and Bartoli et al. (2003). Lorenzen et al. (1998) investigated the influence of microphytobenthos on sediment-water fluxes, documenting high rates of nitrification and tight coupling between nitrification and denitrification, as well as substantial rates of nitrate assimilation by freshwater epipelic diatoms. Positive correlations between temperature, nitrate and epipelic biomass (cp. Søndergaard et al. 2003) might also indicate an increased turnover of nitrogen by stimulation of coupled nitrification-denitrification in the sediment as reported by van Luijn et al. (1995). Nitrogen generally appears to be the limiting factor for benthic algae in the studied swamps (cp. table 2.3), though the apparent trend could not be verified on a significance level of $p \leq 0.05$ for epiphyton communities. Deviations in this case might be due to nutrient release by certain macrophyte species, as discussed earlier, or slight variation in benthic community composition.

In contrast to bogs, where tychoplankton likely accounted for chlorophyll-*a* measured in the water column, a distinct phytoplankton community developed in swamps. Differences in the relative proportions of plankton and benthic biomass indicate a different taxonomic composition of the phytoplankton, which is supposedly limited by phosphorus rather than nitrogen. It is also apparent that, where benthic biomass is low, phytoplankton biomass is high and vice versa (figure 2.2b). This indicates direct competition between planktonic algae and the benthic biofilm, which might deplete soluble reactive phosphorus in the water column to concentrations at or near the detection limit. On the other hand, phytobenthos might be constrained by decreased light availability at higher plankton densities. There is no evidence however, that humic matter concentrations had an effect on benthic primary production. Deviations between the relative proportions of phytoplankton and phytobenthos biomass could also result from different grazing pressure (Goldsborough and Robinson 1996).

2.5.5 Representativeness of biomass estimates from artificial substrata

Periphyton grown on artificial substrata allow for the standardisation of both time and substrate characteristics, reducing the variation found in epiphyton, epipelon and phytoplankton samples and thus providing more accurate site-to-site comparisons. Even though epiphyton samples are more representative of the natural benthic algal community, many unquantified factors such as successional stage, senescence, or seasonal internal community changes influence biomass estimates. Epiphyton samples require more processing time at collection, and chlorophyll-*a* measurements may be confounded by incomplete removal of algae from the vascular plant material. In addition, estimating surface area of submergent plants is difficult and subject to greater measurement error in comparison with artificial substrata. In agreement with McNair and

Chow-Fraser (2003), periphyton grown on inert synthetic material provided the most precise data and the relative proportions of microphytobenthos on natural substrates were well represented in all wetlands. However, a crucial factor in the use of artificial substrata is the specification of an appropriate exposure time. Biomass measurements on artificial substrata often underestimate biomass development on natural substrates (Aloi 1990, Toetz 1995), and even though the polyethylene slides were exposed for twelve weeks in the course of this study, chlorophyll-*a* concentrations in periphyton (as) communities were significantly lower than epiphytic biomass estimates. It is concluded that periphyton grown on artificial substrata allows for comparison of algal biomass between wetlands, but is not suitable for the specification of absolute chlorophyll-*a* concentrations.

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3 Benthic diatom diversity in New Zealand lowland wetlands

3.1 Abstract

Diversity of microphytobenthos in New Zealand lowland wetlands has been poorly studied in the past. To quantify benthic diatom diversity in ombrotrophic and minerotrophic wetland ecosystems, epiphyton, epipelon and periphyton grown on polyethylene slides were sampled from a range of bog and swamp habitats. Community composition was analysed with respect to dominance structure, relative abundance, redundancy patterns, and taxonomic hierarchy. In addition, commonly applied diversity indices and univariate measures of taxonomic distances were evaluated with respect to their performance. Patterns in diatom diversity were linked and interpreted with reference to abiotic environmental conditions.

Between diatom communities from different substrates, no significant differences were observed in any aspect of community structure. At higher spatial scales, bog and swamp diatom communities exhibited slightly different dominance patterns, being characterised by a distinct species composition. Significant differences in the taxonomic composition between wetlands and wetland types were also obtained at the genus level. Among the measured environmental variables, pH, alkalinity, calcium, and silica explained most of the variability in diatom data comprising both wetland types. Bog diatom communities were distributed along a gradient related to ion supply, while diatom community composition in swamps was related to benthic primary production, silica concentrations, and alkalinity. Environmental conditions in swamps were be inferred from predominance of *Chamaepinnularia soehrensis* var. *soehrensis*, *Eunotia incisa*, *Encyonema neogracile*, *Fragilaria construens* f. *venter*, *Navicula heimansioides*, *Nitzschia gracilis*, and *Tabellaria flocculosa*. In contrast, *Eunotia paludosa* var. *paludosa*, *Eunotia paludosa* var. *trinarcria*, *Frustulia saxonica morphotype II*, *Naviculadicta parasubtilissima*, and *Naviculadicta subtilissima* constitute a bog indicator group, referring to highly acidic, and ombrotrophic conditions. Furthermore, transfer functions were developed for pH, alkalinity, gilvin, and silica. Diversity indices differentiated between wetlands and wetland types indicating significantly higher values in swamps, yet species richness and taxonomic diversity indices were most distinctive. In terms of biodiversity conservation, both wetland types are valuable freshwater habitats that exhibit a range of unique features.

3.2 Introduction

Since New Zealand was first settled, its unique biodiversity has been in retreat, from the destruction of habitat, harvest by humans, and successive waves of pests, weeds and diseases. Extinctions have been rapid and the threats to biodiversity have continued unabated for several decades. In recent years, the New Zealand government and

population have become conscious about the values inherited by its indigenous fauna and flora, and a range of research programmes dealing with biodiversity issues were initiated (Ministry of the Environment 1997, Department of Conservation 2000). However, at the scale of microorganisms very little is known as yet, though bacteria and algae constitute essential components in terrestrial, marine and freshwater habitats (World Conservation Monitoring Centre 1998).

The overall aim of this study is to analyse the distribution and diversity of freshwater algal species inhabiting unmodified lowland wetlands in New Zealand and to interpret their habitat requirements with respect to wetland management and conservation policies. To date no comprehensive data exist in this field, even though wetlands represent some of New Zealand's most diverse but most threatened ecosystems. Swamps, bogs and marshes now extend over approximately 1000 square kilometres, but more than 90 % of the original area covered by wetland systems has been lost. Remaining wetlands are often degraded by weed invasions, stock access, and modifications to hydrological regimes. It is also likely that, in the last 100 years, some characteristic New Zealand wetland types have been lost completely, while very few examples are left of others, such as kahikatea (*Dacrycarpus dacrydioides*) swamp forest and some kinds of flax (*Phormium tenax*) swamp and salt marsh (Cromarty and Scott 1996).

Among benthic algae, which are fundamental primary producers in shallow freshwater systems (Allen 1971, Sheldon and Boylen 1975, Cattaneo and Kalff 1980, Stevenson et al. 1996), diatoms often constitute the dominant life-forms in epiphyton, periphyton (as) and epipelon. Benthic diatom communities therefore represent significant elements in biodiversity and ecosystem research, and, in combination with their excellent bio-indicative attributes and the well-developed and revised taxonomic system, they form ideal study objects.

3.3 Material and Methods

3.3.1 Sample collection and sample processing

Benthic diatom samples were collected in December 2002 and March 2003 from all sites and stored at -20 °C in the dark before processing at the NIWA Christchurch laboratory. In addition to periphyton grown on polyethylene slides, epipelon and epiphyton samples were collected if available. Primarily, macrophytes that were common in either wetland type were sampled to ensure sufficient replication across sites. Wherever possible, plant fragments of a variety of macrophyte forms such as rushes, aquatic bryophytes, and other hydrophytes were gathered to assess potential morphological impacts on epiphyton communities. Taxa such as *Juncus* spp. and *Carex* spp. were summarized in the family *Cyperaceae*. A list of substrates taken at the studied wetlands is given in table 3.1 (for a more detailed chart see Appendix, Part B); sampled plant specimens were also catalogued

in a herbarium (IDs NZ-01/01 to NZ-15/01), which is held at the collection of the Limnological Station Iffeldorf (Technical University of Munich). Epipelon samples generally comprised the upper 0-3 cm layer of the sediment.

To separate the diatom valves and to eliminate any organic residuals that might interfere with microscopic identification of the frustules, plant fragments, polyethylene slides and sediment samples were oxidised using concentrated sulphuric acid and hydrogen peroxide according to the method described in Biggs and Kilroy (2000). Cleaned diatom subsamples were dried onto cover slips and subsequently embedded in Naphrax® on pre-cleaned microscope slides for further examination under the light microscope. For scanning electron microscopy (SEM), dried diatom material on Millipore filters was mounted on aluminium stubs and sputtered with gold (Au).

Table 3.1. List of macrophytes and sediment sampled in each wetland; * bryophytes other than *Sphagnum* spp.

	B1	B2	B3	B4	S1	S2	S3	S4
Macrophytes								
Aponogeton distachyus					✓			
Callitriche petriei							✓	
Cyperaceae	✓	✓	✓	✓	✓	✓	✓	✓
*Bryophyta**			✓					
Gratiola sexdentata						✓		
Ludwigia palustris					✓		✓	
Myriophyllum propinquum					✓		✓	✓
Nitella hookeri					✓			
Phormium tenax					✓	✓		
Potamogeton suboblongus						✓		
Sphagnum cristatum	✓	✓	✓	✓	✓			
Typha orientalis								✓
Sediment	✓	✓	✓	✓		✓		✓

3.3.2 Light Microscopy (LM) and Scanning Electron Microscopy (SEM)

At least 400 to 450 diatom valves were counted in random transects in each sample and identified at 1000x magnification, using a Leica DMRBE microscope. According to Lund et al. (1958), statistical bias in the counts does not exceed 10 % in this range. If S_i is the number of individuals of the *i*th taxon and S_n is the total number of individuals counted in the sample, the abundance of each taxon N_i is calculated as:

$$N_i = \frac{S_i}{S_n} \qquad \text{(equation 3.1)}$$

Photographic documentation of the dominant and subdominant taxa was carried out at 100x magnification (objective 100x/1.3 oil immersion) and inferential contrast, using a Kappa DX 20 H-FW digital camera attachment and the corresponding software Kappa Image Base v.2.7.2. Identification and nomenclature followed Cassie (1984, 1989), Cholnoky (1957, 1959), Edlund and Brant (1997), Foged (1978, 1979), Kilroy et al. (2003), Krammer (1992, 1997a,b, 2000, 2002, 2003), Krammer and Lange-Bertalot (1986, 1988, 1991a,b), Lange-Bertalot (1993, 2001), Lange-Beratlot and Krammer (1989), Lange-Bertalot and Metzeltin (1996), Lange-Bertalot and Moser (1994), Lange-Bertalot and Sterrenburg (2004), Lange-Bertalot et. al. (1996), Metzeltin and Lange-Bertalot (1998, 2002), Moser (1998, 1999), Moser et al. (1995), Reichhardt (1997, 1999), Reichhardt and Lange-Bertalot (1991), Rumrich et al. (2000), Sabbe et al. (2001), van de Vijver et al. (2002), Vyverman (1991), Vyverman et al. (1995, 1998), and Wydrzycka and Lange-Bertalot (2001). Critical diatom taxa were cross-checked and documented with a Hitachi S-4500 Scanning Electron Microscope (SEM) at the Botanical Institute of the Johann Wolfgang Goethe Universität, Frankfurt am Main, in collaboration with Prof. Dr. Horst Lange-Bertalot and Manfred Ruppel.

3.3.3 Numerical methods

3.3.3.1 Distributional techniques

A range of distributional techniques, also termed graphical or curvilinear plots, were used to summarise the set of species counts for a single sample by a curve or histogram. The purpose of graphical distributional representations is to extract information on patterns of relative species abundances without reducing that information to a single summary statistic, such as a diversity index.

Geographic abundance plots were used as a measure of community stress at the site level and to assess differences in benthic community structure on different macrophyte hosts. Species were combined in geometric abundance classes, i.e. the number of species represented by only 1 individual in the sample (class 1), 2-3 individuals (class 2), 4-7 individuals (class 3), 8-15 individuals (class 4) etc. are illustrated in the graphs (cp. Gray and Pearson 1982). If the biotic communities are not disturbed or impacted, it is assumed that there are many rare species, and the geometric abundance curve will be smooth with its mode well to the left (Clarke and Warwick 2001). On the other hand, if there is any impact or disturbance, fewer rare and more abundant species are expected, so the higher geometric abundance classes are more strongly represented, and the curve may become irregular or jagged.

k-dominance curves are cumulative ranked abundances plotted against species rank (Lambshead et al. 1983), the species being ranked in decreasing order of abundance. Therefore, the most elevated curve will have the lowest diversity.

3.3.3.2 Multidimensional Scaling (MDS)

Differences in the taxonomic composition of the studied benthic diatom communities were analysed and illustrated by non-parametric *Multidimensional Scaling* (MDS). The main advantage of this method as opposed to other ordination techniques is thought to be its greater ability to represent more complex relations accurately in low-dimensional space, and, as a non-parametric approach, it has few assumptions about the nature and quality of the data (Clarke and Warwick 2001). This is important with respect to the analysis of biotic communities, as multivariate species data commonly do not meet the requirements of parametric statistical test. Furthermore, MDS does not demand deletion of rare taxa, thus all information available in the species data is used in the analysis.
Multidimensional Scaling operates with an non-parametric algorithm, which constructs a 2-dimensional ordination plot by successively refining the positions of sample points until they satisfy, as closely as possible, the dissimilarity relations between samples. The relative distances apart of all points in the MDS graph are in the same rank order as the relative dissimilarities of the samples, which are calculated as Bray-Curtis coefficients (cp. equation 3.6). It follows that points that are close together represent samples very similar in species composition, while points that are far apart correspond to very different communities. Stress values that are shown in the MDS plots serve as an indicator of the quality of the presented information and are defined by the following goodness-of-fit measure of the regression:

$$Stress = \sqrt{\sum_j \sum_k \left(d_{jk} - \hat{d}_{jk}\right)^2 \Big/ \sum_j \sum_k d_{jk}^2} \qquad \text{(equation 3.2)}$$

where $\hat{d}_{jk}$ is the distance predicted from the fitted regression line corresponding to dissimilarity δ_{jk}. If $d_{jk} = \hat{d}_{jk}$ for all of the *n(n-1)/2* distances in this summation, the stress is zero. Large scatter leads to large stress, which can be interpreted as a measure of the difficulty involved in compressing the sample relationships into two dimensions. To avoid the iterative process getting trapped in a local stress minimum, the MDS was repeated 30 times to get as close as possible to the global minimum of the stress function, starting with different random positions of samples in the original configuration. Clarke and Warwick (2001) specify that stress < 0.1 corresponds to a good ordination with no real prospect of a misleading interpretation, while stress < 0.2 still holds a potentially useful 2-dimensional picture. However, for values at the upper end of this range, too much reliance should not be placed on detail of the plot. A cross-check of any conclusions derived from MDS against those from an alternative technique is recommended (Clarke and Warwick 2001), which in this study is implemented by the analysis of similarities introduced in the previous chapter 2.3.4.5.

Bubble plots are used to display the effect of a single environmental or biotic factor on the distribution of samples in an ordination. The value of the variable is superimposed as circles of different sizes onto the multivariate MDS, and the larger the bubble, the greater the value of the superimposed variable.

3.3.3.3 Multivariate Dispersion (IMD)

Variability in the distribution of diatom samples and diversity measures within wetland types was quantified by the Index of Multivariate Dispersion (IMD), which is calculated with the MVDISP routine included in the PRIMER v5 statistical package. The index is based on a similarity matrix and contrasts the average rank of the similarities among samples of one group ($\bar{r}_t$) with the average rank among samples of another group ($\bar{r}_c$), having re-ranked the full triangular matrix and ignoring all between-group similarities.

$$IMD = 2\left(\bar{r}_t - \bar{r}_c\right)/\left(N_t + N_c\right) \qquad \text{(equation 3.3)}$$

where

$$N_c = n_c\left(n_c - 1\right)/2, \quad N_t = n_t\left(n_t - 1\right)/2 \qquad \text{(equation 3.4)}$$

n_c, n_t are the number of samples in the respective groups. The denominator ensures that the IMD has a maximum value of +1 when all similarities among impacted samples are lower than any similarities among control samples. The converse case gives a minimum IMD of -1, and values near zero imply no difference between the treatment groups.
The Index of Multivariate Dispersion is principally restricted to the comparison of only two groups, but it can be extended by the following dispersion sequence

$$\bar{r}_1/k, \quad \bar{r}_2/k, \quad ..., \quad \bar{r}_g/k, \qquad \text{(equation 3.5)}$$

which defines the relative variability within each of g groups. Therefore, the larger values correspond to greater within-group dispersion. The denominator scaling factor k is $(N+1)/2$, i.e. the mean of all N ranks involved, so that a relative dispersion of unity corresponds to the average dispersion.

3.3.3.4 Similarity percentages (SIMPER)

For two different sample groups, an important practical requirement is to identify which species primarily account for the observed assemblage difference. The SIMPER routine (PRIMER v5) calculates how much each individual species contributes to the average sample dissimilarity between two groups (Clarke and Warwick 2001). For Bray-Curtis dissimilarity δ_{jk} between two samples j and k, the contribution from the ith species, $\delta_{jk}(i)$,

is defined as:

$$\delta_{jk}(i) = \frac{100\left|y_{ij} - y_{ik}\right|}{\sum_{i=1}^{p}(y_{ij} + y_{ik})} \qquad \text{(equation 3.6)}$$

$\delta_{jk}(i)$ is then averaged over all pairs (j, k), with j in the first and k in the second group, to give the average contribution δ_i from the ith species to the overall dissimilarity δ between groups one and two. Typically, there are many pairs of samples (j, k) making up the average δ_i, and a useful measure of how consistently a species contributes to δ_i across all such pairs is the standard deviation SD(δ_i) of the $\delta_{jk}(i)$ values. If the average δ_i is large and SD(δ_i) small, i.e. the ratio δ_i/ SD(δ_i) is large, then the ith species is a good discriminator: it consistently contributes a high percentage to the dissimilarity in inter-comparisons of all samples in the two groups.

The initial tables in the SIMPER output (cp. Appendix, Part B) take each group on its own and decompose the similarities of all within-group sample comparisons into their contributions from each species. This gives species which typify a group, in the sense that they are found at consistent high abundances in most samples, i.e. the standard deviation of the contribution of the ith species SD(S_i) is low and the ratio of the average S_i/SD(S_i) high.

In the present study, wetland and wetland type groups were defined *a priori* and confirmed by MDS and ANOSIM tests. SIMPER was applied to the full set of 199 species, but only higher contributing taxa were included in the results log (cp. Appendix, Part B). The implemented cut-off percentage of 90 % means that species are listed in decreasing order of their importance, in contributing to the average dissimilarity between two groups, until the point is reached at which 90 % of the dissimilarity is accounted for. The relative abundance data were square root transformed and are based on Bray-Curtis similarities (cp. equation 2.3).

3.3.3.5 Univariate diversity measures

Diversity indices reduce the multivariate complexity of species assemblage data into a single index, which can then be handled statistically by univariate analysis. In the present study, the following diversity measures were calculated (PRIMER v5) and compared to assess the impact of emphasising species richness or equitability components of diversity to varying degrees.

The most commonly applied index is that of ***Shannon-Wiener***, where p_i is the proportion of the total count arising from the ith species:

$$H' = -\sum_i p_i \log(p_i \log(p_i)) \qquad \text{(equation 3.7)}$$

Species richness is given as the total number of species (*S*), which is strongly dependent on sample size. Additionally, ***Margalef's index*** (*d*) was calculated, which incorporates the total number of individuals (*N*) and is a measure of the number of species present for a given number of individuals:

$$d = (S-1)/\log_e N \qquad \text{(equation 3.8)}$$

Equitability is expressed as ***Pielou's evenness*** index:

$$J' = H'/H'_{\max} = H'/\log_e S \qquad \text{(equation 3.9)}$$

where H'_{max} is the maximum possible value of Shannon diversity, i.e. that which would be achieved if all species were equally abundant. It is thus a measure of how evenly individuals are distributed among the different species.
Another commonly used measure is the ***Simpson index*** (cp. Simpson 1949), which in this study was calculated as:

$$1-\lambda = 1-(\sum p_i^2) \qquad \text{(equation 3.10)}$$

where p_i is the proportion of the total count arising from the *i*th species, as in Shannon index. In the form 1-λ, the Simpson index is an equitability measure, taking its largest value when all species have the same abundance.
The ***average taxonomic diversity*** of a sample is defined (Warwick and Clarke 1995) as

$$\Delta = \left[\sum\sum_{i<j} \omega_{ij} x_i x_j\right] / \left[N(N-1)/2\right] \qquad \text{(equation 3.11)}$$

where the double summation is over all pairs of species *i* and *j* ($i,j = 1, 2, \ldots, S$; $i<j$), and $N = \Sigma_i x_i$, the total number of individuals in the sample. Δ is the average taxonomic distance (ω_{ij}) apart of every pair of individuals in the sample, i.e. the expected path length between any two individuals chosen at random. The average taxonomic distance, therefore, is a natural extension of the Simpson index, from the case where the path length between individuals is either 0 (same species) or 100 (different species), to a more refined scale of intervening relatedness values (0 = same species, 20 = different species in the same genera, 40 = different genera but same family, etc.).
Clarke and Warwick (1999) advocate a simple linear scaling, whereby the largest number of steps in the tree (two species at greatest taxonomic distance apart) is set to $\omega = 100$. Thus, for a sample consisting only of 5 species as shown in figure 3.1, the path between individuals in species 3 and 4 is $\omega_{34} = 100$, between species 1 and 2 is $\omega_{12} = 50$, and between two individuals of species 5 is $\omega_{55} = 0$.

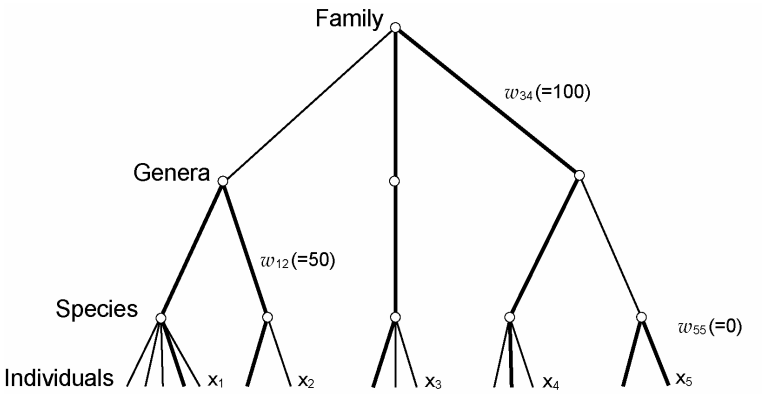


Figure 3.1. Familiy tree illustrating taxonomic distances for a set of five species (modified, Clarke and Warwick 2001)

To remove the dominating effect of the species abundance distribution $\{x_i\}$, leaving a measure which is more nearly a pure reflection of the taxonomic hierarchy, Warwick and Clarke (1995) proposed a formula for the ***average taxonomic distinctness***:

$$\Delta^* = \left[\sum\sum_{i<j} \omega_{ij} x_i x_j\right] / \left[\sum\sum_{i<j} x_i x_j\right] \quad \text{(equation 3.12)}$$

Both average taxonomic diversity (Δ) and average taxonomic distinctness (Δ*) inherit the sample-size independence seen in the Simpson index, from which they are generalised. Whatever the hierarchy or subsample size, Δ is unbiased (Clarke and Warwick 1998) and Δ* is close to being so, except for very small subsamples.

3.3.3.6 Linking biological data to environmental patterns (BIO-ENV)

The premise adopted in the BIO-ENV routine (PRIMER v5) is that, if the suite of environmental variables responsible for structuring the community were known, then samples having rather similar values for these variables would be expected to have rather similar species composition. An ordination based on abiotic information would group sites in the same way as for the biotic plot. The implicit assumption, therefore, is that the observed sample patterns are not dominated by internal stochastic forces, e.g. competitive interactions within the assemblage constituting the biotic data matrix (Clarke and Warwick 2001). Interrelations between biota and their environment are thus examined by employing rank correlation between a fixed species similarity matrix and a data matrix containing abiotic variables.

In the present study, the elements of the respective rank similarity matrices $\{r_i;\ i = 1, \ldots, N\}$ and $\{s_i;\ i = 1, \ldots, N\}$ are connected by the Spearman coefficient, where $N = n(n\text{-}1)/2$ and n is the number of samples (equation 3.13, p. 49).

$$\rho_s = 1 - \frac{6}{N(N^2-1)} \sum_{i=1}^{N} (r_i - s_i)^2 \qquad \text{(equation 3.13)}$$

The constant terms are defined such that ρ lies in the range (-1, 1), with the extremes of ρ = -1 and +1 corresponding to the cases where the two sets of ranks are in complete opposition or complete agreement, respectively. Values of ρ around zero correspond to the absence of any match between the two patterns. Combinations of the environmental variables are considered at steadily increasing levels of complexity, i.e. k variables at a time (k = 1, 2, 3, …, υ).
The BIO-ENV analysis presented in this thesis was run with the environmental parameters included in the principal components analysis of wetland sites (cp. Appendix, Part B). Since this approach requires an exhaustive search over

$$\sum_{k=1}^{\nu} \frac{\nu!}{k!(\nu-k)!} = 2^{\nu} - 1 \qquad \text{(equation 3.14)}$$

combinations, an iterative application of the BIO-ENV routine was adopted, starting from the single variable which best groups the sites in a manner consistent with the biotic patterns, to the maximum number of variables above which no further improvement could be attained. Furthermore, the analysis was carried out at different levels of taxonomic aggregation to find out if species delineated the environmental gradient more clearly than diatom families and genera. Rare taxa with relative abundances below 2 % were generally excluded. The best ten combinations of abiotic variables are listed in the results log of every analysis (Appendix, Part B).
Given the lack of assumptions underlying the BIO-ENV procedure, the support of any conclusions by significance tests is problematic. To bypass this difficulty, the method was first applied to diatom samples from artificial substrates to suggest an optimal combination of abiotic variables and subsequently utilised for an independent set of diatom samples from natural substrates to verify the primary results.

3.3.3.7 Stepwise matching of ordinations (BVSTEP)

This procedure can be thought of as a generalisation of the SIMPER approach to the case of continuous multivariate patterns rather than a clearly defined clustering of samples. The BVSTEP algorithm (PRIMER v5) is an extension of the BIO-ENV routine, allowing for the sequential analysis of data sets with a large number of variables. As opposed to BIO-ENV, this stepwise algorithm does not search over every possible combination of samples but some more limited space, involving forward and backward stepping phases. At each stage, a selection is made of the best single variable to add or to drop from the existing selected set. The process continues until the stopping criterion is met, which, in

this study, is defined as $\rho = 0.95$. However, the aim is not to maximise ρ, but to find the smallest possible subset of variables, which in combination explain most of the pattern in the full data set. The algorithm terminates when a species subset is found with a match of $\rho > 0.95$ to the pattern of the full data set or if no further species can be found that increases ρ by more than 0.001. Since it is possible that the iterative search procedure will get trapped in a local optimum and miss the true best solution, it is recommended to begin the search at several different, random starting points (Clarke and Warwick 2001). For the purpose of the present study, BVSTEP was repeatedly carried out with the full set of diatom species, starting from either a random point in the entire list of taxa or from a randomly selected subset of 25 % and 50 % of the species (cp. Appendix, Part B).
The BVSTEP procedure was also used to analyse structural redundancy in the benthic algal communities studied. Therefore, the initial selection of species was therefore discarded, and another search was run for a second subset of species that produces an equally good match ($p \geq 0.95$).

3.3.3.8 Detrended and Canonical Correspondence Analysis (DCA, CCA, DCCA)

The classical and widely applied approach of linking biotic and environmental data by means of detrended correspondence analysis (DCA) and (detrended) canonical correspondence analysis (CCA, DCCA) was adopted to allow for comparison with results derived by recently developed non-parametric procedures (BIO-ENV, BVSTEP).
Prior to ordination, species data were square root transformed and rare species were down-weighed. With respect to abiotic data, the same set of environmental variables was used as for PCA (cp. Appendix, Part B). Significance of ordination axes and bivariate correlations with the environmental variables extracted by manual forward selection was tested by unrestricted Monte Carlo permutations ($p = 0.05$; $n = 999$). Graphs were constructed using CanoDraw 3.1 and CanoPost 1.0.
Detrended Correspondence Analysis (Canoco 4.0) was consulted to confirm whether species actually respond to the expected unimodal model (cp. ter Braak 1996), which assumes that species distributions reflect some environmental optimum. Detrending by segments was applied according to DECORANA's default detrended correspondence analysis (Hill and Gauch, 1980), therefore a gradient length of 4 SD (standard deviation units of species turnover) is considered to represent a strong unimodal relationship (ter Braak and Smilauer 1998). Data consequently require direct gradient analysis if this criterion is met.
CCA (Canoco 4.0) is a constrained unimodal ordination method, with species representing the dependent variables and environmental factors constituting explanatory variables. The algorithm is a converging sequence of multiple weighted average regressions and calibrations. As for PCA (cp. chapter 2.3.4.4), canonical axes represent linear combinations of environmental variables. Sample scores are the values that the

theoretical variable takes in the samples. Species scores reflect the centre of species curves in the ordination. Eigenvalues are a measure of the importance of ordination axes, corresponding to the amount of variation 'explained'. Scaling focussed on inter-sample distances, in which Hill's scaling proved to be appropriate for the respective gradient length.

Detrended CCA (DCCA) was used to identify environmental variables that are valid for the development of transfer functions by reference to the percentage of species variance explained and the ratio of the first to second eigenvalues ($\lambda_1/\ \lambda_2$), when each variable was included as the sole explanatory variable in DCCA (Birks 1998). Variables found to contribute more than 5 % to species variance and with $\lambda_1/\ \lambda_2$ ratios in excess of 0.5 (cp. Appendix, Part B) were deemed suitable for developing transfer functions by weighted averaging (Hall and Smol 1992, Bennion 1994, Reid 2005).

3.3.3.9 Weighted averaging regression (WA)

Weighted averaging (WA) techniques are commonly used to infer environmental conditions from species data by calculating transfer functions. Simple weighted averaging and calibration (C2 v1.4, Juggins 2003) with classical deshrinking (Birks et al. 1990) was applied to calculate species optima for the abiotic variables accounting for most of the variation in multivariate species data space (cp. previous chapter). Cross-validation by bootstrapping was applied in each case.
When a species shows a unimodal curve against a particular environmental variable, the presences of the species will most frequently occur near the optimum of the curve. By weighted averaging, the average of the values of a specific environmental variable is taken over those sites where the species is present. For abundance data, values are weighted proportional to species abundance, i.e.

$$u* = \left(y_1x_1 + y_2x_2 + ... + y_nx_m\right)/\left(y_1 + y_2 + ... + y_n\right) \qquad \text{(equation 3.15)}$$

where

$y_1, y_2, \ldots, y_n$ are the abundances of the species
$x_1, x_2, \ldots, x_n$ the values of the environmental variable at sites $i = 1, 2, \ldots, n$.

Species absences are disregarded. This method has been shown to be about as efficient as the respective regression techniques for estimating the species optimum 1) when a taxon is rare and has a narrow ecological amplitude and 2) when the distribution of the environmental variable among sites is reasonably homogeneous over the whole range of occurrence of the species along the environmental variable (ter Braak and Looman 1986).
For the assessment of model performance the correlation coefficient (r^2), root-mean squared error of prediction (RMSEP) and plots of predicted against observed values derived for cross-validated models for predicted variable are given in the Appendix, Part B.

3.4 Results

3.4.1 Seasonal variation

Diatom data from December 2002 and March 2003 were highly correlated ($R = 0.907$, $p = 0.001$) as shown by the comparison of similarity matrices (cp. chapter 2.3.4.1). Therfore, differences between early and late summer are even less pronounced in benthic community composition than in environmental data (cp. chapter 2.4.1), as diatoms integrate environmental conditions over a time period of several days or weeks. Therefore, diatom data were averaged for the subsequent analysis of different spatial levels to match with the abiotic data presented in chapter 2.

3.4.2 Taxonomic structure and composition of benthic diatom communities

The diatom taxa presented in this thesis comprise species and their varieties, forms, and morphotypes. Species subunits were only separated if morphologically and ecologically distinct and consequently assigned species rank to simplify analysis. A total of 199 diatom taxa, belonging to 35 genera and 9 families, were found in the studied diatom communities. Among these, 11 centric taxa commonly occurred in microphytobenthos, while pennate diatoms were represented by 188 taxa. An alphabetical list of all species is enclosed in the Appendix, Part B.

3.4.2.1 Dominance patterns

Universal features of community structure that are not a function of the specific taxa present are commonly used to assess the impact of certain stressors, e.g. organic or toxic pollutes, on biota. The results of a range of dominance measures presented in this chapter are structured from wetland type specific patterns down to more detailed analyses of variation between sites and substrates.

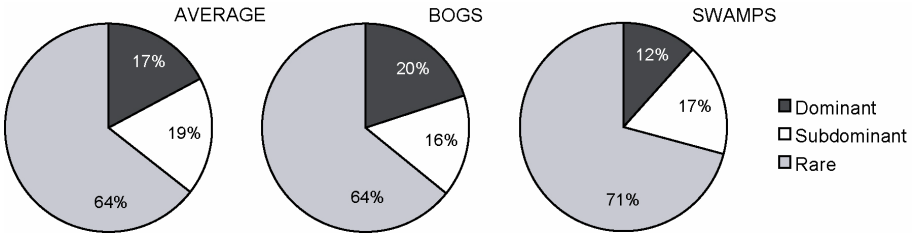


Figure 3.2. Proportions of dominant, subdominant and rare taxa in wetland classes.

Differences between wetlands and wetland types

The largest group in all habitats comprises rare taxa (figure 3.2), which per definition occur in at least one sample with a relative abundance of less than 2 %. Subdominant taxa

are characterised by relative abundances of 2-10 %, while dominant taxa occur at relative abundances above 10 %. The proportions of these groups are commensurate but small in comparison to rare taxa, accounting for 36 % of all diatom communities. In total, 128 rare taxa were determined alongside 37 subdominant and 34 dominant taxa.
The comparison of dominant, subdominant and rare taxa groups between wetland classes reveals that bogs feature a more pronounced dominance structure than swamps. In ombrotrophic conditions, 20 % of the taxa belong to the dominant category, while this group comprises only 12 % in minerotrophic wetlands (figure 3.2). On the other hand, a larger percentage of rare taxa occur in swamps. The total number of taxa exceeds that of ombrotrophic wetlands by almost 100 %, with 178 taxa in swamps as opposed to 95 taxa in bogs.

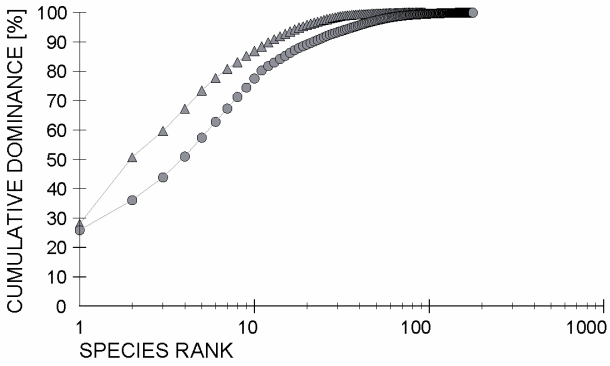


Figure 3.3. *k*-dominance curves for bog (▲) and swamp (●) communities

Universal features of community structure which are not a function of the specific taxa present can also be extracted from distributional plots. In the *k*-dominance curves for benthic diatom communities from New Zealand lowland wetland types (figure 3.3), the cumulative ranked abundances of diatom taxa are plotted against the log species rank (cp. Lambshead et al. 1983). In contrast to the previous approach of breaking down the relative proportions of diatom taxa into three dominance categories, species are now ranked in decreasing order of their importance in terms of abundance. The slightly elevated curve for the bog communities thus points to a stronger emphasis of common taxa in this wetland class, also indicating lower diatom diversity in comparison to swamps.
A more detailed picture of the dominance structure in bogs and swamps provide geometric class plots at the site level (figures 3.4-3.6). Geometric abundance classes are defined by the number of individuals of a taxon, thus species in class 1 are represented by only one individual, species in class 2 by 2-3 individuals, species in class 3 by 4-7

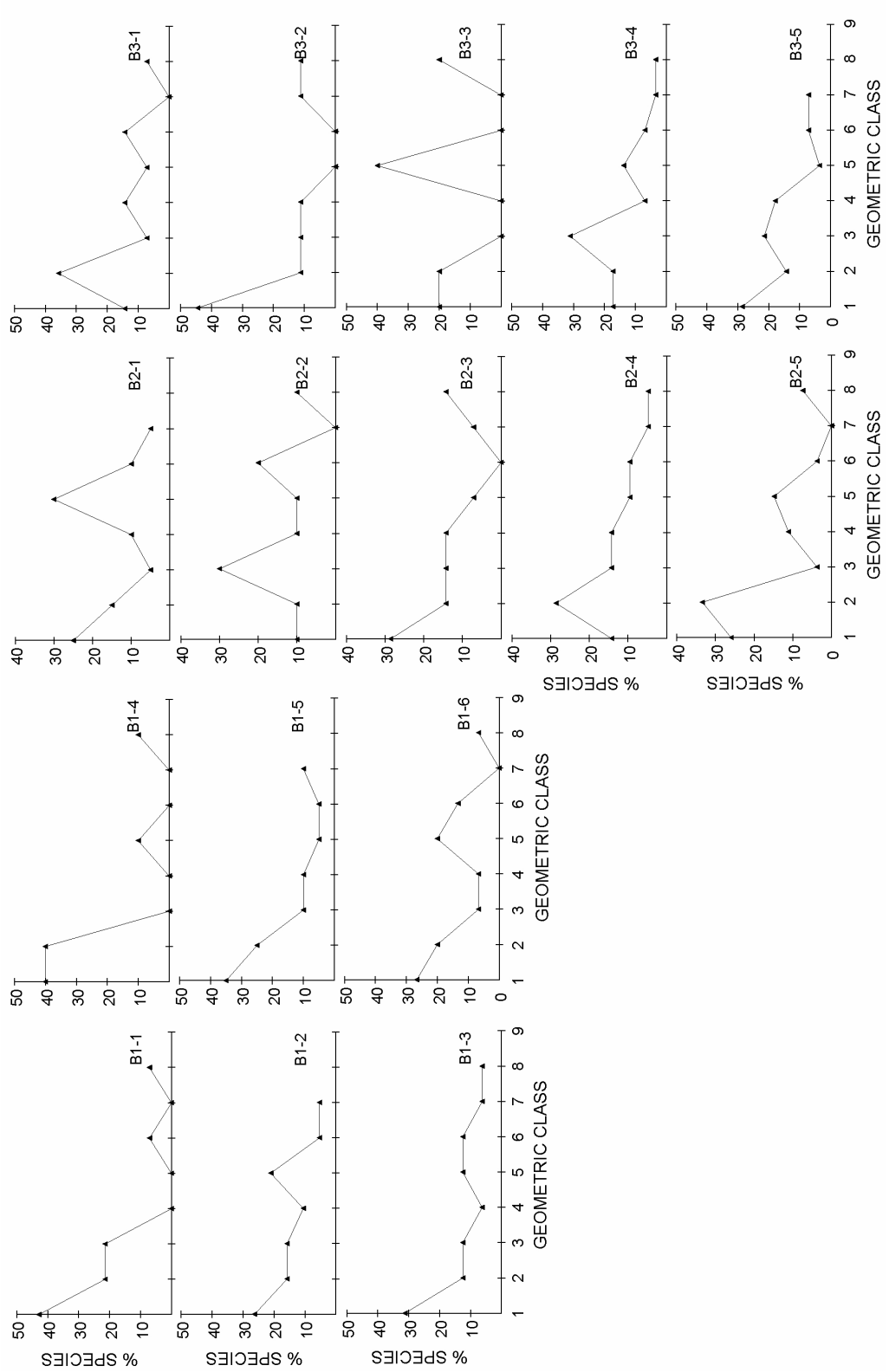


Figure 3.4. Geometric class plots of bog sites B1-B3.

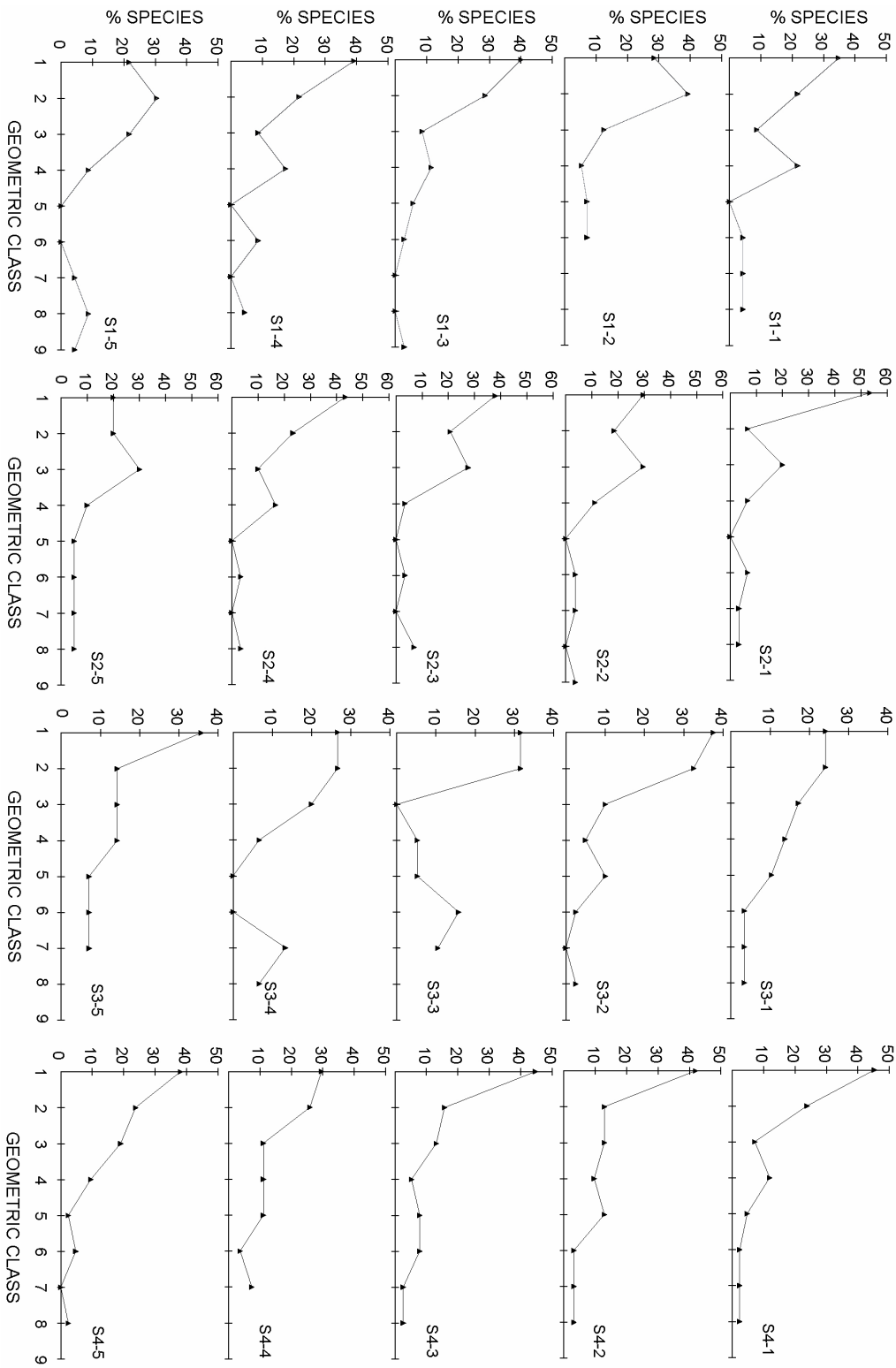


Figure 3.5. Geometric class plots of swamps sites

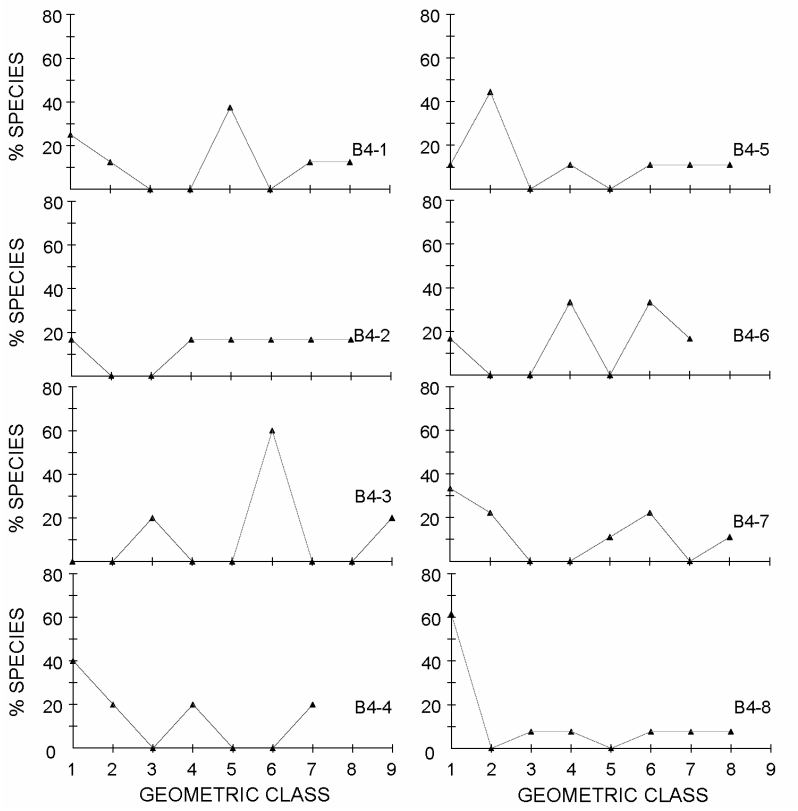


Figure 3.6. Geometric class plots of bog sites in B4

individuals etc. Numbers of individuals in higher classes conform to the lower boundary in the respective next lower class x2. It is suggested that impact on biota tends to change the form of this distribution, lengthening the right tail and giving a more jagged curve (Clarke and Warwick 2001).

Swamp sites are characterised by relatively smooth curves, the mode being well to the left of the graph. In contrast, higher geometric classes are more strongly represented in bogs, and the curves are often irregular and jagged, which is an indication for community stress (Gray and Pearson 1982). From the graphs it is also apparent that geometric classes are uniformly distributed within swamps, whereas variation between replicate sites in ombrotrophic wetlands is distinctly higher. For example, the distribution of species abundances at site B4-8 is heavily left skewed, while at site B4-3 all taxa belong to the geometric classes 3 (20 %), 6 (60 %), and 9 (20 %).

Differences between substrates

Variation in the proportions of taxa groups between substrates is generally low within each wetland class (figure 3.7). Distinctive discrepancies only occur in ombrotrophic wetlands, where periphyton (as) communities contain about 10 % more rare taxa in

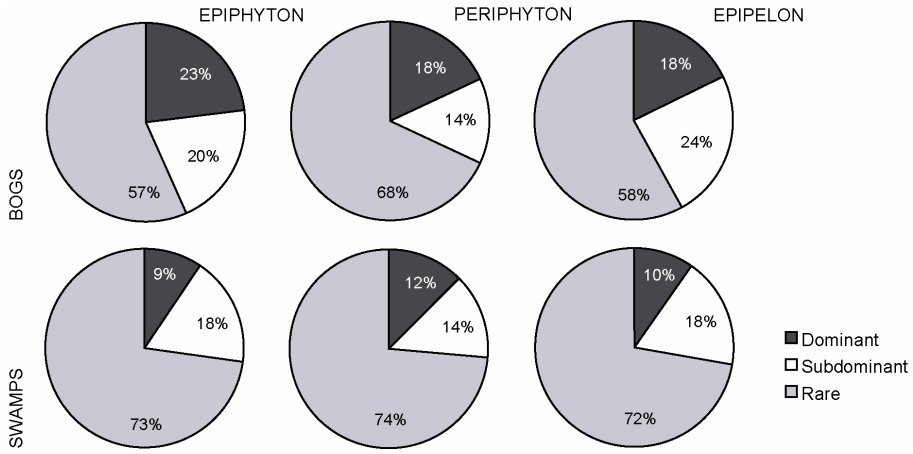


Fig. 3.7. Proportions of dominant, subdominant, and rare taxa from different substrates; periphyton refers to benthic algae on artificial substrata.

comparison to microphytobenthos on plants and sediment. This difference is due to a decreasing number of subdominant taxa, while the percentage of dominant taxa levels off.

The *k*-dominance curves for benthic diatom communities from different substrates (figure 3.8) show that there are only minor differences in the ranked species abundance distribution in swamps. However, epipelon assemblages appear to be more stable than periphytic and epiphytic diatom communities. In bogs, differences between substrates occur within the lower ranks, that is the relative proportions of the most abundant species. As in swamps, epipelon communities are less impacted than diatom assemblages from other substrates. The dominance structure of periphyton (as) and epiphyton is similar, though the cumulative abundance curve of the biofilm grown on polyethylene slides is slightly more elevated.

A detailed comparison of diatom communities from different submersed macrophyte taxa reveals that the dominance structure of the algal biofilm is rather similar between substrates (figure 3.9). However, *Nitella hookeri*, *Callitriche petriei* and bryophytes other than *Sphagnum* stand out because they host a strikingly high percentage of diatom species in the lower geometric classes, that is more than 70 % in classes 1-3, but few diatom taxa with more than 30 individuals. On the other hand, *Potamogeton suboblongus* and *Aponogeton distachyus*, species which have floating leaves, feature over 40 % of diatom species in the mid and upper abundance ranks.

In terms of the overall number of taxa found on different substrates, bog periphyton (as) communities contained the largest number of taxa with 78 species, whereas epiphytic diatom associations enclosed the largest amount of taxa in swamps, comprising 159 species (figure 3.10). The lowest total number of taxa was generally detected in sediment samples, with 62 species in bogs and 104 species in swamps.

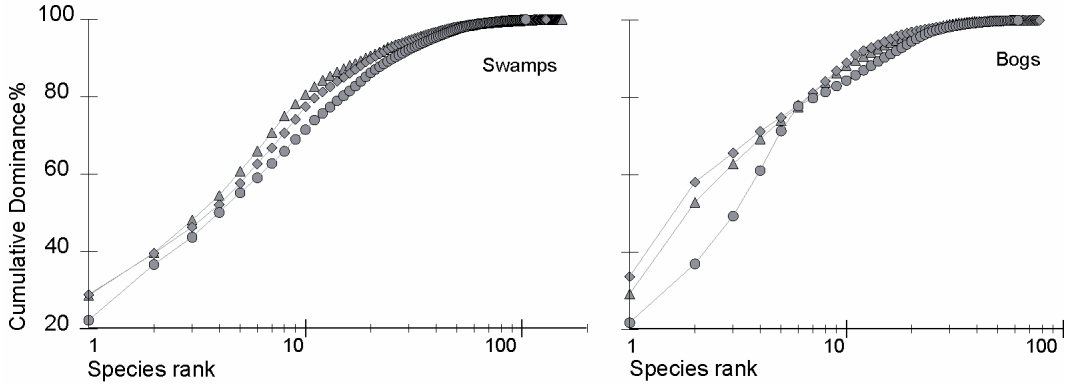


Figure 3.8. *k*-dominance plots of benthic diatom communities. ○ Epipelon, △ Epiphyton, ◇ Periphyton (as)

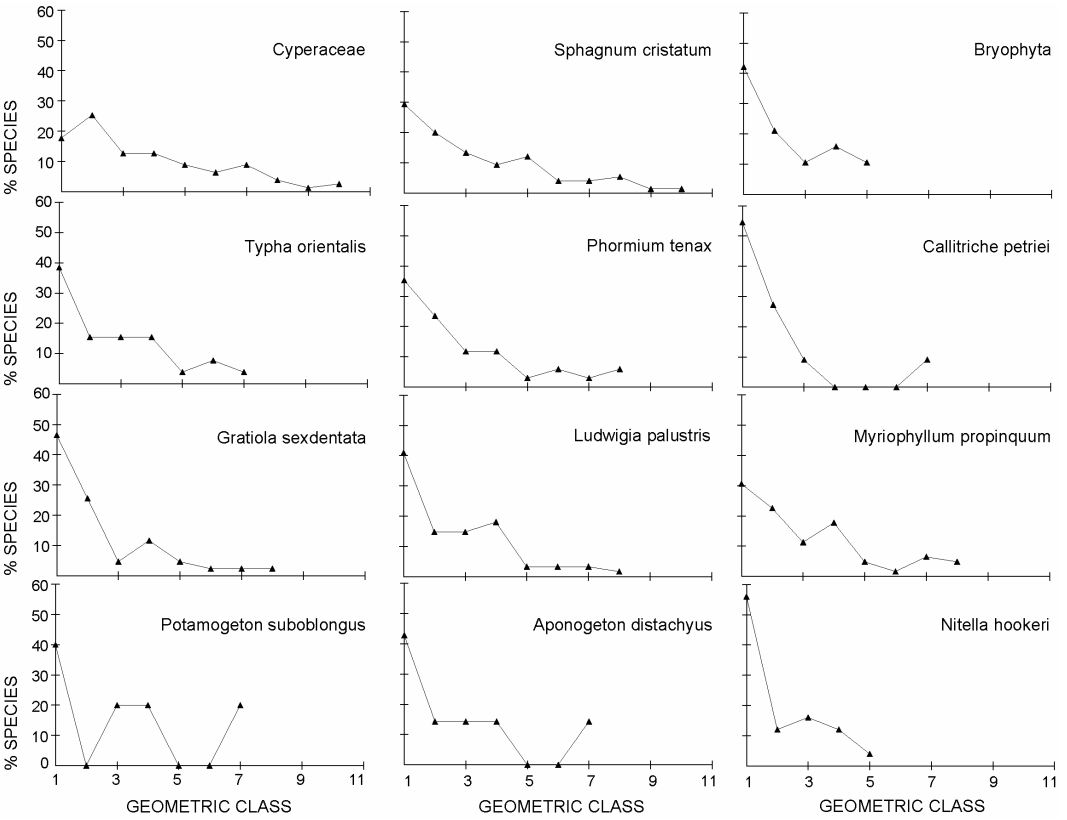


Figure 3.9. Geometric abundance plots of benthic diatom communities from different macrophyte hosts

3.4.2.2 Species composition of benthic diatom communities

In contrast to general dominance patterns in algal assemblages that may be related to community stress, high resolution data of the taxonomic composition in microphyto-benthos provide insight in the habitat preferences of certain diatom species.

The taxonomic composition of benthic diatom communities from New Zealand lowland wetlands was analysed by multivariate nonparametric techniques such as analysis of

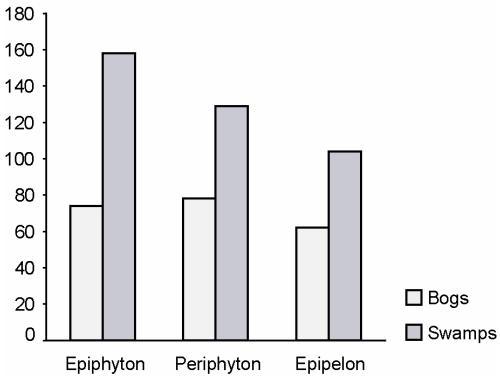


Fig. 3.10. Total number of taxa found in benthic diatom communities from different substrates; periphyton refers to benthic algae on artificial substrata

similarities (ANOSIM), similarity percentages (SIMPER), and multidimensional scaling (MDS). Significance tests were first applied to the lowest spatial scale and consecutively calculated at higher spatial levels, which allows for the optimisation of analytical procedures. Accordingly, differences between substrates are addressed in the first instance, followed by the analysis of taxonomic variation between sites, wetlands, and wetland types.

Differences between substrates

An analysis of similarities (2-way crossed ANOSIM layout with no replication) was carried out to test for differences in the taxonomic composition of benthic diatom communities from sediment, artificial substrata, and a variety of macrophyte species. The test statistic was calculated on the lowest spatial scale to account for deviations between sampling sites. As this approach ruled out any significant differences between substrates ($R = 0.067$; $p = 0.067$), diatom samples from different substrates were treated as replicates in subsequent analysis to increase the power of the tests. The high level of similarity between diatom communities from sediment, macrophytes and polyethylene slides is also illustrated in figures 3.11 and 3.12, which compare the relative proportions of dominant and subdominant taxa in bogs and swamps. The charts demonstrate quite impressively that, even though the proportions at which each taxon is represented may vary between substrates, the taxonomic composition of the benthic biofilm does not change much, if at all.

Differences between wetland sites

One-way ANOSIM tests between sites were calculated separately for each wetland to avoid confounding by wetland specific or type specific properties. However, pairwise comparisons between wetland sites are not discussed in detail, since in most cases there were not enough replicates to ensure significant test results (cp. Appendix, Part B).

Slight differences between sampling sites were detected at swamp S2 ($R = 0.423$; $p = 0.001$), whereas a high degree of variation typified the other wetlands studied ($R \geq 0.577$; $p = 0.001$). The largest deviations between sites occurred in bog B3 ($R = 0.939$; $p = 0.001$), indicating that differences between sites were significantly larger than between replicates of the same site. In fact, small deviations between replicates of a sample will invariably cause more pronounced differences between samples; henceforth, significant differences arising in spite of high variation at lower spatial scales were assigned more weight.

It is also emphasized that the changing degree of similarity between sites provides justification for the application of the multivariate non-parametric ANOSIM instead of the commonly utilised ANOVA (analysis of variance), since the assumption of equal variances between samples is not met. This criterion, although exemplified just in this case, likewise applies to all other comparisons involving different spatial scales, i.e. variation at different spatial levels can not be expected to coincide in this study.

Differences between wetlands

Building up on the analysis of diatom distribution among sites, the nested analysis of similarities revealed significant differences with respect to the taxonomic composition of benthic diatom communities from different wetlands (global test statistic: $R = 0.841$; $p = 0.001$). 75 taxa, thereof six subdominant and one dominant species appear to be wetland specific and were absent in all habitats but the respective bog or swamp.

The global ANOSIM test statistic for bogs ($R = 0.560$; $p = 0.001$) points to a high level of similarity between the ombrotrophic wetlands studied, and the diatom communities are poorly separated from each other in the MDS ordination (figure 3.15 AI). The largest taxonomic differences within the bog wetland class were detected by pairwise tests (table 3.2) between wetlands B2 and B3 ($R = 0.872$; $p \leq 0.05$), thus verifying the alignment of diatom samples in the MDS ordination of bogs. However, the reduction of multidimensional space onto a single plane causes some deterioration in the configuration of samples, and details in the graph might not be entirely reliable (*stress* = 0.18). Therefore the statistics for pairwise ANOSIM tests are not in complete agreement with the sample relationships suggested by MDS, and the degree of overlap between wetlands B1, B3 and B4 could only be resolved to close proximity.

Wetland B1 is characterised by comparably high abundances of *Eunotia exigua* and *Pinnularia microstauron*. Among the dominant taxa, an undulate form resembling small specimens of *Eunotia siolii* is unique to this wetland. This taxon, referred to as *Eunotia* spec. aff. *siolii* f. *bidens*, has not yet been described in the literature and might be restricted to that habitat. Wetland B2 is dominated by *Naviculadicta subtilissima* and *Frustulia saxonica* morphotype I and comprises only small numbers of *Eunotia paludosa* var. *trinarcria* and *Pinnularia perriorata* in comparison to the other bogs studied. A

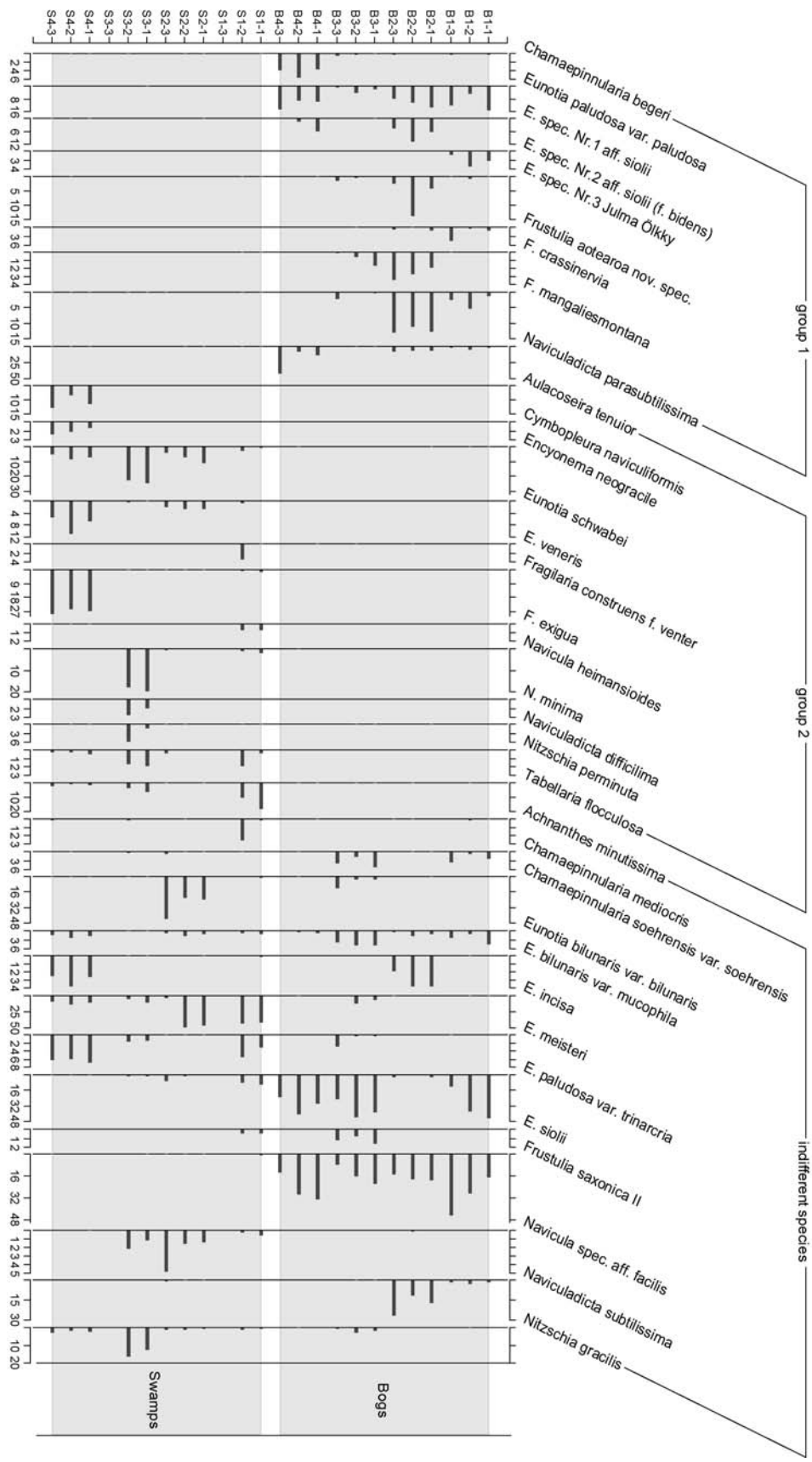


Figure 3.11. Stratigraphic plots of dominant species occurring in bogs and swamps (x-axis represents relative abundance in %). Substrate types are indicated by sample name affixes (y-axis): 1 = epiphyton, 2 = periphyton (as), 3 = epipelon.

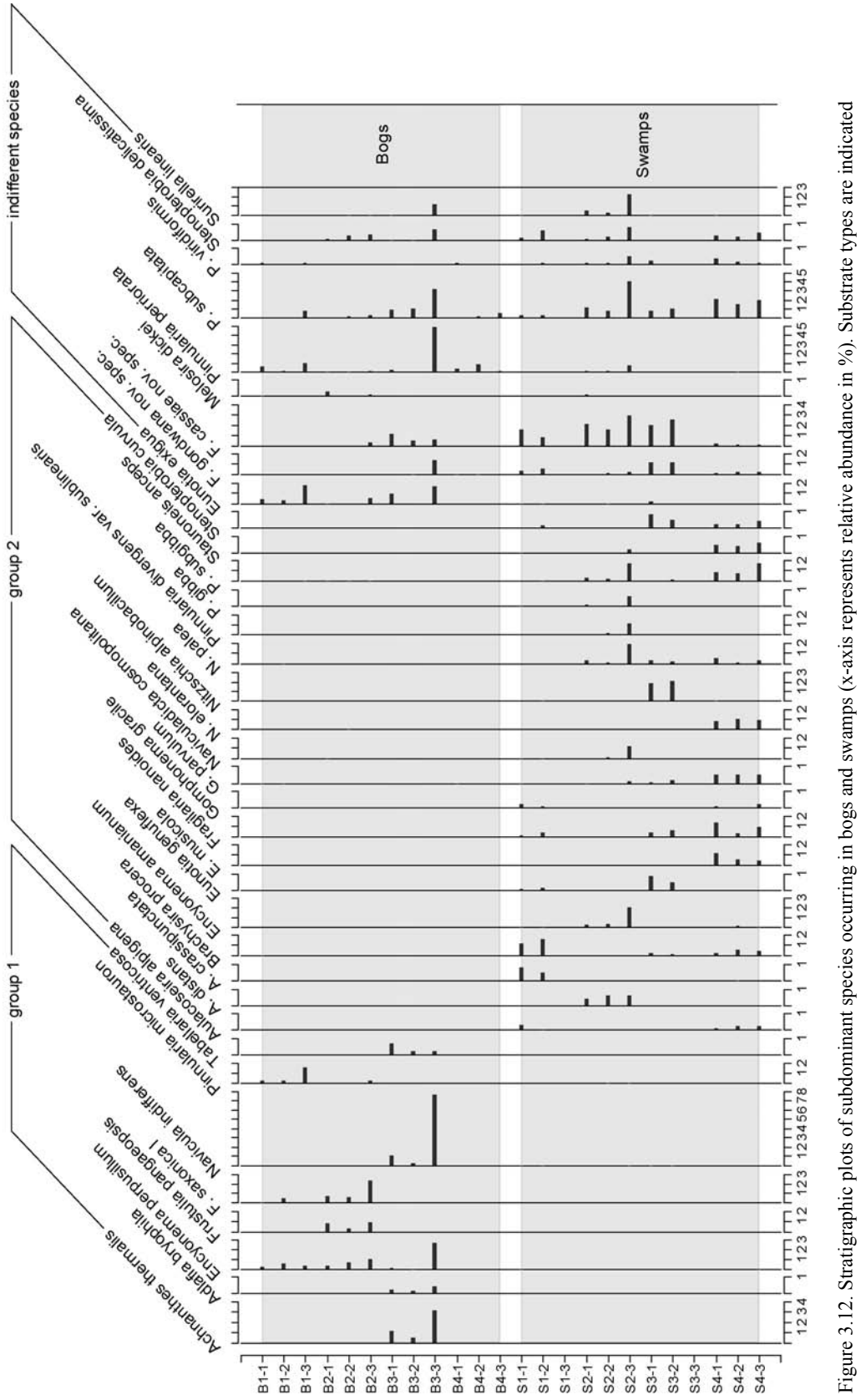


Figure 3.12. Stratigraphic plots of subdominant species occurring in bogs and swamps (x-axis represents relative abundance in %). Substrate types are indicated by sample name affixes (y-axis): 1 = epiphyton, 2 = periphyton (as), 3 = epipelon.

subdominant taxon that exclusively occurred in this ombrotrophic bog is *Frustulia pangaeopsis* (cp. figures 4.11-13, 4.55-60). Species specific to wetland B3 were *Achanthes thermalis* and *Tabellaria ventricosa*, accompanied by more common taxa such as *Adlafia bryophila* and *Navicula indifferens*. Bog B4 is characterised by high percentages of *Navicula parasubtilissima*, *Chamaepinnularia begeri*, *Pinnularia periorrata*, and *Pinnularia subcapitata*. *Navicula praeterita* and *Pinnularia divergentissima* var. *minor* were only found in this wetland, but occurred in just one sample.

Table 3.2. Pairwise comparisons of benthic diatom associations from bogs and swamps. 2-sided significance levels $p \leq 0.05$ (*bonferroni* adjusted).

	B2	B3	B4	S1	S2	S3	S4
B1	0.717	0.357	0.431	0.992	1.000	1.000	1.000
B2		0.872	0.845	1.000	1.000	1.000	1.000
B3			0.497	0.788	0.956	0.992	0.996
B4				0.999	1.000	1.000	1.000
S1					0.676	0.608	0.664
S2						0.932	0.956
S3							0.836

According to the analysis of similarities, the composition of swamp communities on average is more distinctive than in bogs ($R = 0.779$; $p = 0.001$). This is depicted in the MDS ordination of diatom samples from swamp sites (figure 3.15 BI), which clearly separates all minerotrophic wetlands from each other (*stress* = 0.15).

Mahinapua Swamp (S1) is characterised by large proportions of *Tabellaria flocculosa*, *Frustulia saxonica* morphotype II, *Eunotia praerupta*, *Aulacoseira crassipunctata*, and *Brachysira procera*, relative to their occurrence in other minerotrophic wetlands. 22 taxa are specific to this swamp and, even though only represented by a few individuals, this fraction accounts for the largest percentage among all wetlands. Wetland S2 is the only swamp where *Aulacoseira distans* was found. This taxon frequently occurred together with *Navicula* aff. *facilis* and *Chamaepinnularia soehrensis* var. *soehrensis*. *Encyonema amanianum*, *Navicula subtilissima*, *Naviculadicta cosmopolitana*, *Pinnularia divergens* var. *sublinearis*, and *Surirella linearis* were also among the prevalent taxa that characterise this wetland. In swamp S3, *Nitzschia gracilis*, *Navicula difficilima*, *Navicula heimansioides*, *Stenopterobia curvula*, *Nitzschia alpinobacillum*, *Eunotia genuflexa*, and *Chamaepinnularia mediocris* were more numerous than in the other swamps studied. Only eight taxa with relative abundances below 2 % were specific to this wetland.

Eunotia musicola exclusively occurred in Back Creek Swamp (S4). Other subdominant taxa such as *Eunotia bilunaris* var. *mucophila*, *Fragilaria nanoides*, *Navicula elorantana*, and *Stauroneis anceps* also predominated in this wetland. Among the group of dominant taxa, *Fragilaria construens* f. *venter*, *Eunotia schwabei*, *Aulacoseira tenuior*, *Cymbopleura naviculiformis*, and *Eunotia meisteri* were abundant.

Differences between wetland types

From the bar charts presented earlier in this chapter (figures 3.11 and 3.12) it becomes apparent that benthic diatom community composition does not only vary between wetlands but also between wetland types. A nested analysis of similarities confirms that the differences between types are highly significant ($R = 1$; $p = 0.029$), the high *R*-value indicating that all replicates within one wetland type are more similar to each other than any replicates from different wetland types. This is also illustrated by the MDS ordination of diatom samples from bogs and swamps (figure 3.15 CI), in which the microphytobenthos from different wetland types is clearly separated. According to the analysis of similarity percentages (SIMPER), the best type discriminating species are *Eunotia incisa*, *Eunotia paludosa* var. *trinarcria*, *Frustulia saxonica* morphotype II, and *Encyonema neogracile*, which together account for more than 25 % of the average dissimilarity between groups (Bray-Curtis dissimilarity = 87.04). *Eunotia paludosa* var. *paludosa*, *Tabellaria flocculosa*, *Naviculadicta parasubtilissima*, *Nitzschia gracilis*, *Chamaepinnularia soehrensis* var. *soehrensis*, *Navicula heimansioides*, *Fragilaria construens* f. *venter*, and *Naviculadicta subtilissima* also occur at higher abundances in either wetland class, adding another 25 % of the average dissimilarity between groups (see Appendix, Part B for details). The SIMPER result does not generally exclude any overlap in the taxonomic composition of bog and swamp communities, but even though some species might reach dominance in a few samples in one wetland type, they are much more abundant in the other group of wetlands (figures 3.11 and 3.12).

3.4.2.3 Structural redundancy in diatom samples

Redundancy patterns in diatom community structure were analysed by repeated stepwise matching of ordinations (BVSTEP), which can be thought of as a generalisation of the SIMPER approach to the case of continuous multivariate patterns rather than a clearly defined clustering of samples (cp. chapter 3.2.3.4).

In the ordination of diatom samples from both wetland types (Figure 3.15 CI), a minimum set of 8 species explains most of the variation in sample pattern ($p = 0.954$), that is *Chamaepinnularia soehrensis* var. *soehrensis*, *Encyonema neogracile*, *Eunotia bilunaris* var. *bilunaris*, *Eunotia incisa*, *Eunotia paludosa* var. *paludosa*, *Eunotia paludosa* var. *trinarcria*, *Frustulia saxonica* morphotype II, and *Nitzschia gracilis*. If these species are eliminated from the original data set and the analysis is repeated with

the reduced species subset, the best match comprises a minimum of 29 species, which together explain only 84.1 % of the sample pattern.
Similarly, a set of 10 species produce the best match with the ordination of bog samples based on the whole data set (figure 3.15 BI). *Achnanthes thermalis*, *Chamaepinnularia begeri*, *Eunotia incisa*, *Eunotia paludosa* var. *paludosa*, *Eunotia paludosa* var. *trinarcria*, *Frustulia magaliesmontana*, *Frustulia saxonica* morphotype II, *Naviculadicta parasubtilissima*, *Naviladicta subtilissima*, and *Nitzschia gracilis* thus explain 95.1 % of the variation in the data, while with the reduced data, the best matching set of species consists of 21 species which explain a mere 50.5 % in the ordination of diatom samples.
In the MDS ordination of swamps (figure 3.15 AI), a subset of 11 species account for 95.2 % of the sample pattern based on the original data. If *Chamaepinnularia soehrensis* var. *soehrensis*, *Encyonema neogracile*, *Eunotia incisa*, *Eunotia meisteri*, *Eunotia paludosa* var. *trinarcria*, *Fragilaria construens* f. *venter*, *Fragilaria nanoides*, *Navicula heimansioides*, *Navicula difficilima*, *Pinnularia subcapitata*, and *Tabellaria flocculosa* are discarded, the best match is obtained with another set of 19 taxa explaining 83.8 % of the variation in the species data.

3.4.2.4 Community analysis at higher taxonomic levels

In the course of managing and monitoring freshwater ecosystems, it is often not practicable to identify diatom taxa to species level because of financial or time constraints. It is therefore tested, if the results obtained by species analysis are reproducible at higher taxonomic levels. The statistical procedures generally follow those described in chapter 3.3.2.2.

Differences between substrates

As for species composition, no significant differences between substrates were indicated by the analysis of similarities based on either diatom genera ($R = 0.037$; $p = 0.180$) or diatom families ($R = -0.009$; $p = 0.566$). This is expected, since the loss of information by aggregating species to higher taxonomic levels usually leads to weaker test statistics. However, it is of particular interest if the detected spatial differences between samples remain significant with reference to diatom genera or diatom families (see below).

Differences between wetland sites

In the majority of wetland ecosystems studied, the relative proportions of genera and families (table 3.3) differed significantly between sampling sites; yet, at swamp S2 significant deviations in the taxonomic composition of benthic diatom communities were only detectable at the species level, while the relative proportions of genera and families were alike. Overall, the ANOSIM test among wetland sites yielded similar results at the

species, genus, and family level, though a trend of diminishing subtleties with increasing taxonomic aggregation has been observed across all wetlands, and the dissimilarities between wetlands diverge if diatom families are concerned.

Table 3.3. One-way ANOSIM test statistics (*R*-values) for differences among sites within each wetland, applied to diatom data at species, genus, and family level (*bonferroni* corrected $p \leq 0.05$).

R-values	B1	B2	B3	B4	S1	S2	S3	S4
Species	0.665	0.778	0.939	0.848	0.577	0.423	0.844	0.719
Genera	0.530	0.667	0.858	0.762	0.567	ns	0.761	0.631
Families	0.489	0.620	0.822	0.372	0.450	ns	0.713	0.608

Differences between wetlands

The global test statistic of the two-way nested analysis of similarities between benthic ***diatom genera*** occurring in different wetlands ($R = 0.621$; $p = 0.001$) is highly significant, but clearly not as strong as the *R*-statistic obtained at the species level.
This is caused by the relatively equal distribution of diatom genera across bogs (cp. figure 3.13), even though a range of characteristic but rare taxa occur in these wetlands. For example, genera such as *Mayamaea* and *Sellaphora* were exclusively found in bog B1, while *Adflafia* solely occured in bog B3. However, three genera, i.e. *Eunotia*, *Frustulia*, and *Navicula*, account for more than 90 % of all diatom taxa in these ecosystems. The MDS ordination of diatom genera found in bogs (figure 3.15 AII) is barely distinguishable from the sample pattern derived from species data (figure 3.15 AI), but in contrast to the ANOSIM test applied to the full set of species, bogs could not be significantly differentiated at the genus level ($R = 0.107$; $p = 0.084$). In the pairwise comparisons between bogs (table 3.4), significant test results were only obtained for wetlands B2 and B3, which have been shown to feature the largest differences in species composition (cp. table 3.2).
A clear separation of swamps was obtained in an MDS applied to the genus level (figure 3.15 BII), resembling that derived from species samples (figure 3.15 BI). Correspondingly, the analysis of similarities (table 3.4) indicates significant differences between swamps, the global test statistic being marginally weaker than for species data ($R = 0.677$; $p = 0.001$). Wetland S1 is dominated by over 60 % *Eunotia* and *Tabellaria*, while taxa belonging to *Cymbella* sensu lato are underrepresented in comparison to the other swamps studied (cp. figure 3.13). Although present in this wetland, *Fragilaria* attains much higher abundances (> 20 %) in swamp S4, which is also typified by large proportions of *Aulacoseira*. The percentage of centric diatoms exceeds 30 % in this wetland. Wetlands S2 and S3 are characterised by equally high abundances of *Navicula*

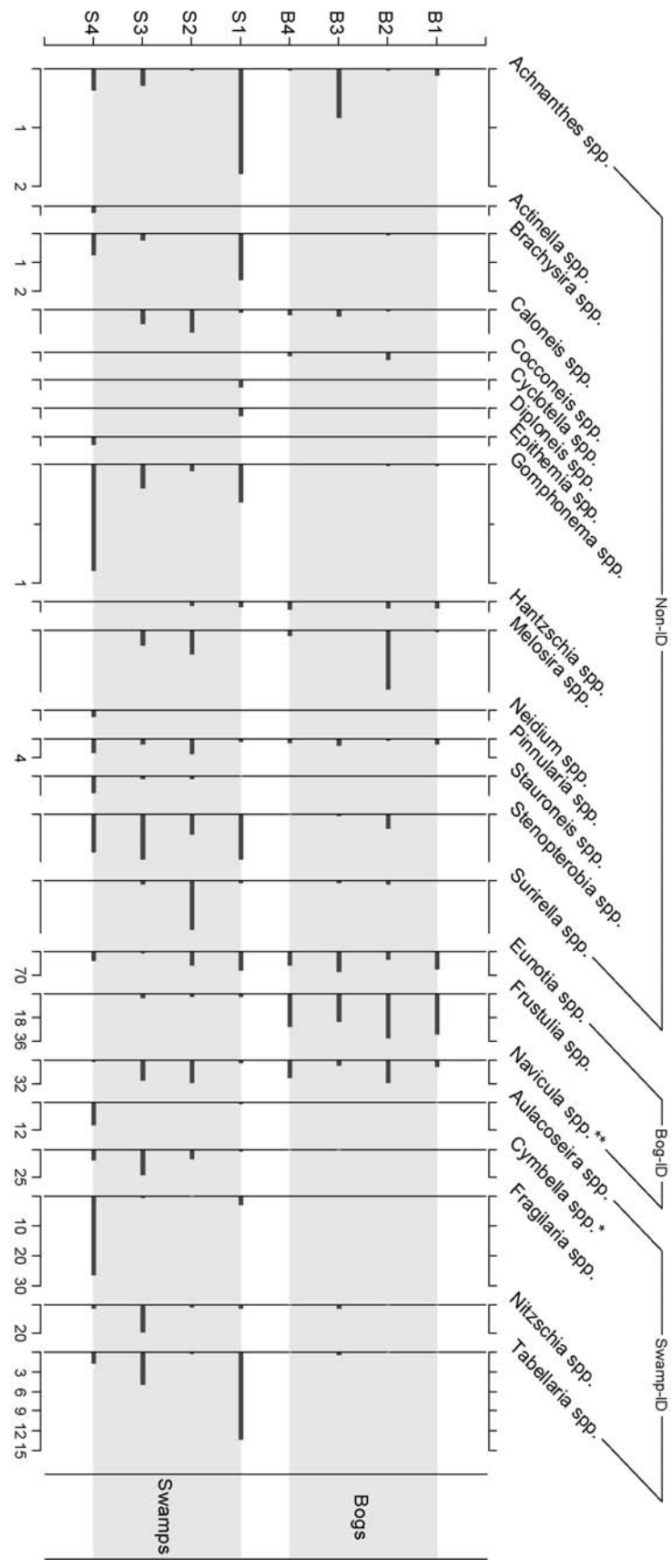


Figure 3.13. Relative proportions and type-specific indicator groups (ID) of benthic diatom genera in bogs and swamps. * Taxa belonging to the genera *Cymbella, Cymbopleura, Encyonema, Encyonopsis*; ** Taxa belonging to the genera *Adlafia, Chamaepinnularia, Diadesmis, Fallacia, Hippodonta, Luticula, Mayamaea, Navicula, Naviculadicta, Sellaphora*

sensu lato, but S3 features larger proportions of *Cymbella* sensu lato, *Nitzschia*, and *Tabellaria*. On the other hand, S2 holds more than 50 % *Eunotia* and a larger percentage of *Pinnularia*.

Table 3.4. Pairwise ANOSIM comparisons of diatom samples from bogs and swamps (genus level); 2-sided significance levels $p \leq 0.05$ (**) and $p \leq 0.1$ (*); adjusted with *bonferroni* correction.

	B2	B3	B4	S1	S2	S3	S4
B1	ns	ns	ns	0.613**	0.888**	0.979**	0.955**
B2		0.444*	ns	0.732*	0.956*	0.976*	0.976*
B3			ns	0.404*	0.652*	0.920*	0.896*
B4				0.634**	0.791**	0.963**	0.951**
S1					0.636**	0.608**	0.468**
S2						0.908**	0.800**
S3							0.728**

If ***diatom families*** are considered in the analysis of similarities between wetlands, the observed differences at the species level (chapter 3.3.2.2) can not be reproduced. Although the global test statistic is still significant ($R = 0.491$; $p = 0.001$), a clear separation of the different wetland sites at the family level is not feasible.

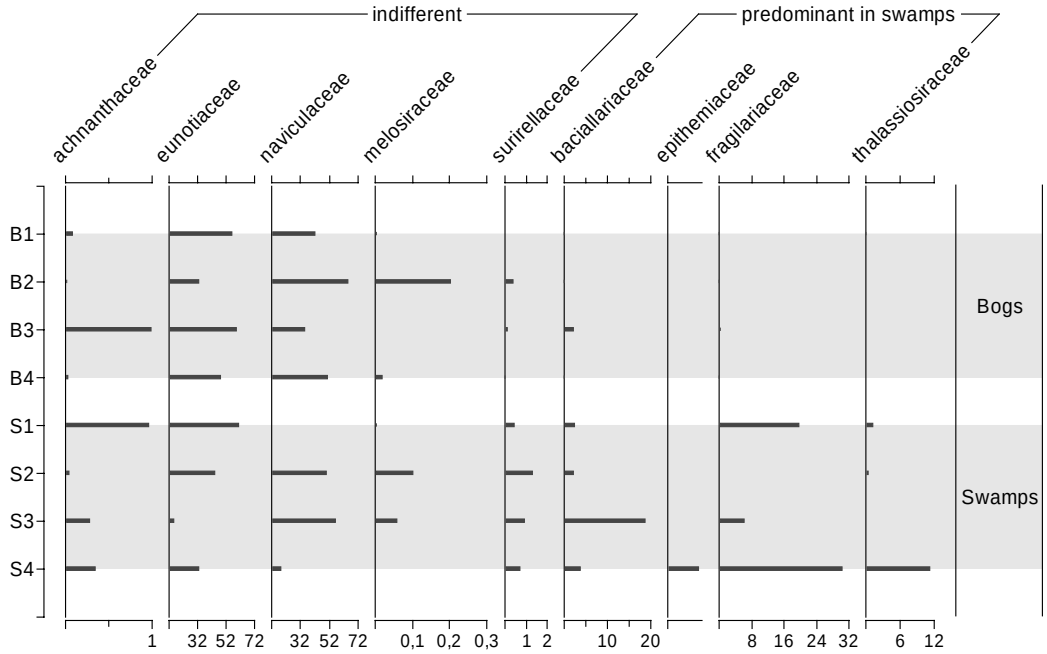


Figure 3.14. Relative proportions of benthic diatom families in bogs and swamps

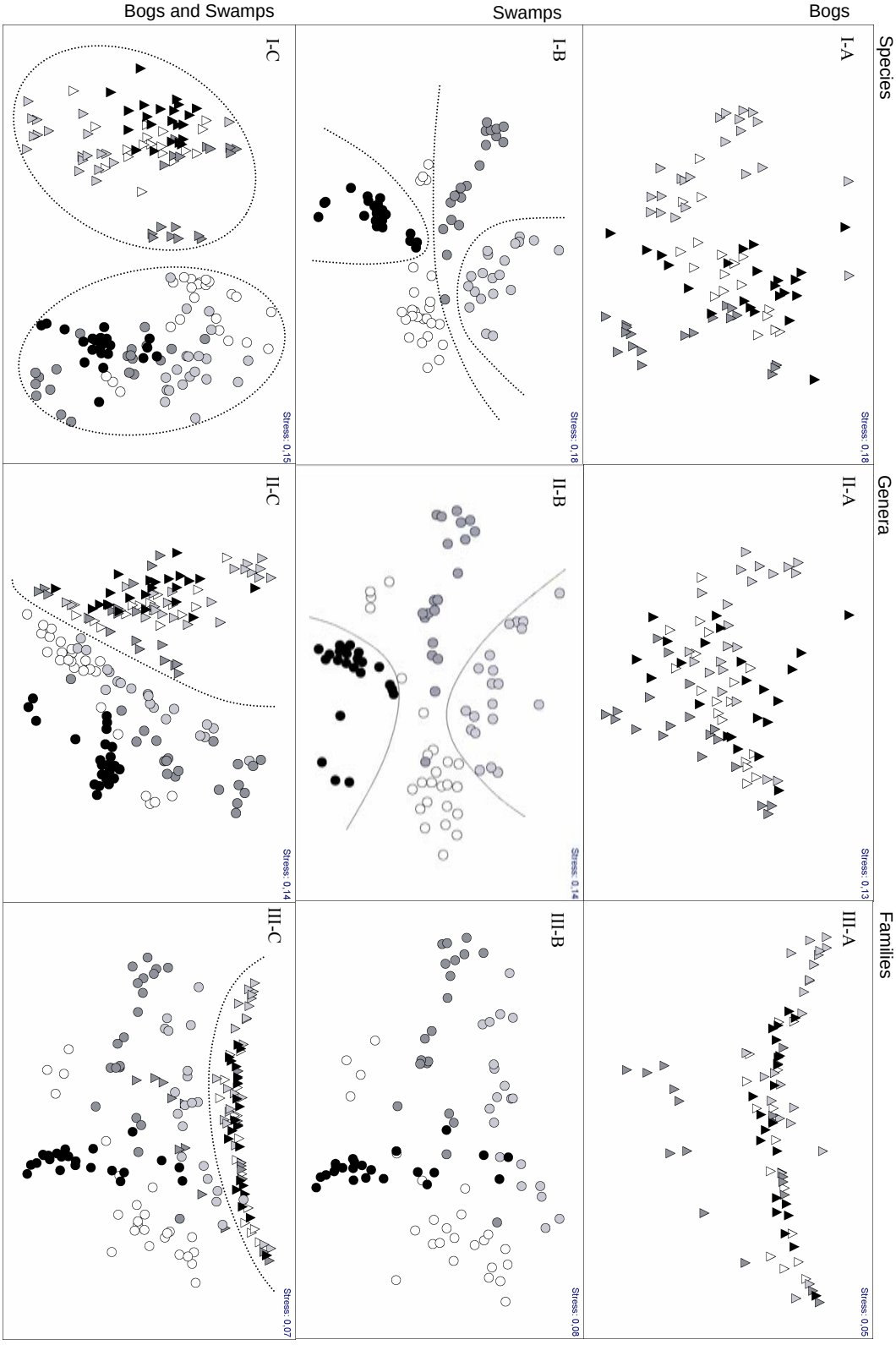


Figure 3.15. MDS ordination including diatom samples from either bogs (A), swamps (B) or both wetland types (C) on the basis of diatom species (I), genera (II) and families (III). B1 (△); B2 (▲); B3 (▲); B4 (▲); S1 (○); S2 (●); S3 (●); S4 (●).

The MDS ordination of bog samples based on diatom families (figure 3.15 AIII) is very different from that obtained by analysis of species (figure 3.15 AI), and apart from a few samples belonging to B3, sample points can barely be separated. Correspondingly, no significant differences among diatom families in bogs could be detected by either the global ANOSIM test ($R = 0.062$; $p = 0.181$) or pairwise comparisons (table 3.5) in contrast to the analysis of similarities at the species level.
Similarly, swamp samples close ranks in the MDS based on the relative proportions of diatom families (figure 3.15 BIII), and the separation of wetland groups is less obvious than for species data (figure 3.15 BI). This result is also reflected by the analysis of similarities over all swamps ($R = 0.581$; $p = 0.001$) and pairwise comparisons between minerotrophic wetlands (table 3.5).

Table 3.5. Pairwise ANOSIM comparisons of diatom samples from bogs and swamps (family level); 2-sided significance levels $p \leq 0.05$ (**), $p \leq 0.1$ (*); adjusted with *bonferroni* correction.

	B2	B3	B4	S1	S2	S3	S4
B1	ns	ns	ns	0.603**	ns	0.803**	0.851**
B2		ns	ns	0.768*	ns	0.684*	0.896*
B3			ns	0.432*	ns	0.540*	0.672*
B4				0.795**	0.409**	0.799**	0.903**
S1					0.640**	0.588**	0.348**
S2						0.580*	0.760*
S3							0.660**

Differences between wetland types

As with species data, significant differences between wetland types could also be detected by analysis of similarities ($R = 0.750$; $p = 0.029$) and multidimensional scaling (figure 3.15 CII) at the ***genus level***. Most genera occur in both wetland classes, but the relative proportions differ with respect to habitat type (cp. figure 3.13). For example, *Frustulia* is less abundant in swamps, whereas *Aulacoseira*, *Cymbella* sensu lato, *Melosira*, *Nitzschia*, and *Tabellaria* occur in larger numbers than in bogs. *Cyclotella*, *Cymbella*, *Cymbopleura*, *Diploneis*, *Encyonopsis*, *Epithemia*, *Fragilaria*, *Hippodonta*, *Neidium*, and *Stauroneis* appear to be specific to the swamp wetland type.
Wetland classes could also be differentiated by multidimensional scaling of samples based on ***diatom families*** (figure 3.15 CIII), even though some sites of wetland B3 intermix with swamp communities. This is due to larger proportions of *Bacillariaceae* and *Fragilariaceae*, which predominate in minerotrophic wetlands (figure 3.14).

Naviculaceae, *Eunotiaceae*, and *Surirellaceae* are present in both wetland types, leading to a significant mid-range value in the analysis of similarities ($R = 0.573$; $p = 0.029$).

3.4.3 Univariate measures of benthic diatom diversity

Diversity indices provide a univariate measure of the number and distribution of species in a sample. The most frequently applied indices, i.e. Margalef's index, Shannon-Wiener diversity, Pielou's evenness, and the Simpson index were calculated for benthic bog and swamp diatom communities to assess patterns in species diversity across wetlands. Diversity thereby refers to α–diversity, which, according to Whittaker (1972), is defined as the diversity of species within community sample plots. In addition, biodiversity measures based on the relatedness of species provide a measure of the taxonomic distinctness and taxonomic diversity among diatom assemblages.

Interrelation between diversity indices

Diversity measures are based on attributes of community structure, such as the total number of individuals (N), total number of species (S) or the average number of individuals per species (N/S). In contrast, the average taxonomic distinctness and average taxonomic diversity indices are not just based on species abundances, but take into account the taxonomic distances within species assemblages (cp. chapter 3.3.3.5). Therefore, it is important to compare the performance of the different methods, if they are applied to the same set of samples.

Table 3.6. Pearson correlation coefficients between univariate diversity measures ($n = 44$ sites; 2-sided *bonferroni* corrected significance level: $p \leq 0.05$). S = species number, d = Margalef's index, J' = Pielou's evenness, H' = Shannon diversity, 1-λ = Simpson diversity, Δ = Taxonomic diversity, Δ* = Taxonomic distinctness.

	N	d	J'	H'	1-λ	Δ	Δ*
S	0.804	1.000	0.675	0.887	0.680	0.777	0.522
N		0.799	0.582	0.735	0.557	0.601	0.373
d			0.676	0.889	0.683	0.780	0.523
J'				0.932	0.956	0.859	0.393
H'					0.919	0.893	0.464
1-λ						0.894	0.412
Δ							0.751

The perfectly linear relationship between the number of species (S) and Margalef's index (d) verifies that slight deviations in the number of individuals counted per sample do not affect species numbers (figure 3.16). Within the actual range of valves identified on

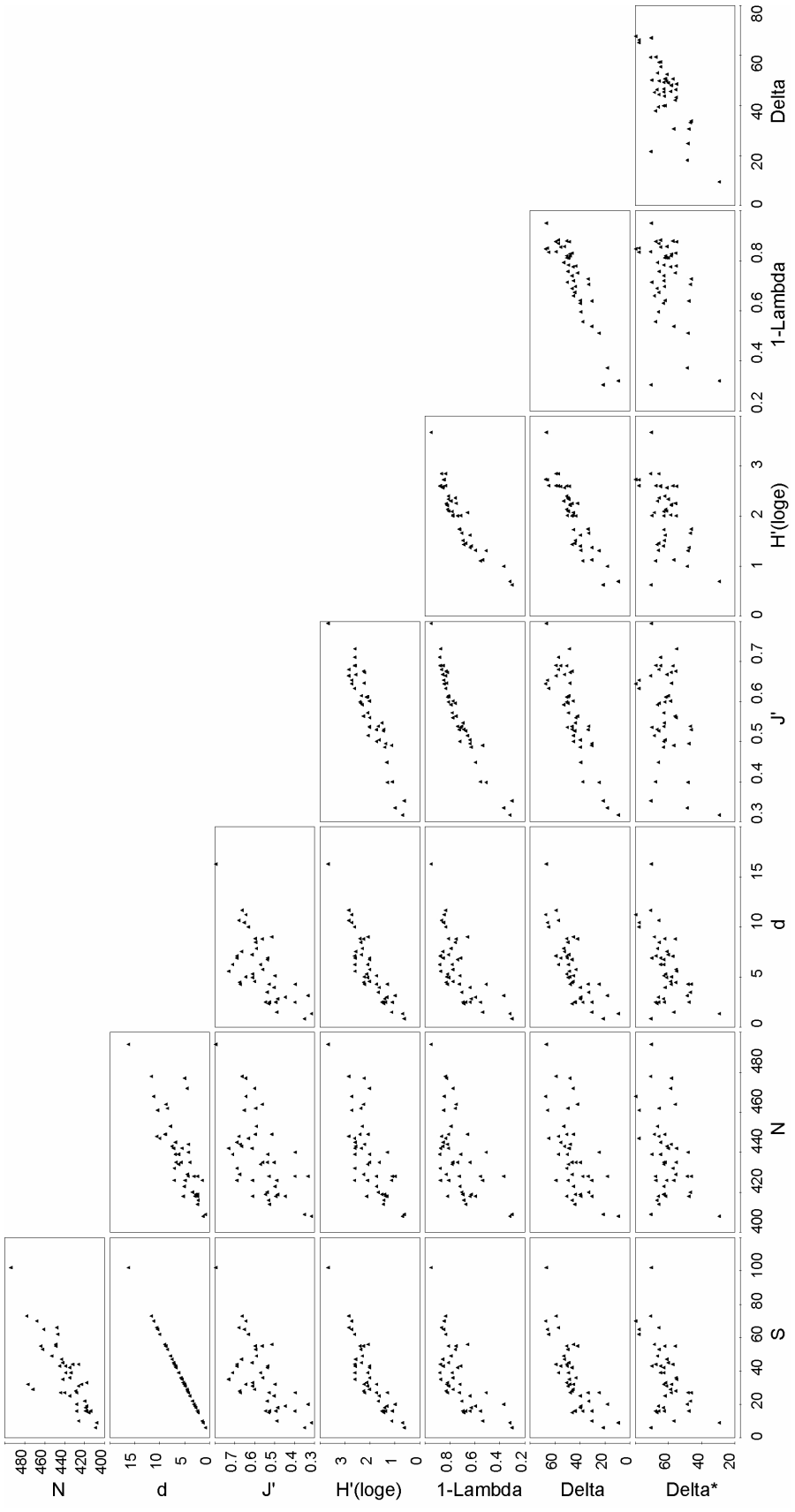


Figure 3.16. Scatter plots of the diversity measures applied to benthic diatom communities from bog and swamp sites (n = 44)

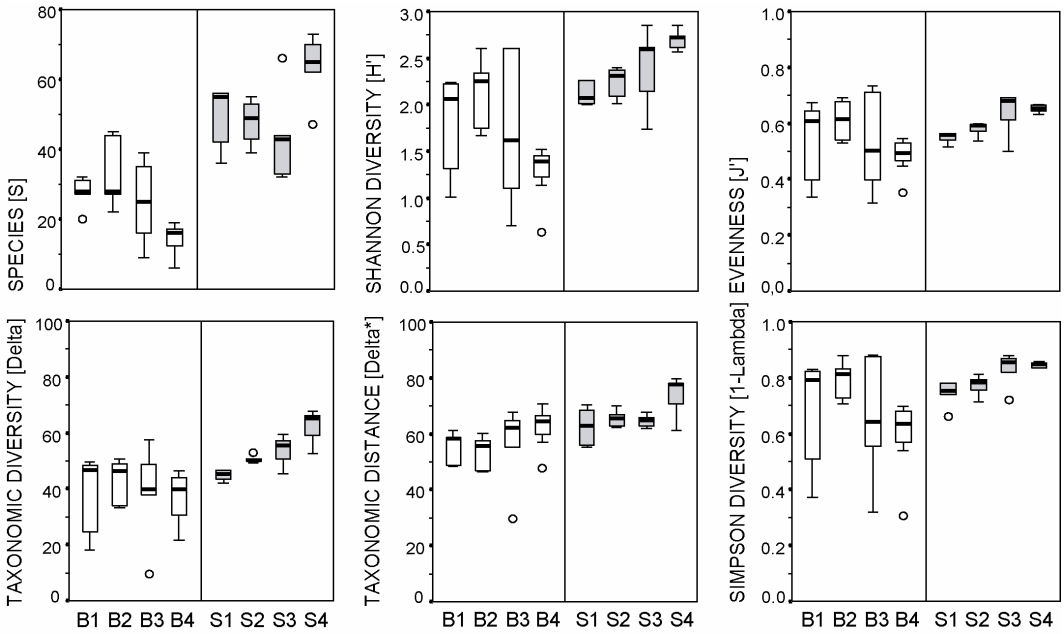


Figure 3.17. Box and whiskers plots for different diversity measures applied to benthic diatom communities from bogs and swamps. Number of replicate sites in bogs (white bars): n = 6 (B1), 5 (B2), 5 (B3), 8 (B4); number of replicate sites in swamps (filled bars): n = 5 (S1, S2, S3, S4). Taxonomic levels in Δ and Δ* are equally weighed.

Table 3.7. Means and standard deviations for diversity index values. S = species numbers, d = Margalef's index, J' = Pielou's evenness, H' = Shannon diversity, 1-λ = Simpson diversity, Δ = Taxonomic diversity, Δ* = Taxonomic distinctness.

	Bogs					Swamps				
	B1	B2	B3	B4	Mean	S1	S2	S3	S4	Mean
n	*6*	*5*	*5*	*8*	*24*	*5*	*5*	*5*	*5*	*20*
S	28 ± 2	33 ± 5	25 ± 6	15 ± 2	24 ± 2	58 ± 12	48 ± 3	44 ± 6	63 ± 5	53 ± 4
d	4.37 ± 0.28	5.31 ± 0.77	3.92 ± 0.92	2.24 ± 0.25	3.76 ± 0.35	9.32 ± 1.85	7.67 ± 0.48	7.01 ± 0.99	10.17 ± 0.72	8.54 ± 0.60
J'	0.54 ± 0.06	0.61 ± 0.03	0.53 ± 0.08	0.48 ± 0.02	0.54 ± 0.02	0.59 ± 0.05	0.58 ± 0.01	0.63 ± 0.04	0.65 ± 0.01	0.62 ± 0.02
H'	1.82 ± 0.21	2.12 ± 0.18	1.73 ± 0.39	1.28 ± 0.10	1.68 ± 0.12	2.41 ± 0.32	2.24 ± 0.08	2.39 ± 0.20	2.70 ± 0.05	2.43 ± 0.10
1-λ	0.69 ± 0.08	0.79 ± 0.03	0.66 ± 0.11	0.60 ± 0.05	0.67 ± 0.03	0.78 ± 0.05	0.77 ± 0.02	0.83 ± 0.03	0.85 ± 0.00	0.81 ± 0.02
Δ	39 ± 6	43 ± 4	39 ± 8	37 ± 3	39 ± 2	49 ± 5	51 ± 1	54 ± 3	62 ± 3	54 ± 2
*Δ**	56 ± 2	53 ± 3	56 ± 7	62 ± 3	57 ± 2	63 ± 3	66 ± 1	65 ± 1	73 ± 3	67 ± 1

average per site, that is 408 to 494 individuals, the denominator in equation 3.8 (chapter 3.3.3.5) varies between 6.01 and 6.20, thus remaining reasonably stable. Pielou's evenness, Shannon diversity and Simpson diversity are also highly correlated (cp. figure

3.16), either measure being equally valid for estimating species diversity of the benthic diatom assemblages studied. The average taxonomic diversity tracks Simpson diversity fairly closely; yet the average taxonomic distinctness should be seen as a subsidiary, independent diversity measure, as the dominating effect of the species abundance distribution is removed and the taxonomic hierarchy within samples is more purely reflected.

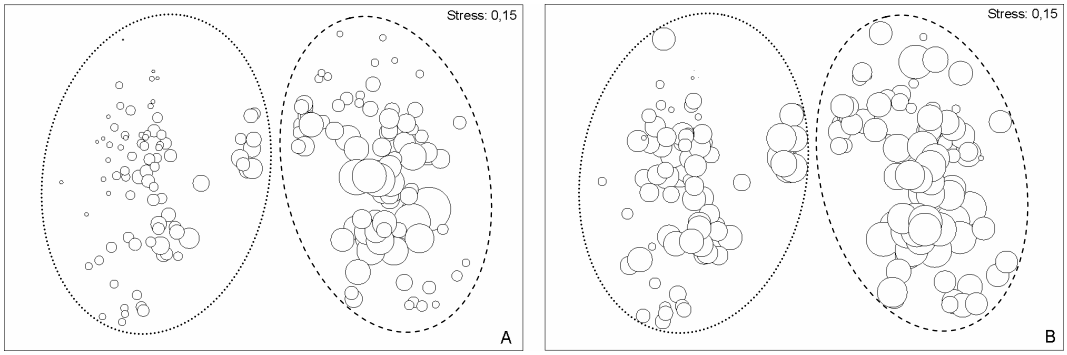


Figure 3.18. Bubble plots based on the MDS ordination of diatom samples (cp. figure 3.15 I-C) from bogs (- - - -) and swamps (— —). A: number of species (S); B: Taxonomic diversity (Δ)

Spatial differences and variability

At a significance level of $p = 0.05$, the Mann-Whitney U test (cp. chapter 2.3.4.7) indicated that all of the applied diversity measures differentiated between ***wetland types*** (for details see Appendix, Part B), i.e. diversity is consistently higher in swamps (cp. table 3.7). However, most distinctive were species numbers and taxonomic diversity observed in the diatom communities studied, while Pielou's evenness, Shannon diversity, Simpson diversity and average taxonomic distinctness revealed only minor differences, their ranges overlapping to a large degree (cp. figure 3.17). Apart from species numbers and the average taxonomic distinctness, variability in the distribution of species across wetland sites appeared to be higher in ombrotrophic wetlands. Increased variability in this type of wetland is quantified by the Index of Multivariate Dispersion (IMD), the relative dispersion of bog sites being 0.826 as opposed to 1.200 in swamps for the respective diversity measures. Bubble plots (cp. chapter 3.3.3.2, p. 45) of the most distinctive diversity measures overlying the MDS ordination of diatom samples (figure 3.18) produce a good match with respect to the separation of wetland types, yet some information in the structure of the diatom communities is not adequately represented by applying univariate diversity measures.

Benthic diatom diversity also differed among ***wetlands*** of a specific type. Within ombrotrophic wetlands, B4 maintained the smallest species numbers, therefore being characterised by the lowest average evenness, Shannon, Simpson, and taxonomic diversity, while diatom communities in B2 were the most diverse within this wetland

type. On the other hand, taxonomic distinctness was highest in B4 and lowest in B2, pointing to a larger proportion of closely related taxa, i.e. species relative to diatom genera or families. Among wetlands of the swamp type, S4 comprised the most diverse diatom communities in terms of abundances and taxonomic distances in species assemblages. In contrast, wetland S1 featured the lowest diversity and taxonomic distinctness, but hosted a comparably large number of species.

3.4.4 Links between diatom diversity and the abiotic environment

Multivariate interrelations between benthic diatoms and their environment were examined by employing rank correlation between a fixed species similarity matrix and a data matrix containing abiotic variables (BIO-ENV). Canonical Correspondence Analysis (CCA) served as a cross-check between parametric and non-parametric techniques. Additional information was obtained by correlating univariate diversity measures with the environmental data acquired.

3.4.4.1 Relating multivariate data sets

Environmental gradients influencing diatom distribution across wetland types

Corresponding to the results of the PCA shown in chapter 3.4.3 (figure 2.5), the BIO-ENV procedure points to pH being the most important single abiotic factor in the ordination of benthic diatom communities from bogs and swamps ($\rho = 0.788$). With a maximum of four variables included, pH, alkalinity, calcium, and gilvin explain most of the variability in diatom community structure ($\rho = 0.775$). If the analysis is carried out at the genus level, the best correlation between biotic and abiotic variables is obtained with pH and alkalinity ($\rho = 0.608$), though inclusion of calcium and silica does not alter the result (cp. Appendix, Part B). At the family level, the same set of environmental variables most closely relates to the ordination of diatom samples. However, the correlation is distinctly weaker ($\rho = 0.483$) at this level of taxonomic resolution.

Canonical correspondence analysis yielded the same result in the ordination of diatom samples at the species level. Bogs and swamps were differentiated along the first canonical axis (figure 3.19), which is highly correlated to pH ($\rho = -0.960$), alkalinity ($\rho = -0.876$), gilvin ($\rho = 0.760$), and calcium ($\rho = -0.756$), explaining 29.8 % of the species-environment correlation. Taxa tolerating highly acidic conditions and low light penetration are *Chamaepinnularia begeri*, *Eunotia paludosa*, and *Frustulia saxonica*, while *Gomphonema gracile*, *Fragilaria nanoides*, and *Stenopterobia curvula* are situated at the other end of this gradient. CCA axis 2 accounts for another 12.1 % and is significantly correlated with chloride ($\rho = -0.523$), thus representing a gradient in ion supply by rainfall (cp. chapter 2). Taxa such as *Cymbopleura naviculiformis*, *Eunotia musicola*, and *Stauroneis anceps* appear to be better adopted to low ion concentrations

than *Adlafia bryophila*, *Navilula indifferens*, or *Tabellaria ventricosa*. By forward selection, a subset of abiotic variables comprising pH, alkalinity, gilvin, calcium, silica, water depth, periphytic chlorophyll-*a*, magnesium, and chloride were included in the analysis, resulting in 58.1 % of variation explained by the first two axes, i.e. 43.5 % by axis 1 and 14.6 % by axis 2.

Environmental controls on the distribution of benthic diatoms within wetland types

The distribution of diatom species in ***bogs*** is best matched by a combination of sulphate deficit, calcium concentrations, ca:mg ratio, and corrected conductivity ($\rho = 0.611$). A rather different set of abiotic variables, that is plankton chlorophyll-*a*, sulphate, calcium, ca:mg ratio, anion deficit, and sodium surplus, produces the best match with the ordination of bog samples based on diatom genera, but the correlation in this case is very low ($\rho = 0.366$). At the family level, the correlation between the smallest set of environmental variables and diatom data is even weaker ($\rho = 0.359$). Periphyton (as) chlorophyll-*a*, corrected conductivity, ca:mg ratio, anion deficit, and sodium surplus produce the best match with the ordination of diatom samples. The inclusion of alkalinity and calcium deteriorates the result only marginally, if at all.
In the CCA of bog samples (figure 3.20) 40.1 % of the variation in species data are explained by the first two axes, in which axis 1 accounts for 20.7 % and axis 2 for another 19.4 %. Calcium ($\rho = -0.835$), chloride ($\rho = -0.648$), and the total sum of ions ($\rho = -0.579$) were significantly correlated to axis 1, while sulphate deficit ($\rho = -0.590$), gilvin ($\rho = -0.573$), and pH ($\rho = 0.514$) contributed significantly to axis 2. If canonical correspondence analysis is restricted to these variables, the proportion of the variation explained by the first two axes mounts to 64.3 %, with 33.6 % contributed by axis 1 and 30.7 % by axis 2. Higher ion concentrations seem to be preferred by *Chamaepinnularia mediocris* and *Pinnularia perriorata*, which are also present in the swamp wetland type (cp. figures 3.11 and 3.12), while *Frustulia pangaeopsis* and *Frustulia saxonica* morphotype I grow under poorest conditions.

In the ***swamp wetland type***, potassium, silica, and water temperature were most closely related to the ordination of diatom samples at the species ($\rho = 0.592$) and genus ($\rho = 0.533$) level. With respect to diatom families, water temperature was replaced by corrected conductivity ($\rho = 0.561$).
Canonical correspondence analysis yielded similar results in comparison to the non-parametric approach (figure 3.21), though the environmental variables described for the BIO-ENV procedure represent only part of the abiotic discriminators obtained by CCA. Periphyton (as) chlorophyll-*a* concentrations ($\rho = 0.710$), alkalinity ($\rho = 0.650$), corrected conductivity ($\rho = 0.597$), and sulphate ($\rho = -0.525$) were significantly correlated to axis 1, accounting for 21.6 % of the variation in the biotic data set. On the other hand, the second

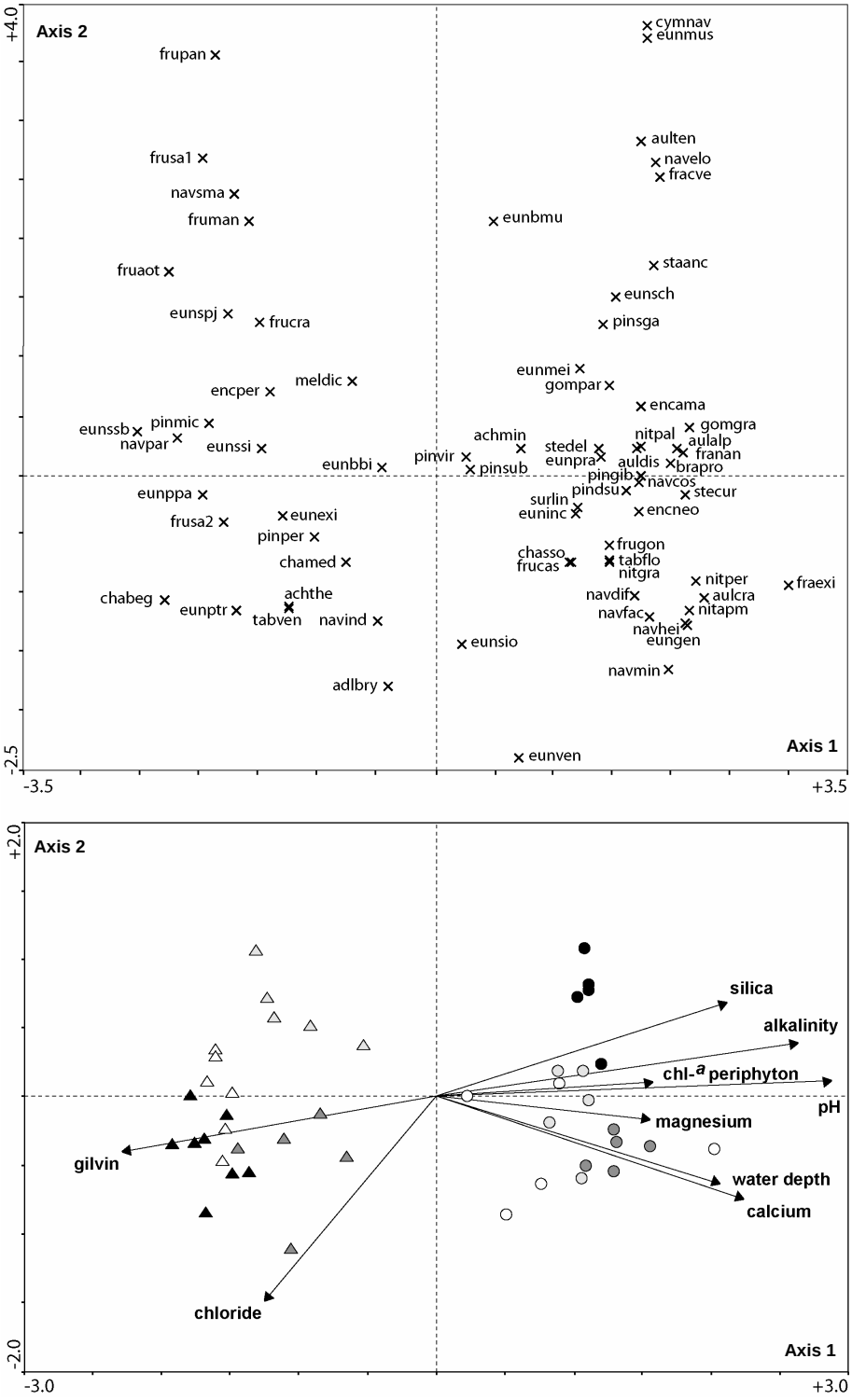
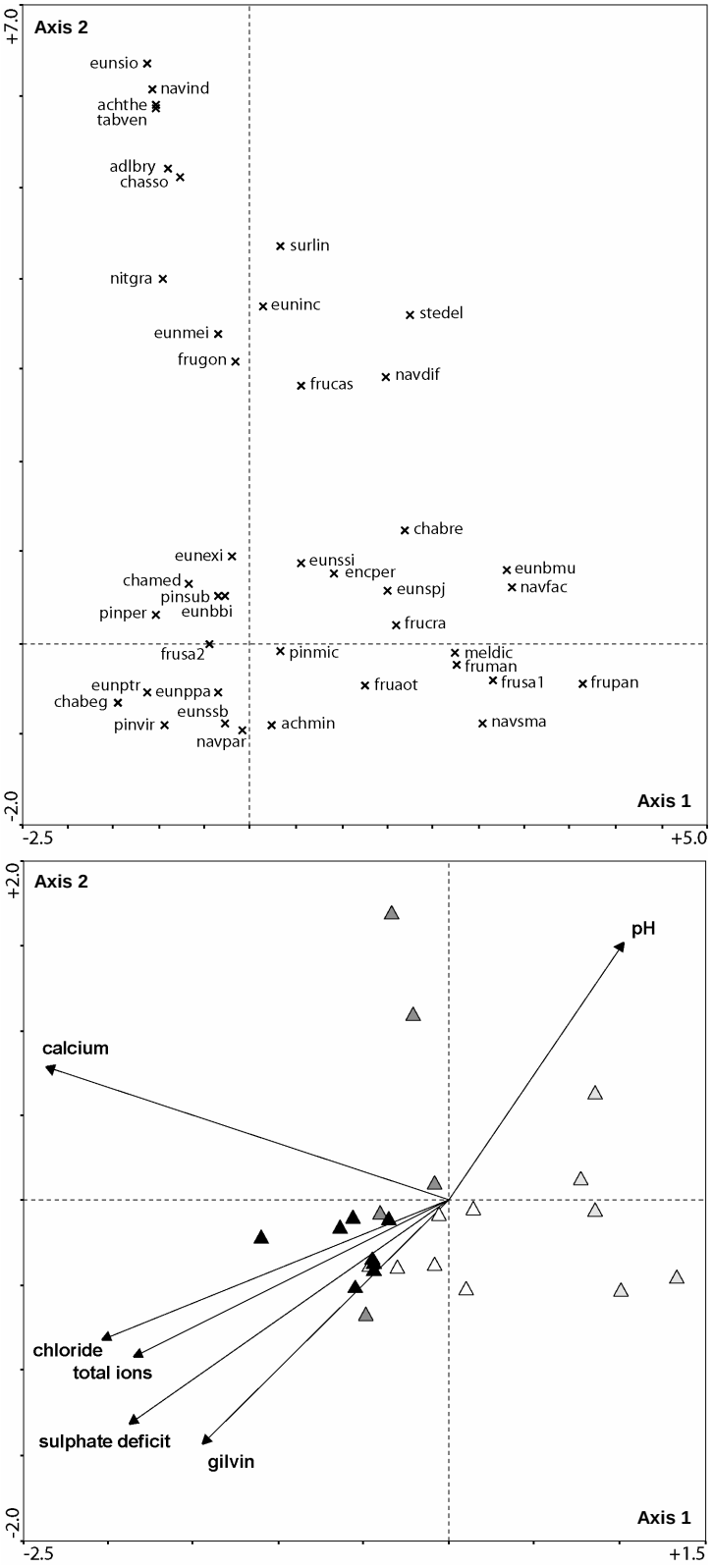


Figure 3.19. CCA wetlands; species plot reduced to dominant and subdominant taxa. B1 (△); B2 (▲); B3 (▲); B4 (▲); S1 (○); S2 (●); S3 (●); S4 (●). Abbreviations cp. figure 3.20.



achmin *Achnanthes minutissima*
achthe *A. thermalis*
adlbry *Adlafia bryophila*
aulalp *Aulacoseira alpigena*
auldis *A. distans*
aulcra *A. crassipunctata*
aulten *A. tenuior*
brapro *Brachysira procera*
chabeg *Chamaepinnularia begeri*
chamed *C. mediocris*
chasso *C. soehrensis* var. *soehrensis*
cymnav *Cymbopleura naviculiformis*
encama *Encyonema amanianum*
encneo *E. neogracile*
encper *E. perpusillum*
eunbil *Eunotia bilunaris* var. *bilunaris*
eunbmu *E. bilunaris* var. *mucophila*
eunexi *E. exigua*
eungen *E. genuflexa*
euninc *E. incisa*
eunmei *E. meisteri*
eunmus *E. musicola*
eunpal *E. paludosa* var. *paludosa*
eunptr *E. paludosa* var. *trinarcria*
eunsch *E. schwabei*
eunsio *E. siolii*
eunspj *E.* spec. Nr.3 Julma Ölkky
eunssb *E.* spec. Nr.2 siolii (f. bidens)
eunssi *E.* spec. Nr.1 aff. siolii
eunven *E. veneris*
fracve *Fragilaria construens* f. *venter*
fraexi *F. exigua*
franan *F. nanoides*
fruaot *Frustulia aotearoa* nov. spec.
frucas *F. cassiae* nov. spec.
frucra *F. crassinervia*
frugon *F. gondwana* nov. spec.
fruman *F. magaliesmontana*
frupan *F. pangaeopsis*
frusa1 *F. saxonica* morphotype I
frusa2 *F. saxonica* morphotype II
gomgra *Gomphonema gracile*
gompar *Gomphonema parvulum*
meldic *Melosira dickei*
navfac *Navicula* spec. aff. *facilis*
navhei *N. heimansioides*
navind *N. indifferens*
navmin *N. minima*
navcos *Naviculadicta cosmopolitana*
navdif *N. difficilima*
navelo *N. elorantana*
navpar *N. parasubtilissima*
navsub *N. subtilissima*
nitapm *Nitzschia alpinobacillum*
nitgra *N. gracilis*
nitpal *N. palea*
nitper *N. perminuta*
pindsu *Pinnularia divergens* var. *sublinearis*
pingib *P. gibba*
pinmic *P. microstauron*
pinper *P. perriorata*
pinsga *P. subgibba*
pinsub *P. subcapitata*
pinvir *P. viridiformis*
staanc *Stauroneis anceps*
stecur *Stenopterobia curvula*
stedel *S. delicatissima*
surlin *Surirella linearis*
tabfloc *Tabellaria flocculosa*
tabven *T. ventricosa*

Figure 3.20. CCA bogs; species plot reduced to dominant and subdominant species. B1 (△); B2 (▲); B3 (▲); B4 (▲).

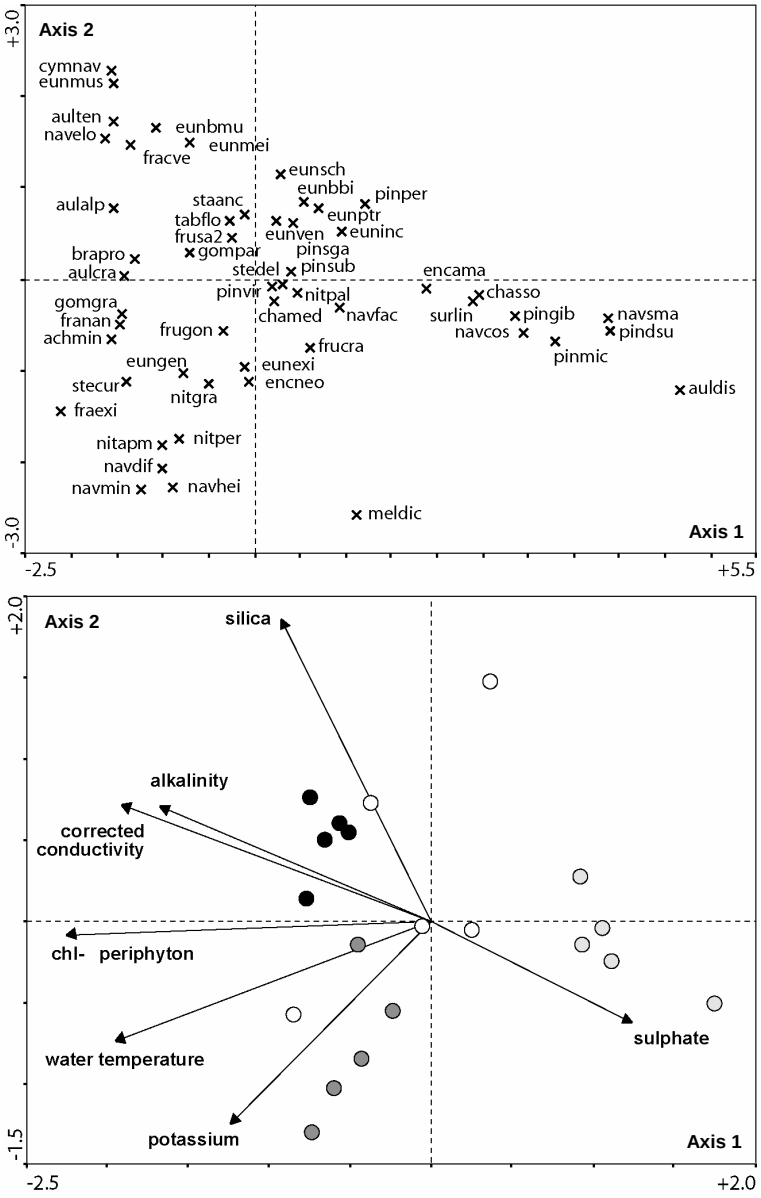


Figure 3.21. CCA swamps; species plot reduced to dominant and subdominant taxa. S1 (○); S2 (●); S3 (●); S4 (●). Abbreviations cp. figure 3.20.

canonical axis is significantly related to potassium ($\rho = 0.548$), water temperature ($\rho = 0.533$), and silica ($\rho = -0.526$), explaining another 19.6 % of the variation. Forward selection lead to an increase from 40.2 % to 51.3 % of the total variation explained, in which 28.9 % are contributed by axis 1 and 21.4 % by axis 2. Of the dominant and subdominant species present, *Achnanthes minutissima*, *Aulacoseira crassipunctata*, and *Gomphonema gracile* have their average distribution maximum in a highly productive environment, whereas *Chamaepinnularia soehrensis* var. *soehrensis* and *Encyonema amanianum* mainly occur at cooler and less productive sites.

3.4.4.2 Bivariate correlations

In ***bogs***, significant correlations were derived between the total sum of ions, sodium, chloride, sulphate deficit, and pH on the one hand, and the number of species (S), Margalef's index (d), Pielou's evenness (J'), Shannon index (H'), and Simpson index (1-λ) on the other hand (table 3.8). Diversity generally increased with pH, while the other environmental factors that are related to ion supply and productivity, were negatively correlated to the abundance and distribution of species. This corresponds to the results obtained by the PCA of abiotic features in ombrotrophic wetlands; yet pH did not play a significant role in the ordination of chemistry and biomass samples (cp. figure 2.6). Taxonomic diversity was also higher at less acidic sites, whereas the average taxonomic distinctness did not show any significant relationship to either of the environmental variables.

In ***swamps***, species richness is positively correlated to calcium, alkalinity, pH, and nitrate. Evenness increases with epipelon chlorophyll-*a* concentrations, pH, and alkalinity, while Shannon diversity is related to pH, alkalinity, and calcium concentrations. Simpson diversity and average taxonomic distinctness did not show any significant correlation with the environmental variables studied.

Table 3.8. 2-sided Pearson correlation coefficients (*bonferroni* corrected $p \leq 0.05$) between diversity measures and environmental variables for bogs (n = 24 sites) and swamps (n = 20 sites; Chl 4: n = 10 sites); suldef = sulphate deficit, Chl 4 = Chl-*a* epipelon, S = species number, d = Margalef's index, J' = Pielou's evenness, H' = Shannon diversity, 1-λ = Simpson diversity, Δ = Taxonomic diversity, Δ* = Taxonomic distinctness.

	Bogs						Swamps			
	ionsum	suldef	pH	Na^+	Cl^-	NO_3^-	Chl 4	alk	pH	Ca^{2+}
S	-0.685	-0.695	0.760	-0.650	-0.668	0.649	-	0.697	0.693	0.703
d	-0.683	-0.694	0.763	-0.647	-0.667	0.648	-	0.697	0.693	0.705
J'	-0.662	-0.650	0.631	-0.693	-0.626	-	0.878	0.640	0.640	-
H'	-0.713	-0.714	0.709	-0.720	-0.683	-	-	0.720	0.789	0.683
1-λ	-0.645	-0.625	0.624	-0.644	-0.628	-	-	-	-	-
Δ	-	-	0.611	-	-	-	-	-	0.690	-
Δ*	-	-	-	-	-	-	-	-	-	-

3.4.4.3 Weighted averaging

Detrended canonical correspondence analysis revealed that pH, alkalinity, silica, and gilvin fulfilled the criteria for the establishment of transfer functions (cp. chapter 3.3.3.8). The model for pH performed best ($R^2 = 0.95$, RMSEP = 0.19 pH units), though alkalinity ($R^2 = 0.89$, RMSEP = 0.52 sqr.rt μeq l^{-1}), gilvin ($R^2 = 0.76$, RMSEP = 2.57 g_{440} m^{-1}), and

silica (R^2 = 0.76, RMSEP = 0.38 sqr.rt mg l^{-1}) models also predicted the observed values sufficiently well (cp. Appendix, Part B). The transfer function for silica was refined by removing an outlier.

3.5 Discussion

Future wetland management and the design of elaborate research programmes dealing with wetland ecosystems in New Zealand require fundamental knowledge of the abiotic and biotic characteristics and processes operating within the area of interest. Appropriate sampling strategies and cost efficiency can only be accomplished by taking into account temporal variability and habitat heterogeneity at various levels. The following discussion covers critical points with respect to the use of artificial substrates in the assessment of benthic diatom diversity and the indicative capacities of benthic diatom communities in New Zealand lowland wetlands. In addition, aspects influencing stability and resilience of microphytobenthos and affiliated implications for future wetland research and monitoring are addressed.

3.5.1 Representativeness of diatom communities from artificial substrata

Algal characteristics can vary considerably among habitats within wetlands or wetland sites. During the last decades there has been wide discussion whether periphyton grown on artificial substrata is representative in terms of species composition and abundance, if compared to naturally occurring substrates (e.g. Castenholz 1960, Tippet 1970, Weitzel et al. 1979, Stevenson and Lowe 1986, Aloi 1990, Cattaneo and Amirault 1992). Artificial substrates allow for a more standardised sampling design (Tuchman and Stevenson 1980, Meier et al. 1983), and temporal variation as well as substrate specific features, e.g. the potential release of nutrients (Allen 1971, Harlin 1973, McRoy and Goering 1974, Howard-Williams and Davies 1978, Pip and Robinson 1982, Ács and Buczkó 1994, Ács et al. 2003) or allelopathic substances (Wium-Anderson et al. 1982, Burkholder and Wetzel 1990) can be eliminated or at least controlled. Stevenson et al. (2002) presume that, even though periphyton communities developing on introduced substrata may differ in certain respects from those growing on natural substrates, this type of sampling provides a reliable indicator of wetland nutrient status and other changes in water chemistry (see also McCormick et al. 1996). Recent evidence also indicates that samples from targeted habitats, i.e. artificial substrates, more precisely indicate wetland change than composite samples from multiple habitats (Stevenson et al. 2002).

However, there are no definite guidelines concerning exposure times or material and texture of the artificial substrate (cp. Biggs 1988, Cattaneo and Amireault 1992, Kelly et al. 1998). As a consequence, sloughing or insufficient biomass accrual can pose severe problems depending on ambient nutrient levels and the growth rate of algae constituting

the biofilm. Stevenson et al. (2002) state, that the determination of a standardised incubation period can be difficult when working in wetlands of widely varying trophic status as in the present study. The development of periphyton (as) at the studied wetland sites and thus representativeness of benthic diatom communities from artificial substrates, therefore, depend on a range of intrinsic factors such as colonisation processes, substrate characteristics, and natural variation.

3.5.1.1 Colonisation processes and community development

Whether benthic diatom communities from artificial substrates are representative of natural assemblages depends on the developmental stage of the biofilm. Both periphyton (as) community structure and biomass are indicative of the maturity, and thus representativeness of microphytobenthos assemblages.
Biofilms form through a complex succession of organisms, usually starting with carbohydrates, followed by bacteria, photoautotrophs, and microzoobenthos. Patrick (1976) found that prostrate diatoms colonised surfaces during the initial period of biofilm development, followed by the attachment of taxa possessing mucilaginous pads or stalks (cp. Howard-Williams and Davies 1978, Korte and Blinn 1983, Ács and Kiss 1993, Albay and Akcaalan 2003). Stevenson and Peterson (1989) also stated that the initial colonisers were species which dispersed effectively, while taxa which reproduced rapidly were the dominant forms at later succession stages. At last, highly competitive species immigrate, and niche diversification and competitive interaction eventually lead to a more diverse taxonomic composition in the microphytobenthos (Patrick 1976, Hoagland et al. 1982, Korte and Blinn 1982, Sekar et al. 2004). These late successional stages usually support the highest biomass (cp. chapter 2).

Sampling routines mostly require that mature benthic communities are sampled (e.g. Kelly et al. 1998). This is usually given for epiphyton on fully developed but not senescent aquatic plants, epilithon and epipelon assemblages. However, sampling requirements are not easily implemented using artificial substrates, since colonisation rates and community development depend on nutrient availability (Biggs 1988, DeAngelis et al. 1989, Cattaneo and Amireault 1992) and dispersion parameters, that is the distribution of the present species pool within a given habitat.
Most of the wetland macrophytes sampled in early and late summer in 2002/2003 were characterised by a large percentage of rare diatom taxa, which is typical for late successional stages. Only plant species with floating leaves such as *Potamogeton suboblongus* and *Aponogeton distachyus* featured comparatively high proportions of diatom taxa in the mid and upper abundance ranks, which might be due to immaturity of the shoots or increased grazing pressure at the water surface. Epipelon assemblages proved to be the most stable benthic communities in both wetland types as indicated by

their cumulative abundance curves and highest average diversity. This is evidence of surface sediments acting as a natural integrator of the spatial and ecological patchiness of wetlands (Stevenson et al. 1998, Stevenson et al. 2002).
Periphyton (as) communities in the low productive bogs were characterised by a larger percentage of dominant taxa relative to epipelon and epiphyton, while the dominance structure of diatom assemblages in swamps did not differ between substrates. This might be an indication that, in ombrotrophic ecosystems, community development on polyethylene slides was still in a transitional stage after twelve weeks of exposure. For example, Rodríguez (1992) observed that mature microphytobenthos communities and pioneer stages on perspex slides took 29 weeks to converge towards a single, highly dynamic equilibrium in a slightly acidic, oligotrophic lake. However, it is assumed that equilibrium is reached somewhat earlier in the studied lowland wetlands, since no significant differences could be detected in the taxonomic composition of diatom communities from artificial and natural substrates. This might be explained by the increased dispersion and equal distribution of benthic algae and bacteria due to wind-induced mixing of the extremely shallow wetland pools (cp. chapter 2); potential changes in the community structure of bog periphyton (as) assemblages in the course of ongoing succession are likely to pertain to minor shifts in the relative abundances of diatom taxa, while the characteristic pattern of species occurrences should not be severely affected. Therefore, it is suggested that an incubation period of twelve weeks is sufficient to obtain representative periphyton samples from polyethylene slides in New Zealand lowland wetlands. Interannual climate variability, i.e. potential shifts in temperature during the growing season yet have to be considered, and an extension of exposure times may be sensible if mesotrophic or eutrophic wetlands are excluded from the analysis.

3.5.1.2 Material, texture, and orientation of artificial substrata

The choice of expedient material and exposure of the sampling device is essential to attain quick attachment and maximum growth of benthic algae on artificial substrata in low productivity environments. In this context, the promoting effect of bacterial films on the attachment and growth of diatoms on glass and other surfaces has been reported by many authors (Tosteson and Corpe 1975, Hunt and Parry 1998, Sekar et al. 2004) and was found to be most pronounced if conditions for algal community development were unfavourable (Fukami et al. 1989).
The surface texture of polyethylene proved to ameliorate colonisation by bacteria and diatoms, of which most attach by the production of EPS (Extracellular Polymeric Substances) in the form of stalks, apical pads, mucilage pads and cell coatings (Hoagland et al. 1993). Becker and Wahl (1991) and Becker (1996) found that the adherence of aquatic microorganisms was generally enhanced on hydrophobic surfaces, e.g. stainless steel, perspex and polyethylene, if compared to hydrophilic surfaces such as glass.

Wranstadeth et al. (1996) substantiated this observation, attributing the better attachment on hydrophobic surfaces to water exclusion mechanisms. On the other hand, water adsorption to hydrophilic substrata is thought to result in weaker accretion (Burchard et al. 1990). Furthermore, Characklis et al. (1990, cited in Sekar et al. 2004) found increased bacterial attachment on rough texture in comparison to smooth surfaces, ascribing it to increased convection associated with such surfaces. Thus, the slides used in this survey were abraded with coarse sandpaper before deployment to facilitate adhesion of microorganisms. It has also been shown that biomass accumulation in lentic environments is enhanced by horizontal orientation of the substratum (Newcombe 1950, Castenholz 1960, Cattaneo 1990), though this effect was not observed consistently (Cattaneo and Amireault 1992). Therfore, the potential advantage of horizontally orientated slides was foregone, given the major drawback of increased accumulation of planktonic diatoms and dead cells.

3.5.1.3 Natural substrate specificity and variation

Because of their small size, microorganisms perceive their environment as highly heterogeneous, and many hypotheses involve environmental heterogeneity as the key factor affecting species diversity (Miller 1987, Kotliar and Wiens 1990, Burkovsky et al. 1994, Azovsky 2002). Differences in benthic community composition and diversity thus might arise from differences in host morphology (Rho and Gunner 1978, Roos et al. 1981), surface texture (Brown 1976, Rosemarin and Gelin 1978, Nielson et al. 1984), and small-scale variations in light and nutrient availability.

Several studies reported definite host specificity by epiphytes (Godward 1937, Prowse 1959, Foerster and Schlichting 1965, Rautiainen and Ravenko 1972, Allanson 1973, Gough and Woelkerling 1976, Moss 1976, Ramm 1977, Eminson and Moss 1980, Pip and Robinson 1984, Cazaubon 1989), though other researchers disputed this theory of specificity (Cholnoky 1927, Fritsch 1931, Main and McIntire 1974, Siver 1977, Gons 1979, Millie and Lowe 1983, Blindow 1987, Buczkó and Ács 1994). Although the influence of macrophyte hosts on epiphyton communities is expected to be most pronounced where external nutrient concentrations are low, i.e. abiotic stress and competition for nutrients is high (Eminson and Moss 1980, Lovett et al. 1989, Tang et al. 1995, Raigosa et al. 1999), there is no indication that the macrophytes sampled in lowland wetlands interact with benthic algal assemblages by releasing growth inhibiting substances or nutrients. Taxonomic composition and structure of the benthic diatom communities were similar on different plant species, including *Myriophyllum* and *Typha*, of which some species have been shown to produce allelopathic substances to inhibit algal growth (Fitzgerald 1969, Planas et al. 1981, Agami and Waisel 1985, Saito et al. 1989, Aliotta et al. 1990, 1992, Della Greca et al. 1990, 1996, 1998, Gross and Sütfeld 1994, Gross et al.

1996, Nakai et al. 1996, 1999, 2000, Gallardo et al. 1998, Leu et al. 2002, Gross 2003). It has been shown, however, that exudates of *Myriophyllum spicatum* loose their inhibitory activity on algae over time, indicating bacterial degradation (Gross et al. 1996, Nakai et al. 1999, Gross 2003). It is therefore suspected that either detoxification and complexation by humic compounds (Ervin and Wetzel 2003) or elevated bacterial activity, as indicated by the high sulphate deficit (cp. chapter 3), might mask allelopathic effects. Light, oxygen, and redox conditions might influence the stability of allelochemicals as well, and transformations such as oxidation, polymerisation, or cleavage could hinder allelopathic impact. The assumption of Planas (1996) that *Sphagnum* would not be colonised by algae at all was also disproved. In fact, the pH-lowering qualities of *Sphagnum* plants neither impaired biomass accumulation, nor taxonomic composition of epiphyton communities. The results of this survey further contradict findings of Cattaneo (1978) and Cattaneo and Kalff (1978), who demonstrated that epiphyte communities of natural and artificial macrophytes differed significantly in diversity and structure. Similarly, Foerster and Schlichting (1965), Tippet (1970), Brown (1976), and Siver (1977) found apparent differences between the epiphyte communities on macrophytes and adjacent glass slides, though Godward (1937), Whitford (1956), and Castenholz (1960) emphasized similarities between natural and artificial substrates.

Epipelon communities have also been reported to differ significantly from algal assemblage growing on other substrates (Carrick and Steinman 2001, Stevenson et al. 2002, Potapova and Charles 2005), but this was not observed in the current project, either. For example, Lim et al. (2001) and Michelutti et al. (2003) reported that *Nitzschia perminuta, Navicula minima, Navicula soehrensis, Nitzschia palea*, *Pinnularia microstauron*, and *Stauroneis anceps* exclusively occurred on rock and sediment; yet those species did not show any habitat specificity in the studied New Zealand lowland wetlands. Thus, benthic diatom composition may be only marginally affected by the substrate itself, but by hydrological and hydrochemical conditions, instead. This is in line with findings of Kitner and Poulíčková (2003) and Millie and Lowe (1983) who assigned the observed lack of significant specificity for either artificial substrata or macrophytes to the instability of physical and chemical conditions. In the shallow water bodies studied at the West Coast, wind induced resuspension of the sediment likely contributes to a rather uniform dispersion of algae, and the available species pool as well as ambient environmental conditions might have been similar for epipelon, epiphyton and periphyton (as) communities throughout the study period.

3.5.2 Benthic diatoms as wetland indicators

Diatoms are well suited for use as biological indicators of environmental conditions in aquatic habitats (Dixit et al. 1992), since they preserve well, reproduce rapidly and

therefore respond quickly to environmental changes. Among the environmental variables that characterise freshwater habitats, pH (Kingston and Birks 1990, Sweets 1992, Cumming et al. 1992), salinity (Fritz et al. 1991, Cumming and Smol 1993), and nutrient concentrations (Hall and Smol 1992, Reavie et al. 1995) have been shown to severely influence diatom distribution.

The challenge to develop suitable models to infer environmental conditions in wetlands is that algal attributes may vary considerably among different wetland types within the same ecoregion (Stewart et al. 1985). Among the major variables affecting the abundance and predominant structure of wetland algae, the hydrodynamics and physical properties of the system, the supply of colonisable substratum and nutrients, and herbivory vary depending on wetland type and, to some degree, are wetland specific (Goldsborough and Robinson 1996).

3.5.2.1 Confounding by substrate specificity and grazing

For the studied lowland wetlands, it could be shown that substrate characteristics had no significant influence on diatom composition in microphytobenthos (cp. chapter 3.5.1).

It cannot definitely be excluded, however, that grazing by microzoobenthos had an effect on community composition, since several studies have demonstrated changes in epiphytic assemblages through differential grazing (Dickman 1968, Allanson 1973, Kesler 1981, Sumner and McIntire 1982, Lowe and Hunter 1988, Marks and Lowe 1989, Winterbourn and Fegley 1989, Brönmark et al. 1992, Rosemond et al. 1993, Biggs and Lowe 1994, Greens 1995, Gilbert et al. 2003). Wetlands typically support a diverse aquatic insect fauna (Mason and Bryant 1975, Hann 1991, Blinn et al. 2004, Stanczak and Keiper 2004), of which chironomids are probably the most abundant (Wrubleski 1987, cited in Goldsborough and Robinson 1996). Severe alterations of benthic diatom community composition by grazers in the studied wetland ecosystems yet are unlikely for a number of reasons. To begin with, benthic invertebrates have been shown to preferentially graze certain types of substrates (Mason and Bryant 1975, Conides et al. 1999, Kelly and Hawes 2005), but no substrate-specific effects in benthic diatom community composition were detected in either bogs or swamps. Furthermore, chironomids, which presumably constitute the dominant grazers in the studied systems, were reported to have only minor impact on benthic algal communities compared to other microinvertebrates (Hann 1991). Finally, a large and significant portion of the total variation in benthic diatom community composition is explained by the environmental variables measured, which points to chemical and physical parameters exerting control on species distribution.

3.5.2.2 Statistical bias

With reference to the potential use of diatoms for wetland classification, John and Helleren (1998) state that Canonical Correspondence Analysis (CCA) is extremely

powerful in detecting patterns of species distribution related to the associated physical and chemical parameters. However, analyses based on straight-line relationships such as Canonical Correspondence Analysis are often used uncritically (Austin 2002). The assumptions implicit to CCA (ter Braak 1986), that is equal species tolerances or niche breadths, equal species amplitudes, and homogeneously distributed species optima, are rarely met in diatom community data. Therefore, non-parametric statistical methods such as multidimensional scaling (MDS) are better adapted to complex ecological models of species responses (Austin 2002), though CCA is considered to be robust to changes in the assumptions (Palmer 1993; ter Braak 1987, ter Braak and Juggins 1993).
The primary environmental gradients explaining species abundance patterns in New Zealand wetlands generally were reflected by parametric and non-parametric statistical methods, indicating high reproducibility of the results obtained. MDS and CCA proved to complement each other and, consequently, were combined in the interpretation of species-environment relationships.

3.5.2.3 Differentiation of wetland types

Across the studied ***wetland types***, species composition changed with pH, alkalinity, calcium, silica, and water colour. Observations thus coincide with results obtained for small subarctic lakes, where pH, calcium, and silica were reported to correlate with diatom distribution (Korhola et al. 1999). Water colour and alkalinity have also been shown to determine diatom community structure in electrolyte-poor, oligotrophic freshwater ecosystems (Fallu et al. 2002), and Stevenson et al. (1998, 2004) stated that light, pH, available nutrients, and the mineral content of the water determine the type of algal community that develops in wetlands.

Among the environmental factors influencing diatom distribution, ***pH and alkalinity*** are commonly the variables that explain the greatest part of diatom assemblage variability (e.g. Dixit et al. 1992, Vyverman et al. 1996, Lotter et al. 1997, Weckström et al. 1997, Korhola et al. 1999, Negro et al. 2003, Poulíčková et al. 2003). Hydrogen ion concentrations have direct, species-specific effects on physiology and might also indirectly affect watershed conditions. Hence, diatom species composition is well known to respond to changes in pH at all ranges between 3.5 and 9.5 (Dixit et al. 1992), and most taxa show preferences for a fairly narrow pH range (Battarbee et al. 1986, van Dam et al. 1994).
For example, species of the genera *Eunotia*, *Frustulia*, and *Pinnularia* are usually considered acidophilous (Patrick 1977, van Dam et al. 1994, DeNicola 2000). The optima and tolerances calculated for *Chamaepinnularia begeri*, *Eunotia paludosa* var. *paludosa*, *Frustulia aotearoa* spec. nov., *Frustulia pangaeopsis*, *Navicula parasubtilissima*, and *Pinnularia microstauron* were well within the range of pH values that typify the

ombrotrophic bogs studied (cp. Appendix, Part B). Among those, *Eunotia paludosa* var. *paludosa* was reported by van de Vijver and Beyens (1997, 1999) as a major component of moss diatom communities in acidic stagnant pools. Associated bryophilous taxa that commonly occurred in the studied bogs were *Eunotia exigua* (cp. Wuthrich and Matthey 1978, Kingston 1982, Kapfer 1998, Muñoz et al. 2003) and *Pinnularia perriorata*. *Achnanthes minutissima*, *Eunotia exigua*, *Eunotia bilunaris*, *Frustulia saxonica*, *Pinnularia microstauron*, and *Pinnularia subcapitata* have also been reported to be fairly widespread at highly acidic pH (Wuthrich and Matthey 1978, DeNicola 2000, Verb and Vis 2000), though these taxa were not a restricted to the bog wetland type in this study.
Muñoz et al. (2003) reported taxa such as *Aulacoseira distans*, *Frustulia saxonica*, *Gomphonema gracile*, *Nitzschia gracilis*, *Pinnularia subcapitata*, and *Surirella linearis* from fen hollows in the northern hemisphere, which resemble the studied swamps in their physical properties and hydrochemistry. Thereof, *Aulacoseira distans* and *Gomphonema gracile* were characteristic of the swamp wetland type, while the other taxa were common in both minerotrophic and ombrotrophic wetlands. *Encyonema neogracile, Eunotia musicola*, *Gomphonema parvulum*, *Navicula minima*, and *Nitzschia palea* were also restricted to slightly acidic systems, although they proved to tolerate much lower pH (DeNicola 2000, Poulíčková et al. 2003). The results of this study further circumstantiate the assumption that *Tabellaria flocculosa* is indicative of slightly acidic brown-water conditions (Faulkenham et al. 2003). *Fragilaria construens* f. *venter* is another taxon that is typical for strongly coloured lakes with low alkalinity conditions (Fallu et al. 2002).
In comparison to Schönfelder et al. (2002), who investigated pristine freshwater floodplains and lakes, species optima regarding pH (Appendix, Part B) are probably more accurately represented in this study, since a larger variety of acidic habitats were included in the analysis (see also Vyverman et al. 1996). With few exceptions, species tolerances are distinctly narrower, and the absolute pH values are somewhat lower than the expected optimum in Schönfelder et al. (2002).

Although ***water colour*** and ***mineral content*** have been shown to affect benthic diatom growth and community structure (e.g. Moss 1972, Fallu et al. 2002, Stevenson et al. 2004), any direct relationship with diatom community composition in bogs and swamps is unlikely. Calcium, silica, and gilvin absorption coefficients simply coincide with wetland type specific features (cp. chapter 2), therefore passively accounting for variation in the diatom data, whereas pH as a single variable proved to be highly correlated with community patterns. Among wetlands of the same type, however, pH gradients are short in comparison to other components, and abiotic variables associated with ion or nutrient supply and the physical environment become more important. These findings agree with observations by Blinn et al. (2004), who state that salinity tended to override other determinants of diatom community structure except in wetlands with pH < 4.

3.5.2.4 Species-environment relationships within bogs

Diatom distribution among bogs was largely influenced by inorganic ion concentrations, gilvin, and pH. Microphytobenthos communities thus appear to be regulated by competition for dissolved ions and light, which is intuitively explained by the high dissolved humic matter concentrations in the presence of peaty substrates (cp. chapter 2) and the dependence of ion supply on rainfall. Sulphate deficit and pH are also coupled through precipitation, which is the major driving force in ombrotrophic wetlands.

Estimates of total ion concentrations such as ***conductivity*** and ***salinity*** have long been related to great shifts in species composition from marine to freshwater habitats (e.g. Fritz et al. 1991, Juggins et al. 1994). Stephenson et al. (1998) further conclude that variables measuring the ionic strength of waters were most important in explaining diatom species variance in wetlands. By affecting osmotic pressure on cells and cell membranes, conductivity has a direct effect on algal physiology and is often related to nutrient supply (Dixit et al. 1992). The major impact of conductivity gradients on benthic diatom community composition in the wetlands studied thus may be due to low water volumes and rapidly changing supply of water, which causes extensive temporal and spatial gradients of ion concentrations. Moreover, ombrotrophic wetland ecosystems that are influenced by oceanic climate are particularly susceptible to atmospheric influxes of salts and nutrients. High sulphate deficit and low nitrogen levels further indicate that the supply of ions by rainfall might increase bacterial activity, and, as a consequence, enhance competition for abiotic resources in bogs.

With respect to ***gilvin*** absorbance, it could not be resolved if the response of benthic diatoms to differences in light availability is determined by a direct causal relationship, as yellow substance concentrations increased with ion supply (cp. chapter 2). However, light availability is fundamental to photosynthesis, and potential synergistic effects of humic matter and ion concentrations on microphytobenthos likely occur. In strongly coloured waters, short wavelengths are absorbed by dissolved organic matter (Watrasa and Baker 1988), thus benthic algae might be limited by reduced transmission of photosynthetically active radiation (PAR). Correspondingly, Goldsborough and Robinson (1996) and Hill (1996) suggest that variation in the quantity and quality of light accounts for much of the variation in community structure of microphytobenthos assemblages. Effects of water colour on benthic diatom distribution were also reported by Fallu et al. (2002) for electrolyte-poor, oligotrophic freshwater ecosystems. Further indication for direct effects of humic matter concentrations on benthic diatom community structure is given by the prevalence of *Chamaepinnularia begeri* and *Naviculadicta parasubtilissima* at strongly coloured sites. Admiraal and Peletier (1979) demonstrated that the growth of taxa belonging to the diatom genera *Navicula* and *Nitzschia* was supplemented by facultative

heterotrophy at low light levels, which possibly accounts for the competitive advantage of *Navicula* spp. in bogs with high humic matter concentrations.

3.5.2.5 Species-environment relationships within swamps

In swamps, diatom distribution primarily changed along a gradient related to productivity. Variation in periphytic biomass, alkalinity, ion concentrations, and water temperature reflected differences in diatom community composition. Similarly, Pan and Stevenson (1996) and Blinn et al. (2004) reported that salinity and TP concentrations predicted diatom community structure in minerotrophic wetlands.

Taxa abundant in New Zealand lowland swamps such as *Aulacoseira alpigena*, *Encyonema neogracile*, *Fragilaria exigua*, *Gomphonema parvulum*, *Stauroneis anceps, Stenopterobia curvula*, *Surirella linearis*, and *Tabellaria flocculosa* were commonly reported from low ***alkalinity*** and low ***salinity*** habitats (van de Vijver et al. 2001, Negro et al. 2003, Blinn et al. 2004, Owen et al. 2004). Furthermore, *Gomphonema gracile* and *Nitzschia gracilis,* which have been shown to tolerate large amounts of dissolved inorganic ions (Blinn et al. 2004, Izaguirre et al. 2004), occurred at the most productive sites among the studied minerotrophic wetlands.

Species diversity and evenness, as reflected by univariate diversity measures, were significantly correlated to pH, alkalinity, sediment chlorophyll-*a* concentrations, calcium, and nitrate. This indicates the major influence of groundwater on primary production and diatom community structure in minerotrophic systems. Similar results were obtained by Owen et al. (2004), who found significant correlations between diatom distribution and pH, conductivity, nitrate, and water temperature in Kenyan swamps. In addition, DeNicola (1996) reported that local input from groundwater and solar heating in shallow areas can have significant effects on ***temperature*** in aquatic ecosystems and, therefore, affect periphyton community structure.

Any direct relationship between phosphorus or nitrogen and multivariate patterns in species distribution could not be observed in the studied wetland ecosystems, though ***nutrient concentrations*** appear to be coupled with ion supply (cp. chapter 2). Pringle (1985) and Cattaneo (1987) suggest that nutrients available to benthic algae may differ from the open water, and nutrient concentrations measured in the water column might not directly relate to benthic diatom assemblages (cp. Revsbech and Jorgenson 1986, Cattaneo 1987, Bothwell 1988, Hansson 1988, 1992). Moreover, Stevenson et al. (2004) state that the effects of nutrient changes in systems with high biotic variability may effectively mask species specific response by cascading effects through other algal groups. TP may also be highly variable and difficult to characterise in wetlands, because of wind-induced resuspension of particulates and diurnal fluctuations in algal abundance. ***Chlorophyll-a concentrations*** yet give a good estimate of the actual nutrient levels and

were significantly correlated to diatom distribution in the studied wetlands. For example, *Achnanthes minutissima*, a taxon that has been shown to prefer a nitrogen and phosphorus enriched environment (Pringle and Bowers 1984, Fairchild et al. 1985, McCormick and Stevenson 1989, Stevenson et al. 1991, Peterson and Grimm 1992), typically occurred at highly productive sites within the swamp wetland class. In contrast, *Aulacoseira distans* is considered indicative of oligotrophic conditions (Hall and Smol 1992) and was only found at low productive swamp sites.

Correlations between ***silica*** and species distribution might be arbitrary, since silica concentrations vary depending on groundwater and surface water inflow; yet silica limitation has been shown to occur in epiphyton communities inhabiting shallow waters (Zimba 1998). Negro et al. (2003) observed that silica content was among the most significant variables explaining phytoplankton diatom composition in mires in north-western Spain. Among the tychoplanctonic taxa present in acidic, low alkalinity habitats, many were also found in the microphytobenthos communities in New Zealand lowland swamps, e.g. *Aulacoseira distans*, *Eunotia bilunaris*, *Eunotia exigua*, *Eunotia veneris*, *Navicula minima*, *Pinnularia gibba*, *Pinnularia subgibba*, and *Stenopterobia delicatissima*. Moreover, *Aulacoseira* species have been shown to require high silica concentrations in comparison to other diatom taxa (Kilham 1990), which corresponds to the distribution of *Aulacoseira* spp. within the studied lowland swamps.

3.5.2.6 Species indicator groups

The hydrochemical and hydrophysical features that characterise the studied wetland types were shown to coincide with benthic diatom species distribution, in which eleven taxa account for a total of 50 % of the average dissimilarity between bogs and swamps. Indifferent species, that is diatom taxa occurring in both wetland types, also proved to be suitable indicators, unless their relative abundance maxima were equally distributed across habitat types. Slightly acidic conditions and low alkalinity, calcium, and silica concentrations in New Zealand lowland wetlands can be inferred from the predominance of *Chamaepinnularia soehrensis*, *Eunotia incisa*, *Encyonema neogracile*, *Fragilaria construens* f. *venter*, *Navicula heimansioides*, *Nitzschia gracilis*, and *Tabellaria flocculosa*. In contrast, *Eunotia paludosa* var. *paludosa*, *Eunotia paludosa* var. *trinarcria*, *Frustulia saxonica morphotype II*, *Naviculadicta parasubtilissima*, and *Naviculadicta subtilissima* constitute the bog indicator group, referring to highly acidic, and ombrotrophic conditions.

According to species abundance distributions, wetland types can further be subdivided into units that exhibit varying, though type specific, abiotic features. This will be of interest with respect to biodiversity conservation issues, as each of the studied wetlands contains diatom species specific to that habitat, some of which possibly are endemic to

the southern hemisphere (cp. chapter 4). Slight changes in the hydrological regime or nutrient charge in lowland wetlands might severely alter species composition and diversity, therefore causing further losses in biodiversity.
Benthic diatom species indicating low conductivity and humic matter concentrations in bogs e.g. are *Frustulia* cf. *magaliesmontana*, *Frustulia pangaeopsis*, and *Navicula subtilissima*, while taxa such as *Chamaepinnularia begeri*, *Eunotia paludosa* var. *trinarcria*, and *Pinnularia perriorata* are located at the other end of the gradient. Among swamps, highly productive sites i.a. are indicated by *Achnanthes minutissima*, *Fragilaria nanoides*, and *Gomphonema gracile*, whereas diatoms such as *Aulacoseira distans*, *Chamaepinnularia soehrensis* var. *soehrensis*, and *Pinnularia subgibba* characterise oligotrophic conditions.
It is suggested that species optima calculated by weighted averaging (Appendix, Part B) may be used to infer changes of environmental conditions in the studied wetlands; yet the establishment of transfer functions and their application to a larger set of wetland ecosystems requires sampling of a continuous gradient spanning the whole range of possible values for the relevant environmental variables. As long as the current set of reference sites is not extended to other wetland types, canonical correspondence analysis provides additional means for assessing the response of benthic diatoms to changes in significant environmental gradients.

3.5.3 Redundancy patterns at the genus and family level

Taxonomic characteristics of algal assemblages provide some of the most sensitive and robust indications of wetland nutrient status (e.g. McCormick and O'Dell 1996). Species-level assessments, although requiring the greatest taxonomic expertise to perform, yield the most precise indicators of environmental conditions and biological integrity. However, it has been shown that considerable information can be obtained from assessments performed at the genus level or higher (e.g. Prygiel and Coste 1993, van der Borgh 1999, cited in Stevenson et al. 2002, Clarke and Warwick 2001).

The results of this study indicate that observations at the genus level were sufficient to differentiate between wetland types in south-western New Zealand. Although most genera occurred in both wetland classes, their relative proportions differed significantly between habitat types. Within the swamp wetland class, the approach also proved to be sensitive enough to reproduce the outcome of species-level analyses, yet variation in diatom community composition among bogs could only be detected at the species level.
Thus, indicator groups can also be established at the genus level, which increases the time- and cost efficiency of monitoring programmes. Furthermore, taxonomic bias is largely reduced, as diatom genera are readily identified by non-specialists, while experts are required for the identification of diatom species. Variation in wetlands of a specific

type, however, should be assessed at the species level, as differences could not be resolved in the distribution of diatom genera in bogs.
Ombrotrophic lowland wetlands are identified by the predominance of *Eunotia*, *Frustulia*, and *Navicula*, which together make up more than 90 % of the genera occurring in benthic diatom assemblages of this wetland type. This is by no means surprising, since species of the genera *Eunotia* and *Frustulia* are usually considered acidophilous (Planas 1996, DeNicola 2000), and the genus *Eunotia* is often well represented in acidic waters (Moss 1973, Mulholland et al. 1986, Marker and Willoughby 1988, Planas et al. 1989, Winterbourn et al. 1992). In contrast, *Aulacoseira*, *Cymbella*, *Fragilaria*, *Nitzschia*, and *Tabellaria* are designated swamp indicators, given that at least one genus accounts for more than 10 % of the taxa present. This is in line with observations of Faulkenham et al. (2003), who found that *Tabellaria* and *Eunotia* spp. were indicative of slightly acidic, brown-water conditions, though taxa of the genus *Eunotia* were abundant in all wetlands studied in south-western New Zealand. Furthermore, Goldsborough and Robinson (1996) state that dominant algal groups in the epiphyton of nutrient-rich temperate freshwater wetlands typically include genera such as *Cymbella*, *Fragilaria*, and *Nitzschia*. The genus *Aulacoseira* characteristically occurs in shallow nutrient-rich wetland ecosystems (Wolin and Duthie 1999), indicating the establishment of a true phytoplankton community. The large rivers and lakes to which the studied swamps are connected, e.g. Mahinapua River or Lake Kaniere, might serve as sources of inocula and nutrients (cp. Klarer and Millie 1992), mediating the deposition of phytoplanktonic cells into the benthic communities (cp. Moss 1981).

If diatom families are concerned, pattern observed at lower taxonomic levels could not be adequately reproduced. Even though wetland types differed significantly, the separation of samples proved to be unsatisfactory compared to the analysis based on species and genera. The effect of diverging dissimilarities was even more pronounced among wetlands of the same type and, consequently, environmental variability is not accurately reflected at such high level of aggregation.

3.5.4 Univariate description of diversity

The application of ecological indices as a monitoring tool has a long history (for review see Washington 1984). In this context, the relative abundance distribution, which characterises the total number and abundance of species in a community, is generally considered the most fundamental measure in ecology (Hillebrand and Sommer 2000, Pachepsky et al. 2001). Species richness and evenness of taxa distributions are important characteristics of many diversity indices that are used to describe biological assemblages. Therefore, diversity indices provide substantial information on community structure that is represented by a simple index value. However, the reduction of multivariate patterns

into univariate measures of diversity will invariably result in a loss of information, and diversity indices might not adequately reproduce the patterns obtained by unrestricted statistical approaches.

Stevenson et al. (2002) point to the fact that species records obtained by standard cell counts might not be sufficient for the assessment of diatom species diversity, since many taxa usually will not be identified. Therefore, richness is more a function of evenness than evenness a function of richness (Archibald 1972, Stevenson and Lowe 1986). Total species numbers have also been shown to increase with the size of the sampled area (e.g. Clarke and Warwick 2001, Holt et al. 2002, Peintinger et al. 2003), which must be taken into account when dealing with biodiversity conservation. In the present study, the perfectly linear relationship between the number of species and Margalef's index verified that slight deviations in the number of individuals counted per sample did not affect species numbers. Diversity measures based on species richness thus are assumed to reliably indicate relative differences between benthic diatom communities from the studied wetland habitats. However, absolute species numbers and taxonomic diversity were likely underestimated; yet no statistical framework exists for departure of species numbers from expectation, as there is no absolute standard (Clarke and Warwick 2001).

Non-monotonic responses of algal diversity can also occur along environmental gradients (Archibald 1972, Connell 1978, McCormick 1996, Clarke and Warwick 2001), introducing ambiguity into the interpretation of diversity indices. Both increases and decreases in species diversity arise as the independent variable, e.g. nutrient loads and disturbance, increases (cp. figure 3.22). This ambiguity seems to be related to the maximum evenness of tolerant and sensitive taxa at midpoints along environmental gradients, and subsidy-stress perturbation gradients (Odum et al. 1979). According to Archibald (1972), diversity in pristine oligotrophic freshwater ecosystems can be highly variable, covering the whole range of diversity. This is explained by the simultaneous impact of a range of environmental variables on community structure. Disturbance intensity and frequency, i.e. abiotic stress, have also been shown to influence pattern in species richness (Gaedeke and Sommer 1986, McCormick 1996, Watanabe et al. 2000). That is, diversity and evenness are reduced by environmental stress, the results within a given system often being species-specific (Perry et al. 1987). The high degree of variability in species diversity observed in the studied bogs as compared to swamps thus might be attributed to highly acidic conditions and the exposure to rapid environmental fluctuations. For example, temporary and locally restricted drought events or changes in pH in shallow water zones could severely affect species numbers and abundances. Support for these assumptions are given by Watanabe et al. (2000), who report species such as *Eunotia incisa*, *Fragilaria construens* f. *venter*, *Fragilaria exigua*, *Gomphonema gracile*, *Navicula minima*, *Pinnularia subgibba*, and *Surirella linearis* as typical for mires

with low disturbance frequencies. The results of this study further coincide with observations by Planas (1996), Vyverman et al. (1996), John and Helleren (1998), and Poulíčková (2003), who found that Shannon diversity increased with pH in wetlands. Shannon index values that are comparable to diversity in New Zealand lowland swamps e.g. were reported for pristine marshes by Zheng et al. (2004). Our findings also agree with a model proposed by Büssenschütt and Pahl-Wostl (1999), which predicts that maximum diversity in an ecosystem increases with nutrient input. Negative correlations between ion supply and diatom diversity in bogs might be attributed to the dilution of ambient nutrient levels by precipitation.

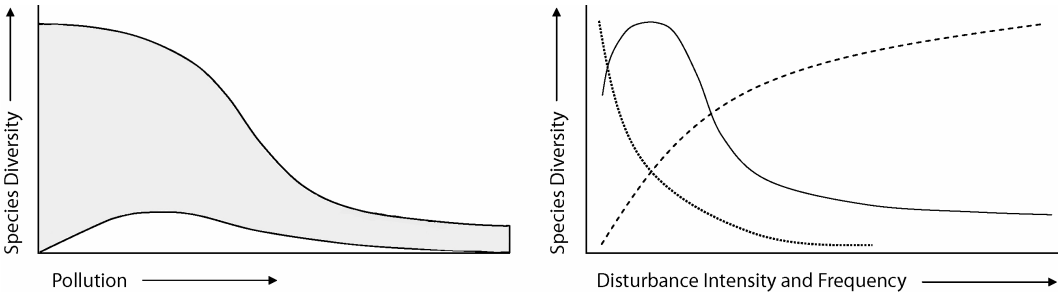


Figure 3.22. Idealised relationship between species diversity and the degree of pollution (left graph, Archibald 1972) and disturbance (right graph, McCormick 1996). The dotted line illustrates the decreasing importance of competitive interactions in determining species composition with increasing disturbance, whereas the dashed line shows the increasing importance of adaptations for coping with disturbance.

Among the univariate diversity measures employed, average taxonomic diversity and species numbers were most distinctive, indicating significant differences between wetland types. In contrast, the application of Shannon diversity, Simpson diversity, Pielou's evenness, and taxonomic distance indices is rather critical, as the delineation of wetland classes is constrained by high variability and large overlaps in the range of index values. If diversity is to be correlated with environmental variables, species numbers perform best. Therefore, a combination of of species numbers and taxonomic diversity supposedly gives the best estimate of benthic diatom diversity in New Zealand lowland wetlands, as both species occurrences and taxonomic distances are encompassed, and the average taxonomic diversity is independent of sample size (cp. Clarke and Warwick 2001).

3.5.5 Stability and resilience of the studied biomes

Conservation and management of biodiversity in New Zealand wetlands as emphasised by the New Zealand Biodiversity Strategy (Department of Conservation 2000) requires information on the stability and resilience of biological communities in these ecosystems. Experience with wetlands in western Canada suggests that each wetland has a

characteristic dominant algal assemblage that, without major environmental changes such as water level fluctuation, can persist for decades (Goldsborough and Robinson 1996). However, stability and resilience of biological communities are connected to a variety of processes related to dispersion, diversity, population dynamics, habitat heterogeneity, disturbance, and developmental equilibria, which are not easily discernible and have been widely discussed in the literature.

Ellner and Fussmann (2003) state that understanding spatial population dynamics and the role of spatial structure in population persistence is one of the central problems in ecology. The classical metapopulation scenario, where species persist in a network of habitat patches through a balance between frequent local within-patch extinctions and recolonisation, yet is not likely to be relevant for the studied New Zealand ecosystems due to the effective dispersal of diatoms (cp. Kristiansen 1996, Earn et al. 2000). In addition, within-patch variability in terms of the distribution and duration of successional stages in wetland microphytobenthos communities is high, which allows for persistence of refractory populations (cp. Ellner and Fussmann 2003). However, endemism has been shown to occur in different regions of the world (cp. Sabbe et al. 2001, Kilroy et al. 2003 etc.), and habitat loss and fragmentation might have reduced certain diatom species to isolated patches within their range (cp. chapter 4). Therefore, species persistence in a patchy habitat through metapopulation dynamics will be strongly affected by the biological causes of local extinctions, and the processes whereby patches regain the properties that made them suitable to support a local population. Niche partitioning within a spatially-structured community and continual invasion by competitively inferior species may contribute to the maintenance of diversity.

Disturbance is another key factor determining pattern and processes in freshwater algal communities, but again, the precise nature of this influence is complex and not easily compartmentalised into discrete categories of effects (Peterson 1996). Following Rykiel (1985), disturbance may be defined as a biotic or abiotic causal mechanism or stress, which results in a perturbation or response of a biological system. In addition, the mechanism must force one or more system parameters beyond what is expected under normal temporal and spatial variation (Gerritsen and Patten 1985). In most systems, recovery of benthic algae initiates from multiple starting points, which are spatially distributed across the respective ecosystem and dictated by the resistance of algae prior to disturbance. Just as benthic algal resistance changes with successional time, it is also likely that autogenic changes occurring during community development would affect recovery. If taxa have autecological characteristics that dictate reliance on recycled nutrients, allowing for slow, steady growth in the low-resource environment of late-successional biofilms (cp. Stevenson et al. 1998), then these taxa would not likely respond rapidly when re-exposed to resource-replete conditions. Therefore, individual

water bodies may have characteristic recovery rates that primarily reflect local growth conditions, being relatively insensitive to the identity of component species (Rodríguez 1992). With respect to the studied wetlands, this means that nutrient enrichment might not be picked up immediately by changes in benthic diatom community composition, since individuals are adjusted to low nutrient levels. Anthropogenic impact, or more generally speaking, increased levels of abiotic stress, might therefore be indicated by slow competitive displacement or reduction of taxa in the diatom genera *Eunotia* and *Pinnularia*, which are often found in relatively undisturbed wetlands (cp. Stevenson et al. 2002). In contrast, Odum (1979) pointed out that many types of disturbance act as system subsidies, that is they trigger a positive response of the system if the causal mechanism represents a usable input. Increased nutrient loads charging oligotrophic or mesotrophic wetlands, therefore, may result in an overall increase in diatom species richness. Stress can also be manifested in reversion to an earlier successional stage (Perry et al. 1987), which might be reflected in the skewed dominance structure in bogs being caused by physiological stress, e.g. low pH. Correspondingly, Woodwell (1970) presumes that a system might response to stress by simplification of community structure and changes in the system's relative position along the successional continuum.

One of the most frequently suggested non-equilibrium explanations for the maintenance of species diversity in ecological communities is the intermediate-disturbance hypothesis (IDH), which predicts that local species diversity is greatest at intermediate levels of disturbance (Connell 1978). Most commonly, the IDH is interpreted as "intermediate-timescale disturbances", that means coexistence is promoted when disturbances recur through time at intermediate frequencies. Under high-frequency disturbances the better competitor but poorer disperser cannot persist, while under low-frequency disturbances the better competitor excludes the good disperser. For example, Watanabe et al. (2000) demonstrated that high disturbance frequency causes low diversity in epipelon communities, which corresponds to the observations of the present study (cp. chapter 3.5.4). At intermediate frequencies there is a parameter zone where taxa can coexist indefinitely, with the competitively inferior species occupying the recently disturbed sites. This situation might apply to New Zealand lowland swamps, where environmental fluctuations are expected to be less frequent than in bogs according to the comparatively large water volume. In the within-patch context, disturbances are assumed to be global in the sense that all organisms in the system are simultaneously affected by the disturbance, regardless of the spatial locations of those organisms (cp. Roxburgh et al. 2004). The threshold of perception of temporal heterogeneity thus may be different at different levels of organisation, e.g. small heterogeneity in nutrient supply may have consequences for nutrient uptake but not necessarily for the outcome of competition between algal species (Gaedeke and Sommer 1986). This might explain the high level of homogeneity between

benthic diatom communities from different types of substrates, though other factors should also be taken into account (cp. chapter 3.4.1). Correspondingly, Rodríguez et al. (1992) suspect that convergence of initially differing periphyton (as) communities towards a single equilibrium might result from the susceptibility of interspecific interactions to the influence of external abiotic factors.

Considering the combined aspects that influence stability and resilience in the studied wetland ecosystems, patterns in community structure and diversity of the benthic diatom assemblages point to higher disturbance frequencies, i.e. relative instability of periphyton communities in bogs. Nutrient deficiency and low pH are interpreted as negative stress, whereas higher ambient nutrient levels in swamps, as reflected by biomass estimates, may sustain a more complex community composition. Assumptions on the response of benthic diatoms to environmental changes in the studied wetlands yet are speculative, as evidence by manipulative experiments is needed to support the conclusions derived by any mensurative study design. However, bog communities are supposed to be less resilient than swamp assemblages, due to their high susceptibility to environmental fluctuations. Increases in pH and nutrient concentrations will eventually lead to invasion of other diatom species that are better adapted to induced abiotic conditions. Moreover, benthic diatom community stability and resilience are coupled to the habitats dynamic load capacity, and the effects generated by altering the hydrologic regime or by anthropogenic pollution are not easily reversed to oligotrophic or ombrotrophic conditions.

3.5.6 Implications for wetland monitoring and protection

With the development and intensification of land use practises in New Zealand, the demand to protect and manage the remaining indigenous wetland ecosystems steadily increases. Therefore, it is necessary to develop a realistic and ecologically sound approach to monitor the current status and trends of ecological conditions in wetlands.

Diatom community characteristics have been used to monitor and assess water quality and biotic integrity in lakes and streams, but little work has tested their utility in the spatially complex habitats of wetlands. However, quantitative measures of algal standing crop, nutrient content, and productivity were shown to provide valuable insight into wetland function and the relative importance of periphyton processes, and taxonomic composition, when combined with specific environmental tolerances of taxa, can be used to calculate stressor indicators to infer environmental conditions in wetlands (Pan and Stevenson 1996, Stevenson et al. 1998).

The sampling intensity required to adequately assess algal conditions is related to the complexity and spatial variability of the algal community, which in turn is a function of habitat heterogeneity. Sampling effort will be relatively low in instances where a single algal community predominates and is distributed in a relatively homogenous manner

across the wetland. In most instances, however, multiple communities will coexist and be distributed patchily within and among habitats as shown in the present study. Sampling intensity also is affected by the presence of nutrient or other disturbance gradients within the wetland. For example, point-source nutrient inputs can produce localised zones of enrichment that will support an algal community quite different from that in unenriched portions of the same wetland, whereas non-point source inputs, or those that are exceedingly high relative to the size of the wetland, may enrich the entire system. Accordingly, Kotliar and Wiens (1990) suggest that, when focusing investigations at any particular spatial level, at least three levels of patchiness, i.e. spatial variation should be considered.

Therefore, the present study accounts for four spatial scales, assessing the variability at the substrate, site, wetland, and type levels. Although no significant influence of the substrate in both bogs and swamps could be observed, it can not generally be excluded that some epiphytic communities or periphyton on other naturally occurring substrates differ in taxonomic composition and/or dominance structure. Integrated sampling of a range of substrates is therefore recommended to obtain a representative proof of the abundant benthic diatom species present. Nevertheless, sampling effort may be largely reduced by pooling samples from replicate sites in a wetland, if wetland types are to be compared. However, the number of wetlands representative of a certain wetland class should not be reduced to less than four, due to significant variation within types. To reduce natural variability, the use of polyethylene slides in New Zealand lowland wetlands is recommended. This will result in higher precision of statistical analysis, since most of the noise in spatial analyses is eliminated. For ombrotrophic and oligotrophic lowland wetlands, an exposure period of three to four months is recommended, while in mesotrophic to eutrophic wetlands, an exposure period of less than twelve weeks might be sufficient. Sloughing was not observed in the studied pristine wetlands. However, if heavily polluted wetlands or systems with naturally high nutrient levels are explored, further reduction of the exposure period should be considered.

Even though no significant differences were found between benthic diatom diversity in early and late summer, algal communities may exhibit differing seasonal patterns of standing crop and species composition, depending on wetland type (cp. Stevenson 2002). Therefore, some familiarity with the temporal dynamics of algal communities in wetland classes of interest should be gained before initiating routine sampling. Whenever possible, the sampling design should cover more than one season to provide an integrated assessment of periphyton and nutrient conditions. Stevenson et al. (2002) recommend that sampling should be conducted during the peak growing season or at a time when stressor impacts are most likely to occur, if the impact of changes in the environment is to be estimated. With respect to monitoring programmes that routinely measure water

chemistry and benthic diatom community composition in New Zealand lowland bogs and swamps, one-time sampling between December and March will provide representative data for inter-annual comparisons.

The results of this study further indicate that diatoms respond sensitively to environmental conditions in wetlands and may be useful indicators of environmental conditions in wetlands (cp. Pan and Stevenson 1996). Algal diversity, biomass, and algal chemistry have all been studied as indicators of habitat conditions (Lowe and Pan 1996), but Stevenson et al. (1998) state that the most useful indicators in many cases have been the weighted averaging models that are used to infer specific habitat conditions (ter Braak and van Dam 1989, Birks et al. 1990, Korsman and Birks 1996). This quantitative approach, however, requires that a wide and continuous gradient of any habitat along the modelled parameter is sampled. Consequently, the generation and application of transfer functions is not justified with respect to the parameters measured in the present study. However, species optima calculated by weighted averaging may be used to infer environmental conditions in lowland bogs and swamps in south-western New Zealand, thus providing a basis for further investigation. It has to be tested though, if these observations can be extended to wetland types other than the ones studied.

Besides weighted averaging, multivariate analysis of benthic diatom abundances proved to reliably indicate differences in the abiotic environment of wetland ecosystems. Changes in species composition and variation were shown to differentiate between wetlands and wetland types, representing the most accurate but also most time-consuming and cost-intensive approach. Diatom genera also appear to provide effective means for the delineation of wetland types at a low level of taxonomic expertise required. Cost and time efficiency, therefore, can be increased by carefully considering the hypotheses to be tested and deliberating the desired accuracy of the data.

Univariate diversity indices, though more easily implemented than multivariate statistical analysis, did not reflect variation among wetlands of a specific type, thus representing only part of the information available from species abundance data. However, diversity indices may facilitate comparisons between studies and provide substantial information on community structure by a simple index value. In the delineation of New Zealand bogs and swamps, species numbers and taxonomic diversity proved to be most distinctive, yet their performance and applicability to other wetland types in New Zealand has to be tested.

With respect to wetland conservation in south-western New Zealand, special emphasis should be placed on the remaining ombrotrophic lowland bogs, since their oligotrophic status and hydrological regime is not easily restored and the area covered by these ecosystems has severely declined since European settlement. Furthermore, wetlands of that type host a range of specific and perhaps endemic diatom species (chapter 4), which

contribute their share to biodiversity in the New Zealand algal flora. Ombrotrophic bogs are extremely fragile, and even though increases in pH or nutrient levels might lead to a rise in species diversity, rare taxa will diminish and might eventually get extinct (cp. Cairns 1993).

In contrast, benthic diatom communities in swamps may forgive minor changes in ambient conditions due to higher adaptive capacities of the assemblages, though shifts in community composition are likely to occur if the ecosystem is strained by acute anthropogenic disturbance. Pollution and drainage of these wetlands are expected to cause a decrease in diversity, yet part of the effect might be reversed to some degree. The high habitat heterogeneity in the swamp wetland type also entails distinct diatom communities that differ significantly between the minerotrophic wetlands studied. Therefore, each wetland has a characteristic algal assemblage justifying its protection (cp. Maitland and Morgan 1997).

3.6 References

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5 A synopsis of cosmopolitan, rare, and new *Frustulia* species (Bacillariophyceae) from ombrotrophic peat bogs and minerotrophic swamps in New Zealand

5.1 Abstract

Eight *Frustulia* taxa from lowland wetlands located at the south-western coast of New Zealand were examined by LM and SEM microscopy. Thereof, four taxa are described as new species. *F. aotearoa* spec. nov., which is characterised in a differential diagnosis from *F. bahlsii*, occurred exclusively in ombrotrophic peat bogs, while *F. cassieae* spec. nov., *F. gondwana* spec. nov., and *F. maoriana* spec. nov. were restricted to slightly acidic, minerotrophic swamps. *F. cassieae* has been recorded in the past in eastern Australia and the New Zealand North Island but was erroneously identified as *F. rhomboides* var. *elongatissima* (Manguin). *F. gondwana* resembles populations from other regions of the southern hemisphere and the Neotropics that were not specified in detail. In contrast, *F. maoriana* has not been observed elsewhere and may provisionally be regarded as an endemic element of the New Zealand diatom flora like *F. aotearoa*. *F. pangaeopsis* was as yet known only from Central Europe, but proves to be cosmopolitan since its counterpart in the studied wetlands could not be differentiated by any of the observed morphological or ecological features. Conspecificity of *F. magaliesmontana* from South Africa with the New Zealand population, however, remains questionable. As opposed to *F. pangaeopsis*, which is limited to highly acidic, ombrotrophic ecosystems, *F. magaliesmontana* occupies a wider ecological niche and is associated with the cosmopolitan species *F. crassinervia* and *F. saxonica*.

5.2 Introduction

Current diatom research is predominantly based on a paradigm of a cosmopolitan geographic distribution of freshwater diatoms. Kociolek and Spaulding (2000) state that "we are still in a discovery period with regard to diatom morphology, exposing the diversity of all freshwater diatoms, with many areas of the earth largely unknown", and that "careful determination of taxon-based geographic distributions is a starting point for diatom biogeography".

Species diversity in the genus *Frustulia* (Bacillariophyceae) has been underestimated in previous years because of the insufficiently precise taxonomic criteria attributed to this group. Hustedt (1959) recognised eight taxa for the diatom flora of Europe, including only three acidophilous or acidobiontic species. Only recently, the erroneous combination of *Navicula rhomboides* (Ehrenberg 1843) with *Frustulia* has been revised (Lange-Bertalot and Jahn 2000, Lange-Bertalot 2001), and an increasing number of new *Frustulia* taxa has been described in the last decade (e.g. Lange-Bertalot and Metzeltin

1996, Edlund and Brant 1997, Van de Vijver 2002, Lange-Bertalot and Sterrenburg 2004). As demonstrated by studies on the diatom flora of South and Central America (Metzeltin and Lange-Bertalot 1998, Rumrich et al. 2000, Wydrzycka and Lange-Bertalot 2001), Madagascar (Metzeltin and Lange-Bertalot 2002) and New Caledonia (Moser et al. 1995, Moser 1998, 1999), few *Frustulia* species appear to be cosmopolitan and a series of detailed comparative surveys are needed to gain insight into the actual biogeographical distribution of taxa within this genus.

Among the benthic diatom populations observed in the study area, eight taxonomic entities could be separated, which were compared with established and critical taxa. Five *Frustulia* species from ombrotrophic peat bogs and three from minerotrophic swamps were distinguished by using SEM and LM analyses, all of which are either cosmopolitan or restricted to the southern hemisphere. Two taxa appear to be specific to the Australasian region, which is regarded as a major centre of microalgal biodiversity and endemism (Vyverman et al. 1998, Sabbe et al. 2001, Kilroy et al. 2003).

5.3 Material and Methods

Epiphyton and sediment samples were collected in December 2002 and March 2003 from a range of bog and swamp sites located at the south-western coast of New Zealand (table 4.1, see also previous chapters).

Quantitative sub-samples of the epiphytic and epipelic algal communities were fixed in a 3 % glutaraldehyde solution, while a second set of subsamples was processed according to the method of van der Werff (1955). Identical and complete arrays of diatom samples were deposited at both the NIWA Christchurch laboratory (National Institute of Water and Atmospheric Research, New Zealand) and the archive of the Limnological Station Iffeldorf, TUM (Technical University of Munich, Germany) for long-term storage.

Table 4.1: Location of sampling sites, GPS coordinates have been converted from New Zealand Map Grid (NZMG49) into the new national geodetic datum (NZGD2000, Geodetic Reference System 1980), B = bog, S = swamp.

Wetland	Type	Sites	Latitude	Longitude
Arthurstown Road	B	8	42 44 06.6331 S	170 57 44.9609 E
Keogan's Road	B	6	42 41 53.7424 S	171 00 44.5988 E
Kumara	B	5	42 38 33.8741 S	171 10 21.0840 E
Stafford Loop Road	B	5	42 41 11.7633 S	171 10 03.1472 E
Back Creek Swamp	S	5	42 47 33.6798 S	171 01 03.6993 E
Lake Kaniere	S	5	42 48 14.3170 S	171 07 42.5786 E
Mahinapua Swamp	S	5	42 46 21.5387 S	170 55 28.7270 E
Tucker Flat	S	5	42 44 50.9672 S	171 01 05.9379 E

Diatom material was mounted in Naphrax™ for light microscopy (Leica Diaplan, Objective Planapochromat 63/1.4) or dried onto millipore filters that were mounted on aluminium stubs and sputtered with Au for SEM analysis (Hitachi S-4500). Photographs were taken on 25 ASA Agfa Ortho Professional film (LM) and as digital images (SEM). Type material and slides are available from the archive of the Limnological Station of the TUM or the Lange-Bertalot collection (FR), respectively.

5.4 Observations

5.4.1 ***Frustulia aotearoa*** T. Beier and Lange-Bertalot spec. nov. (figures 4.1, 4.26-31)

DIAGNOSIS: Diagnosis differens vs. *Frustulia bahlsii* Edlund and Brant 1997
Valvae lanceolatae sive rhombico-lanceolatae apicibus simpliciter obtuse rotundatis (non vel protractis inconspicue numquam leviter rostratis). Longitudo circiter 110-210 µm, latitudo 25-38 µm. Striae transapicales 25-26 in 10 µm parallelae in mediis partibus et subparallelae denique paulo convergentes ad apices versus, sed distincte radiantes circum apices (id est medietate aliquid densius sitae quam 20-26 in *F. bahlsii*). Striae apicales id est series punctorum longitudinales in mediis partibus distincte densius sitae enim 22-24 (nec 16-19) in 10 µm. Complexus continens raphe, area axialis centralisque alias sternum cum costis axialibus parallelis fere similis *F. bahlsii* sed differt nodulis centralibus generaliter convexis interdum paululum incurvatis in medio (nec fortiter concavis). Item differt quoad nodulos terminales cum helictoglossis integratis simpliciter obtuse vel aliquid cuneate rotundatos (nec expansos spathulatiformes id est late ad plane retusos).
Aspectus ultramicroscopicus: Externe raphe cum extremis centralibus terminalibusque ad instar litterae T. Area centralis (vide figures 4.28-29) formata seriebus apicalibus areolarum adaxialibus hic moderate sed satis distincte curvatis ad margines versus (nec rectis ita area centralis non formata vide Edlund et Brant figure 7). Areae terminales (figure 4.30) anguste elongatae (nec transverse late expansae vide figure 9 loc. cit.). Aspectus internus (vide figures 4.27, 4.29, 4.31): Areolae circum nodulum centralem plus minusve irregulariter formatae.

TYPUS: Slide Oz-51 (figure 4.1) in Lange-Bertalot collection (FR). Isotype slide NZ-111c and residual type sample NZ-111f in the collection of the Limnological Station, Technical University of Munich.

LOCUS TYPICUS: Ombrotrophic peat bog ("pakihi") at Stafford Loop Road near Dillmanstown, West Coast District, South Island, New Zealand.

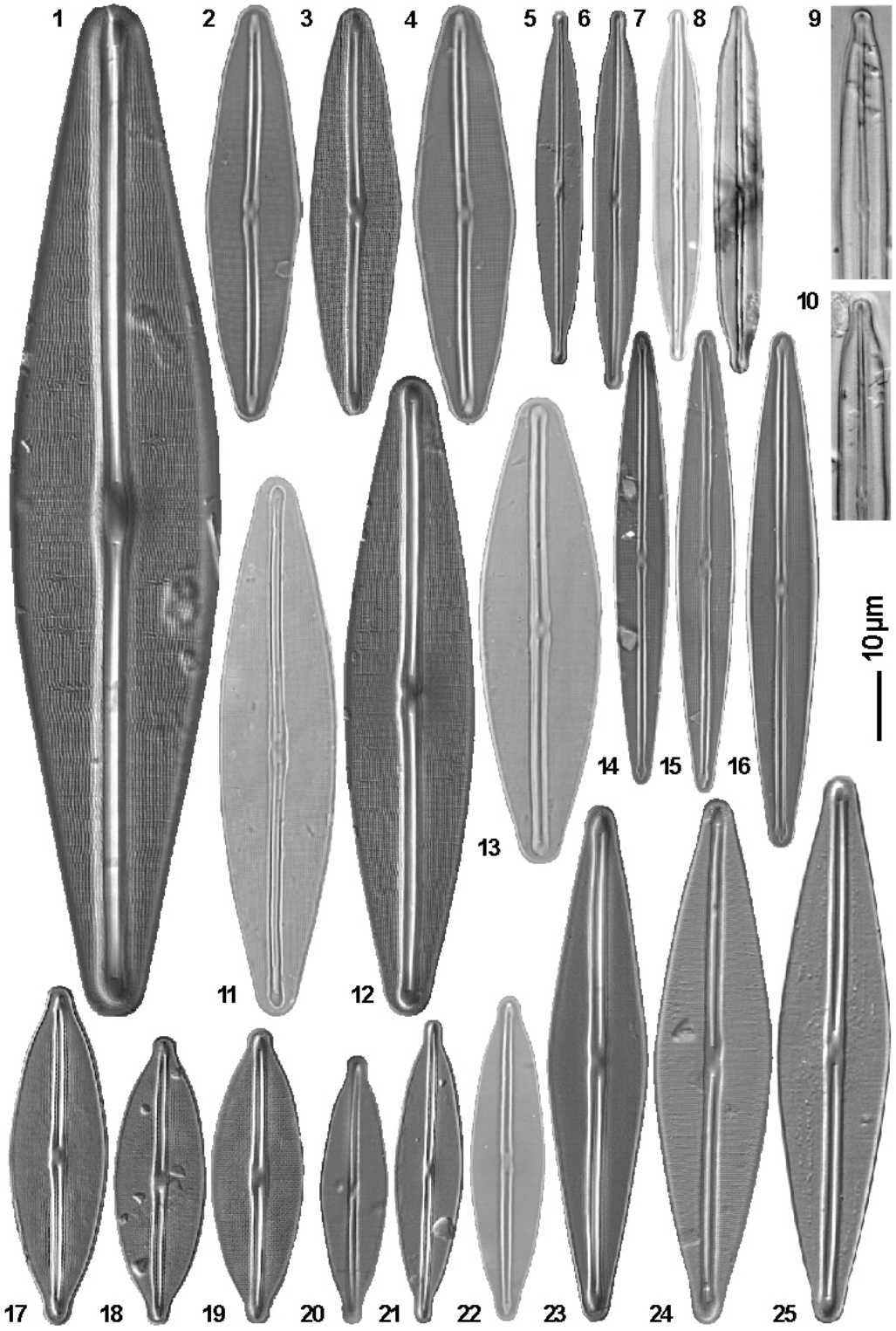
ETYMOLOGY: "Aotearoa" is a common Maori name for New Zealand, meaning "land of the long white cloud".

SPECIES DESCRIPTION: Differential diagnosis vs. *Frustulia bahlsii* Edlund and Brant 1997

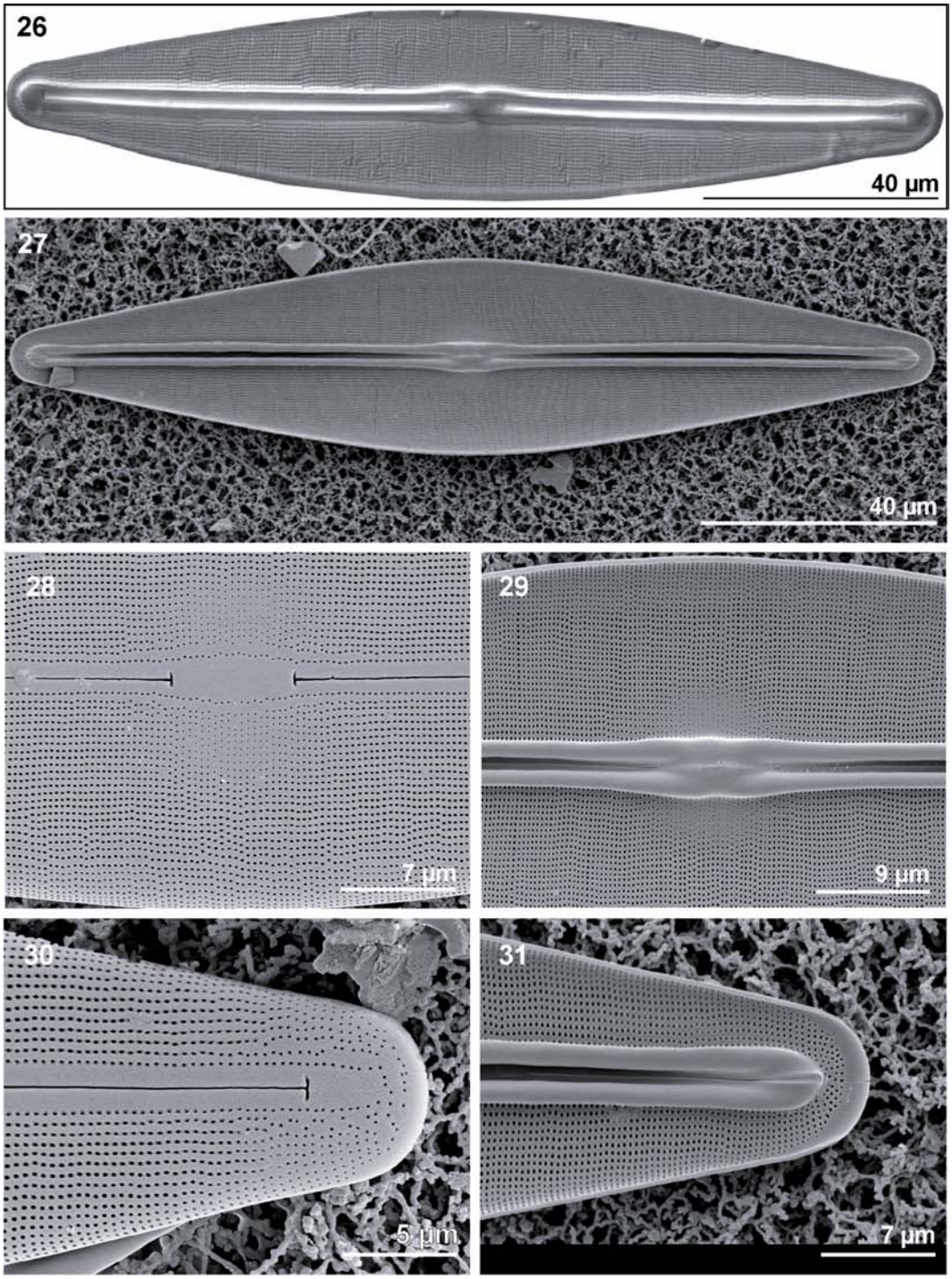
Valve outlines lanceolate to rhombic-lanceolate with obtusely rounded ends (at most inconspicuously protracted, but never slightly rostrate). Length 110-210 µm, breadth 25-38 µm (i.e. maxima moderately higher than 98-193 and 24-33 µm, respectively). Transapical striae 25-26 (i.e. on average denser than 20-26) in 10 µm, parallel, becoming subparallel to slightly convergent towards the ends, continuous and radiate around apices. Apical series of puncta, i.e. longitudinal striae more or less undulate, consistently 22-24 (not 16-19) in 10 µm, if the proximal parts of valves are compared. Raphe sternum forming a convex central nodule that may be slightly constricted (but is not generally strongly constricted). Terminal nodules are obtusely or cuneately rounded (rather than spatulate or truncate).
SEM external view (figures 4.28, 4.30): Raphe slit with T-shaped ends conforms to most *Frustulia* taxa. Narrow linear axial area expanded in the middle, forming a distinct narrow-elliptical central area (cp. figure 4.28 to figure 7 in the protologue of *F. bahlsii*). Terminal areae (cp. figure 4.30 to figure 9 loc. cit.) narrow, apically elongated (rather than transapically expanded and broadly rounded).
SEM internal view (figures 4.27, 4.29, 4.31): Areolae around central nodule irregular, forming a "pseudo area". Helictoglossae appear as very narrow lips fused with the apical parts of the sternum, where they may slightly protrude in the largest specimens.

REMARKS: The few other species that conform in the position of the helictoglossae, e.g. *F. chilensis*, *F. pangaeopsis*, or *F. lacatosii* from tropical South America, differ by their entire complex of characters. The valves of *F. aotearoa* nov. spec. and *F. bahlsii* are similar in outlines and dimensions, with comparatively coarse striae and puncta pattern. Frustules of either species feature more or less compact and rounded distal ends of the raphe sternum, rather than the "porte-crayon" shape usually present in the genus. *F. bahlsii* as yet has only been recorded from the North American subcontinent.

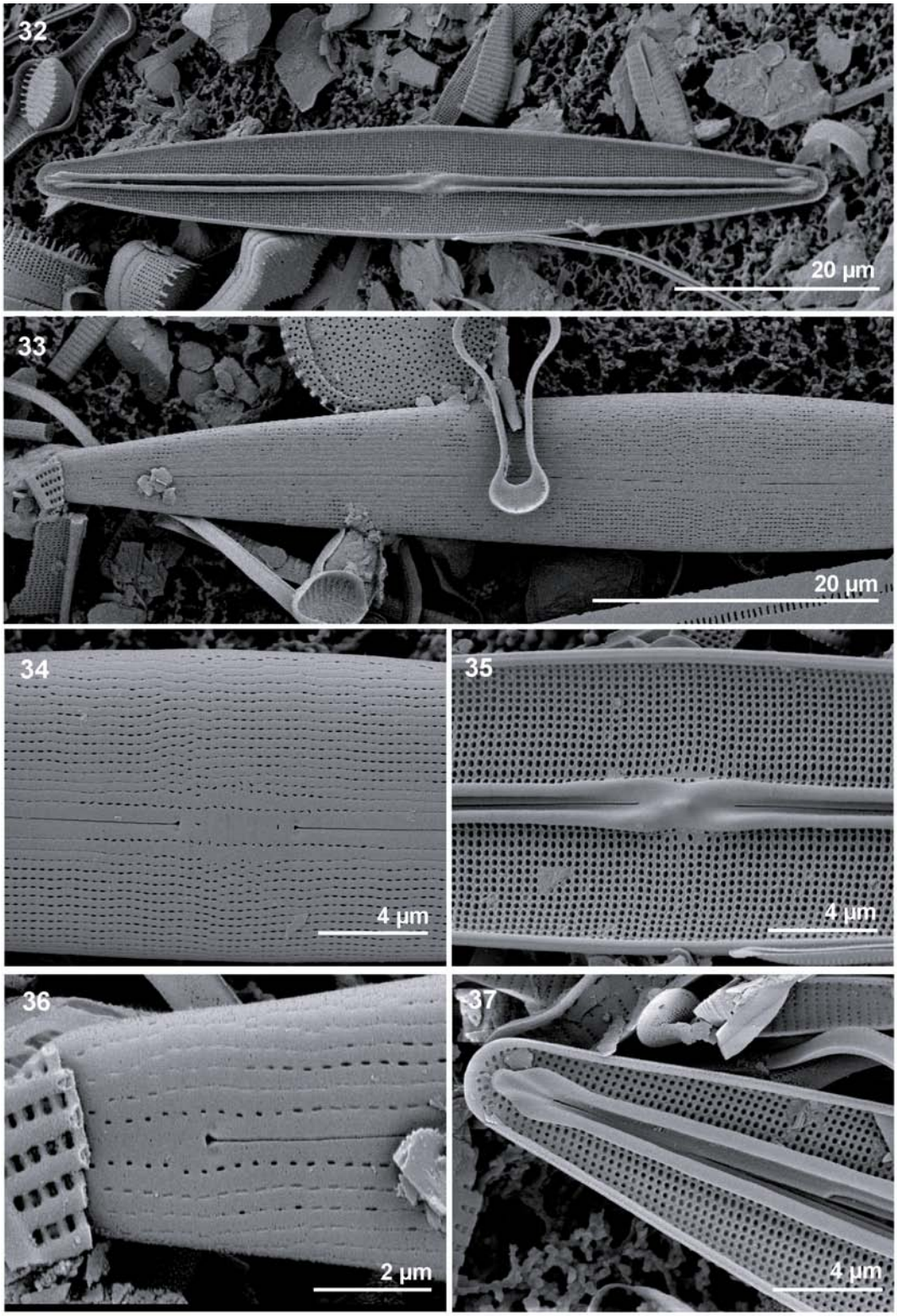
DISTRIBUTION AND ECOLOGY: So far only known from highly acidic, ombrotrophic peat bogs (with transitions to the "pakihi" wetland type, cp. Johnson and Gerbeaux 2004) at the south-western coast of New Zealand. The habitat is characterised by extremely low nutrient concentrations and biomass. *F. aotearoa* occurs in epipelon and epiphyton on *Sphagnum* spp. and *Juncus* spp.



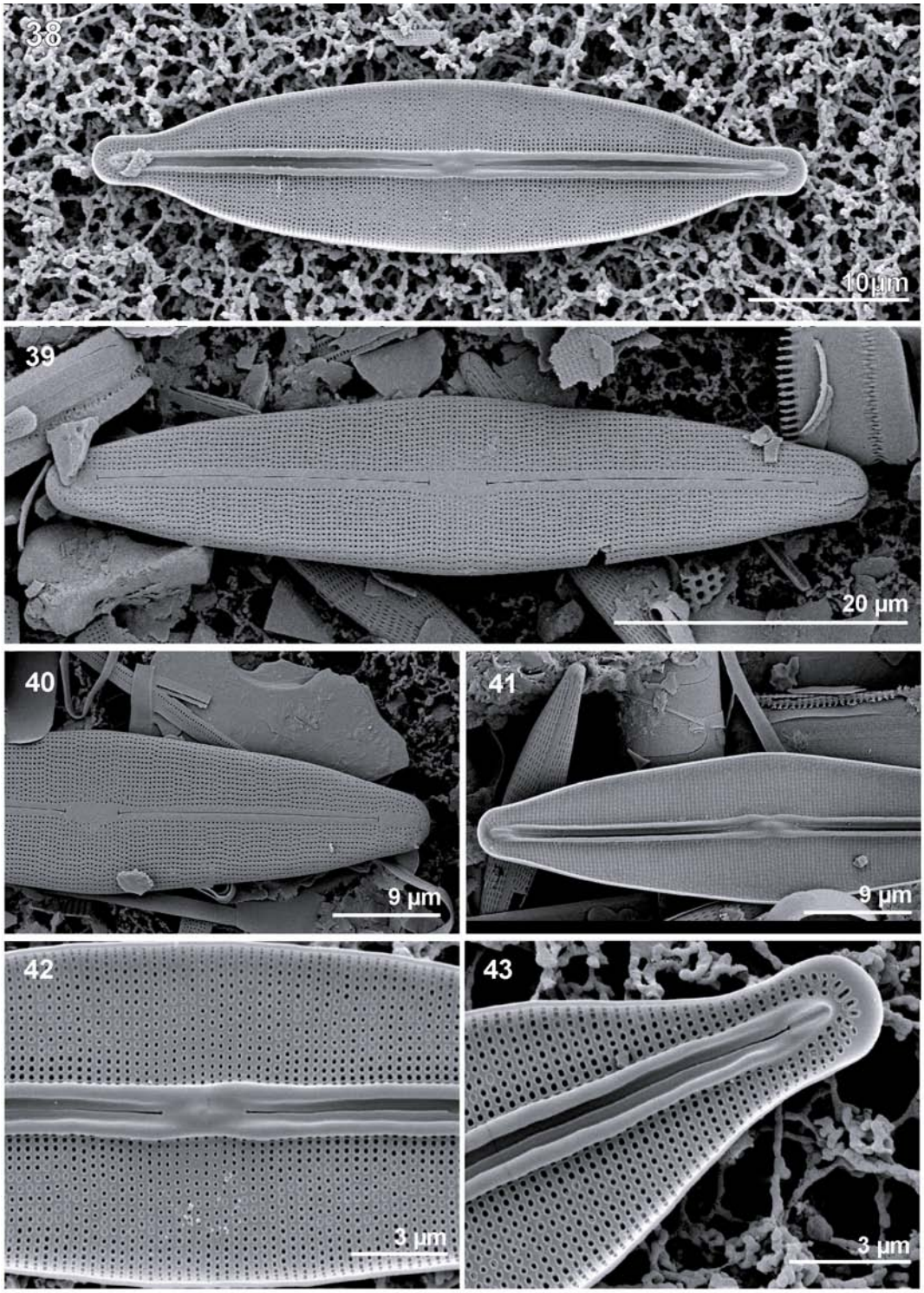
Figures 4.1-25 (LM, x1000): *Frustulia* taxa from New Zealand wetlands. Figure 4.1: *F. aotearoa* T. Beier and Lange-Bertalot spec. nov. Figures 4.2-4: *F. gondwana* Lange-Bertalot and T. Beier spec. nov. Figures 4.5-7: *F.* cf. *magaliesmontana*. Figures 4.8-10 *F. magaliesmontana* Cholnoky 1959. Figures 4.11-13: *F. pangaeopsis*. Figures 4.14-16: *F. cassieae* Lange-Bertalot and T. Beier spec. nov. Figures 4.17-19: *F. maoriana* Lange-Bertalot and T. Beier spec. nov. Figures 4.20-22: *F. crassinervia*. Figures 4.23-25: *F. saxonica.*



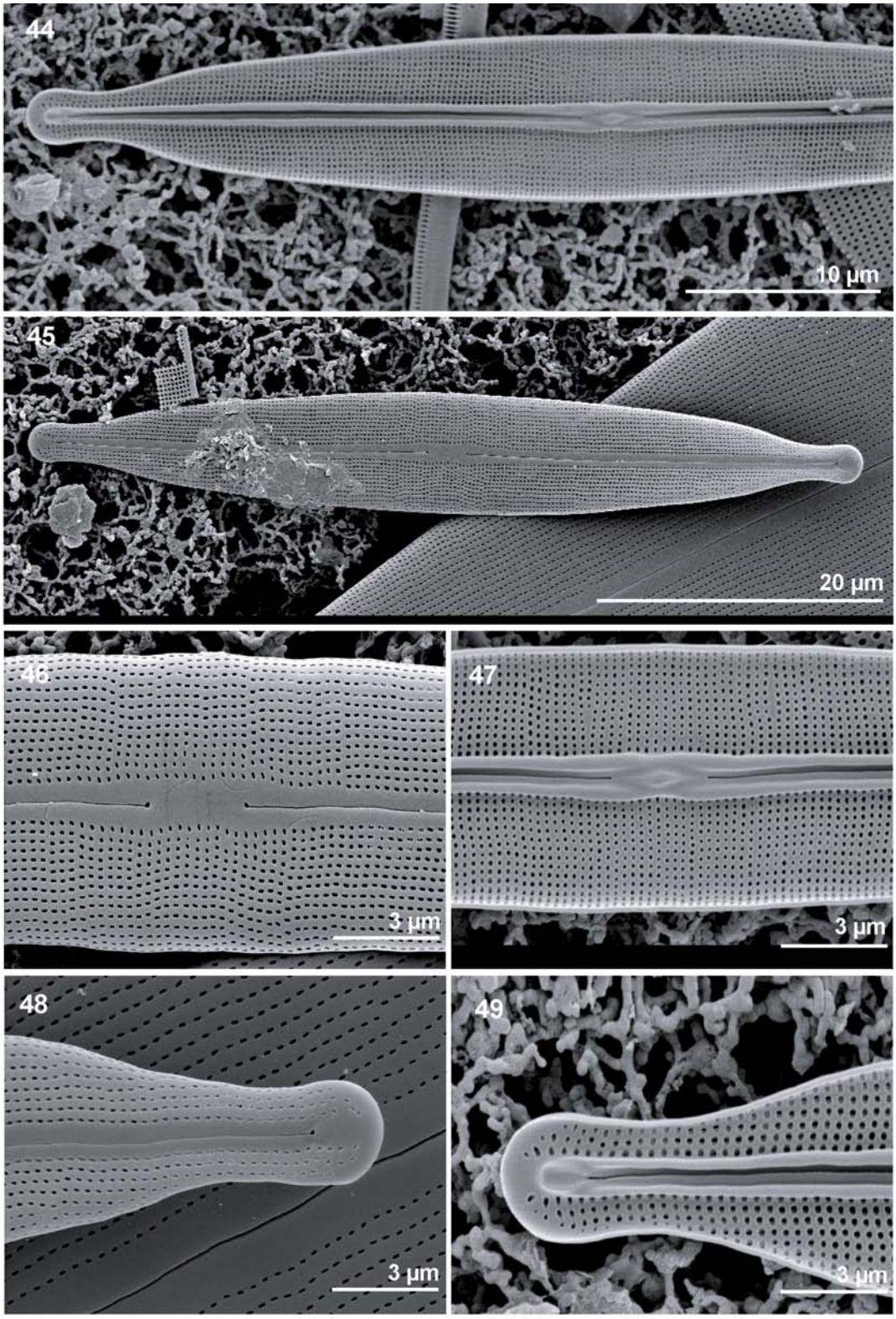
Figures 4.26-31: *Frustulia aotearoa* T. Beier and Lange-Bertalot spec. nov. Figure 4.26 LM (interference contrast). Figures 4.27, 4.29, 4.31 SEM internal, Figures 4.28, 4.30 SEM external view of the valve with particular aspects of the central and terminal raphe ends, areae, central nodule, axial costae and helicto-glossae.



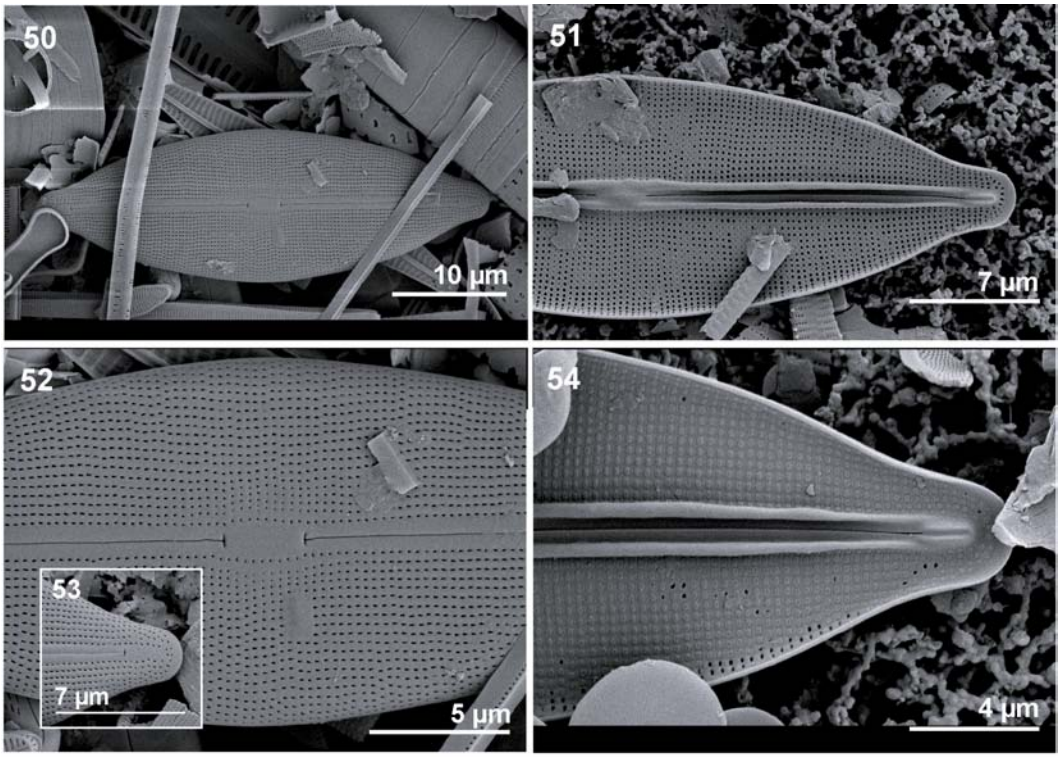
Figures 4.32-37: *Frustulia cassieae* Lange-Bertalot and T. Beier spec. nov. Figures 4.32, 4.35, 4.37 SEM internal, figures 4.33-34, 4.36 SEM external view of the valve; aspects as in figures 4.27-31.



Figures 4.38, 4.42-43: *Frustulia crassinervia*. SEM internal view of the valve with aspects of the central and terminal raphe ends, areae, central nodule, axial costae and helictoglossae.
Figuress 4.39-41: *Frustulia gondwana* Lange-Bertalot and T. Beier spec. nov. Figures 4.32-33 SEM external, figure 4.34 SEM external view of the valve.



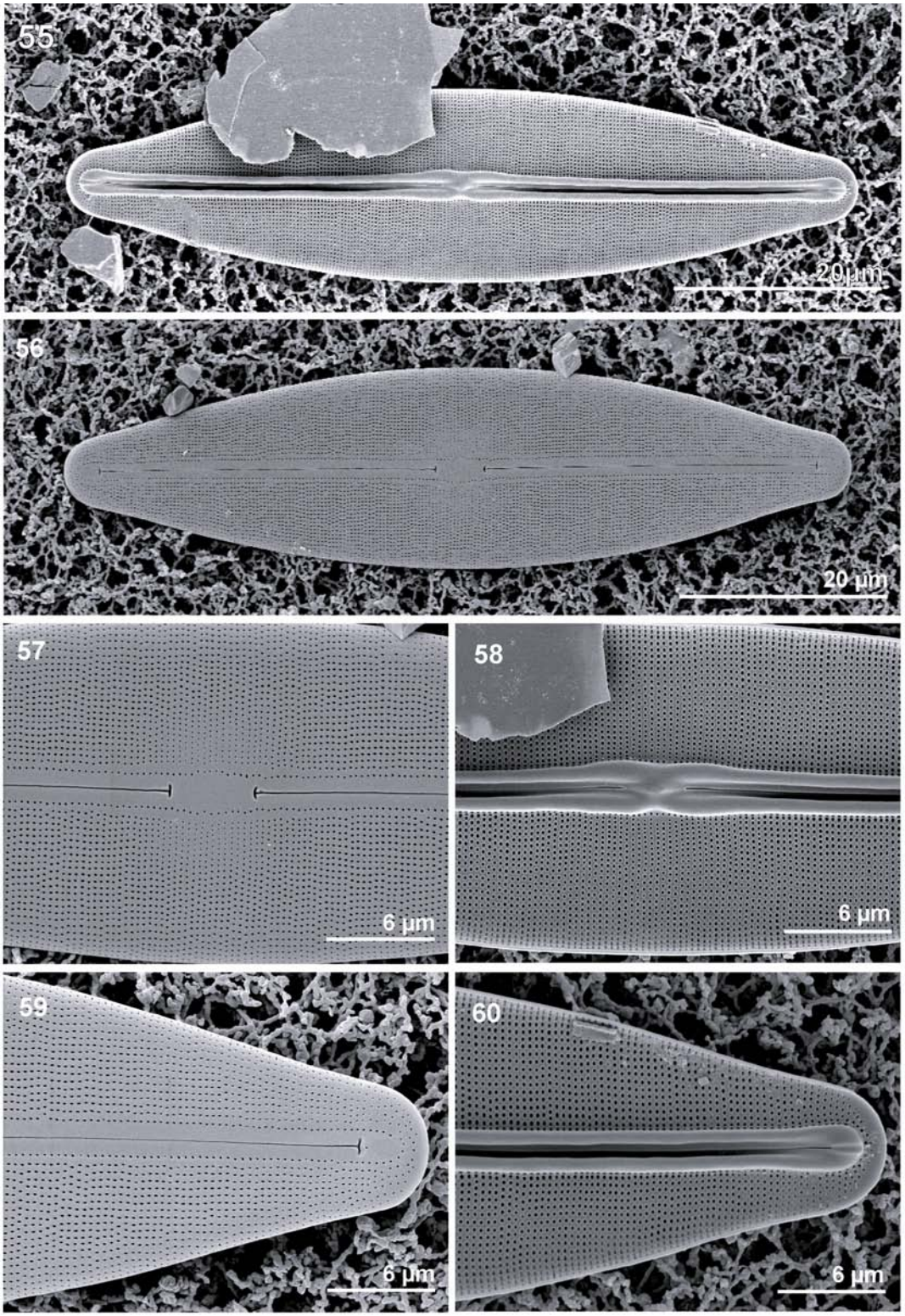
Figures 4.44-49: *Frustulia* cf. *magaliesmontana*. Figures 4.44, 4.47, 4.49 SEM internal, figures 4.45-46, 4.48 SEM external view; aspects as in figures 4.27-31.



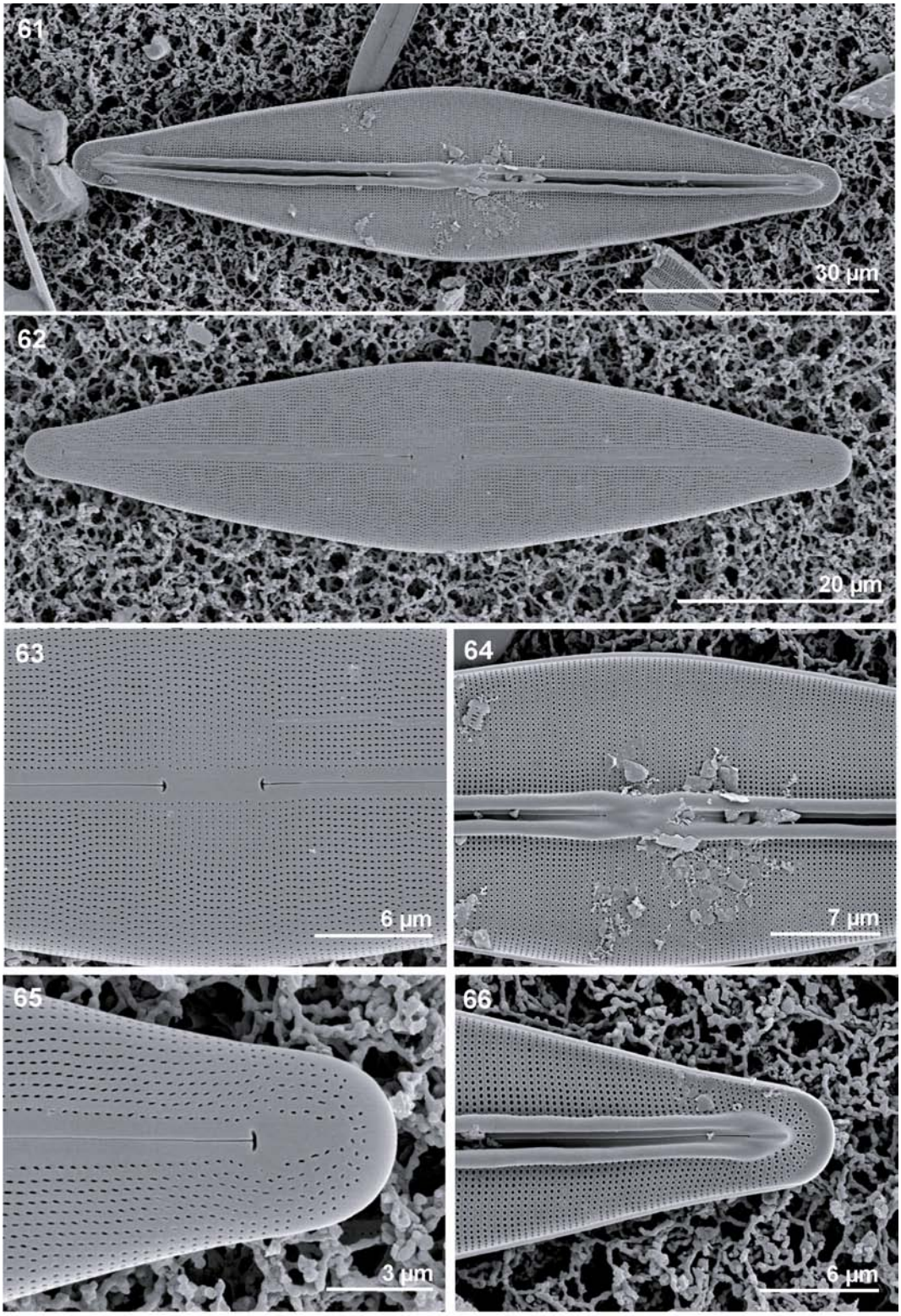
Figures 4.50-54: *Frustulia maoriana* Lange-Bertalot and T. Beier spec. nov. Figures 4.50, 4.52-53 SEM external, figures 4.51, 4.54 SEM internal view of the valve; aspects as in figures 4.27-31.

Table 4.2: Morphological features of the studied *Frustulia* species

taxon	valve outlines	length/width in µm	transap./apical striae in 10µm
F. aotearoa	lanceolate/rhombic-lanceolate, ends obtusely rounded, slightly protracted	110-210/25-38	25-26/22-24
F. cassiae	narrow-lanceolate/rhombic lanceolate, ends accutely rounded, non-protracted	70-100/11-14	29-31/30-33
F. crassinervia	lanceolate/elliptic-lanceolate, (triundulate), ends protracted rostrate/subrostrate/subcapitate	30-55/8-12.5	30-35/30-35
F. gondwana	lanceolate/rhombic-lanceolate, (triundulate), ends broadly protracted and rounded	48-57/11.5-16	25-27/25-27
F. cf. *magaliesmontana*	narrow-lanceolate, ends capitate	47-51/7-9	37-39/32-35
F. maoriana	broad-elliptic/elliptic-lanceolate, ends narrowly short-protracted, rostrate	36-53/12.5-14	28-30/27-29
F. pangaeopsis	elliptic-lanceolate/lanceolate, (triundulate), ends abruptely protracted, subrostrate/subcapitate	75-90/16-18.5	26-27/23-27
F. saxonica	broad-lanceolate/rhombic-lanceolate, ends broad- and short protracted, weakly subcapitate or subrostrate	28-105/10-18	29-32/28-31



Figures 4.55-60: *Frustulia pangaeopsis.* Figures 4.55, 4.58, 4.60 SEM internal, figures 4.56-57, 4.59 SEM external view of the valve; aspects as in figures 4.27-31.



Figures 4.61-66: *Frustulia saxonica*. Figures 4.61, 4.64, 4.66 SEM internal, figures 4.62-63, 4.65 SEM external view of the valve; aspects as in figures 4.27-31.

5.4.2 ***Frustulia cassieae*** Lange-Bertalot and T. Beier spec. nov. (Figs 4.14-16, 4.32-37)

Syn. *Frustulia rhomboides* var. *elongatissima* Manguin sensu Foged 1978, figure 20:10, Foged 1979, figures 18:4, 5 (non Manguin in Bourelly and Manguin 1952, p. 54, figure 3:47)

DIAGNOSIS:

Valvae fusiformes id est anguste et plus minusve rhombico-lanceolatae sensim attenuatae usque ad apices fere acute rotundatos non protractos. Longitudo 70 ad circiter 100 µm, latitudo 11-14 µm. Costa axialis cum nodulo centrali leviter constricto. Noduli terminales circiter triangulati apparentes. Striae transapicales parallelae in mediis partibus valvae, fortiter convergentes in partibus distalibus, circumradiantes ad polos, 29-31 in 10 µm. Striae apicales id est puncta striarum paene pariter sitae, 30-33 in 10 µm.

Aspectus ultramicroscopicus vide figures 4.32-37. Externe fissurae raphis cum poris simplicibus ad nodulos centrales terminalesque et cum depressionibus parvis utroque (nec ad instar litterae T). Extrema terminalia interna distincte dilatata cum helictoglossis prolongatis ex costa ad apices versus.

DIAGNOSIS DIFFERENS:

Paucae species similes ad instar et quoad dimensiones structurasque. *F. rhomboides* var. *elongatissima* (syn. *F. elongatissima* Lange-Bertalot) differt dimensionibus maioribus et quoad nodulos centrales terminalesque cum extremis centralibus raphis magis remotis inter se et helictoglossis distinctissime remotis a polis. *F. blancheana* Maillard ex Moser et al. differt apicibus distincte protractis et nodulis centralibus magis constrictis etiam striis transapicalibus distalibus minus convergentibus.

TYPUS: Slide Oz-53 (figure 4.16) in Collection Lange-Bertalot (FR). Isotype slide NZ-42c and residual type sample NZ-42f in the collection of the Limnological Station, Technical University of Munich.

LOCUS TYPICUS: Back Creek Swamp, West Coast District, South Island, New Zealand.

SPECIES DESCRIPTION:

Valves spindle-shaped, i.e. narrow-lanceolate or rhombic-lanceolate, from the middle tapering to the non-protracted, almost accutely rounded ends. Length 70-100 µm, breadth 11-14 µm. Axial costa complex straight with slightly constricted central nodule and approximately triangulate terminal nodules. Transapical striae parallel in proximal parts becoming progressively more convergent towards the valve ends, circumradiate at the poles, 29-31 in 10 µm. Apical striae, i.e. puncta of the striae, 30-33 in 10 µm.

SEM cp. figures 4.32-37. The central and terminal endings of the external raphe slit are not T-shaped, as in the great majority of *Frustulia* species, but form simple pores, which are comparable with *F. magaliesmontana* s. lato or *F. blancheana*. However, a pair of small shallow grooves flanking the terminal pores could only be detected in *F. cassieae*.

A second isolated porus, possibly coinciding with the internal raphe ends, appears about 1 µm proximally of each central raphe end. Internally, the apical ends of the sternum appear spatulate and the helictoglossae are distinctly protracted "porte-crayon-like".

DIFFERENTIAL DIAGNOSIS:

Only two established taxa are similar with respect to dimensions and valve outlines and might be confused with *F. cassieae*. *F. rhomboides* var. e*longatissima* Manguin (syn. *F. elongatissima* Lange-Bertalot) differs by larger dimensions. The valves are 110-127 µm long, 13-15 µm broad and the ends bluntly rounded, the central nodule is broader and longer and the terminal nodules are in a more distant position from the poles. *F. blancheana* Maillard ex Moser et al. 1995 (cp. figures 35:1-6, 36:1-3, 6) differs by distinctly protracted ends and more strongly constricted central nodules, whereas the distal transapical striae are less convergent.

REMARKS: Additional pores in an elongated central nodule are rarely observed in other *Frustulia* taxa (cp. *F. amphipleuroides* in Rumrich et al. 2000, figures 93:3-5, *F. blancheana*, Maillards drawing in the protologue, figure 3:5). Small, shallow grooves at either side of the central pores are known from *Frustulia vulgaris*, *F. pumilio* and *F. kosmolliana*. This feature usually lacks in taxa with T-shaped raphe ends and might serve as a substitute stability feature, preventing rupture of the terminal endings.

DISTRIBUTION AND ECOLOGY: This taxon appears to be restricted to slightly acidic, minerotrophic swamps at the south-western coast of New Zealand. Its habitat is characterised by low to medium nutrient concentrations and low productivity. *F. cassieae* was found on a variety of substrates, including sediment and a range of aquatic plants. Compared to the other benthic diatom taxa present, *F. cassieae* always occurred in low abundances and hence might constitute a taxon that is generally rare.

5.4.3 ***Frustulia crassinervia*** (Brébisson) Lange-Bertalot and Krammer

(Figures 4.20-22, 4.38, 4.42-43)

LM (figures 4.20-22) and SEM (figures 4.38, 4.42-43) photographs of the New Zealand population are shown for comparison with *Frustulia maoriana* Lange-Bertalot and T. Beier spec nov (cp. figures 4.17-19, 4.50-54). A detailed description of *F. crassinervia* can be found in Lange-Bertalot (2001, cp. figures 127:7-15). Further specifications are given in the differential diagnosis of *F. maoriana* (cp. table 4.2) and in the discussion.

5.4.4 *Frustulia gondwana* Lange-Bertalot and T. Beier spec. nov. (Figs 4.2-4, 4.39-41)

Syn. *Frustulia rhomboides* var. *lacustris* Maillard 1978 pro parte, p. 152, figure 3:1 d-f (nec lectotypus, figures 3:1 a-c)

DIAGNOSIS: Diagnosis differens versus *Frustulia saxonica* Rabenhorst 1853

Valvae lanceolatae ad parum rhombico-lanceolatas marginibus fere leviter triundulatis apicibus minime late protractis semper obtusissime rotundatis (nec apicibus acutius rotundatis et plus minusve subrostratis vel subcapitatis). Longitudo 48-75 µm, latitudo 11.5-16 µm. Nodulus centralis constrictus. Striae transapicales comparate distantius sitae inter se, 25-27 (nec 28-32) in 10 µm, parallelae in media parte valvae, tum minime denique modice convergentes ad apices versus, ibi circumradiales. Puncta striarum pariter striae apicales etiam comparate crassiores, 25-27 (nec 28-31) in 10 µm.

Aspectus ultramicroscopicus vide figures 4.39-41. Structurae externae vix differentes. Interne helictoglossae distinctissime longiuns anguste protractae ex costa axiali (nec compacte integratae in costa axiali, confer Lange-Bertalot 2001, figure 126:3).

TYPUS: Slide Oz-52 (figure 4.4) in Collection Lange-Bertalot (FR). Isotype slide NZ-171c and residual type sample NZ-171f in the collection of the Limnological Station, Technical University of Munich.

LOCUS TYPICUS: Mahinapua Swamp, West Coast District, South Island, New Zealand.

ETYMOLOGY: Gondwana refers to the southern counterpart of the ancient North continent Laurasia.

SPECIES DESCRIPTION: Differential diagnosis versus *Frustulia saxonica* Rabenhorst

Valve outlines lanceolate to slightly rhombic-lanceolate with moderately triundulated margins. Ends inconspicuously broadly protracted and broadly rounded (not subrostrate to subcapitate). Length 48-75 µm, breadth 11.5-16 µm. Central nodule constricted. Transapical and apical striae (i.e. puncta) comparatively coarse, 25-27 (not 28-32) in 10 µm, parallel in the middle of the valve becoming gradually more but moderately convergent towards the poles.

SEM cp. figures 4.39-41. External structures very similar. Internally, the helictoglossae are significantly longer narrowly protracted towards the apices (not compactly integrated into the apical end of the axial costa system, cp. Lange-Bertalot 2001, figure 126:3).

REMARKS: The following taxa from the northern and southern hemispheres possess similarly undulated valve outlines, but can hardly be confused if the entire combination of characters displayed is considered: *F. undosa* Metzeltin and Lange-Bertalot 1998 from South America, *F. crassiundosa* Metzeltin and Lange-Bertalot 2002 from Madagascar and South America, *Frustulia quadrisinuata* Lange-Bertalot 1996 ssp. *quadrisinuata* from the northern hemisphere and *F. quadrisinutata* ssp. *meridiana* Metzeltin and Lange-

Bertalot 1998 from South America. Several other taxa with triundulate margins were found in New Caledonia. These species, however, differ even more conspicuously.

DISTRIBUTION AND ECOLOGY: *F. gondwana* is abundant in minerotrophic swamps in the western part of the New Zealand South Island, but rare in ombrotrophic habitats. Populations that were not readily distinguished have been reported as *Frustulia rhomboides* or *F*. (cf.) *saxonica* from New Caledonia (Moser et al. 1995, figures 42:1, 2), Costa Rica (Wydrzycka and Lange-Bertalot 2001, figure 11:4), and Chile (Rumrich et al. 2000, figures 96:5,6). Its distribution coincides with that of *F. magaliesmontana*, which is restricted to the southern hemisphere (see below).

5.4.5 *Frustulia* **cf.** ***magaliesmontana*** Cholnoky 1957 (Figures 4.5-10, 4.44-49)

It cannot definitely be ascertained whether or not Cholonky's taxon from South Africa is conspecific with the populations of *Frustulia* cf. *magaliesmontana* found at the South- and North Island of New Zealand. In this context, images of specimens from the type slide (figures 4.8-10) are presented for the first time to facilitate comparison with other populations. The exactness of Cholnoky's drawings may not be out of doubt, a count of the fine structures in the drawings and the number of striae given in the diagnosis do not agree completely. Moser et al. (1995, figures 36:4-5, 7, figures 37:1, 2, and figure 39:7) show LM and SEM microphotographs of another population from South Africa, identified as *F. magaliesmontana*. However, conspecificity with the type specimens is also arguable, though valve dimensions and outlines are very similar. They differ by the lower number of transapical striae, 29-33 in 10 µm, which coincides with the number of puncta. In contrast, the population from the type locality is characterised by 37-39 transapical striae in 10 µm, which are very difficult to resolve even when using DIC equipment (personal communication with J. Taylor, who photographed the type specimens), whereas the apical stria system with 32-35 puncta in 10 µm is much easier to resolve (figures 4.8-10). When creating line drawings from other localities of the Cape Province, Cholnoky (1959) drew the transapical striae strictly parallel (i.e. in a 90 ° angle to the apical costa) from the centre through to the apices, whereas the populations from New Zealand possess strongly convergent striae, except for the central part of the valve (see also Foged 1979, figures 17: 11-12 and 1978, figures 19:12-14, from East Australia). These conform better to the type specimens of *F. magaliesmontana*, if the density of striae is considered, but exhibit narrowly lanceolate valve outlines tapering to capitate ends, instead of a linear-lanceolate to linear shape with cuneately protracted rostrate ends. *Frustulia magaliesmontana* from the Columbian Andes (Rumrich et al. 2000, figure 98:7) largely corresponds to the type material, whereas for *F. magaliesmontana* ssp. *americana* (Metzeltin and Lange-Bertalot 1998, figures 116:4-6) that has been reported from tropical Brazil and Venezuela, the assignment of species rank would be more appropriate. This

taxon differs with respect to the number of transapical striae (29-31 in 10 µm), and the apical striae and puncta are coarser (15.5-26.5 in 10 µm) than in the type specimens. Another similar species is *Frustulia pseudomagaliesmontana* Camburn and Charles 2000, which is as yet only known from North America. It is distinguished by a shorter valve width (5-6.5 µm) and 37-40 parallel striae in 10 µm. The populations from the southern hemisphere generally feature broader valves from 7-9 µm and are characterised by distinctly convergent striae, except for the central part.

5.4.6 ***Frustulia maoriana*** Lange-Bertalot and T. Beier spec. nov.

(Figures 4.17-19, 4.50-54)

DIAGNOSIS: Diagnosis differens versus *Frustulia crassinervia* (Brébisson) Lange-Bertalot and Krammer

Valvae comparate latius ellipticae vel aliquid elliptico-lanceolatae quoad individua longissima apicibus semper protractis anguste rostratis (marginibus numquam triundulatis). Longitudo 36-53 µm, latitudo 12.5-14 (non 8-12.5) µm. Nodulus centralis vix constrictus. Striae transapicales parallelae usque sub apices, ibi circumradiales sed nullo loco distincte convergentes, 28-30 (non 30-35) in 10 µm ita ut striae apicales pariter puncta striarum, 27-29 in 10 µm, facile discernandae microscopio photonico etiam sine illuminatione obliqua.
Aspectus ultramicroscopius externus internusque (vide figures 4.50-54). Structurae praecipuae vix differentes comparate *F. crassinervia*.

TYPUS: Slide Oz-52 (figure 4.17) in Lange-Bertalot collection (FR). Isotype slide NZ-171c and residual type sample NZ-171f in the collection of the Limnological Station, Technical University of Munich.

LOCUS TYPICUS: Mahinapua Swamp, West Coast District, South Island, New Zealand.

ETYMOLOGY: The epithet “maoriana” is derived from Maori, the native population and native language of New Zealand

SPECIES DESCRIPTION: Differential diagnosis versus *Frustulia crassinervia* (Brébisson) Lange-Bertalot and Krammer

Valve outlines broad-elliptic or moderately elliptic-lanceolate if the longest specimens of the cell cycle are concerned (never triundulate). Ends narrowly short-protracted, rostrate. Length 36-53 µm, breadth 12.5-14 (not 8-12.5) µm. Central nodule at most very little constricted. Transapical striae parallel up to the ends, nowhere distinctly convergent, around the apices circumradiate, 28-30 (not 30-35 or even 36-40 as noted by some authors) in 10 µm. Apical striae 27-29 in 10 µm. Easily discernible in LM as opposed to *F. crassinervia*, even without oblique lighting.

SEM (cp. external and internal view in figures 4.50-54): Regarding the vital fine structures, there are no significant features that differentiate between *F. maoriana* and *F. crassinervia*.

REMARKS: Other small-celled taxa known from the northern or southern hemisphere can hardly be confused with *F. maoriana*, since the combination of characters differs significantly (cp. *Frustulia* spp. in Moser et al. 1995, 1998 and Moser 1999 from New Caledonia, Metzeltin and Lange-Bertalot 1998 from the Neotropics, Rumrich et al. 2000 from the Andes in South America, Wydrzycka and Lange-Bertalot 2001 from Costa Rica). *Frustulia saxonica* is associated at the type locality but is easy to distinguish from *F. maoriana*.

DISTRIBUTION AND ECOLOGY: This taxon is known as yet from various acidic, oligo- to mesotrophic lowland wetlands at the south-western coast of New Zealand. *F. maoriana* spec. nov. was found in sediment samples and on a variety of submerged macrophytes, i.e. it does not appear to be host specific.

5.4.7 ***Frustulia pangaeopsis*** Lange-Bertalot 2001 (Figures 4.11-13, 4.55-60)

LM (figures 4.11-13) and SEM (figures 4.55-60) photographs of the New Zealand population are shown for comparison with *Frustulia aotearoa* (cp. figures 4.1, 4.26-31). A detailed description of *F. pangaeopsis* can be found in Lange-Bertalot (2001, cp. figures 130:1-6). For further information refer to remarks in the observations of *F. aotearoa* (cp. table 4.2) and in the discussion.

5.4.8 ***Frustulia saxonica*** Rabenhorst 1853 (Figures 4.23-25, 4.61-66)

LM (figures 4.23-25) and SEM (figures 4.61-66) photographs of the New Zealand population are shown for comparison with *Frustulia gondwana* (cp. figures 4.2-4, 4.39-41). A detailed description of *F. saxonica* can be found in Lange-Bertalot (2001, cp. figures 126:1-7, 127:1-6). Further specifications are referred to in the differential diagnosis of *F. gondwana* (cp. table 4.2) and in the discussion.

5.5 Discussion

With few exceptions, *Frustulia* populations from the southern hemisphere have been erroneously identified as holarctic taxa in the past. Most of the photographically documented taxa from Australasia were assigned to *F. vulgaris* or varieties of the 'catch-all' taxon *F. rhomboides*. According to this erroneous assumption, the vast majority of *Frustulia* species would be cosmopolitan, yet the opposite is exemplified by the Pacific island New Caledonia. After revision of the 17 species present (Moser 1999), only *F.*

vulgaris, *F. spicula*, and *F. weinholdii* proved to be cosmopolitan. Interestingly, none of these taxa is acidophilous or acidobiontic and characteristic of electrolyte-poor habitats. The other 14 taxa likely are endemic or restricted to Australasia. In the Neotropics, the biogeographical situation is comparable. However, because of the larger area and habitat diversity, more zonal and presumably endemic acidobiontic *Frustulia* taxa occur. Most of them have been described recently (Metzeltin and Lange-Bertalot 1998, Wydrzycka and Lange-Bertalot 2001). It is also remarkable that New Caledonia and the Neotropics have no acidobiontic *Frustulia* taxa in common, either with Europe or with each other. Occurrence of acidobiontic cosmopolitan taxa of this genus in the neotropical area of South America is generally not evident. *F. pangaea* was misleadingly interpreted in this respect. Revision with SEM revealed that the populations of Central Europe are morphologically heterogeneous, relating to *F. pangaeopsis*.

In ombrotrophic peat bogs and minerotrophic lowland wetlands in south-western New Zealand, we found eight acidophilous or acidobiontic taxa, of which four were described as new species. *F. gondwana* spec. nov. was previously reported as *Frustulia rhomboides* from New Caledonia (Moser et al. 1995). Morphologically very similar populations that supposedly belong to this taxon were also found in the Neotropics (Rumrich et al. 2000, Wydrzycka and Lange-Bertalot 2001). *F. magaliesmontana* was originally described from South Africa but has also been reported from other (sub)continents and islands in the southern hemisphere (Foged 1978, 1979, Moser et al. 1995, Rumrich et al. 2000). Conspecificity with the New Zealand population is not unlikely but remains questionable (see also chapter 4.4). Irrelevant of the homogeneity of those populations, *F. magaliesmontana* is apparently absent in the northern hemisphere and the holarctic plant kingdom. However, three of the studied New Zealand taxa appear to be identical with populations from Europe, since there are no significant features that justify differentiation. Among these, *F. saxonica* and *F. crassinervia* are known to be cosmopolitan in temperate climate zones. However, *F. pangaeopsis* is an overlooked and perhaps neglected taxon that, on occasion, might have been mistaken for *F. rhomboides*. In fact, there is hardly any doubt that '*F. rhomboides*' in Vyverman et al. (1995, figures 29:2,4) from Tasmanian mountain lakes belongs to *F. pangaeopsis*. The specimen in figure 29:1 (loc. cit.) is another misidentified '*F. rhomboides*' that resembles *F. aotearoa* spec. nov., but differs by the terminal nodules, which exhibit distinctly protracted helictoglossae. While this taxon might represent another species new to science, figure 29:5 (loc. cit.), which is designated as *F. rhomboides* var. *elongatissima*, it presumably ranks among *F. cassieae* spec. nov. (as far as recognisable at the microphotograph). The line drawings and SEM photographs of the same taxon (Vyverman 1991) from Papua New Guinea can hardly serve for effective comparison because of their poor quality. Foged (1978, 1979) erroneously reported Manguin's taxon from East Australia and the North Island of New Zealand. Observation of the type slide by Metzeltin and Lange-

Bertalot (unpublished) definitely excludes any conspecificity between the Caribbean and Australasian populations. *F. aotearoa* spec. nov. and *F. maoriana* spec. nov. could not be retrieved in any iconographical documentation from the southern hemisphere or elsewhere in the literature. However, inaccurate line drawings of specimens that have been determined as '*F. rhomboides* var. *saxonica*' or '*F. rhomboides* var. *crassinervia*' might actually refer to *F. maoriana*. Nevertheless, both newly described taxa may provisionally be regarded as endemic to New Zealand or the Australasian region.

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APPENDIX

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Glossary

α-diversity	diversity of species within community sample plots
a priori	prior to sampling and statistical analysis
acidobiontic	organisms occurring at pH < 7, with the optimum distribution at pH 5.5 or below
acidophilous	organisms occurring at pH 7, but widest distribution at lower pH
adnate	closely attached
alkalinity	measure of a solution's resistance to changes in pH
allelopathic substances	growth inhibiting chemicals released by plants
alluvial	created or deposited by either glacial or stream activity
anaerobic	anoxic
anion deficit	difference between the total sum of cations and anions
ANOSIM	Analysis of Similarities
ANOVA	Analysis of Variance
anthropogenic	caused by men
aotearoa	Maori name of New Zealand, “land of the long white cloud”
apical	relating to or located at the valve end
(as)	artificial substrate
ASA	American Standard Association; measure of film speed
Au	chemical symbol for gold
Aufwuchs	plants and animals adhering to submersed surfaces
axial area	unornamented area along the apical axis of a diatom valve
B, b	bog
B1	wetland site at Keogan’s Road
B2	wetland site at Stafford Loop Road
B3	wetland site at Kumara
B4	wetland site at Arthurstown Road
Bacillariophyceae	class of marine and freshwater eukaryotic algae: diatoms
benthic	living at or near the bottom of freshwater or marine systems
BIO-ENV	numerical algorithm matching biological and environmental data
bog	highly acidic, ombrotrophic/oligotrophic wetland type
bootstrapping	randomisation procedure in statistical testing
boxplot	box and whiskers plot
bubble plot	ordination diagram with superimposed variables
BVSTEP	stepwise matching of ordinations, numerical algorithm
CCA	Canonical Correspondence Analysis
chelates	organic molecules trapping or encapsulating highly reactive trace metals
Chl-*a*	chlorophyll-*a*
cingulum	all elements of the girdle region of a diatom valve
Cond	corrected conductivity
costae	thickened bands or ribs on the diatom valve
d	species richness, Margalef’s Index
DAAD	German Academic Exchange Service
DCA	Detrended Correspondence Analysis
DCCA	Detrended Canonical Correspondence Analysis

DECORANA	software providing Detrended Correspondence Analysis
Delta Δ	average taxonomic diversity
Delta Δ*	average taxonomic distinctiveness
Delta ΔΦ	intensity of relative water level fluctuations
DIC	differential contrast
DOC	dissolved organic carbon
dominant	species with relative abundances > 10 %
draftsman plot	pairwise scatter plots of correlated variables
endemic	species distribution restricted to a specific area
epipelon	benthic algae inhabiting sediment
epiphyton	benthic algae growing on aquatic macrophytes
EPS	Extracellular Polymeric Substance
eq	equivalent
Euclidean distance	dissimilarity measure
eutrophic	highly productive freshwater ecosystems
fen	acidic, minerotrophic wetland type with low to moderate nutrient status
FR	France
frustule	diatom valves and their associated cingulum elements
fulvic acid	low molecular weight yellow substance
g_{440}	gilvin absorbance coefficient at 440 nm wavelength
geographic class plot	distributional plot measuring community stress
gilvin	water colour; substitute measure for DOC
girdle	part of the diatom frustule separating the epi- and hypovalves
gley	soil influenced by groundwater
Gondwana	southern super continent in the late Mesozoic era
GPS	Global Positioning System
granite	mineral mainly consisting of quartz and feldspar
granodiorite	intrusive igneous rock similar to granite
greywacke	impure sandstone consisting of rock fragments and grains of quartz and feldspar in a matrix of clay-sized particles
H’	Shannon-Wiener diversity index
helictoglossae	pores at the terminal raphe endings of a diatom valve
herbarium	collection of preserved plants or plant parts
heterotrophy	Nutritional mode in which absorption of organic matter is required for growth, metabolism and reproduction
humic acid	complex mixture of organic acids
hydrophilic	exhibiting affinity to water
hydrophobic	water repelling
ID	Identification number
IDH	intermediate disturbance hypothesis
IMD	Index of Multivariate Dispersion
inert	not readily reactive with other elements
J’	Pielou’s Evenness Index
k-dominance plot	distributional plot of summarised ranked abundances
Lambda λ	Simpson diversity index
λ_1/λ_2	ratio of the first and second eigenvectors in DCCA

Laurasia	northern supercontinent in the late Mesozoic era
LM	light microscope
loess	aeolian sediment
$\log_e$	logarithm to the base e
macrophytes	vascular aquatic plants and macroscopic algae
Mantel test	parametric method testing correlation of two distance matrices
Maori	native language and people of New Zealand
MDS	Multidimensional Scaling
mensurative	descriptive
mesothermal climate	temperate climate; coldest month between −3°C and 18°C
mesotrophic	moderately productive freshwater ecosystems
metaphyton	floating algal mats
metapopulation	cluster of connected populations
microphytobenthos	microscopic algae growing on submersed substrates
minerotrophic	water supply by non-atmospheric water sources
morainic	refers to moraine: glacial gravel deposit
MVDISP	Multivariate Dispersion
N	number of individuals
n	number of replicates
Neotropics	tropical zones of the Americas
nitrification	process by which ammonia reacts to nitrite, nitrate, and nitrogen gas
NIWA	National Institute of Water and Atmospheric Research
NZ	New Zealand
NZGD	New Zealand Geodatic Datum
NZMG	New Zealand Map Grid
non-parametric	statistical test without restrictions in probability distributions
oceanic climate	maritime climate; typically found along continental and island west coasts at middle latitudes
oligotrophic	low productive freshwater ecosystems
ombrotrophic	water supply depends on precipitation
ordination	projection of samples from multivariate space
p	significance level for statistical tests
pakihi	bog wetland type in south-western New Zealand
PAR	photosynthetically active radiation
parametric	statistical test that requires normal distribution of samples
permutation	repeated randomised statistical testing procedure
PCA	Principal Components Analysis
PC axis	Principal Components axis
periphyton	assemblage of microorganisms attached to submerged surfaces
periphyton (as)	periphyton attached to artificial substrata
perspex	polymethyl-2-methylpropanoate; plexiglas, acrylic glass
photoautotroph	organisms using light as energy source
phytoplankton	algal component of the plankton drifting in the water column
podzol	acidic soil which is heavily leached in its upper layers
polyethylene	chemically inert plastic polymer of ethylene
prostrate	laying flat on the ground

puncta	perforation through diatom valves
PVC	polyvinyl chloride
R^2	regression coefficient
R, ρ	correlation coefficient
raphe	median groove of a diatom valve
rare	species with relative abundances of less than 2 %
redundancy	fail-safe design providing a secondary standby structural member
RELATE	numerical algorithm relating similarity and dissimilarity matrices
replicates	repeated samples at the same ecological and experimental level
resilience	ability for an ecosystem to rebound from disturbance
RMSEP	root mean square error of prediction
rostrate	beaklike
salinity	total amount of dissolved ions
S, s	swamp
S1	Mahinapua Swamp
S2	wetland site at Tucker Flat
S3	wetland site at Lake Kaniere
S4	Back Creek Swamp
schist	fine-grained metamorphic rock with laminations similar to slate
SD	standard deviation
SEM	scanning electron microscope
SIMPER	numerical algorithm calculating similarity percentages
sloughing	autogenically induced senescence and detachment of algal cells
sqr.rt	square root
SRP	soluble reactive phosphorus
standardisation	normalisation across different scales of environmental variables
striae	rows of puncta/areolae at diatom valves
subdominant	species with relative abundances between 2 % to 10 %
succession	sequence of developmental states in biological communities
sulphate deficit	difference between expected sulphate concentration induced by sea spray and the actual sulphate content
superhumid climate	high rainfall area: annual precipitation 3000-5000mm
swamp	slightly acidic, minerotrophic/meso- to eutrophic wetland type
temp	temperature
TP	total phosphorus
transapical	axis from the centre of the epivalve to that of the hypovalve
transfer function	mathematical representation of the relation between input and output of a linear time-invariant system
TUM	Technical University of Munich
tychoplankton	temporarily suspended benthic organisms
Type I error	probability of rejecting a true hypothesis
UV-VIS	spectroscopic method using ultraviolet and visible wavelengths
valve	siliceous part of the diatom frustule
WA	weighted averaging
Waimea	latest period of glaciation in New Zealand
yellow substance	organic matter decomposition product

Alphabetical list of taxa

ID-tax	Taxon	Bogs				Swamps			
		B1	B2	B3	B4	S1	S2	S3	S4
achcar	*Achnanthes carissima* (Lange-Bertalot in Lange-Bertalot & Krammer 1989)					x			
achdid	*Achnanthes didyma* (Hustedt 1933)					x			
achhel	*Achnanthes helvetica* (Hustedt) Lange-Bertalot in Lange-Bertalot & Krammer 1989					x	x	x	x
achkra	*Achnanthes kranzii* (Lange-Bertalot in Lange-Bertalot & Krammer 1989)							x	
achlae	*Achnanthes laevis* (Oestrup)			x					
achlan	*Achnanthes lanceolata* (Brébisson) Grunow in Cleve & Grunow 1880					x	x	x	
achlev	*Achnanthes levanderi* (Hustedt 1933)					x			
achmar	*Achnanthes marginulata* (Grunow in Cleve & Grunow 1880)					x		x	x
achmin	*Achnanthes minutissima* var. *minutissima* (Kützing 1833)	x	x		x	x	x	x	x
achobl	*Achnanthes oblongella* (Oestrup 1902)					x		x	
achpus	*Achnanthes pusilla* (Grunow) De Toni 1891				x	x	x		
achsac	*Achnanthes saccula* (Carter in Carter & Bailey-Watts 1981)								x
achsub	*Achnanthes subatomoides* (Hustedt) Lange-Bertalot & Archibald in Krammer &					x		x	
	Lange-Bertalot 1985								
achthe	*Achnanthes* cf. *thermalis* (Rabenhorst) Schoenfeld 1907			x					
actspe	*Actinella* spec. aff. *Eunotia cuneiformis* (Manguin 1962) Moser et al. 1995								x
adlbry	*Adlafia bryophila* (Petersen) Lange-Bertalot in Moser et al. 1998			x		x			
aulalp	*Aulacoseira alpigena* (Grunow) Krammer 1990					x			x
aulcra	*Aulacoseira crassipunctata* (Krammer 1990)					x			x
aulcre	*Aulacoseira crenulata* (Ehrenberg) Thwaites 1848						x		
auldis	*Aulacoseira distans* (Ehrenberg) Simonsen 1979						x		
aullac	*Aulacoseira lacustris* (Grunow) Krammer 1990					x			x
aulten	*Aulacoseira tenuior* (Grunow) Krammer 1990	x				x			x
brabre	*Brachysira brebissonii* (Ross in Hartley 1986)					x			x
braneo	*Brachysira neoexilis* (Lange-Bertalot)	x				x			x
brapro	*Brachysira procera* (Lange-Bertalot & Moser)	x				x		x	x
brawyg	*Brachysira wygaschii* (Lange-Bertalot)		x						x
calaer	*Caloneis aerophila* (Bock 1963)		x	x			x		
calbac	*Caloneis bacillum* (Grunow) Cleve 1894		x	x	x	x	x	x	
calbra	*Caloneis branderii* (Hustedt) Krammer 1985						x		
calhya	*Caloneis hyalina* (Hustedt 1938)					x	x	x	
chabeg	*Chamaepinnularia begeri* (Krasske 1932) Lange-Bertalot	x	x	x	x	x	x	x	x
chabre	*Chamaepinnularia bremensis* (Hustedt 1957) Lange-Bertalot	x	x			x			x
chamed	*Chamaepinnularia mediocris* (Krasske 1932) Lange-Bertalot	x	x	x	x	x	x	x	x
chasha	*Chamaepinnularia soehrensis* var. *hassica* (Krasske 1925) Lange-Bertalot		x	x		x	x		x
chasso	*Chamaepinnularia soehrensis* var. *soehrensis* (Krasske 1923) Lange-Bertalot &		x	x	x	x	x	x	x
	Krammer								
cocpla	*Cocconeis placentula* var. *lineata* (Ehrenberg 1838)		x		x				
cyccom	*Cyclotella comensis* (Grunow in Van Heurck 1882)					x			
cycste	*Cyclotella stelligera* (Cleve & Grunow in Van Heurck 1882)					x			
cymasp	*Cymbella aspera* (Ehrenberg) H. Peragallo 1889								x
cymcus	*Cymbopleura cuspidata* (Kützing)						x		
cymnav	*Cymbopleura naviculiformis* (Auerswald)					x	x	x	x
diacon	*Diadesmis contenta* (Grunow) D.G. Mann	x		x	x	x	x	x	x
dipell	*Diploneis elliptica* (Kützing) Cleve 1891					x			
dipspe	*Diploneis* spec. aff. nov. spec. Nr. 1 Julma Ölkky					x			
encama	*Encyonema amanianum* (Krammer)					x	x	x	x
encmin	*Encyonema minutum* (Hilse in Rabenhorst) D. G. Mann 1990								x
encneo	*Encyonema neogracile* (Krammer)	x	x		x	x	x	x	x
encper	*Encyonema perpusillum* (A. Cleve) D. G. Mann in Round & al. 1990	x	x	x		x			x
encrum	*Encyonopsis rumrichae* (Krammer)								x
episor	*Epitemia sorex* (Kützing 1844)								x
eunarl	*Eunotia arculus* (Grunow) Lange-Bertalot & Nörpel		x						
eunars	*Eunotia arcus* (Ehrenberg 1837)		x	x			x	x	x
eunbbi	*Eunotia bilunaris* var. *bilunaris* (Ehrenberg) Mills 1934	x	x	x	x	x	x	x	x
eunbmu	*Eunotia bilunaris* var. *mucophila* (Lange-Bertalot & Nörpel 1991)	x	x	x		x	x	x	x
eunbot	*Eunotia* aff. *botuliformis* (Wild, Nörpel & Lange-Bertalot)							x	
euncri	*Eunotia crista-galli* (P.T. Cleve 1891)					x			
eundio	*Eunotia diodon* (Ehrenberg 1837)					x			
eunexi	*Eunotia exigua* (Brébisson ex Kützing) Rabenhorst 1864	x	x	x	x	x	x	x	

ID-tax	Taxon	Bogs				Swamps			
		B1	B2	B3	B4	S1	S2	S3	S4
eunfle	*Eunotia flexuosa* (Brébisson) Kützing 1849							x	x
eungen	*Eunotia genuflexa* (Nörpel-Schempp)					x		x	
eungro	*Eunotia groenlandica* (Grunow) Nörpel-Schemgg & Lange-Bertalot		x	x	x	x	x		
eunimp	*Eunotia implicata* (Nörpel, Lange-Bertalot & Alles 1991)		x						x
euninc	*Eunotia incisa* (Gregory 1854)	x	x	x	x	x	x	x	x
eunmei	*Eunotia meisteri* (Hustedt 1930)	x	x	x		x	x	x	x
eunmin	*Eunotia minor* (Kützing) Grunow in Van Heurck 1881	x			x				
eunmon	*Eunotia monodontiforma* (Lange-Bertalot & Nörpel-Schempp)					x			
eunmus	*Eunotia musicola* (Krasske 1939)								x
eunnae	*Eunotia naegeli* (Migula in Thomé 1907)							x	x
eunppa	*Eunotia paludosa* var. *paludosa* (Grunow in Van Heurck 1881)	x	x	x	x			x	x
eunptr	*Eunotia paludosa* var. *trinacria* (Krasske) Nörpel 1991	x	x	x	x	x	x	x	x
eunpra	*Eunotia praerupta* (Ehrenberg 1843)					x			x
eunsch	*Eunotia schwabei* (Krasske 1939)	x				x	x	x	x
eunsio	*Eunotia siolii* (Hustedt)			x		x		x	
eunspe	*Eunotia* spec. Nr.4	x							x
eunspj	*Eunotia* spec. Nr.3 Julma Ölkky	x	x	x	x	x			x
eunssb	*Eunotia* spec. Nr.2 aff. siolii (f. bidens)	x							
eunssi	*Eunotia* spec. Nr.1 aff. siolii		x	x	x		x		x
eunste	*Eunotia steineckii* (Petersen 1950)	x	x		x				
eunsub	*Eunotia subarcuatoides* (Alles, Nörpel & Lange-Bertalot 1991)	x	x	x		x			
eunven	*Eunotia veneris* (Kützing) De Toni 1892		x	x	x	x			
falvit	*Fallacia vitrea* (Østrup) Mann	x		x		x	x		
fracap	*Fragilaria capucina* v. *capucina* (Desmazières 1825)					x	x		
fracex	*Fragilaria construens* f. *exigua* (W. Smith) Hustedt 1959					x			
fracve	*Fragilaria construens* f. *venter* (Ehrenberg) Hustedt 1957					x	x	x	x
fraexi	*Fragilaria exigua* (Grunow in Cleve & Möller 1878)					x			x
franan	*Fragilaria nanoides* (Lange-Bertalot)					x		x	x
fraold	*Fragilaria oldenburgioides* (Lange-Bertalot)								x
frapar	*Fragilaria parasitica* (W. Smith) Grunow in Van Heurck 1881					x			x
frapse	*Fragilaria pseudoconstruens* (Marciniak 1982)					x			
frauln	*Fragilaria ulna* (Nitzsch) Lange-Bertalot 1980					x			x
fravir	*Fragilaria virescens* (Ralfs 1843)					x			
fruaot	*Frustulia aotearoa* spec. nov. T. Beier & Lange-Bertalot	x	x	x					
frucas	*Frustulia cassieae* spec. nov. Lange-Bertalot & T. Beier					x			x
frucor	*Frustulia corneliae* (Lange-Bertalot & Rumrich) 2000	x	x	x	x				
frucra	*Frustulia crassinervia* (Brébisson) Lange-Bertalot & Krammer in Lange-Bertalot &	x	x	x		x			x
	Metzeltin 1996								
frugon	*Frustulia gondwana* spec. nov. Lange-Bertalot & T. Beier		x	x	x	x	x	x	x
frumag	*Frustulia* cf. *magaliesmontana* (Cholnoky)	x	x	x		x	x	x	x
frumao	*Frustulia maoriana* spec. nov. Lange-Bertalot & T. Beier		x	x		x	x	x	x
frumar	*Frustulia marginata* (Amossé 1932)							x	
frupan	*Frustulia pangaeopsis* (Lange-Bertalot 2001)		x						
frupum	*Frustulia pumilio* (Lange-Bertalot & Rumrich)			x		x		x	
frusa1	*Frustulia saxonica* morphotype I (Rabenhorst 1853)	x	x						
frusa2	*Frustulia saxonica* morphotype II (Rabenhorst 1853)	x	x	x	x	x	x	x	x
fruvul	*Frustulia vulgaris* (Twaites) De Toni 1891		x			x			
gomcym	*Gomphonema* spec. aff. *cymbelliclinum* (Reichardt & Lange-Bertalot)					x			x
gomgra	*Gomphonema gracile* (Ehrenberg 1838)		x			x		x	x
gompar	*Gomphonema parvulum* (Kützing) Kützing 1849	x			x	x	x	x	x
gomtru	*Gomphonema truncatum* (Ehrenberg 1832)					x			
hanamp	*Hantzschia amphioxys* (Ehrenberg) Grunow in Cleve & Grunow 1880	x	x		x	x	x		
hipsub	*Hippodonta subcostulata* (Hustedt) Lange-Bertalot, Metzeltin & Wittkowski 1996								x
lutmut	*Luticula mutica* (Kützing) Mann	x			x	x	x	x	x
mayaat	*Mayamaea atomus* var. *atomus* (Kützing) Lange-Bertalot 1997	x				x	x		
mayape	*Mayamaea atomus* var. *permitis* (Hustedt) Lange-Bertalot 1997					x	x	x	
mayfos	*Mayamaea fossalis* (Krasske) Lange-Bertalot 1997							x	
melare	*Melosira arentii* (Kolbe) Nagumo & Kobayasi 1977					x			
meldic	*Melosira dickei* (Thwaites) Kützing 1849	x	x		x		x	x	
melvar	*Melosira varians* (Agardh 1827)						x		
navcos	*Naviculadicta cosmopolitana* (Lange-Bertalot)		x			x	x		
navdif	*Naviculadicta difficilima* (Hustedt 1950)		x	x		x	x	x	x

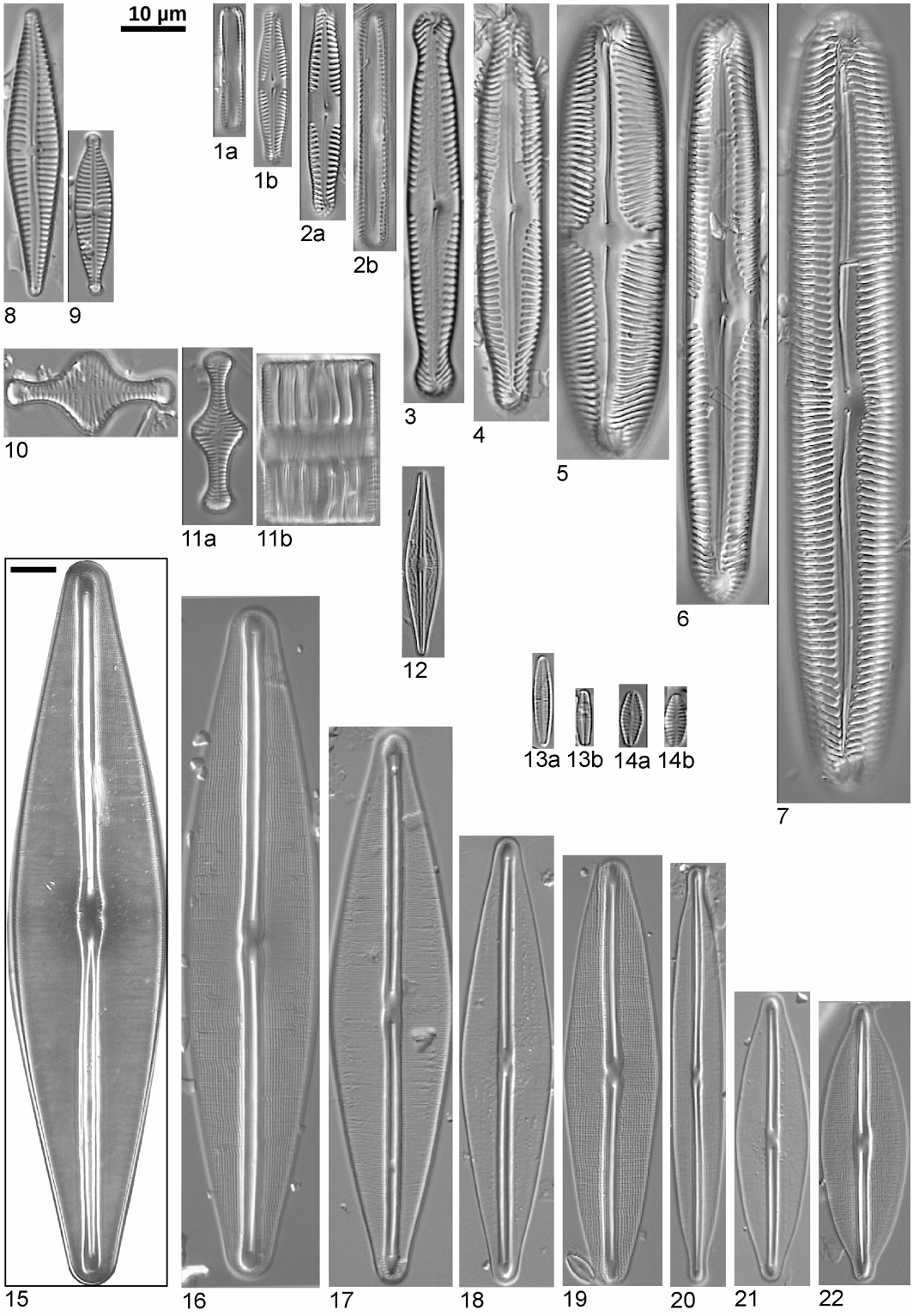
ID-tax	Taxon	Bogs				Swamps			
		B1	B2	B3	B4	S1	S2	S3	S4
navdig	*Naviculadicta digitulus* (Hustedt 1943)							x	
navelo	*Naviculadicta elorantana* (Lange-Bertalot)		x			x			x
naveva	*Navicula evanida* (Hustedt 1942)					x			
navfac	*Navicula* spec. aff. *facilis* (Krasske 1949)		x			x	x	x	x
navfen	*Naviculadicta fennica* (Hustedt)					x			
navgall	*Navicula gallica* var. *laevissima* (Cleve) Lange-Bertalot 1985					x			
navham	*Naviculadicta hambergii* (Hustedt)						x		
navhei	*Navicula heimansioides* (Lange-Bertalot 1993)				x	x	x	x	x
navind	*Naviculadicta indifferens* (Hustedt 1942)			x		x	x	x	
navjaa	*Navicula* aff. *jaagii* (Meister 1934)		x						
navjae	*Navicula jaernefeltii* (Hustedt 1942)					x			
navmin	*Navicula minima* (Grunow in Van Heurck 1880)					x	x	x	x
navobs	*Navicula* aff. *obsoleta* (Hustedt 1942)	x		x		x		x	
navpar	*Naviculadicta parasubtilissima*	x	x	x	x	x	x		x
navpra	*Navicula praeterita* (Hustedt 1945)				x				
navrad	*Navicula radiosa* (Kützing 1844)					x			x
navrhy	*Navicula rhynchocephala* (Kützing 1844)					x		x	x
navsax	*Navicula saxophila* Bock ex Hustedt 1966					x	x		
navsma	*Navicula subtilissima* (Cleve 1891) Lange-Bertalot 1996	x	x	x			x		
navsub	*Navicula submuralis* (Hustedt 1945)						x	x	
navten	*Navicula tenelloides* (Hustedt 1937)						x		
navute	*Naviculadicta utermoehlii* (Hustedt)					x			
navwil	*Navicula* aff. *willeri* (Krasske 1939)		x						
navwit	*Naviculadicta witkowskii* (Lange-Bertalot & Metzeltin)					x			x
neiamp	*Neidium ampliatum* (Ehrenberg) Krammer 1985								x
nitaci	*Nitzschia acidoclinata* (Lange-Bertalot 1976)					x		x	x
nitalp	*Nitzschia alpina* (Hustedt 1943 emend. Lange-Bertalot 1980)					x	x	x	
nitapm	*Nitzschia alpinobacillum* (Lange-Bertalot)					x		x	x
nitbre	*Nitzschia brevissima* (Grunow in Van Heurck 1881)							x	
nitfle	*Nitzschia flexa* (Schumann 1862)						x		
nitgra	*Nitzschia gracilis* (Hantzsch 1860)	x		x	x	x	x	x	x
nithan	*Nitzschia hantzschiana* (Rabenhorst 1860)					x		x	
nitint	*Nitzschia intermedia* (Hantzsch ex Cleve & Grunow 1880)		x			x	x	x	x
nitnan	*Nitzschia nana* (Grunow in Van Heurck 1881)					x		x	
nitpal	*Nitzschia palea* (Kützing) W. Smith 1856	x				x	x	x	x
nitper	*Nitzschia perminuta* (Grunow) M. Peragallo 1903					x	x	x	x
nitpla	*Nitzschia paleacea* (Grunow) Grunow in Van Heurck 1881					x	x	x	
nitpls	*Nitzschia palaeformis* (Hustedt 1950)			x					
nitsub	*Nitzschia subacicularis* (Hustedt in A. Schmidt et al. 1922)					x			x
pinbac	*Pinnularia brebissonii* var. *acuta* (Cleve-Euler 1955)					x	x		
pinbbr	*Pinnularia brebissonii* var. *brebissonii* (Krammer 1992)					x			
pinbic	*Pinnularia biceps* (Gregory 1856)	x	x	x			x	x	
pinbmi	*Pinnularia brebissonii* var. *minuta* (Krammer 1992)		x	x	x				
pinbor	*Pinnularia borealis* (Ehrenberg 1843)				x		x		
pinbra	*Pinnularia brauniana* (Grunow) Mills 1934						x		
pincar	*Pinnularia carteri* (Krammer 2000)						x		
pincru	*Pinnularia cruxarea* (Krammer 2000)						x		
pinddi	*Pinnularia divergens* var. *divergens* (W. Smith 1853)						x		
pindsu	*Pinnularia divergens* var. *sublinearis* (Cleve 1895)						x		
pindid	*Pinnularia divergentissima* var. *divergentissima* (Grunow) Cleve 1895	x	x		x	x	x		x
pindim	*Pinnularia divergentissima* var. *minor* (Krammer 1992)				x				
pindit	*Pinnularia divergentissima* var. *triundulata* (Krammer 2000)						x		
pingib	*Pinnularia gibba* (Ehrenberg 1843)					x	x		x
pingis	*Pinnularia gibbiformis* (Krammer 1992)						x		
pinmic	*Pinnularia microstauron* (Ehrenberg) Cleve 1891	x	x	x			x		
pinmno	*Pinnularia microstauron* var. *nonfasciata* (Krammer 2000)					x		x	
pinobs	*Pinnularia obscura* (Krasske 1932)						x		
pinper	*Pinnularia perirrorata* (Krammer 2000)	x	x	x	x	x	x	x	x
pinsga	*Pinnularia subgibba* (Krammer 1992)	x	x			x	x	x	x
pinsin	*Pinnularia sinistra* (Krammer 1992)	x	x	x				x	x
pinsto	*Pinnularia stomatophora* (Grunow) Cleve 1891								x
pinsub	*Pinnularia subcapitata* (Gregory 1856)	x	x	x	x	x	x	x	x

ID-tax	Taxon	Bogs				Swamps			
		B1	B2	B3	B4	S1	S2	S3	S4
pintra	*Pinnularia transversa* (A. Schmidt) Mayer 1940		x						
pinvir	*Pinnularia viridiformis* (Krammer 1992)	x	x	x	x	x	x	x	x
selmut	*Sellaphora mutata* (Krasske) Lange-Bertalot					x			
selpup	*Sellaphora pupula* var. *pupula* (Kützing) Mereschkowsky	x				x	x	x	x
staanc	*Stauroneis anceps* (Ehrenberg 1843)					x	x	x	x
stagra	*Stauroneis* aff. *gracilior* (Reichardt)70								x
stakri	*Stauroneis kriegeri* (Patrick 1945)							x	
stapho	*Stauroneis phoenicenteron* (Nitzsch) Ehrenberg 1843					x	x	x	x
stecur	*Stenopterobia curvula* (W. Smith) Krammer 1987					x		x	x
stedel	*Stenopterobia delicatissima* (Lewis) Brébisson ex Van Heurck 1896		x	x		x	x	x	x
steden	*Stenopterobia densestriata* (Hustedt) Krammer 1987				x	x	x	x	x
surbis	*Surirella biseriata* (Brébisson in Brébisson & Godey 1836)		x						
surbre	*Surirella brebissonii* (Krammer & Lange-Bertalot 1987)							x	
surlin	*Surirella linearis* (W. Smith 1853)		x	x		x	x	x	x
surrob	*Surirella roba* (Leclercq 1983)		x						
surten	*Surirella tenera* (Gregory 1856)								x
tabflo	*Tabellaria flocculosa* (Roth) Kützing 1844	x	x	x	x	x	x	x	x
tabven	*Tabellaria ventricosa* (Kützing 1844)			x					

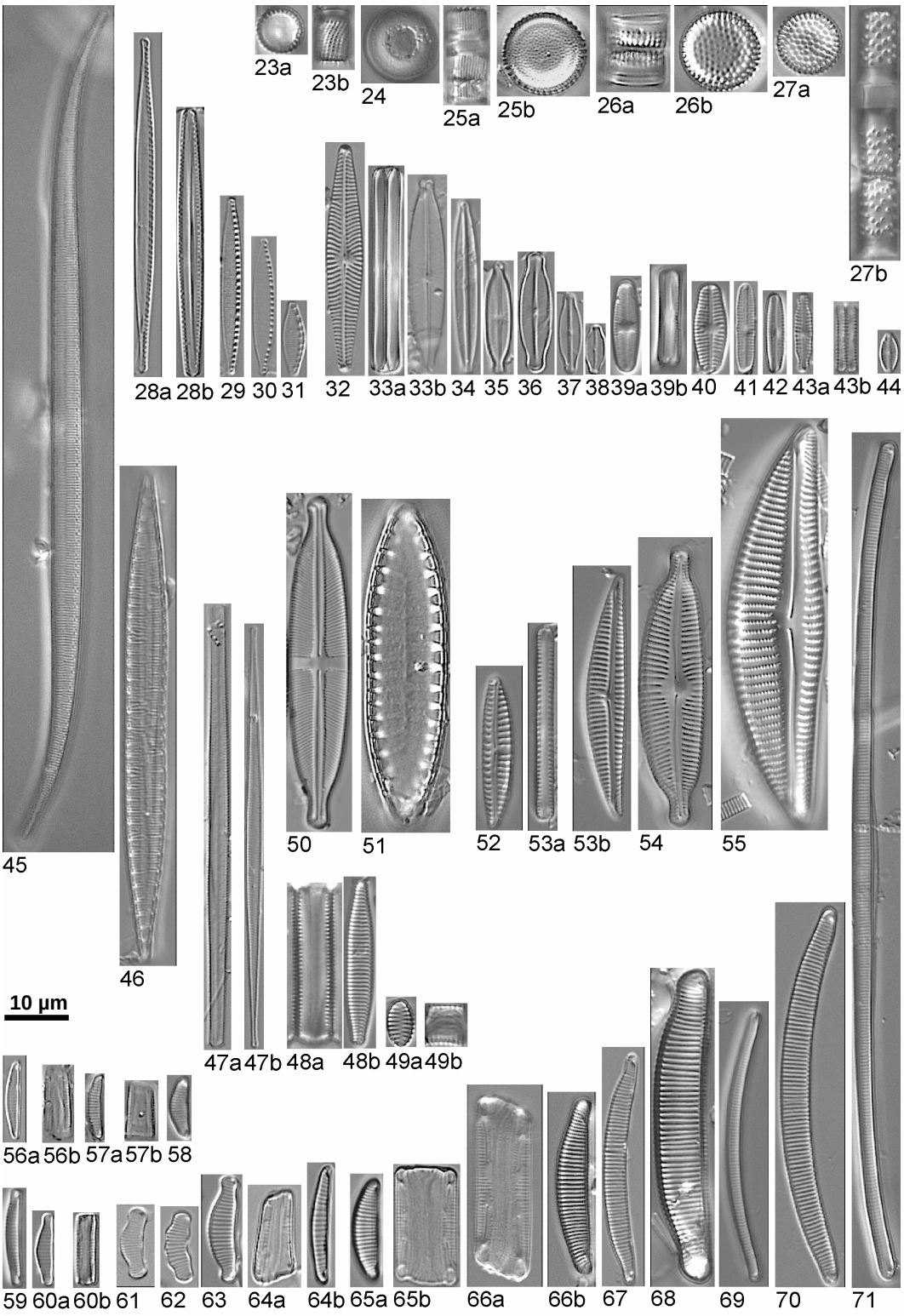
Substrate catalogue

Species	Family	Sampling location	Herbarium-ID
Aponogeton distachyus	Aponogetonaceae	Mahinapua Swamp	NZ-01/01
Baumea teretifolia	Cyperaceae	Stafford Loop Road	NZ-02/01
Gratiola sexdentata	Scrophulariaceae	Lake Kaniere	NZ-03/01
Isolepis prolifer	Cyperaceae	Tucker Flat	NZ-04/01
Juncus acuminatus	Cyperaceae	Lake Kaniere	NZ-05/01
Juncus acuminatus	Cyperaceae	Stafford Loop Road	NZ-05/02
Juncus acuminatus	Cyperaceae	Back Creek Swamp	NZ-05/03
Juncus bulbosus	Cyperaceae	Kumara	NZ-06/01
Juncus bulbosus	Cyperaceae	Arthurstown Road	NZ-06/02
Juncus bulbosus	Cyperaceae	Keogan's Road	NZ-06/03
Juncus bulbosus	Cyperaceae	Back Creek Swamp	NZ-06-04
Juncus bulbosus	Cyperaceae	Mahinapua Swamp	NZ-06/05
Juncus bulbosus	Cyperaceae	Stafford Loop Road	NZ-06/06
Juncus canadensis	Cyperaceae	Keogan's Road	NZ-07/01
Juncus canadensis	Cyperaceae	Arthurstown Road	NZ-07/02
Juncus canadensis	Cyperaceae	Kumara	NZ-07/03
Juncus prismatocarpus	Cyperaceae	Back Creek Swamp	NZ-08/01
Ludwigia palustris	Onagraceae	Lake Mahinapua	NZ-09/01
Ludwigia palustris	Onagraceae	Tucker Flat	NZ-09/02
Myriophyllum propinquum	Haloragaceae	Lake Mahinapua	NZ-10/01
Myriophyllum propinquum	Haloragaceae	Back Creek Swamp	NZ-10/02
Myriophyllum propinquum	Haloragaceae	Tucker Flat	NZ-10/03
Nitella hookeri	Characeae	Lake Mahinapua	NZ-11/01
Phormium tenax	Agavaceae	Lake Kaniere	NZ-12/01
Potamogeton suboblongus	Potamogetonaceae	Lake Kaniere	NZ-13/01
Sphagnum cristatum	Sphagnaceae	Keogan's Road	NZ-14/01
Typha orientalis	Typhaceae	Back Creek Swamp	NZ-15/01
unidentified aquatic moss	Bryophyta	Kumara	NZ-16/01

I Photographic plates (LM) of dominant and subdominant benthic diatom taxa



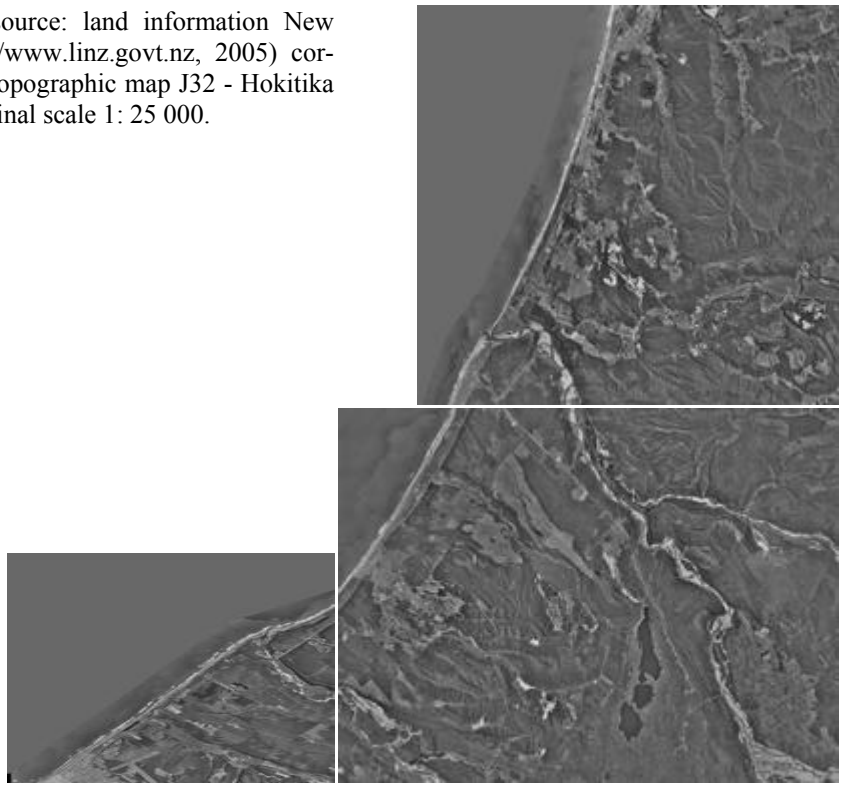
II Photographic plates (LM) of dominant and subdominant benthic diatom taxa



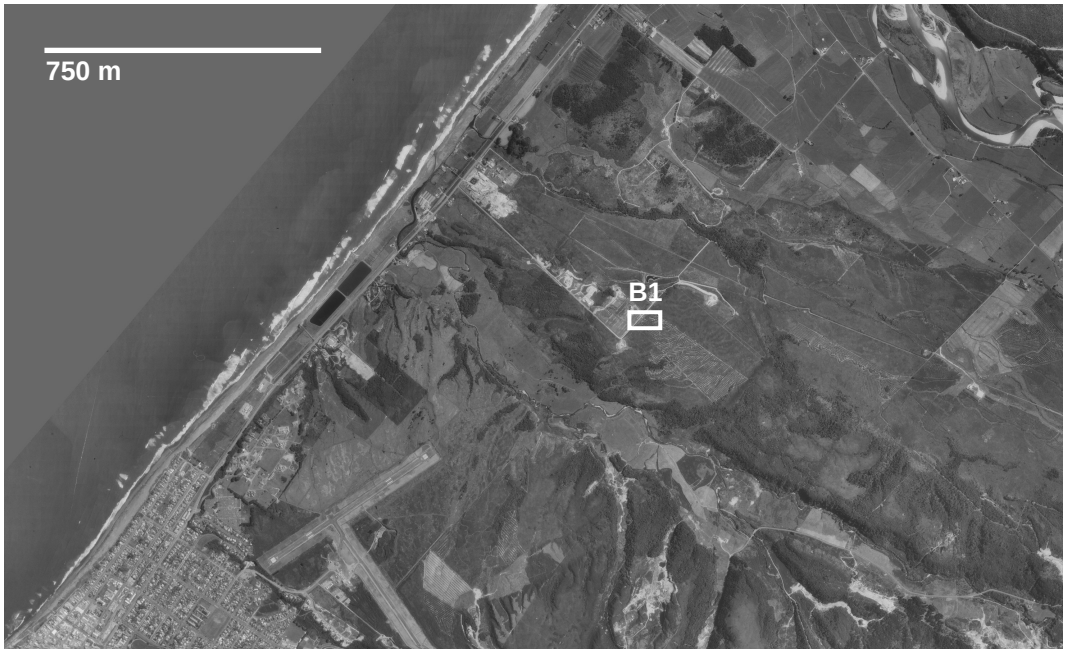
Legend to the photographic plates I and II (LM)

1a *Pinnularia perriorata*, gurdle view
1b *P. perriorata*
2a *P. subcapitata*
2b *P. subcapitata*, gurdle view
3 *P. gibba*
4 *P. microstauron*
5 *P. divergens* var. *sublinearis*
6 *P. subgibba*
7 *P. viridiformis*
8 *Gomphonema gracile*
9 *G. parvulum*
10 *Tabellaria ventricosa*
11a *T. flocculosa*
11b *T. flocculosa*, gurdle view
12 *Brachysira procera*
13a *Achnanthes minutissima* var. *minutissima*, L-valve
13b *A. minutissima* var. *minutissima*, R-valve
14a *A. thermalis*, R-valve
14b *A. thermalis*, L-valve
15 *Frustulia aotearoa* spec. nov.
16 *Frustulia pangaeopsis*
17 *F. saxonica* morphotype II
18 *F. saxonica* morphotype I
19 *F. gondwana* spec. nov.
20 *F.* cf. *magaliesmontana*
21 *F. crassinervia*
22 *F. maoriana* spec. nov.
23a *Aulacoseira alpigena*
23b *A. alpigena*, gurdle view
24 *Melosira dickei*
25a *Aulacoseira tenuior*, gurdle view
25b *A. tenuior*
26a *A. distans*, gurdle view
26b *A. distans*
27a *A. crassipunctata*
27b *A. crassipunctata*, gurdle view
28a *Nitzschia gracilis*
28b *N. gracilis*, gurdle view
29 *N. palea*
30 *N. perminuta*
31 *N. alpinobacillum*
32 *Navicula heimansioides*
33a *Naviculadicta subtilissima*, gurdle view
33b *N. subtilissima*
34 *N. parasubtilissima*
35 *Adlafia bryophila*
36 *Naviculadicta cosmopolitana*
37 *N. difficilima*
38 *Navicula indifferens*
39a *N. minima*
39b *N. minima*, gurdle view
40 *Naviculadicta elorantana*
41 *Chamaepinnularia mediocris*
42 *C. begeri*
43a *C. soehrensis* var. *soehrensis*
43b *C. soehrensis* var. *soehrensis*, gurdle view
44 *Navicula* spec. aff. *facilis*
45 *Stenopterobia curvula*
36 *S. delicatissima*
47a *Fragilaria nanoides*, gurdle view
47b *F. nanoides*
48a *F. exigua*, gurdle view
48b *F. exigua*
49a *F. construens* f. *venter*
49b *F. construens* f. *venter*, gurdle view
50 *Stauroneis anceps*
51 *Surirella linearis*
52 *Encyonema perpusillum*
53a *E. neogracile*, gurdle view
53b *E. neogracile*
54 *Cymbopleura naviculiformis*
55 *Encyonema amanianum*
56a *Eunotia* spec. Nr. 1 aff. *siolii*
56b *E.* spec. Nr. 1 aff. *siolii*, gurdle view
57a *E.* spec. Nr. 2 aff. *siolii* (f. bidens)
57b *E.* spec. Nr. 2 aff. *siolii* (f. bidens), gurdle view
58 *E.* spec. Nr. 3 Julma Ölkky
59 *E. paludosa* var. *paludosa*
60a *E. paludosa* var. *trinarcria*
60b *E. paludosa* var. *trinarcria*, gurdle view
61 *E. exigua*
62 *E. musicola*
63 *E. meisteri*
64a *E. siolii*, gurdle view
64b *E. siolii*
65a *E. veneris*
65b *E. veneris*, gurdle view
66a *E. incisa*, gurdle view
66b *E. incisa*
67 *E. schwabei*
68 *E. praerupta*
69 *E. bilunaris* var. *mucophila*
70 *E. bilunaris* var. *bilunaris*
71 *E. genuflexa*

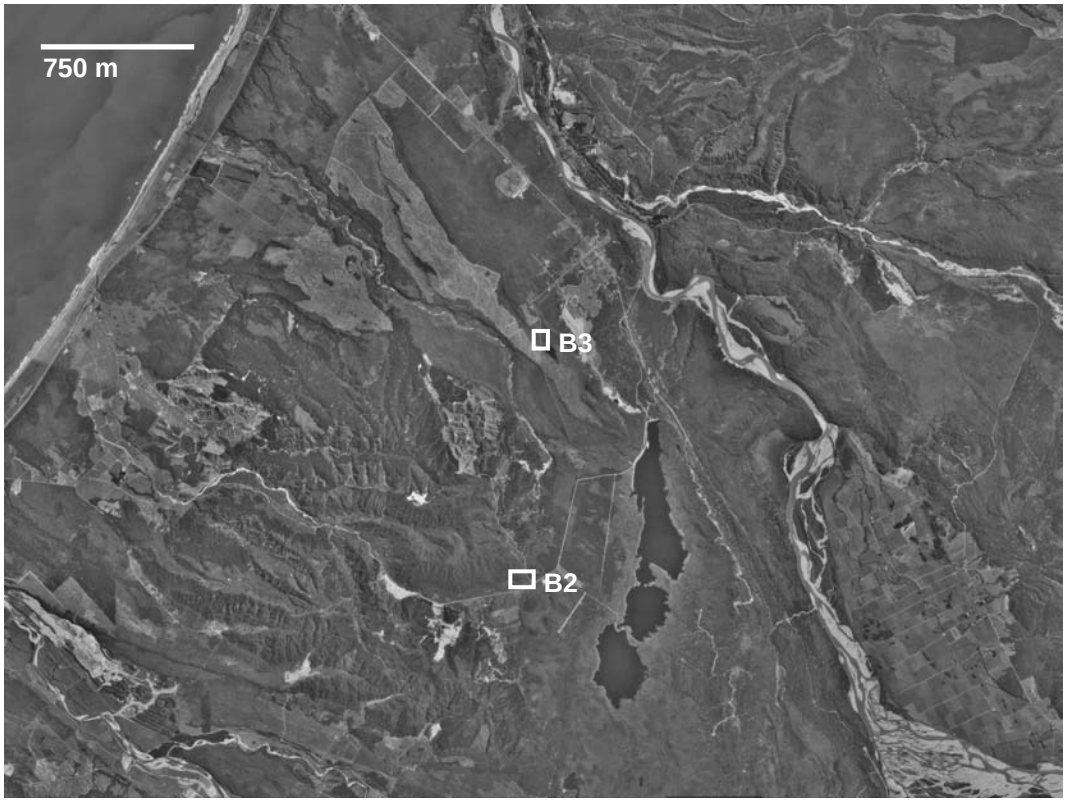
Orthophotos (source: land information New Zealand, http://www.linz.govt.nz, 2005) corresponding to topographic map J32 - Hokitika (1995/96); original scale 1: 25 000.



Orthophotos (source: land information New Zealand, http://www.linz.govt.nz, 2005) corresponding to topographic map J33 - Kaniere (2001/02); original scale 1: 25 000.



Aerial photograph (cp. preceding overview; original source b/w) showing the sampling area of wetland B1.



Aerial photograph (cp. preceding overview; original source b/w) showing the sampling areas of wetlands B2 and B3.

Aerial photograph (cp. preceding overview) showing the sampling areas of wetlands B4, S1, S3, and S4.

Aerial photograph (cp. preceding overview) showing the sampling area of wetland S2.

Photographs of the studied bogs (from top to bottom): B1 = Keogans's Road, B2 = Stafford Loop Road, B3 = Kumara, B4 = Arthurstown Road.

Photographs of the studied swamps from top to bottom): S1 = Mahinapua Swamp, S2 = Lake Kaniere, S3 = Tucker Flat, S4 = Back Creek Swamp.

Geographic coordinates of sampling locations (E = easting, S = southing); NZMS 260: 1:50 000 map references; NZGD49: New Zealand map grid; NZGD2000: New Zealand geodetic datum, geodetic reference system 1980.

	NZMS 260	NZGD49 - S	NZGD49 - E	NZGD2000 - S	NZGD2000 - E
A1	J32 4719 3242	2347190	5832415	42 41 53.3428	171 00 45.8421
A2	J32 4717 3241	2347167	5832410	42 41 53.4870	171 00 44.8267
A3	J32 4715 3245	2347152	5832445	42 41 52.3417	171 00 44.2044
A4	J32 4718 3242	2347176	5832420	42 41 53.1700	171 00 45.2324
A5	J32 4720 3242	2347202	5832417	42 41 53.2872	171 00 46.3712
A6	J32 4709 3230	2347086	5832303	42 41 56.8911	171 00 41.1576
B1	J32 5973 3394	2359731	5833935	42 41 13.3679	171 09 58.1349
B2	J32 5984 3399	2359836	5833986	42 41 11.7900	171 10 02.7950
B3	J32 5985 3399	2359848	5833989	42 41 11.7013	171 10 03.3248
B4	J32 5993 3402	2359926	5834024	42 41 10.6227	171 10 06.7838
B5	J32 5988 3400	2359881	5834001	42 41 11.3359	171 10 04.7855
C1	J32 6013 3880	2360127	5838800	42 38 36.0313	171 10 20.1861
C2	J32 6015 3865	2360147	5838649	42 38 40.9376	171 10 20.9193
C3	J32 6015 3877	2360146	5838766	42 38 37.1463	171 10 20.9874
C4	J32 6016 3899	2360160	5838990	42 38 29.8990	171 10 21.8161
C5	J32 6015 3913	2360150	5839130	42 38 25.3562	171 10 21.5113
G1	J33 4317 2815	2343173	5828154	42 44 08.2521	170 57 44.8635
G2	J33 4316 2814	2343155	5828140	42 44 08.6914	170 57 44.0575
G3	J33 4311 2813	2343108	5828126	42 44 09.1079	170 57 41.9770
G4	J33 4307 2805	2343074	5828054	42 44 11.4135	170 57 40.4058
G5	J33 4320 2816	2343199	5828160	42 44 08.0782	170 57 46.0125
G6	J33 4323 2834	2343233	5828344	42 44 02.1443	170 57 47.7034
G7	J33 4321 2825	2343207	5828248	42 44 05.2337	170 57 46.4581
G8	J33 4324 2840	2343244	5828402	42 44 00.2740	170 57 48.2488
D1	J33 4026 2391	2340262	5823907	42 46 23.5167	170 55 32.3124
D2	J33 3994 2423	2339944	5824232	42 46 12.7328	170 55 18.6842
D3	J33 4022 2392	2340222	5823922	42 46 22.9986	170 55 30.5699
D4	J33 4030 2395	2340295	5823948	42 46 22.2150	170 55 33.8081
D5	J33 4017 2382	2340173	5823819	42 46 26.2959	170 55 28.3029
E1	J33 5695 2090	2356948	5820899	42 48 13.7101	171 07 43.1253
E2	J33 5694 2090	2356938	5820897	42 48 13.7676	171 07 42.6833
E3	J33 5694 2088	2356940	5820877	42 48 14.4171	171 07 42.7516
E4	J33 5692 2087	2356919	5820870	42 48 14.6286	171 07 41.8208
E5	J33 5694 2086	2356937	5820858	42 48 15.0304	171 07 42.6009
F1	J33 4777 2694	2347771	5826935	42 44 51.3189	171 01 05.6627
F2	J33 4777 2688	2347771	5826882	42 44 53.0359	171 01 05.6075
F3	J33 4779 2696	2347790	5826962	42 44 50.4588	171 01 06.5259
F4	J33 4779 2696	2347793	5826963	42 44 50.4287	171 01 06.6588
F5	J33 4776 2699	2347760	5826990	42 44 49.5287	171 01 05.2364
H1	J33 4783 2196	2347829	5821962	42 47 32.4689	171 01 03.0341
H2	J33 4784 2191	2347836	5821911	42 47 34.1265	171 01 03.2889
H3	J33 4784 2191	2347836	5821908	42 47 34.2237	171 01 03.2857
H4	J33 4784 2191	2347835	5821906	42 47 34.2877	171 01 03.2397
H5	J33 4789 2194	2347887	5821937	42 47 33.3233	171 01 05.5593

PCA Wetlands

Eigenvalues

PC	Eigenvalues	%Variation	Cum.%Variation
1	7,31	30,5	30,5
2	4,86	20,2	50,7
3	2,86	11,9	62,6
4	2,16	9,0	71,6
5	1,50	6,2	77,9

Eigenvectors

Variable	PC1	PC2	PC3	PC4	PC5
aniondef	0,046	-0,096	-0,122	-0,451	0,307
nasur	-0,183	-0,269	-0,005	-0,123	-0,115
ionsum	-0,164	0,391	0,076	0,080	0,048
so4def	0,197	0,274	-0,107	0,007	-0,219
tp	-0,117	0,062	-0,505	0,025	-0,041
srp	-0,108	0,135	-0,420	0,145	-0,090
amm	-0,143	0,133	-0,154	0,021	-0,444
nit	-0,222	0,069	-0,196	-0,182	0,014
chla1	-0,178	-0,097	-0,366	-0,011	0,193
chla3	-0,243	0,025	-0,217	-0,239	-0,283
alk	-0,331	-0,080	0,178	-0,081	-0,113
ph	-0,308	-0,184	0,122	-0,069	0,010
ca	-0,306	0,079	0,149	-0,110	0,105
mg	-0,248	0,203	0,273	-0,158	0,001
k	-0,218	0,128	-0,205	-0,245	0,234
na	-0,061	0,400	-0,023	0,068	0,110
sulphate	-0,169	0,031	0,004	0,370	0,372
cl	0,054	0,429	-0,038	0,103	0,148
cond	-0,084	0,315	0,189	-0,117	-0,230
gilvin	0,250	0,238	0,089	-0,168	-0,005
silica	-0,308	-0,001	0,205	0,112	-0,265
temp	0,032	0,169	0,110	-0,473	0,242
relpeg	-0,174	0,045	0,039	0,304	0,217
depth	-0,273	-0,016	0,083	0,175	0,193

Principal Component Scores

Sample	SCORE1	SCORE2	SCORE3	SCORE4	SCORE5
B1-1	2,959	1,086	0,749	0,365	0,367
B1-2	4,362	-1,405	3,590	1,201	-0,708
B1-3	3,008	1,275	1,792	-0,755	-0,275
B1-4	3,338	-0,008	1,454	0,329	-0,429
B1-5	4,001	-1,301	1,168	0,130	-0,114
B1-6	2,653	-0,136	0,261	-1,644	0,813
B2-1	1,903	-1,742	0,062	-1,101	-0,132
B2-2	1,659	-2,017	-1,919	-0,525	0,040
B2-3	1,555	-2,425	-2,551	0,286	-0,327
B2-4	3,450	-3,255	0,565	1,150	0,031
B2-5	2,100	-2,286	0,659	-0,120	-0,904
B3-1	-1,273	5,214	-2,987	2,276	-0,687
B3-2	-0,295	1,063	-3,760	1,040	0,372
B3-3	-0,465	5,742	-3,151	2,509	-1,358
B3-4	0,393	-1,586	-1,904	0,223	0,610
B3-5	0,913	-1,324	-3,112	0,024	-0,586
B4-1	2,520	1,129	-0,301	0,494	-0,918
B4-2	1,875	2,144	-0,477	-1,677	1,320
B4-3	2,612	2,492	0,080	-0,671	0,773
B4-4	3,223	1,926	1,058	0,380	0,146
B4-5	1,953	1,693	-0,373	-0,619	-0,760
B4-6	2,306	3,430	0,686	-2,378	0,989
B4-7	1,230	2,507	-0,536	-2,046	1,088
B4-8	2,616	2,135	1,265	-0,932	0,830
S1-1	-1,652	0,222	0,604	0,556	0,489
S1-2	-8,070	1,451	2,307	-1,933	3,253
S1-3	-3,458	1,956	2,844	0,427	0,285
S1-4	-1,213	0,393	0,682	1,479	0,989
S1-5	-3,556	3,750	3,852	3,623	-1,233
S2-1	-0,298	-2,223	0,618	2,455	0,707
S2-2	-2,690	-2,042	-0,627	2,061	2,693
S2-3	-1,193	-2,787	-0,360	1,953	1,098
S2-4	-1,263	-3,598	0,154	1,816	0,173
S2-5	-1,082	-2,222	-0,093	2,156	0,930
S3-1	-2,180	-1,127	-1,160	-1,097	0,661
S3-2	-2,910	-0,593	-0,460	-1,167	-2,200
S3-3	-1,999	-0,344	-2,465	-1,494	0,910
S3-4	-1,584	-0,611	-1,343	-1,453	0,866
S3-5	-0,632	-2,003	0,774	-1,118	-0,170
S4-1	-2,604	-1,155	0,587	-1,039	-1,739
S4-2	-2,792	-1,120	0,571	-1,270	-1,691

S4-3	-2,387	-1,688	0,562	-1,027	-1,880
S4-4	-3,924	-0,222	-0,130	-1,412	-3,415
S4-5	-3,109	-0,391	0,766	-1,456	-0,909

PCA Bogs

Eigenvalues

PC	Eigenvalues	%Variation	Cum.%Variation
1	7,91	34,4	34,4
2	5,19	22,5	56,9
3	2,67	11,6	68,5
4	1,47	6,4	74,9
5	1,17	5,1	80,0

Eigenvectors

Variable	PC1	PC2	PC3	PC4	PC5
aniondef	-0,125	0,201	0,347	0,309	0,260
nasur	-0,231	-0,201	0,194	0,138	0,332
ionsum	0,345	0,079	0,007	-0,056	0,019
so4def	0,303	0,193	0,017	-0,052	0,025
tp	0,208	-0,290	0,154	0,123	-0,023
srp	0,243	-0,196	0,104	-0,015	0,101
amm	0,217	-0,189	-0,186	0,084	-0,170
nit	0,103	-0,193	0,409	-0,153	-0,095
chla1	0,071	-0,267	0,268	0,283	-0,266
chla3	0,125	-0,256	0,239	-0,111	0,119
ph	-0,215	-0,055	0,227	-0,448	-0,187
ca	0,207	0,160	0,186	-0,235	-0,339
mg	0,213	0,304	0,101	-0,115	-0,036
k	0,262	-0,047	0,247	0,148	0,237
na	0,325	0,051	0,067	0,055	0,180
sulphate	0,152	-0,244	-0,219	0,030	0,105
cl	0,340	0,112	-0,016	-0,058	-0,010
cond	0,228	0,168	-0,252	-0,076	0,121
gilvin	0,046	0,352	0,004	0,230	0,290
silica	0,113	-0,255	-0,281	-0,192	0,040
temp	0,018	0,257	0,346	-0,111	-0,125
relpeg	0,129	-0,076	-0,050	0,516	-0,396
depth	0,095	-0,237	0,032	-0,265	0,404

Principal Component Scores

Sample	SCORE1	SCORE2	SCORE3	SCORE4	SCORE5
B1-1	-0,056	1,545	-0,641	0,372	0,989
B1-2	-2,745	1,384	-4,026	0,034	-2,004
B1-3	-0,349	1,901	-0,573	-1,188	1,408
B1-4	-1,153	1,350	-1,627	0,640	1,172
B1-5	-2,579	0,969	-1,609	0,779	1,150
B1-6	-1,508	1,157	0,976	0,699	-0,069
B2-1	-2,906	-0,977	1,090	-0,704	-0,158
B2-2	-2,301	-2,344	1,340	2,067	1,289
B2-3	-2,325	-3,356	0,702	2,190	-0,274
B2-4	-4,130	-1,173	-1,428	-0,059	-0,493
B2-5	-3,316	-2,125	-0,402	-3,879	0,883
B3-1	6,705	-2,885	-1,459	-0,064	-0,413
B3-2	2,391	-3,545	0,810	0,686	0,694
B3-3	7,021	-2,538	-2,146	-0,494	0,095
B3-4	-1,360	-3,184	1,358	-0,406	-1,250
B3-5	-1,081	-2,354	1,791	-0,637	-2,126
B4-1	0,546	0,838	-1,199	0,476	0,090
B4-2	1,361	1,674	1,857	0,413	1,258
B4-3	1,595	2,088	0,050	0,864	-0,610
B4-4	0,681	2,309	-1,258	0,839	-0,579
B4-5	1,044	0,610	0,404	-1,557	1,153
B4-6	2,013	3,796	2,238	-0,619	-1,591
B4-7	1,748	1,782	2,730	-0,354	0,481
B4-8	0,703	3,081	1,022	-0,097	-1,095

PCA Swamps

Eigenvalues

PC	Eigenvalues	%Variation	Cum.%Variation
1	8,61	34,5	34,5
2	5,57	22,3	56,7
3	3,15	12,6	69,3
4	2,47	9,9	79,2
5	1,53	6,1	85,3

Eigenvectors

Variable	PC1	PC2	PC3	PC4	PC5
aniondef	0,044	0,284	-0,297	-0,041	-0,051
nasur	-0,063	0,235	0,117	0,183	0,419
ionsum	-0,309	-0,128	-0,015	0,060	0,056
so4def	0,080	-0,125	0,364	-0,333	0,100
seadist	0,229	0,223	0,141	0,206	0,098
tp	0,138	0,171	-0,083	-0,384	0,071
srp	0,205	0,134	0,020	-0,047	-0,444
amm	-0,119	0,263	0,271	0,068	-0,307
nit	-0,286	0,201	-0,024	-0,026	0,038
chla1	0,122	0,137	-0,340	-0,096	0,233
chla3	-0,151	0,321	0,104	-0,235	-0,014
alk	-0,251	0,223	0,079	0,187	0,037
ph	-0,084	0,353	-0,210	0,112	-0,109
ca	-0,283	0,100	-0,171	0,064	-0,206
mg	-0,318	0,047	0,035	0,086	0,047
k	-0,098	0,228	-0,341	-0,147	-0,022
na	-0,259	-0,156	-0,048	0,016	0,173
sulphate	-0,074	-0,172	-0,343	0,267	-0,049
cl	-0,206	-0,286	-0,113	-0,177	-0,068
cond	-0,299	0,078	0,125	-0,143	0,079
gilvin	-0,207	-0,046	0,236	-0,262	-0,324
silica	-0,260	0,001	0,247	0,250	0,129
temp	-0,203	0,068	-0,108	-0,437	0,009
relpeg	-0,076	-0,172	-0,102	0,210	-0,454
depth	-0,153	-0,296	-0,235	-0,137	0,133

Principal Component Scores

Sample	SCORE1	SCORE2	SCORE3	SCORE4	SCORE5
S1-1	-0,730	-2,358	-0,051	-1,578	0,244
S1-2	-7,571	2,167	-4,826	1,550	-0,659
S1-3	-4,180	-2,669	0,498	-0,123	0,626
S1-4	0,013	-3,386	-0,248	-1,666	-1,154
S1-5	-5,069	-5,276	2,525	0,313	0,234
S2-1	3,469	-2,181	0,010	1,555	-2,232
S2-2	1,815	-0,502	-2,345	2,292	1,568
S2-3	3,500	-1,015	-0,850	1,254	-0,025
S2-4	3,582	-0,089	-0,212	2,200	-0,071
S2-5	3,133	-1,650	-0,533	1,310	-0,493
S3-1	0,995	1,134	-1,076	-2,155	0,204
S3-2	-0,565	2,915	1,711	-0,630	-2,599
S3-3	1,938	1,384	-1,673	-3,072	-0,266
S3-4	1,274	0,442	-1,294	-2,476	0,502
S3-5	1,289	-0,129	0,191	-1,188	1,082
S4-1	-0,187	1,725	1,459	0,460	1,322
S4-2	-0,335	1,719	1,177	0,313	1,803
S4-3	0,335	1,675	1,452	0,289	1,773
S4-4	-1,102	3,793	2,684	0,884	-0,244
S4-5	-1,605	2,302	1,402	0,469	-1,615

Canoco – DCA wetlands

```
Number of segments                26
Nonlinear rescaling of axes
Rescaling threshold             0.00
Number of axes in biplot           2
No samples omitted
Number of samples                 44
Number of species                199
Number of occurrences           1641
No. of environmental variables:  26
No interaction terms defined
Squareroot-transformation of species data
No species-weights specified
No sample-weights specified
Downweighting of rare species

No. of active  samples:     44
No. of passive samples:      0
No. of active  species:    199
Sum of all eigenvalues of CA =    2.77880

**** Weighted correlation matrix (weight = sample total) ****
SPEC AX1    1.0000
SPEC AX2    -.3922     1.0000
SPEC AX3    -.1644      .2385     1.0000
SPEC AX4     .4701     -.0805     -.1057     1.0000
ENVI AX1     .9854     -.4000     -.1792      .4936     1.0000
ENVI AX2    -.4085      .9649      .2212     -.1066     -.4145     1.0000
ENVI AX3    -.1880      .2272      .9397     -.1188     -.1908      .2354     1.0000
ENVI AX4     .5590     -.1182     -.1283      .8701      .5673     -.1225     -.1366     1.0000
aniondef     .1043     -.0957      .0486      .2256      .1059     -.0992      .0517      .2593
nasur        .4833     -.6676     -.0204      .0914      .4905     -.6919     -.0217      .1051
ionsum       .0947      .4003      .4500      .1548      .0960      .4148      .4788      .1779
so4def      -.4518      .4496      .3354     -.1970     -.4585      .4660      .3570     -.2264
tp           .2238      .0730     -.1812      .1508      .2271      .0757     -.1929      .1733
srp          .2119      .2388     -.1365      .2238      .2151      .2475     -.1453      .2573
amm          .2252     -.0624      .3673     -.0692      .2286     -.0647      .3908     -.0796
nit          .3503     -.2139      .0923      .3771      .3555     -.2217      .0982      .4334
chla1        .4115     -.3213     -.2396      .2811      .4176     -.3330     -.2550      .3230
chla3        .5421     -.1668      .2540      .2497      .5502     -.1728      .2703      .2870
alk          .8668     -.4054      .1400      .3984      .8797     -.4202      .1489      .4579
ph           .9471     -.4871     -.1593      .5013      .9611     -.5048     -.1696      .5762
ca           .7628     -.0299      .1334      .5163      .7741     -.0310      .1419      .5934
mg           .5227      .0396      .4285      .3869      .5304      .0410      .4560      .4446
k            .4009      .0444      .0532      .3348      .4068      .0461      .0565      .3848
na          -.1587      .4285      .3637      .0412     -.1611      .4441      .3870      .0474
sulphate     .2896     -.0038     -.3146      .0287      .2939     -.0040     -.3348      .0330
cl          -.3780      .7366      .2707     -.0392     -.3836      .7634      .2881     -.0450
cond         .0732      .2567      .7037     -.0410      .0742      .2660      .7489     -.0471
gilvin      -.7458      .6111      .4436     -.4491     -.7568      .6333      .4721     -.5162
silica       .6980     -.3996      .2956      .2596      .7084     -.4142      .3145      .2984
temp        -.1228      .2734      .3037      .1705     -.1246      .2834      .3231      .1959
relpeg       .3294     -.1396     -.1892      .1066      .3343     -.1447     -.2014      .1225
depth        .6936     -.2421     -.1605      .3929      .7039     -.2509     -.1709      .4516
          SPEC AX1   SPEC AX2   SPEC AX3   SPEC AX4   ENVI AX1   ENVI AX2   ENVI AX3   ENVI AX4

**** Summary ****
Axes                                    1     2     3     4 Tot. Inert.
Eigenvalues                        :   .649  .242  .156  .077      2.779
Lengths of gradient                :  3.796 2.316 1.968 1.550
Species-environment correlations   :   .985  .965  .940  .870
Cumulative percentage variance
   of species data                 :  23.3  32.0  37.7  40.4
   of species-environment relation:  29.5  39.9    .0    .0
Sum of all unconstrained eigenvalues                          2.779
Sum of all canonical     eigenvalues                          2.126
```

Canoco – CCA wetlands

```
Forward selection of envi. variables =  0
Scaling of ordination scores         = -1
No samples omitted
Number of samples                      44
Number of species                     199
Number of occurrences                1641
No. of environmental variables:        26
No interaction terms defined
Squareroot-transformation of species data
No species-weights specified
No sample-weights specified
Downweighting of rare species

No rescaling
No detrending
No. of active  samples:     44
No. of passive samples:      0
No. of active  species:    199
Sum of all eigenvalues of CA =    2.77880

**** Weighted correlation matrix (weight = sample total) ****
```

SPEC AX1	1.0000							
SPEC AX2	.0173	1.0000						
SPEC AX3	.0085	-.0128	1.0000					
SPEC AX4	.0052	.0208	.0153	1.0000				
ENVI AX1	.9899	.0000	.0000	.0000	1.0000			
ENVI AX2	.0000	.9662	.0000	.0000	.0000	1.0000		
ENVI AX3	.0000	.0000	.9623	.0000	.0000	.0000	1.0000	
ENVI AX4	.0000	.0000	.0000	.9175	.0000	.0000	.0000	1.0000
aniondef	-.1161	.2132	-.2797	.3156	-.1173	.2206	-.2907	.3439
nasur	-.5130	.5308	.1416	.0382	-.5182	.5494	.1472	.0416
ionsum	-.0794	-.2396	-.4142	-.3486	-.0802	-.2480	-.4304	-.3799
so4def	.4676	-.1140	-.3228	-.1367	.4724	-.1180	-.3355	-.1491
tp	-.2076	-.1908	-.0731	.2347	-.2097	-.1975	-.0759	.2558
srp	-.1922	-.3674	-.0164	-.0654	-.1941	-.3802	-.0170	-.0712
amm	-.2219	.1607	-.2195	-.2532	-.2241	.1663	-.2281	-.2760
nit	-.3536	.1474	-.0816	-.0969	-.3572	.1525	-.0848	-.1056
chla1	-.4095	.0712	.1663	.1704	-.4137	.0737	.1728	.1858
chla3	-.5293	.1205	-.3616	-.0137	-.5347	.1247	-.3758	-.0150
alk	-.8763	.2014	-.2097	-.1284	-.8852	.2085	-.2179	-.1399
ph	-.9597	.1023	-.0196	.0193	-.9695	.1059	-.0203	.0211
ca	-.7556	-.1897	-.3138	-.1665	-.7632	-.1963	-.3260	-.1815
mg	-.5217	.0063	-.4738	-.3011	-.5270	.0065	-.4924	-.3282
k	-.3962	-.0555	-.4214	.2996	-.4002	-.0575	-.4379	.3266
na	.1685	-.2050	-.2829	-.2787	.1702	-.2122	-.2940	-.3038
sulphate	-.2885	-.3608	.3433	-.0243	-.2914	-.3734	.3568	-.0265
cl	.4041	-.5230	-.3064	-.2057	.4082	-.5414	-.3184	-.2242
cond	-.0518	.0219	-.6502	-.3054	-.0523	.0226	-.6756	-.3329
gilvin	.7604	-.1554	-.3275	-.1222	.7681	-.1609	-.3404	-.1332
silica	-.7065	.2718	-.1079	-.4103	-.7137	.2813	-.1121	-.4471
temp	.1285	-.0588	-.4979	.1097	.1298	-.0608	-.5174	.1195
relpeg	-.3365	-.1824	.3872	-.2428	-.3399	-.1888	.4024	-.2647
depth	-.6922	-.1560	.0833	-.0977	-.6992	-.1614	.0866	-.1065
	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4	ENVI AX1	ENVI AX2	ENVI AX3	ENVI AX4

```
**** Summary ****
Axes                                1     2     3     4  Tot. inert.
Eigenvalues                  :   .634  .256  .235  .201       2.779
Species-environment correlations  :   .990  .966  .962  .917
Cumulative percentage variance
   of species data           :  22.8  32.1  40.5  47.7
   of species-environment relation:  29.8  41.9  52.9  62.4
Sum of all unconstrained eigenvalues                          2.779
Sum of all canonical     eigenvalues                          2.126

*** Unrestricted permutation ***
Seeds:  14760 23558; 999 permutations under reduced model

**** Summary of Monte Carlo test ****
Test of significance of first canonical axis: eigenvalue =     .634
                                              F-ratio    =    5.622
                                              P-value    =    .0010

Test of significance of all canonical axes  : Trace      =    2.126
                                              F-ratio    =    2.579
                                              P-value    =    .0010
```

Canoco – CCA wetlands (restricted)

```
Forward selection of envi. variables =    1
Scaling of ordination scores         =   -1
No samples omitted
Number of samples                        44
Number of species                       199
Number of occurrences                  1641
No. of environmental variables:          26
No interaction terms defined
Squareroot-transformation of species data
No species-weights specified
No sample-weights specified
Downweighting of rare species

No rescaling
No detrending
No. of active  samples:     44
No. of passive samples:      0
No. of active  species:    199
Sum of all eigenvalues of CA =    2.77880

**** Weighted correlation matrix (weight = sample total) ****
SPEC AX1    1.0000
SPEC AX2    -.0410     1.0000
SPEC AX3     .0126      .0249     1.0000
SPEC AX4     .0156     -.0006     -.0518     1.0000
ENVI AX1     .9793      .0000      .0000      .0000     1.0000
ENVI AX2     .0000      .8910      .0000      .0000      .0000     1.0000
ENVI AX3     .0000      .0000      .8556      .0000      .0000      .0000     1.0000
ENVI AX4     .0000      .0000      .0000      .8349      .0000      .0000      .0000     1.0000
chla3        .5312      .0412      .3592     -.1796      .5425      .0462      .4198     -.2152
alk          .8824      .1433      .3176     -.0246      .9011      .1608      .3712     -.0294
ph           .9654      .0428      .0378     -.0057      .9859      .0481      .0442     -.0068
ca           .7517     -.2729      .4060     -.0189      .7676     -.3063      .4745     -.0226
mg           .5208     -.0623      .6320     -.0434      .5318     -.0700      .7387     -.0520
cl          -.4195     -.5423      .3655      .0256     -.4284     -.6087      .4272      .0307
gilvin      -.7672     -.1458      .3655     -.0965     -.7835     -.1636      .4271     -.1156
silica       .7099      .2489      .3968      .2773      .7249      .2794      .4637      .3321
depth        .6916     -.2330      .0313      .2570      .7062     -.2615      .0366      .3078
          SPEC AX1   SPEC AX2   SPEC AX3   SPEC AX4   ENVI AX1   ENVI AX2   ENVI AX3   ENVI AX4

**** Summary ****
Axes                                    1     2     3     4  Tot. inert.
Eigenvalues                        :   617  .208  .166  .151       2.779
Species-environment correlations :     979  .891  .856  .835
Cumulative percentage variance
   of species data                 :  22.2  29.7  35.7  41.1
   of species-environment relation:  43.5  58.1  69.8  80.4
Sum of all unconstrained eigenvalues                              2.779
Sum of all canonical     eigenvalues                              1.420

*** Unrestricted permutation ***
Seeds:  12900  1545; 999 permutations under reduced model

**** Summary of Monte Carlo test ****
Test of significance of first canonical axis:eigenvalue =     .617
                                             F-ratio    =    9.713
                                             P-value    =    .0010
Test of significance of all canonical axes  :Trace      =    1.420
                                             F-ratio    =    3.947
                                             P-value    =    .0010
```

Canoco – CCA swamps

```
Forward selection of envi. variables =    0
Scaling of ordination scores         =   -1
No samples omitted
Number of samples                        20
Number of species                       178
Number of occurrences                  1069
No. of environmental variables:          26
No interaction terms defined
Squareroot-transformation of species data
No species-weights specified
No sample-weights specified
Downweighting of rare species

No rescaling
No detrending
No. of active  samples:     20
No. of passive samples:      0
No. of active  species:    178
Sum of all eigenvalues of CA =    1.50918

**** Weighted correlation matrix (weight = sample total) ****
```

SPEC AX1	1.0000							
SPEC AX2	-.0001	1.0000						
SPEC AX3	.0003	.0000	1.0000					
SPEC AX4	-.0001	.0000	.0003	1.0000				
ENVI AX1	1.0000	.0000	.0002	.0000	1.0000			
ENVI AX2	.0000	1.0000	.0000	.0000	.0000	1.0000		
ENVI AX3	.0001	.0000	1.0000	.0002	.0000	.0000	1.0000	
ENVI AX4	.0000	.0000	.0001	1.0000	.0000	.0000	.0000	1.0000
aniondef	.3571	.3065	-.2768	.4591	.3572	.3065	-.2769	.4592
nasur	.4776	-.2869	-.0815	.0533	.4775	-.2869	-.0816	.0532
ionsum	.2059	-.1048	.5050	.3722	.2058	-.1047	.5048	.3718
so4def	.1702	.0046	.3323	-.5765	.1702	.0046	.3323	-.5765
tp	.0141	.5673	-.1943	-.5271	.0141	.5673	-.1942	-.5271
srp	-.3241	.2353	-.4333	-.4544	-.3240	.2353	-.4333	-.4542
amm	.4399	-.1813	.0674	-.2215	.4399	-.1813	.0672	-.2216
nit	.6214	.0655	.3076	.3987	.6213	.0655	.3074	.3985
chla1	.1095	.2525	-.4598	.1617	.1096	.2525	-.4598	.1619
chla3	.7104	.3407	.1750	-.0991	.7105	.3407	.1749	-.0991
alk	.6500	-.0651	.0642	.3602	.6500	-.0650	.0639	.3600
ph	.4327	.3164	-.2528	.5118	.4328	.3165	-.2530	.5118
ca	.3107	.1889	.2976	.6283	.3107	.1890	.2974	.6281
mg	.4885	-.0922	.3485	.3945	.4884	-.0921	.3483	.3943
k	.2990	.5483	-.1334	.2785	.2990	.5483	-.1336	.2784
na	.0591	-.1521	.4753	.2644	.0590	-.1521	.4752	.2640
sulphate	-.5245	.0094	.0764	.5693	-.5245	.0093	.0764	.5691
cl	-.2386	.1122	.6746	.2659	-.2387	.1122	.6746	.2656
cond	.5974	.0232	.5697	.1466	.5973	.0233	.5695	.1464
gilvin	.1824	.0135	.7694	-.1092	.1824	.0136	.7693	-.1094
silica	.4742	-.5260	.2819	.1342	.4741	-.5259	.2818	.1340
temp	.4167	.5327	.6469	.2379	.4167	.5327	.6468	.2378
relpeg	-.4715	-.3594	.1879	.3866	-.4715	-.3594	.1878	.3865
depth	-.2411	.0954	.5966	.5201	-.2412	.0954	.5966	.5199
	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4	ENVI AX1	ENVI AX2	ENVI AX3	ENVI AX4

```
**** Summary ****
Axes                                    1     2     3     4  Tot. inert.
Eigenvalues                        :   .326  .281  .220  .127       1.509
Species-environment correlations   :  1.000 1.000 1.000 1.000
Cumulative percentage variance
   of species data                 :   21.6  40.2  54.7  63.2
   of species-environment relation:   21.6  40.2  54.7  63.2
Sum of all unconstrained eigenvalues                                1.509
Sum of all canonical     eigenvalues                                1.509

*** Unrestricted permutation ***
Seeds:   1620 22945; 999 permutations under reduced model

**** Summary of Monte Carlo test ****
Test of significance of first canonical axis: eigenvalue =     .326
                                              F-ratio    =     .000
                                              P-value    =  1.0000
Test of significance of all canonical axes  : Trace      =    1.509
                                              F-ratio    =     .000
                                              P-value    =  1.0000
```

Canoco – CCA swamps (restricted)

```
Forward selection of envi. variables =    1
Scaling of ordination scores         =   -1
No samples omitted
Number of samples                        20
Number of species                       178
Number of occurrences                  1069
No. of environmental variables:          26
No interaction terms defined
Squareroot-transformation of species data
No species-weights specified
No sample-weights specified
Downweighting of rare species
No rescaling
No detrending
No. of active  samples:     20
No. of passive samples:      0
No. of active  species:    178
Sum of all eigenvalues of CA =    1.50918

**** Weighted correlation matrix (weight = sample total) ****

SPEC AX1    1.0000
SPEC AX2    -.0252     1.0000
SPEC AX3     .0764     -.0403     1.0000
SPEC AX4     .0125      .0909     -.0165     1.0000
ENVI AX1     .9573      .0000      .0000      .0000     1.0000
ENVI AX2     .0000      .8946      .0000      .0000      .0000     1.0000
ENVI AX3     .0000      .0000      .9416      .0000      .0000      .0000     1.0000
ENVI AX4     .0000      .0000      .0000      .9165      .0000      .0000      .0000     1.0000
chla3       -.8294     -.0352     -.1089     -.0482     -.8664     -.0393     -.1157     -.0526
alk         -.6152      .2657     -.2105      .5744     -.6427      .2970     -.2236      .6267
k           -.4551     -.4704     -.2239      .3156     -.4754     -.5258     -.2378      .3443
sulphate     .4574     -.2362      .2950      .6046      .4778     -.2641      .3133      .6597
cond        -.7030      .2661      .3008      .2394     -.7344      .2974      .3194      .2612
silica      -.3398      .6950      .0207      .3885     -.3550      .7768      .0220      .4239
temp        -.7165     -.2773      .5098      .1578     -.7485     -.3099      .5415      .1722
          SPEC AX1   SPEC AX2   SPEC AX3   SPEC AX4   ENVI AX1   ENVI AX2   ENVI AX3   ENVI AX4

**** Summary ****
Axes                                    1     2     3     4   Tot. inert.
Eigenvalues                        :   .280  .218  .193  .099        1.509
Species-environment correlations   :   .957  .895  .942  .916
Cumulative percentage variance
   of species data                 :  18.6  33.0  45.8  52.4
   of species-environment relation:  28.9  51.3  71.2  81.4
Sum of all unconstrained eigenvalues                              1.509
Sum of all canonical     eigenvalues                               .971

*** Unrestricted permutation ***
Seeds:  10540 11934; 999 permutations under reduced model

**** Summary of Monte Carlo test ****
Test of significance of first canonical axis: eigenvalue =     .280
                                              F-ratio    =    2.737
                                              P-value    =    .0020
Test of significance of all canonical axes  : Trace      =     .971
                                              F-ratio    =    3.097
                                              P-value    =    .0010
```

Canoco – CCA bogs

```
Forward selection of envi. variables =    0
Scaling of ordination scores         =   -1
No samples omitted
Number of samples                        24
Number of species                        95
Number of occurrences                   572
No. of environmental variables:          25
No interaction terms defined
Squareroot-transformation of species data
No species-weights specified
No sample-weights specified
Downweighting of rare species

No rescaling
No detrending
No. of active  samples:     24
No. of passive samples:      0
No. of active  species:     95
Sum of all eigenvalues of CA =    1.54961

**** Weighted correlation matrix (weight = sample total) ****
```

SPEC AX1	1.0000							
SPEC AX2	-.0037	1.0000						
SPEC AX3	-.0052	.0147	1.0000					
SPEC AX4	.0038	-.0118	-.0106	1.0000				
ENVI AX1	.9990	.0011	-.0001	-.0003	1.0000			
ENVI AX2	.0010	.9916	-.0001	.0001	.0000	1.0000		
ENVI AX3	.0000	.0000	.9934	.0000	.0000	.0000	1.0000	
ENVI AX4	.0000	.0001	.0000	.9957	.0000	.0000	.0000	1.0000
aniondef	.1635	-.2619	-.1356	.3299	.1634	-.2641	-.1365	.3314
nasur	.6883	.1157	-.1142	.0495	.6883	.1161	-.1149	.0499
ionsum	-.5794	-.4451	-.0184	.0304	-.5785	-.4487	-.0187	.0304
so4def	-.5530	-.5901	.1099	-.0241	-.5522	-.5948	.1105	-.0244
tp	-.1661	.2476	-.1700	.1613	-.1657	.2494	-.1712	.1619
srp	-.4011	.1583	-.0533	.2076	-.4009	.1597	-.0537	.2084
amm	-.1561	.0662	-.2748	.1152	-.1553	.0664	-.2767	.1156
nit	.0399	.3500	.0763	.4108	.0404	.3524	.0768	.4125
chla1	.0782	.4843	-.2643	.1448	.0785	.4880	-.2660	.1454
chla3	-.2065	.4350	-.1433	.1328	-.2065	.4385	-.1442	.1333
ph	.2791	.5141	.4879	.2527	.2784	.5184	.4912	.2538
ca	-.8354	.0766	.2003	.2155	-.8360	.0780	.2015	.2162
mg	-.5708	-.5535	.1998	.1309	-.5704	-.5577	.2010	.1314
k	-.2434	-.3574	-.0267	.2847	-.2424	-.3606	-.0270	.2859
na	-.3774	-.5011	-.0514	.0805	-.3762	-.5055	-.0518	.0807
sulphate	-.2537	.2362	-.3999	-.0244	-.2536	.2382	-.4026	-.0246
cl	-.6482	-.4241	.0291	.0052	-.6474	-.4274	.0292	.0051
cond	-.5123	-.4649	.0574	-.4625	-.5120	-.4684	.0577	-.4646
gilvin	-.3987	-.5726	-.1822	-.1487	-.3990	-.5768	-.1835	-.1494
silica	.1141	.0268	.0846	-.2690	.1148	.0266	.0852	-.2701
temp	-.1441	-.2075	.3171	.1982	-.1441	-.2090	.3191	.1991
relpeg	.0022	.0853	-.2439	-.0762	.0029	.0857	-.2456	-.0766
depth	-.0399	.2305	.3475	-.2091	-.0351	.2188	.3379	-.2004
	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4	ENVI AX1	ENVI AX2	ENVI AX3	ENVI AX4

```
**** Summary ****
Axes                                    1     2     3     4  Tot. inert.
Eigenvalues                        :   .313  .297  .162  .151       1.550
Species-environment correlations   :   .999  .992  .993  .996
Cumulative percentage variance
   of species data                 :   20.2  39.4  49.9  59.6
   of species-environment relation:   20.7  40.1  50.8  60.7
Sum of all unconstrained eigenvalues                              1.550
Sum of all canonical     eigenvalues                              1.524

*** Unrestricted permutation ***
Seeds:  13180 29298; 999 permutations under reduced model

**** Summary of Monte Carlo test ****
Test of significance of first canonical axis: eigenvalue =     .313
                                              F-ratio    =     .254
                                              P-value    =    .2290
Test of significance of all canonical axes  : Trace      =    1.524
                                              F-ratio    =    2.734
                                              P-value    =    .0010
```

Canoco – CCA bogs (restricted)

```
Forward selection of envi. variables =    1
Scaling of ordination scores         =   -1
No samples omitted
Number of samples                        24
Number of species                        95
Number of occurrences                   572
No. of environmental variables:          25
No interaction terms defined
Squareroot-transformation of species data
No species-weights specified
No  sample-weights specified
Downweighting of rare species

No rescaling
No detrending
No. of active  samples:     24
No. of passive samples:      0
No. of active  species:     95
Sum of all eigenvalues of CA =    1.54961

**** Weighted correlation matrix (weight = sample total) ****
SPEC AX1    1.0000
SPEC AX2    -.0036     1.0000
SPEC AX3    -.0031     -.0824     1.0000
SPEC AX4     .0523     -.0579      .0409     1.0000
ENVI AX1     .9418      .0000      .0000      .0000     1.0000
ENVI AX2     .0000      .9295      .0000      .0000      .0000     1.0000
ENVI AX3     .0000      .0000      .8278      .0000      .0000      .0000     1.0000
ENVI AX4     .0000      .0000      .0000      .8749      .0000      .0000      .0000     1.0000
ionsum      -.6582     -.3330     -.0117      .2874     -.6989     -.3582     -.0141      .3285
so4def      -.6669     -.4756      .1906      .2219     -.7081     -.5117      .2302      .2536
ph           .3671      .5482      .5157      .0113      .3898      .5898      .6230      .0129
ca          -.8384      .2819      .1284      .1864     -.8902      .3033      .1551      .2130
cl          -.7226     -.2965      .0326      .1962     -.7672     -.3190      .0394      .2243
gilvin      -.5131     -.5193     -.0851     -.1627     -.5448     -.5587     -.1028     -.1860
         SPEC AX1   SPEC AX2   SPEC AX3   SPEC AX4   ENVI AX1   ENVI AX2   ENVI AX3   ENVI AX4

**** Summary ****
Axes                                    1     2     3     4 Tot. inert.
Eigenvalues                        :   .272  .248  .097  .076      1.550
Species-environment correlations   :   .942  .929  .828  .875
Cumulative percentage variance
   of species data                 :  17.6  33.5  39.8   44.7
   of species-environment relation:  33.6  64.3  76.3   85.7
Sum of all unconstrained eigenvalues                              1.550
Sum of all canonical     eigenvalues                               .809

*** Unrestricted permutation ***
Seeds:   7520  2395; 999 permutations under reduced model

**** Summary of Monte Carlo test ****
Test of significance of first canonical axis: eigenvalue =     .272
                                              F-ratio    =    3.620
                                              P-value    =    .0010
Test of significance of all canonical axes  : Trace      =     .809
                                              F-ratio    =    3.092
                                              P-value    =    .0010
```

BIOENV - Wetland types

Data: species
Rank correlation method: Spearman
Maximum number of variables: 4
Analyse between: Samples
Similarity measure: Norm. Eucl. Dist.
Standardise: No

Variables
1 ca:mg
2 aniondef
3 nasur
4 ionsum
5 so4def
6 seadist
7 tp
8 srp
9 amm
10 nit
11 chla1
12 chla3
13 alk
14 ph
15 ca
16 mg
17 k
18 na
19 sulphate
20 cl
21 cond
22 gilvin
23 silica
24 temp
25 relpeg
26 depth

Best results

No. Vars	Corr.	Selections
1	0,788	14
3	0,781	13,14,22
3	0,778	14,15,22
4	0,775	13-15,22
2	0,770	14,22
4	0,762	13,14,22,26
4	0,756	14,15,22,26
4	0,754	14,15,22,23
4	0,751	12-14,22
2	0,750	13,14

data: genera
Rank correlation method: Spearman
Maximum number of variables: 3
Analyse between: Samples
Similarity measure: Normalised
Euclidean distance
Standardise: No
Transform: None

Best results

No. Vars	Corr.	Selections
2	0,608	13,14
3	0,604	13-15
3	0,597	14,15,23
3	0,586	13,14,23
1	0,583	13
1	0,582	14
2	0,577	14,23
2	0,565	14,15
3	0,565	12-14
3	0,563	13,15,23

Data: families
Rank correlation method: Spearman
Maximum number of variables: 5
Analyse between: Samples
Similarity measure: Normalised
Euclidean distance
Standardise: No
Transform: None

Best results

No. Vars	Corr.	Selections
4	0,483	13-15,23
3	0,483	14,15,23
2	0,466	14,23
5	0,465	13-15,23,26
3	0,465	13,15,23
3	0,464	13,14,23
5	0,463	12-15,23
5	0,461	13-15,21,23
4	0,456	12,14,15,23
5	0,456	13-16,23

BIOENV - Bogs

Data: species
Rank correlation method: Spearman
Maximum number of variables: 5
Analyse between: Samples
Similarity measure: Norm. Eucl. Dist.
Standardise: No
Transform: None

Best results

No. Vars	Corr.	Selections
4	0,611	1,5,15,21
5	0,611	1,5,13,15,21
5	0,611	1,5,6,15,21
4	0,611	1,5,6,15
5	0,611	1,5,6,13,15
3	0,602	1,5,15
4	0,602	1,5,13,15
5	0,598	1,5,6,12,15
5	0,597	1,5,15,16,21
5	0,597	1,5,12,15,21
3	0,596	1,15,21
4	0,596	1,13,15,21
4	0,595	1,6,15,21
5	0,595	1,6,13,15,21
5	0,595	1,5,14,15,21
5	0,592	1,6,15,20,21
5	0,590	1,6,12,15,21
5	0,590	1,14-16,21
4	0,589	1,15,16,21
5	0,589	1,13,15,16,21

Data: genera
Rank correlation method: Spearman
Maximum number of variables: 7
Analyse between: Samples
Similarity measure: Normalised
Euclidean distance
Standardise: No
Transform: None

Best results

No. Vars	Corr.	Selections
6	0,366	1-3,11,15,19
7	0,366	1-3,11,13,15,19
5	0,365	1-3,11,19
6	0,365	1-3,11,13,19
6	0,364	1-3,9,11,19
7	0,364	1-3,9,11,13,19
5	0,362	1,3,9,11,19
6	0,362	1,3,9,11,13,19
7	0,361	1-3,9,11,15,19
7	0,360	1-3,11,12,15,19
6	0,360	1-3,9,19,21
7	0,360	1-3,9,13,19,21
7	0,359	1-3,12,15,19,21
5	0,359	1,3,9,19,21
6	0,359	1,3,9,13,19,21
6	0,359	1-3,12,19,21
7	0,359	1-3,12,13,19,21
5	0,359	1,3,12,19,21
6	0,359	1,3,12,13,19,21
5	0,358	1-3,9,19

Data: families

Rank correlation method: Spearman
Maximum number of variables: 6
Analyse between: Samples
Similarity measure: Norm. Eucl. Dist.
Standardise: No
Transform: None

Best results

No. Vars	Corr.	Selections
5	0,359	1-3,12,21
6	0,359	1-3,12,13,21
5	0,357	1,2,12,15,21
6	0,357	1,2,12,13,15,21
4	0,355	1,2,12,21
5	0,355	1,2,12,13,21
6	0,353	1-3,12,15,21
6	0,350	1-3,11,12,21
6	0,348	1-3,9,12,21
5	0,345	1,2,12,16,21
6	0,345	1,2,12,13,16,21
6	0,344	1,2,11,12,15,21
6	0,344	1-3,6,12,21
6	0,343	1,2,9,12,15,21
5	0,343	1,2,12,21,24
6	0,343	1,2,12,13,21,24
6	0,343	1,2,10,12,15,21
6	0,342	1,2,6,12,15,21
6	0,342	1-3,10,12,21
5	0,341	1,2,6,12,21

BIOENV - Swamps

Data: species
Rank correlation method: Spearman
Maximum number of variables: 4
Analyse between: Samples
Similarity measure: Norm. Eucl. Dist.
Standardise: No
Transform: None

Best results

No. Vars	Corr.	Selections
3	0,592	17,23,24
2	0,575	17,24
4	0,564	12,17,23,24
4	0,563	17,23-25
4	0,562	17,19,23,24
4	0,555	7,17,23,24
4	0,554	15,17,23,24
4	0,539	17,23,24,26
3	0,538	12,17,23
4	0,535	13,17,23,24
4	0,531	11,17,23,24
4	0,530	13,17,19,24
2	0,530	12,17
2	0,527	17,23
3	0,526	13,17,24
3	0,526	15,17,24
3	0,523	12,17,24
4	0,520	7,13,17,24
3	0,517	17,19,24
4	0,517	17,20,23,24

Data: genera
Rank correlation method: Spearman
Maximum number of variables: 4
Analyse between: Samples
Similarity measure: Norm. Eucl. Dist.
Standardise: No
Transform: None

Best results

No. Vars	Corr.	Selections
3	0,533	17,23,24
4	0,508	13,17,23,24
4	0,499	7,17,23,24
2	0,496	17,23
3	0,491	17,21,23
4	0,490	17,19,23,24
4	0,489	17,23-25
4	0,487	15,17,23,24
4	0,486	6,17,23,24
3	0,485	13,17,23
4	0,482	7,13,23,24
2	0,481	17,24
4	0,480	11,17,23,24
4	0,478	14,17,23,24
4	0,477	8,17,23,24
2	0,477	13,17
4	0,476	7,13,17,24
4	0,476	17,21,23,24
4	0,476	12,17,23,24
3	0,476	13,17,24

Data: families
Rank correlation method: Spearman
Maximum number of variables: 4
Analyse between: Samples
Similarity measure: Norm. Eucl. Dist.
Standardise: No
Transform: None

Best results

No. Vars	Corr.	Selections
3	0,561	17,21,23
2	0,555	17,21
4	0,545	17,19,21,23
4	0,543	5,17,21,23
4	0,539	7,17,21,23
3	0,538	17,23,24
4	0,535	15,17,21,23
3	0,532	7,17,21
4	0,531	10,17,21,23
4	0,529	3,17,21,23
3	0,529	15,17,21
4	0,528	7,17,23,24
4	0,524	7,10,17,21
4	0,522	17,21-23
4	0,522	3,7,17,21
4	0,520	5,10,17,23
4	0,520	10,17,19,23
4	0,518	17,19,23,24
4	0,518	7,15,17,21
4	0,517	7,17,19,21

BVSTEP - Swamps

Rank correlation method: Spearman
Termination criteria: rho > 0,95
delta rho < 0,001
Use random selection for starting variables
Number of restarts: 5
Percentage of starting variables: 25
Analyse between: Samples
Similarity measure: Bray Curtis
Standardise: No
Transform: Square root

Variables

1	achthe	37	frucra
2	achmin	38	frumag
3	adlbry	39	frupan
4	aulalp	40	frugon
5	aulcra	41	frusa1
6	auldis	42	frusa2
7	aulten	43	frumao
8	brapro	44	gomgra
9	chabeg	45	gompar
10	chamed	46	meldic
11	chasso	47	navhei
12	cymnav	48	navmin
13	encama	49	navfac
14	encneo	50	navcos
15	encper	51	navdif
16	eunbbi	52	navelo
17	eunbmu	53	navind
18	eunexi	54	navpar
19	eungen	55	navsma
20	eungro	56	nitapm
21	euninc	57	nitgra

22	eunmei	58	nitpal
23	eunmus	59	nitper
24	eunppa	60	pindsu
25	eunptr	61	pingib
26	eunpra	62	pinmic
27	eunsch	63	pinper
28	eunsio	64	pinsub
29	eunssi	65	pinsga
30	eunssb	66	pinvir
31	eunspj	67	staanc
32	eunven	68	stecur
33	fracve	69	stedel
34	fraexi	70	surlin
35	franan	71	tabflo
36	fruaot	72	tabven

Best results

No. Vars	Corr.	Selections
11	0,952	11,14,21,22,25,33, 35,47,51,64,71
11	0,951	11,14,16,20-22,33, 40,43,47,71
11	0,951	7,11,14,21,22,25, 33,40,47,65,71
11	0,950	11,14,16,20,21,33, 43,44,47,57,71
12	0,951	11,14,16,21,24,26, 33,40,42,47,50,71

Redundancy:

No. Vars	Corr.	Selections
20	0,838	2,7,8,12,13,16,24,28, 42-44,46,48,50, 57-60,65,68
19	0,838	2,7,8,12,13,16,24, 28,42, 43,46,48,50, 57-60,65,68
23	0,835	2,7,8,12,13,20,24, 26-28, 42-44,46,48-50, 52,57,59, 60,65,68

BVSTEP - Bogs

Rank correlation method: Spearman
Termination criteria: rho > 0,95
delta rho < 0,001
Use random selection for starting variables
Number of restarts: 5
Percentage of starting variables: 25
Analyse between: Samples
Similarity measure: Bray Curtis
Standardise: No
Transform: Square root

Best results

No. Vars	Corr.	Selections
10	0,951	1,9,21,24,25,38,42, 54,55,57
10	0,950	3,11,15,21,24,25,38, 42,54,55
11	0,950	3,11,24,25,28,31,38, 42,54,55,64
12	0,952	3,10,24,25,29,38,42, 53-55,57,64
12	0,950	9,10,21,22,24,25,37, 42,54,55,57,63

Redundancy:

No. Vars	Corr.	Selections
21	0,505	2,3,10,11,17,20,22, 28,29,31,36,39-41,46, 51,53,63,64,66,72
20	0,504	2,3,10,11,17,20,22, 28,29,31,36,39,41,46, 51,53,63,64,66,72
16	0,486	2,3,10,11,14,16,17,22,28, 29,39,41,53,63,66,72

BVSTEP - Wetlands

Rank correlation method: Spearman
Termination criteria:
rho > 0,95
delta rho < 0,001
Use fixed starting variables
Analyse between: Samples
Similarity measure: Bray Curtis
Standardise: No
Transform: Square root

Best results

No. Vars	Corr.	Selections
8	0,954	11,14,16,21,24,25,42,57

Redundancy:

No. Vars	Corr.	Selections
29	0,841	7,9,10,13,20,22,27,29,31, 33,35,37-39,43,47-51,54, 58,59,63,64,68-71

SIMPER - Similarity Percentages

```
Standardise data: No
Transform: Square root
Cut off for low contributions: 98,00%
Factor name: wetland type
```

Factor groups
1,0 bogs
2,0 swamps

Group 1,0
Average similarity: 41,16

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
eunptr	27,87	10,06	0,91	24,43	24,43
frusa2	22,79	9,86	1,39	23,96	48,39
eunppa	8,98	6,82	1,54	16,56	64,95
navpar	7,55	3,15	0,70	7,66	72,60
eunbbi	2,33	1,37	0,63	3,33	75,93
frumag	4,26	1,32	0,48	3,20	79,13
navsma	6,21	1,26	0,40	3,05	82,18
chabeg	1,42	0,98	0,58	2,39	84,57
chamed	1,50	0,83	0,50	2,02	86,59
pinsub	0,48	0,76	0,71	1,84	88,43
frucra	1,00	0,59	0,43	1,44	89,87
eunspj	1,64	0,52	0,41	1,28	91,15
pinper	0,44	0,42	0,47	1,01	92,16
eunssi	3,12	0,41	0,22	1,00	93,16
fruaot	0,62	0,35	0,41	0,86	94,02
eunexi	0,39	0,31	0,39	0,76	94,78
encper	0,34	0,29	0,39	0,70	95,47
euninc	2,13	0,27	0,28	0,65	96,12
frusa1	0,36	0,21	0,29	0,52	96,64
eunste	0,15	0,20	0,31	0,49	97,13
eunssb	0,72	0,12	0,15	0,29	97,42
frumao	0,30	0,12	0,23	0,28	97,70
pinmic	0,17	0,10	0,24	0,25	97,95
pinvir	0,06	0,10	0,26	0,25	98,19

Group 2,0
Average similarity: 38,24

Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
euninc	25,83	7,36	0,95	19,23	19,23
encneo	10,23	3,98	1,10	10,41	29,64
nitgra	4,54	2,81	1,41	7,34	36,98
tabflo	6,47	2,63	0,81	6,88	43,86
frumao	1,52	2,03	1,33	5,30	49,16
eunmei	3,21	1,59	0,80	4,16	53,32
pinsub	1,23	1,57	1,52	4,11	57,43
chasso	7,09	1,41	0,50	3,68	61,11
eunbbi	1,19	1,36	1,03	3,56	64,66
navhei	5,35	1,34	0,52	3,50	68,16
eunsch	2,70	1,31	0,82	3,41	71,58
eunptr	3,99	1,24	0,51	3,24	74,82
fracve	7,78	0,91	0,34	2,38	77,20
frusa2	0,54	0,58	0,67	1,53	78,73
frugon	0,50	0,57	0,69	1,50	80,23
pinsga	0,46	0,50	0,67	1,30	81,53
nitpal	0,40	0,49	0,66	1,29	82,81
aulten	3,08	0,42	0,27	1,11	83,92
brapro	0,57	0,40	0,57	1,05	84,97
nitper	0,97	0,40	0,47	1,05	86,02
pinvir	0,20	0,33	0,62	0,87	86,90
eunbmu	0,99	0,33	0,36	0,87	87,77
stedel	0,28	0,33	0,60	0,85	88,62
stecur	0,31	0,32	0,49	0,84	89,46
navdif	0,75	0,30	0,38	0,78	90,24
chamed	0,31	0,28	0,46	0,74	90,98
navfac	1,06	0,25	0,31	0,64	91,62
franan	0,47	0,22	0,41	0,57	92,19
navmin	0,58	0,18	0,29	0,47	92,66
eunpra	0,25	0,16	0,30	0,41	93,07
pinper	0,15	0,15	0,34	0,40	93,47
navelo	0,27	0,14	0,29	0,38	93,85
staanc	0,18	0,14	0,38	0,37	94,22
gompar	0,19	0,14	0,36	0,35	94,57

encama	0,23	0,13	0,29	0,34	94,92
eunppa	0,20	0,12	0,28	0,32	95,23
surlin	0,24	0,12	0,28	0,31	95,54
nitapm	0,50	0,10	0,19	0,27	95,80
selpup	0,09	0,10	0,33	0,27	96,07
eunsio	0,14	0,10	0,24	0,25	96,32
eungro	0,14	0,09	0,22	0,23	96,56
eunmus	0,24	0,08	0,21	0,21	96,77
eunfle	0,12	0,08	0,27	0,21	96,98
diacon	0,09	0,07	0,26	0,19	97,17
nitint	0,07	0,07	0,27	0,18	97,35
eungen	0,22	0,07	0,21	0,18	97,53
navpar	0,12	0,07	0,25	0,18	97,70
achmin	0,27	0,06	0,23	0,15	97,85
cymnav	0,48	0,05	0,14	0,13	97,98
nitaci	0,09	0,04	0,19	0,11	98,10

Groups 1,0 & 2,0
Average dissimilarity = 87,04

Species	Group 1,0 Av.Abund	Group 2,0 Av.Abund	Av.Diss	Diss/SD	Contrib%	Cum.%
euninc	2,13	25,83	6,70	1,16	7,70	7,70
eunptr	27,87	3,99	6,22	1,22	7,14	14,84
frusa2	22,79	0,54	5,88	1,41	6,76	21,60
encneo	0,03	10,23	3,99	1,24	4,59	26,19
eunppa	8,98	0,20	3,95	1,52	4,54	30,73
tabflo	0,02	6,47	3,06	1,01	3,51	34,24
navpar	7,55	0,12	3,00	0,86	3,45	37,68
nitgra	0,76	4,54	2,71	1,21	3,12	40,80
chasso	1,07	7,09	2,63	0,75	3,02	43,82
navhei	0,00	5,35	2,24	0,75	2,57	46,39
fracve	0,00	7,78	2,18	0,64	2,50	48,89
navsma	6,21	0,15	2,14	0,65	2,46	51,35
eunmei	0,18	3,21	1,96	0,96	2,25	53,60
frumag	4,26	0,07	1,89	0,74	2,17	55,77
eunsch	0,03	2,70	1,71	0,86	1,96	57,73
eunbbi	2,33	1,19	1,63	1,19	1,87	59,60
frumao	0,30	1,52	1,58	1,51	1,82	61,42
aulten	0,00	3,08	1,25	0,56	1,44	62,85
chamed	1,50	0,31	1,21	0,88	1,38	64,24
eunssi	3,12	0,02	1,18	0,47	1,36	65,60
chabeg	1,42	0,01	1,15	0,69	1,32	66,92
pinsub	0,48	1,23	1,11	1,21	1,27	68,20
eunbmu	0,88	0,99	1,08	0,73	1,24	69,44
eunspj	1,64	0,01	0,97	0,55	1,12	70,56
frucra	1,00	0,02	0,90	0,73	1,04	71,59
nitper	0,00	0,97	0,81	0,70	0,93	72,52
frugon	0,04	0,50	0,76	1,04	0,87	73,39
navfac	0,01	1,06	0,74	0,53	0,85	74,23
navdif	0,02	0,75	0,71	0,57	0,82	75,05
pinsga	0,02	0,46	0,69	0,94	0,79	75,84
pinper	0,44	0,15	0,68	0,88	0,78	76,63
nitpal	0,00	0,40	0,67	0,95	0,77	77,40
brapro	0,00	0,57	0,66	0,83	0,76	78,16
fruaot	0,62	0,00	0,61	0,59	0,70	78,86
eunexi	0,39	0,06	0,56	0,74	0,65	79,51
navmin	0,00	0,58	0,55	0,48	0,64	80,14
stedel	0,09	0,28	0,55	0,95	0,63	80,77
stecur	0,00	0,31	0,53	0,81	0,61	81,38
franan	0,00	0,47	0,50	0,63	0,58	81,96
encper	0,34	0,02	0,49	0,73	0,57	82,53
pinvir	0,06	0,20	0,48	0,97	0,55	83,08
eunssb	0,72	0,00	0,48	0,40	0,55	83,62
frusa1	0,36	0,00	0,45	0,57	0,52	84,14
eunsio	0,32	0,14	0,43	0,51	0,50	84,64
nitapm	0,00	0,50	0,43	0,45	0,49	85,14
eunpra	0,00	0,25	0,41	0,53	0,47	85,61
eungro	0,09	0,14	0,40	0,66	0,46	86,07
navelo	0,00	0,27	0,39	0,60	0,44	86,51
surlin	0,03	0,24	0,38	0,58	0,44	86,95
encama	0,00	0,23	0,36	0,56	0,42	87,36
eunste	0,15	0,00	0,34	0,60	0,39	87,76
gompar	0,01	0,19	0,34	0,66	0,39	88,15
staanc	0,00	0,18	0,33	0,58	0,38	88,52
cymnav	0,00	0,48	0,32	0,31	0,37	88,89
eunmus	0,00	0,24	0,31	0,48	0,36	89,25
achmin	0,03	0,27	0,31	0,51	0,35	89,60
eungen	0,00	0,22	0,28	0,45	0,32	89,92

pinmic	0,17	0,00	0,28	0,51	0,32	90,25
frupan	0,21	0,00	0,26	0,39	0,30	90,54
diacon	0,03	0,09	0,26	0,65	0,29	90,84
eunfle	0,00	0,12	0,24	0,55	0,28	91,12
navind	0,28	0,01	0,24	0,37	0,28	91,40
selpup	0,00	0,09	0,24	0,65	0,28	91,68
eunars	0,01	0,11	0,22	0,46	0,26	91,93
achthe	0,26	0,00	0,20	0,32	0,23	92,17
nitint	0,00	0,07	0,20	0,58	0,22	92,39
eunven	0,01	0,21	0,19	0,26	0,21	92,60
aulcra	0,00	0,22	0,18	0,32	0,21	92,81
navcos	0,00	0,11	0,18	0,40	0,21	93,02
nitaci	0,00	0,09	0,18	0,44	0,20	93,23
gomgra	0,00	0,11	0,17	0,44	0,20	93,43
aulalp	0,00	0,13	0,17	0,37	0,20	93,63
pindsu	0,00	0,09	0,17	0,39	0,19	93,82
auldis	0,00	0,13	0,16	0,28	0,19	94,01
tabven	0,15	0,00	0,16	0,32	0,18	94,19
eunsub	0,04	0,02	0,16	0,45	0,18	94,38
meldic	0,05	0,03	0,16	0,36	0,18	94,56
calbac	0,01	0,05	0,13	0,40	0,15	94,71
chasha	0,03	0,03	0,13	0,41	0,15	94,87
eunnae	0,00	0,05	0,13	0,44	0,15	95,02
fraexi	0,00	0,23	0,13	0,24	0,15	95,17
braneo	0,00	0,05	0,13	0,46	0,14	95,31
pingib	0,00	0,06	0,12	0,34	0,14	95,45
nitalp	0,00	0,05	0,12	0,38	0,14	95,59
achmar	0,00	0,07	0,12	0,35	0,14	95,72
adlbry	0,07	0,01	0,12	0,32	0,14	95,86
steden	0,00	0,04	0,12	0,48	0,13	95,99
gomcym	0,00	0,06	0,12	0,36	0,13	96,13
navobs	0,00	0,05	0,11	0,33	0,13	96,26
frucor	0,04	0,00	0,11	0,40	0,13	96,39
brabre	0,00	0,05	0,11	0,37	0,13	96,52
pindid	0,01	0,03	0,11	0,39	0,12	96,64
navrhy	0,00	0,03	0,11	0,46	0,12	96,76
achlan	0,00	0,03	0,10	0,37	0,11	96,87
navsub	0,00	0,04	0,10	0,29	0,11	96,99
falvit	0,03	0,00	0,09	0,36	0,11	97,09
frubla	0,00	0,03	0,09	0,42	0,10	97,19
pinbic	0,02	0,02	0,09	0,30	0,10	97,29
brawyg	0,04	0,00	0,08	0,29	0,10	97,39
navwil	0,03	0,00	0,08	0,31	0,09	97,48
lutmut	0,01	0,01	0,08	0,38	0,09	97,57
mayaat	0,01	0,01	0,08	0,31	0,09	97,65
hanamp	0,01	0,01	0,07	0,36	0,08	97,73
mayape	0,00	0,02	0,07	0,30	0,08	97,81
achobl	0,00	0,02	0,07	0,33	0,08	97,89
navrad	0,00	0,03	0,07	0,33	0,08	97,96
aullac	0,00	0,02	0,06	0,30	0,07	98,04

Mann-Whitney U test statistics

	Rank sum		MW-U	Z	Asym. sign.	Monte-Carlo sign. (2-sided)			Monte-Carlo sign. (1-sided)		
	bogs	swamps			(2-sided)	sign.	95% l.l.	95% u.l.	sign.	95% l.l.	95% u.l.
RELPEG	422.0	568.0	122.0	-2.781	0.005	0.004	0.003	0.005	0.002	0.001	0.003
TEMP	561.5	428.5	218.5	-0.507	0.612	0.625	0.615	0.634	0.311	0.302	0.320
CA:MG	358.5	631.5	58.5	-4.278	0.000	0.000	0.000	0.000	0.000	0.000	0.000
ANIONDEF	517.5	472.5	217.5	-0.530	0.596	0.598	0.588	0.608	0.300	0.291	0.309
NASUR	387.0	603.0	87.0	-3.606	0.000	0.000	0.000	0.000	0.000	0.000	0.000
IONSUM	541.5	448.5	238.5	-0.035	0.972	0.976	0.973	0.979	0.483	0.474	0.493
SO4DEF	696.5	293.5	83.5	-3.689	0.000	0.000	0.000	0.000	0.000	0.000	0.000
TP	485.0	505.0	185.0	-1.296	0.195	0.202	0.194	0.210	0.105	0.099	0.110
SRP	476.0	514.0	176.0	-1.508	0.131	0.132	0.125	0.138	0.064	0.059	0.069
AMM	485.0	505.0	185.0	-1.296	0.195	0.193	0.185	0.200	0.095	0.089	0.101
NIT	488.0	502.0	188.0	-1.226	0.220	0.226	0.218	0.234	0.114	0.107	0.120
CHLA1	459.5	530.5	159.5	-1.898	0.058	0.059	0.055	0.064	0.030	0.027	0.033
CHLA2	448.0	498.0	172.0	-1.412	0.158	0.159	0.152	0.166	0.080	0.075	0.085
CHLA3	433.0	557.0	133.0	-2.522	0.012	0.011	0.009	0.013	0.005	0.003	0.006
CHLA4	106.0	147.0	28.0	-2.110	0.035	0.037	0.033	0.041	0.019	0.016	0.021
ALK	300.0	690.0	0.0	-6.180	0.000	0.000	0.000	0.000	0.000	0.000	0.000
PH	300.0	690.0	0.0	-5.658	0.000	0.000	0.000	0.000	0.000	0.000	0.000
CA	312.0	678.0	12.0	-5.374	0.000	0.000	0.000	0.000	0.000	0.000	0.000
MG	403.0	587.0	103.0	-3.229	0.001	0.001	0.000	0.001	0.000	0.000	0.001
K	449.0	541.0	149.0	-2.145	0.032	0.032	0.029	0.036	0.015	0.013	0.017
NA	593.0	397.0	187.0	-1.249	0.212	0.218	0.210	0.226	0.113	0.106	0.119
SULPHATE	476.5	513.5	176.5	-1.497	0.134	0.135	0.129	0.142	0.066	0.061	0.071
CL	648.0	342.0	132.0	-2.546	0.011	0.010	0.008	0.012	0.005	0.004	0.006
COND	535.0	455.0	235.0	-0.118	0.906	0.918	0.913	0.923	0.458	0.448	0.468
GILV	748.0	242.0	32.0	-4.903	0.000	0.000	0.000	0.000	0.000	0.000	0.000
SIL	317.0	673.0	17.0	-5.256	0.000	0.000	0.000	0.000	0.000	0.000	0.000
TIEFE	333.0	657.0	33.0	-4.879	0.000	0.000	0.000	0.000	0.000	0.000	0.000
SPECIES	321.5	668.5	21.5	-5.154	0.000	0.000	0.000	0.000	0.000	0.000	0.000
D	320.0	670.0	20.0	-5.185	0.000	0.000	0.000	0.000	0.000	0.000	0.000
EVENNESS	380.0	610.0	147.0	-2.192	0.028	0.026	0.023	0.029	0.013	0.011	0.015
SHANNON	380.0	610.0	80.0	-3.771	0.000	0.000	0.000	0.000	0.000	0.000	0.000
SIMPSON	420.0	570.0	120.0	-2.828	0.005	0.004	0.003	0.005	0.002	0.001	0.003
DELTADIV	364.0	626.0	64.0	-4.148	0.000	0.000	0.000	0.000	0.000	0.000	0.000
DELTADIS	404.0	586.0	104.0	-3.206	0.001	0.002	0.001	0.003	0.001	0.000	0.002

Monte-Carlo tests are based on 10000 randomisations

Wilcoxon test statistics

Chl-*a* periphyton – Chl-*a* epiphyton		N	Mean rank	Rank sum
	Negative ranks	34(a)	23,09	785,00
	Positive ranks	8(b)	14,75	118,00
	Bindings	0(c)		
	Total	42		

a Chl-*a* periphyton < Chl-*a* epiphyton
b Chl-*a* periphyton > Chl-*a* epiphyton
c Chl-*a* periphyton = Chl-*a* epiphyton

Statistics (c)

Z			-4,170(a)
Asymptotic significance (2-sided)			,000
Monte-Carlo significance (2-sided)	significance		,000
	95% confidence intervall	lower limit	,000
		upper limit	,000
Monte-Carlo significance (1-seitig)	significance		,000
	95% confidence intervall	lower limit	,000
		upper limit	,000

a based on positive ranks.
c based on 10000 randomisations.

Bogs	Kolmogorov-Smirnov(a)			Shapiro-Wilk		
	Stat.	df	Sign.	Stat.	df	Sign.
CA:MG	.246	24	.001	.821	24	.001
ANIONDEF	.216	24	.005	.764	24	.000
NASUR	.148	24	.185	.940	24	.160
IONSUM	.175	24	.054	.935	24	.125
SO4DEF	.102	24	.200(*)	.977	24	.839
TP	.171	24	.066	.920	24	.058
SRP	.225	24	.003	.837	24	.001
AMM	.232	24	.002	.856	24	.003
NIT	.209	24	.008	.884	24	.010
CHLA1	.093	24	.200(*)	.963	24	.511
CHLA2	.150	23	.199	.942	23	.203
CHLA3	.128	24	.200(*)	.967	24	.596
CHLA4	.142	12	.200(*)	.932	12	.399
ALK(b)						
PH	.189	24	.026	.892	24	.014
CA	.129	24	.200(*)	.960	24	.430
MG	.098	24	.200(*)	.958	24	.398
K	.144	24	.200(*)	.952	24	.295
NA	.102	24	.200(*)	.960	24	.443
SO4	.186	24	.031	.909	24	.033
CL	.156	24	.137	.927	24	.086
COND	.117	24	.200(*)	.975	24	.795
GILV	.173	24	.061	.922	24	.063
SIL	.199	24	.015	.918	24	.054
TEMP	.202	24	.012	.878	24	.007
RELPEG	.124	24	.200(*)	.923	24	.069
TIEFE	.096	24	.200(*)	.977	24	.842
SPECIES	.106	24	.200(*)	.966	24	.559
N	.157	24	.130	.876	24	.007
D	.104	24	.200(*)	.965	24	.550
EVENNESS	.091	24	.200(*)	.962	24	.480
SHANNON	.112	24	.200(*)	.952	24	.300
SIMPSON	.127	24	.200(*)	.916	24	.048
DELTADIV	.155	24	.140	.926	24	.079
DELTADIS	.154	24	.144	.908	24	.032

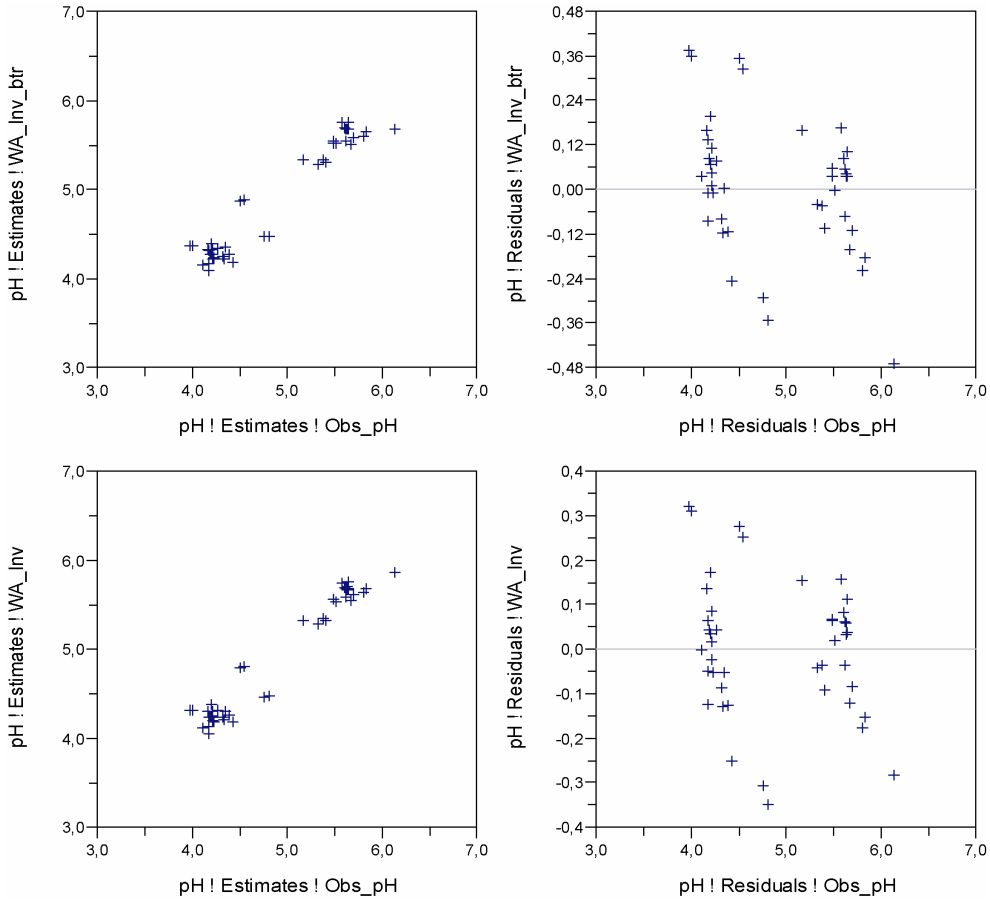
* lower limit of the true significance.
a Lilliefors significance correction
b ALKGES is constant and was omitted.

Swamps	Kolmogorov-Smirnov(a)			Shapiro-Wilk		
	Stat.	df	Sign.	Stat.	df	Sign.
CA:MG	.139	20	.200(*)	.966	20	.664
ANIONDEF	.207	20	.025	.786	20	.001
NASUR	.113	20	.200(*)	.967	20	.684
IONSUM	.250	20	.002	.835	20	.003
SO4DEF	.312	20	.000	.652	20	.000
TP	.191	20	.054	.868	20	.011
SRP	.107	20	.200(*)	.969	20	.731
AMM	.287	20	.000	.751	20	.000
NIT	.116	20	.200(*)	.948	20	.341
CHLA1	.167	20	.146	.965	20	.650
CHLA2	.179	20	.092	.938	20	.218
CHLA3	.145	20	.200(*)	.959	20	.524
CHLA4	.278	10	.028	.852	10	.061
ALK	.181	20	.084	.945	20	.302
PH	.159	20	.200(*)	.943	20	.273
CA	.213	20	.018	.761	20	.000
MG	.244	20	.003	.876	20	.015
K	.244	20	.003	.796	20	.001
NA	.200	20	.035	.929	20	.150
SO4	.210	20	.021	.896	20	.034
CL	.181	20	.084	.915	20	.078
COND	.146	20	.200(*)	.944	20	.283
GILV	.191	20	.054	.931	20	.162
SIL	.139	20	.200(*)	.948	20	.339
TEMP	.199	20	.037	.919	20	.093
RELPEG	.247	20	.002	.838	20	.003
TIEFE	.131	20	.200(*)	.959	20	.515
SPECIES	.134	20	.200(*)	.908	20	.058
N	.140	20	.200(*)	.970	20	.754
D	.131	20	.200(*)	.911	20	.066
EVENNESS	.100	20	.200(*)	.964	20	.626
SHANNON	.117	20	.200(*)	.922	20	.108
SIMPSON	.115	20	.200(*)	.980	20	.929
DELTADIV	.150	20	.200(*)	.930	20	.153
DELTADIS	.109	20	.200(*)	.948	20	.338

* lower limit of the true significance.
a Lilliefors significance correction

Wetlands	Kolmogorov-Smirnov(a)			Shapiro-Wilk		
	Stat.	df	Sign.	Stat.	df	Sign.
CA:MG	.109	44	.200(*)	.975	44	.437
ANIONDEF	.160	44	.006	.780	44	.000
NASUR	.145	44	.022	.934	44	.014
IONSUM	.099	44	.200(*)	.927	44	.009
SO4DEF	.204	44	.000	.748	44	.000
TP	.133	44	.051	.931	44	.011
SRP	.204	44	.000	.834	44	.000
AMM	.233	44	.000	.827	44	.000
NIT	.167	44	.003	.862	44	.000
CHLA1	.108	44	.200(*)	.962	44	.148
CHLA2	.146	43	.022	.957	43	.107
CHLA3	.126	44	.078	.979	44	.605
CHLA4	.161	22	.143	.954	22	.371
ALK	.337	44	.000	.782	44	.000
PH	.202	44	.000	.844	44	.000
CA	.082	44	.200(*)	.958	44	.105
MG	.129	44	.064	.952	44	.068
K	.154	44	.010	.896	44	.001
NA	.110	44	.200(*)	.961	44	.140
SO4	.149	44	.016	.896	44	.001
CL	.146	44	.019	.918	44	.004
COND	.095	44	.200(*)	.971	44	.324
GILV	.126	44	.077	.937	44	.019
SIL	.144	44	.023	.900	44	.001
TEMP	.106	44	.200(*)	.961	44	.139
RELPEG	.096	44	.200(*)	.944	44	.034
TIEFE	.082	44	.200(*)	.970	44	.315
SPECIES	.083	44	.200(*)	.950	44	.055
N	.097	44	.200(*)	.949	44	.051
D	.077	44	.200(*)	.953	44	.071
EVENNESS	.079	44	.200(*)	.969	44	.277
SHANNON	.126	44	.079	.972	44	.360
SIMPSON	.138	44	.034	.874	44	.000
DELTADIV	.125	44	.083	.952	44	.063
DELTADIS	.112	44	.200(*)	.940	44	.024

* lower limit of the true significance.
a Lilliefors significance correction



Results for model: pH

```
Model type                    :  Weighted Averaging
Species data                  :  species transformed
Environmental data            :  environmental transformed
Number of samples in model    :  44
Number of variables in model:  199
```

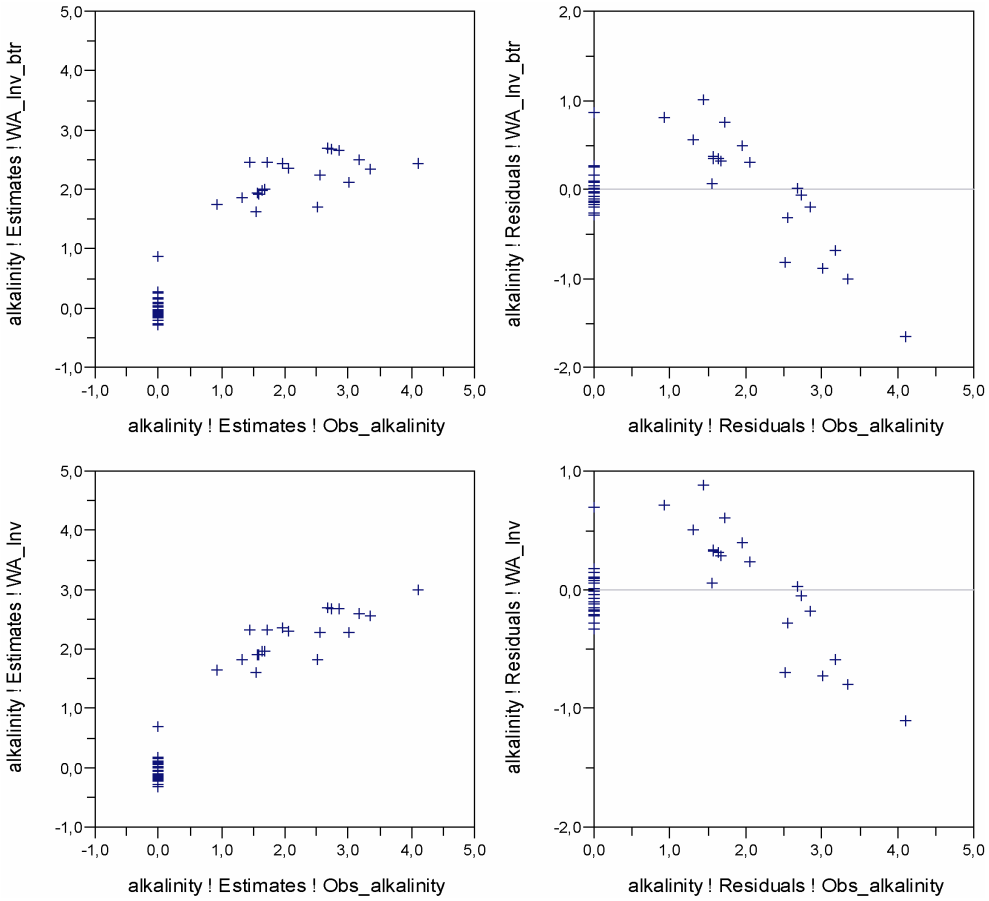
Taxa with only one occurrence have had their tolerances set to 0,33227

Deshrinking regression coefficients

#	Id	WA_b0	WA_b1	WATOL_b0	WATOL_b1
1	Inverse deshrinking	-2,6678	1,5264	-0,94803	1,179
2	Classical deshrinking	1,9058	0,62275	0,99142	0,80985

Model performance

#	Id	WA_Inv	WA_Cla	WATOL_Inv	WATOL_Cla
1	RMSE	0,15109	0,15496	0,14453	0,14791
2	R2	0,9506	0,9506	0,95479	0,95479
3	Ave_Bias	2,9169e-015	2,8361e-015	4,7437e-016	5,5511e-016
4	Max_Bias	0,32866	0,35053	0,38565	0,34446
5	Boot_R2	0,93374	0,93388	0,92756	0,92725
6	Boot_Ave_Bias	-0,0087319	-0,0085416	-0,053752	-0,054764
7	Boot_Max_Bias	0,4697	0,43228	0,52204	0,49033
8	RMSE_s1	0,049694	0,051513	0,15195	0,15913
9	RMSE_s2	0,17653	0,17531	0,19401	0,19141
10	RMSEP	0,18339	0,18273	0,24643	0,24891



Results for model: alkalinity

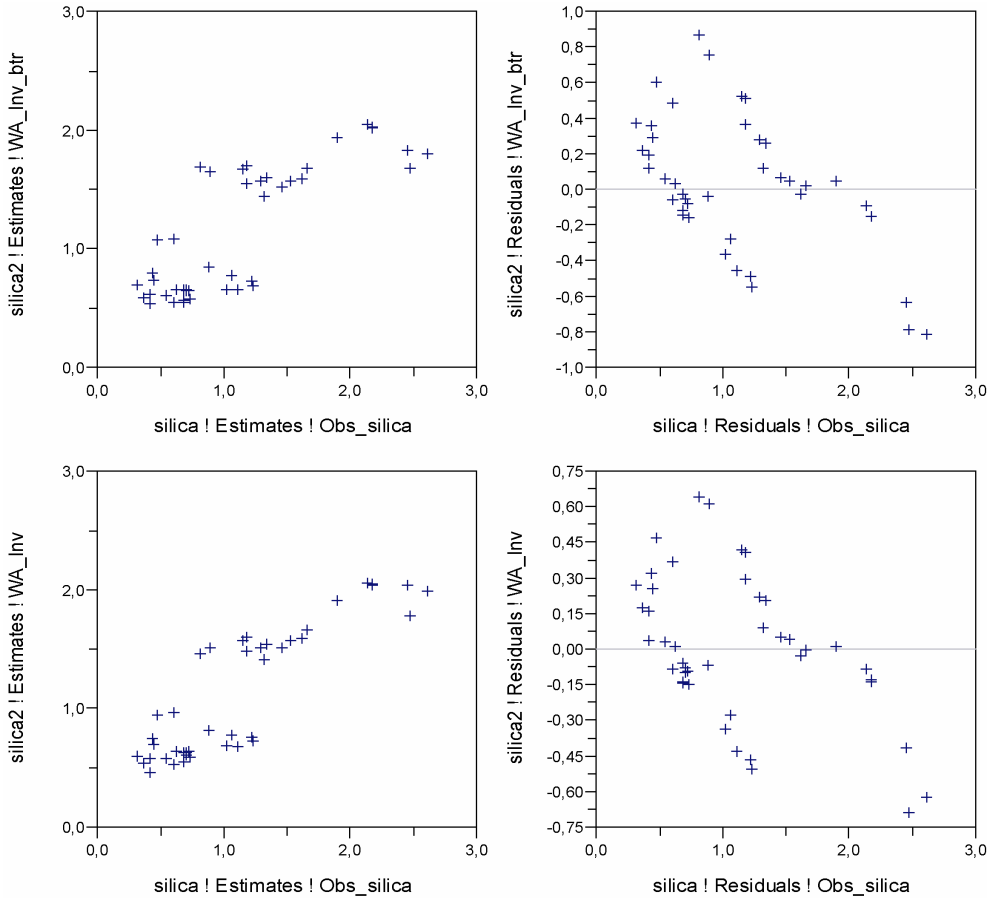
```
Model type                    :  Weighted Averaging
Species data                  :  species transformed
Environmental data            :  environmental transformed
Number of samples in model    :  44
Number of variables in model:  199
Taxa with only one occurrence have had their tolerances set to 0,88278
```

Deshrinking regression coefficients

#	Id	WA_b0	WA_b1	WATOL_b0	WATOL_b1
1	Inverse deshrinking	-0,67924	1,5155	-0,44603	1,333
2	Classical deshrinking	0,52178	0,58695	0,3933	0,69205

Model performance

#	Id	WA_Inv	WA_Cla	WATOL_Inv	WATOL_Cla
1	RMSE	0,40878	0,43342	0,3424	0,3565
2	R2	0,88951	0,88951	0,92248	0,92248
3	Ave_Bias	6,1567e-016	8,0239e-016	2,7756e-016	1,4635e-016
4	Max_Bias	1,1081	0,86185	1,1438	0,9802
5	Boot_R2	0,83184	0,83206	0,85294	0,85242
6	Boot_Ave_Bias	-0,017094	-0,014239	-0,060373	-0,060539
7	Boot_Max_Bias	1,6548	1,5138	1,5238	1,4599
8	RMSE_s1	0,12892	0,14285	0,33027	0,34781
9	RMSE_s2	0,50459	0,51891	0,47958	0,4763
10	RMSEP	0,5208	0,53821	0,5823	0,58977



Results for model: silica

```
Model type                    :  Weighted Averaging
Species data                  :  species transformed
Environmental data            :  environmental transformed
Number of samples in model    :  43
Number of variables in model:  198
```

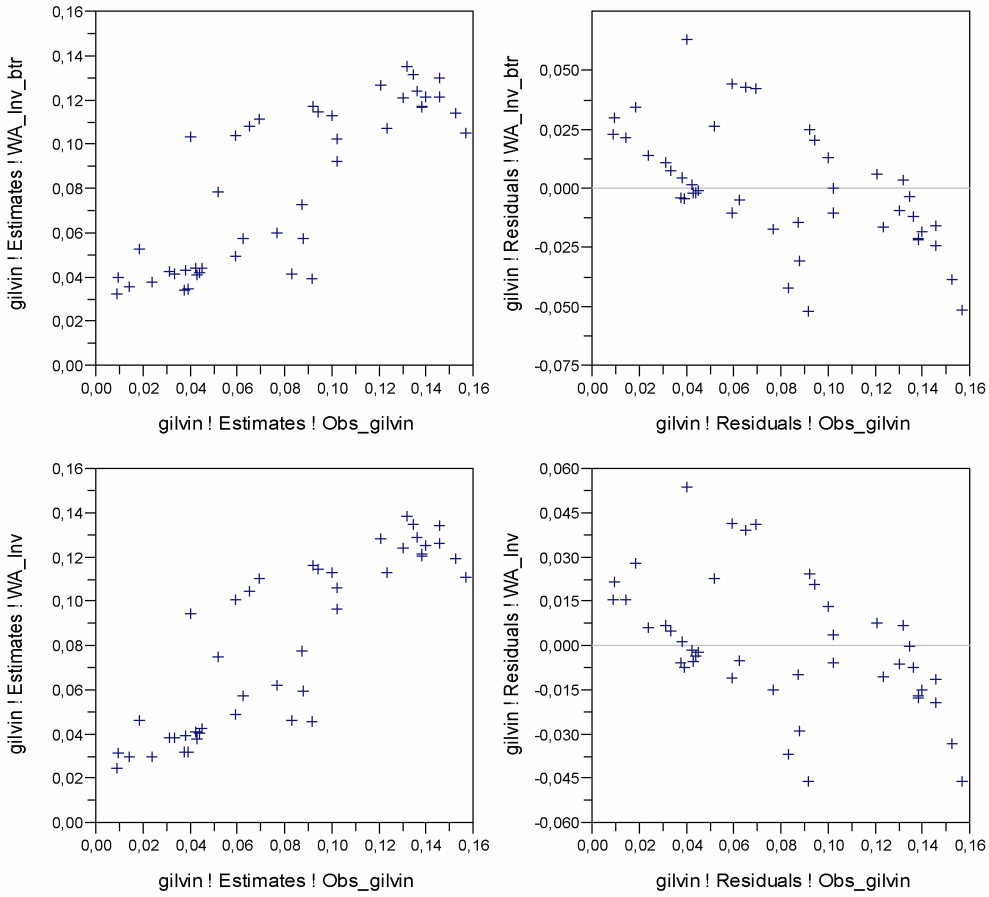
The following training set samples have been excluded from the model: 29 S1-5
The following training set variables have been excluded from the model: 43 dipell
Taxa with only one occurrence have had their tolerances set to 0,3229

Deshrinking regression coefficients

#	Id	WA_b0	WA_b1	WATOL_b0	WATOL_b1
1	Inverse deshrinking	-0,7865	1,6307	-0,24148	1,1673
2	Classical deshrinking	0,64612	0,46673	0,33834	0,73914

Model performance

#	Id	WA_Inv	WA_Cla	WATOL_Inv	WATOL_Cla
1	RMSE	0,30485	0,34943	0,23105	0,24875
2	R2	0,76112	0,76112	0,86278	0,86278
3	Ave_Bias	-6,4806e-016	-8,4170e-016	1,4201e-016	1,9364e-016
4	Max_Bias	0,57751	0,44007	0,27399	0,27737
5	Boot_R2	0,64681	0,65548	0,73752	0,74276
6	Boot_Ave_Bias	-0,024573	-0,026987	-0,045359	-0,050093
7	Boot_Max_Bias	0,74502	0,58176	0,55619	0,4567
8	RMSE_s1	0,089728	0,105	0,20609	0,22999
9	RMSE_s2	0,37275	0,40359	0,32279	0,32697
10	RMSEP	0,3834	0,41702	0,38297	0,39975



Results for model: gilvin

```
Model type                    :  Weighted Averaging
Species data                  :  species transformed
Environmental data            :  environmental transformed
Number of samples in model    :  44
Number of variables in model:  199
Taxa with only one occurrence have had their tolerances set to 0,025681
```

Deshrinking regression coefficients

#	Id	WA_b0	WA_b1	WATOL_b0	WATOL_b1
1	Inverse deshrinking	-0,052112	1,7074	-0,02004	1,3806
2	Classical deshrinking	0,041997	0,44344	0,025515	0,58794

Model performance

#	Id	WA_Inv	WA_Cla	WATOL_Inv	WATOL_Cla
1	RMSE	0,021948	0,025224	0,019323	0,021448
2	R2	0,7571	0,7571	0,81172	0,81172
3	Ave_Bias	-2,6967e-017	-4,0056e-017	4,7311e-019	1,7820e-017
4	Max_Bias	0,027736	0,015018	0,028753	0,019337
5	Boot_R2	0,68007	0,69071	0,72529	0,73105
6	Boot_Ave_Bias	-7,2549e-005	-3,5566e-004	0,001958	0,002189
7	Boot_Max_Bias	0,032655	0,021302	0,031353	0,024703
8	RMSE_s1	0,0059503	0,0066743	0,012583	0,014366
9	RMSE_s2	0,025193	0,026663	0,023449	0,023738
10	RMSEP	0,025886	0,027486	0,026612	0,027747

WA optima of benthic diatom taxa

		pH		alkalinity		silica		gilvin	
Taxon	n	opt.	tol.	opt.	tol.	opt.	tol.	opt.	tol.
achhel	5	5.51	0.16	95	74	3.30	2.06	5.435	2.557
achlan	5	5.59	0.22	86	65	2.97	1.38	6.032	3.197
achmar	5	5.83	0.27	190	117	3.69	1.70	7.547	2.475
achmin	20	5.30	0.83	140	144	3.16	2.55	7.012	4.434
achobl	5	5.60	0.34	130	131	3.77	2.06	6.670	1.598
aulalp	5	5.76	0.30	213	90	5.00	1.50	6.359	2.416
aullac	5	5.65	0.11	160	25	4.63	0.79	4.536	2.635
aulten	10	5.65	0.30	169	65	4.68	1.14	4.485	2.680
brabre	5	5.62	0.11	165	20	4.93	0.88	4.778	2.179
braneo	7	5.61	0.58	181	100	4.31	1.71	6.037	3.066
brapro	13	5.70	0.35	179	104	4.35	1.98	5.523	2.406
calbac	11	5.38	0.54	63	74	1.69	1.38	4.268	4.053
chabeg	29	4.34	0.36	7	31	0.60	0.83	12.163	3.542
chamed	33	4.73	0.68	37	69	1.56	1.86	8.412	4.222
chasha	10	5.21	0.44	60	71	2.78	2.84	4.830	2.679
chasso	22	5.38	0.41	62	61	2.12	1.94	3.412	2.785
cymnav	8	5.71	0.12	201	66	5.79	1.85	4.538	2.238
diacon	21	5.22	0.73	87	106	2.29	2.13	6.608	5.021
encama	10	5.62	0.14	88	71	2.70	1.55	2.237	1.624
encneo	27	5.59	0.32	102	79	2.46	1.84	4.212	2.751
encper	16	4.62	0.54	27	84	1.12	1.61	9.745	3.906
eunars	10	5.42	0.46	66	51	2.08	1.05	4.531	3.860
eunbbi	36	4.87	0.67	49	80	2.00	2.17	7.735	4.330
eunbmu	18	5.26	0.52	89	90	3.10	2.25	5.814	3.132
eunexi	17	4.61	0.54	15	37	0.77	0.77	9.822	4.400
eunfle	8	5.69	0.09	127	48	3.01	1.79	5.295	2.273
eungen	7	5.67	0.25	129	92	3.03	2.53	5.500	1.933
eungro	18	4.92	0.64	53	79	2.76	3.00	6.210	3.329
eunimp	5	5.10	0.65	78	98	2.30	2.11	7.120	3.018
euninc	31	5.43	0.39	87	73	3.05	2.37	5.263	3.321
eunmei	21	5.45	0.45	125	84	4.20	2.84	6.093	2.883
eunmus	5	5.66	0.06	162	28	4.79	0.81	4.002	1.787
eunnae	6	5.68	0.09	160	40	4.26	1.41	4.796	2.493
eunppa	34	4.39	0.42	10	39	0.74	1.10	10.909	3.876
eunptr	37	4.45	0.52	17	47	1.19	1.83	10.796	3.884
eunpra	10	5.52	0.33	152	102	5.75	2.79	6.382	2.146
eunsch	19	5.56	0.33	129	88	4.04	2.44	4.283	3.249
eunsio	8	5.07	0.58	67	107	2.70	3.14	7.300	1.691
eunssi	17	4.59	0.43	12	48	0.87	1.14	8.242	4.294
eunssb	6	4.26	0.06	0	82	0.49	0.38	13.234	2.150
eunspj	20	4.48	0.31	5	32	0.80	1.26	8.768	3.221
eunste	14	4.28	0.13	0	82	0.38	0.20	12.568	2.988
eunsub	12	4.65	0.53	20	52	1.42	1.68	8.071	2.878
eunven	9	5.26	0.54	76	118	3.37	2.86	7.401	2.165
falvit	9	4.42	0.59	26	93	0.86	1.61	12.557	4.485
fracve	13	5.70	0.19	177	69	4.77	1.25	4.363	2.134
franan	12	5.74	0.19	165	87	3.49	2.01	5.779	2.473
frauln	5	5.76	0.21	204	73	5.11	1.18	4.814	2.239
frubah	12	4.31	0.19	0	82	0.60	0.39	10.476	4.129
frubla	7	5.71	0.22	182	84	4.82	1.28	4.681	2.151
frucor	10	4.34	0.16	0	82	0.41	0.35	11.249	3.230
frucra	18	4.51	0.50	16	59	1.06	1.21	8.481	3.067
fruman	25	4.50	0.50	17	66	0.91	1.25	8.637	3.762
frupan	5	4.38	0.25	0	82	0.58	0.22	7.252	2.363
fruqua	25	5.50	0.47	105	89	2.82	2.36	5.625	2.942
frusa1	9	4.40	0.25	0	82	0.59	0.30	8.987	3.380
frusa2	40	4.46	0.44	11	42	0.84	1.20	10.566	3.806
fruspe	27	5.36	0.52	76	78	2.26	2.10	4.750	2.700
gomgra	8	5.75	0.38	190	129	4.29	2.04	4.151	1.023
gompar	16	5.56	0.52	133	89	3.26	2.07	6.285	4.169
gomcym	6	5.80	0.19	220	66	5.28	1.54	5.630	2.662
hanamp	6	4.75	0.85	67	140	1.51	2.38	9.810	4.893
lutmut	10	5.13	0.81	98	122	2.67	2.67	7.483	5.900
mayaat	5	5.07	0.72	32	29	1.37	0.88	6.379	6.500
mayape	7	5.70	0.25	131	113	2.85	2.42	4.833	2.208

		pH		alkalinity		silica		gilvin	
Taxon	n	opt.	tol.	opt.	tol.	opt.	tol.	opt.	tol.
meldic	10	4.80	0.62	19	28	0.75	0.43	6.927	4.244
navobs	8	5.29	0.47	93	66	4.28	3.69	7.095	2.088
navhei	17	5.70	0.21	113	97	2.23	1.98	4.280	1.870
navmin	12	5.65	0.20	106	87	2.36	2.58	4.895	1.931
navrhy	8	5.77	0.21	182	93	4.30	1.84	5.004	2.270
navfac	15	5.60	0.34	113	97	3.01	2.22	4.743	2.927
navsub	5	5.66	0.12	79	38	1.60	0.92	4.689	2.801
navcos	6	5.61	0.29	83	101	2.36	1.55	1.772	1.285
navdif	21	5.55	0.40	98	88	2.26	2.32	4.760	1.971
navelo	8	5.70	0.23	185	70	4.86	1.20	4.755	2.344
navind	7	4.79	0.54	14	31	0.60	0.71	6.651	2.651
navpar	30	4.36	0.40	10	40	0.70	1.11	11.409	3.466
navsma	17	4.45	0.46	6	18	0.70	0.56	8.566	4.306
nitaci	8	5.74	0.23	143	115	2.93	2.44	3.978	0.374
nitalp	8	5.67	0.19	100	74	2.01	1.34	4.663	2.564
nitapm	8	5.68	0.16	116	76	2.32	1.94	5.067	1.783
nitgra	24	5.49	0.42	93	84	2.42	2.28	4.732	2.474
nitint	14	5.69	0.28	141	100	3.38	2.52	5.056	2.400
nitpal	19	5.60	0.27	112	85	3.07	2.15	3.969	2.866
nitper	15	5.75	0.23	145	115	2.90	2.21	4.325	2.128
pinbic	8	4.90	0.73	31	41	1.32	0.64	6.453	5.098
pindsu	5	5.56	0.10	54	4	1.88	0.45	1.343	0.575
pindid	12	5.12	0.64	84	96	2.75	2.75	8.104	4.766
pingib	7	5.61	0.25	97	102	3.03	2.62	2.313	2.426
pinmic	11	4.40	0.39	3	13	0.68	0.52	10.111	4.848
pinper	31	4.73	0.60	33	68	1.45	2.19	9.564	4.801
pinsin	8	4.84	0.70	52	76	1.84	1.95	8.197	4.131
pinsub	41	5.11	0.68	71	85	2.31	2.23	6.279	4.101
pinsga	21	5.52	0.43	116	87	3.43	2.22	4.240	3.309
pinvir	30	5.14	0.67	73	82	2.38	2.51	6.985	4.834
selpup	11	5.64	0.34	142	78	3.80	1.68	4.658	3.354
staanc	14	5.67	0.13	140	84	3.92	2.33	3.816	2.355
stapho	5	5.81	0.20	169	104	3.85	1.47	5.004	3.459
stecur	12	5.71	0.19	141	93	3.09	2.14	4.718	1.850
stedel	21	5.51	0.45	112	108	2.94	1.91	4.605	2.921
steden	11	5.72	0.45	182	113	3.91	2.17	5.283	2.886
surlin	18	5.44	0.41	64	64	2.13	1.54	3.780	3.397
tabflo	25	5.50	0.34	112	83	3.87	2.75	6.066	2.376

CURRICULUM VITAE

Tanja Beier

Date of birth: 13.10.1976, Weilheim in OB.

EDUCATION

1996	Higher education entrance qualification, Gymnasium Weilheim
1996 – 2002	Study in biology at the Technical University of Munich. Area of specialisation: vegetation and soil ecology, limnology, landscape planning
2002	Diploma degree in biology Thesis: „Diatomeengesellschaften auf *Zannichellia palustris* an Fließgewässerstandorten unterschiedlicher Trophie in Bayern“ Supervisor: Dr. Uta Raeder

DISSERTATION

2002 – 2005	PhD scholarship recipient at the Technical University of Munich; Funding by the Margarete-Ammon-Foundation
2002 – 2003	Guest researcher at the National Institute of Water and Atmospheric Research (NIWA) in Christchurch, New Zealand. Financial support by the German Academic Exchange Service (DAAD)
2004	Organising committee of the 18. DDT (meeting of German speaking diatomologists) in Iffeldorf Poster award at the annual conference of the German Society for Limnology (DGL) in Potsdam
2005	PhD degree in natural sciences (Dr. rer. nat.) at the faculty Weihenstephan Center of Food and Life Sciences, Technical University of Munich
from 2005	Associate scientist at the Limnological Station of the Technical University of Munich