

Quantitative relationships between benthic diatom assemblages and water chemistry in Macquarie Island lakes and their potential for reconstructing past environmental changes

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Abstract: This study is the first published survey of diatom-environment relationships on sub-Antarctic Macquarie Island. Fifty-eight sites in 50 coastal and inland lakes were sampled for benthic diatoms and water chemistry. 208 diatom species from 34 genera were identified. Multivariate analyses indicated that the lakes were distributed along nutrient and conductivity gradients. Conductivity, pH, phosphate (SRP), silicate and temperature all explained independent portions of the variance in the diatom data. Transfer functions provide a quantitative basis for palaeolimnological studies of past climate change and human impacts, and can be used to establish baseline conditions for assessing the impacts of recent climate change and the introduction of non-native plants and animals. Statistically robust diatom transfer functions for conductivity, phosphate and silicate were developed, while pH and temperature transfer functions performed less well. The lower predictive abilities of the pH and temperature transfer functions probably reflect the broad pH tolerance range of diatoms on Macquarie Island and uneven distribution of lakes along the temperature gradient. This study contributes to understanding the current ecological distribution of Macquarie Island diatoms and provides transfer functions that will be applied in studies of diatoms in lake sediment cores to quantitatively reconstruct past environmental changes.

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Introduction

Recent research suggests that the Southern Ocean exerts a powerful influence on global climate (Rintoul *et al.* 2001). Macquarie Island is one of the few islands in the Southern Ocean and provides an important site for investigating climate change. An understanding of past magnitudes and rates of climate change is fundamental for putting the present into context and making realistic predictions about the future.

However, to date there have been few attempts at reconstructing past climate change at Macquarie Island, and more generally in the region between 40–65°S. This is surprising as Macquarie Island is well placed to respond to changes in rainfall, temperature and westerly wind patterns associated with changes in the thermal gradient between temperate and polar latitudes, the position of the Polar Frontal Zone and sea ice extent.

Macquarie Island contains numerous lakes and ponds, many of which accumulate sediments that archive a record of past environmental conditions. Unlocking this record can be achieved through palaeolimnological studies. Diatoms are one of the key tools used in these studies as they respond to a wide range of environmental variables including nutrients, pH, conductivity and temperature

(Stoermer & Smol 1999). Quantitative methods have been developed to relate diatom species assemblages to specific environmental variables (i.e. diatom-based transfer functions). With these transfer functions, sub-fossil diatom assemblages in lake sediment cores can be used to reconstruct past environmental conditions and can be applied to investigations of recent climate change and human impacts (see Battarbee *et al.* 2001).

High-latitude diatom-based transfer functions have previously been developed for inferring nutrients (e.g. Lim *et al.* 2007), salinity (e.g. Verleyen *et al.* 2003, Sabbe *et al.* 2004, Hodgson *et al.* 2006), pH (e.g. Jones & Birks 2004), chlorophyll *a* (e.g. Jones & Juggins 1995), temperature (e.g. Kumke *et al.* 2004, Gremmen *et al.* 2007) and soil moisture content (e.g. Van de Vijver *et al.* 2002a). To date, with the exception of Van de Vijver *et al.* (2002a) and Gremmen *et al.* (2007), there are no diatom-based transfer functions from the sub-Antarctic despite good evidence that the composition of diatom assemblages in this region is strongly influenced by environmental gradients (e.g. Van de Vijver *et al.* 2002b, 2004).

The relationships between diatom community composition and environmental variables on Macquarie Island have not yet been fully explored. In this paper we

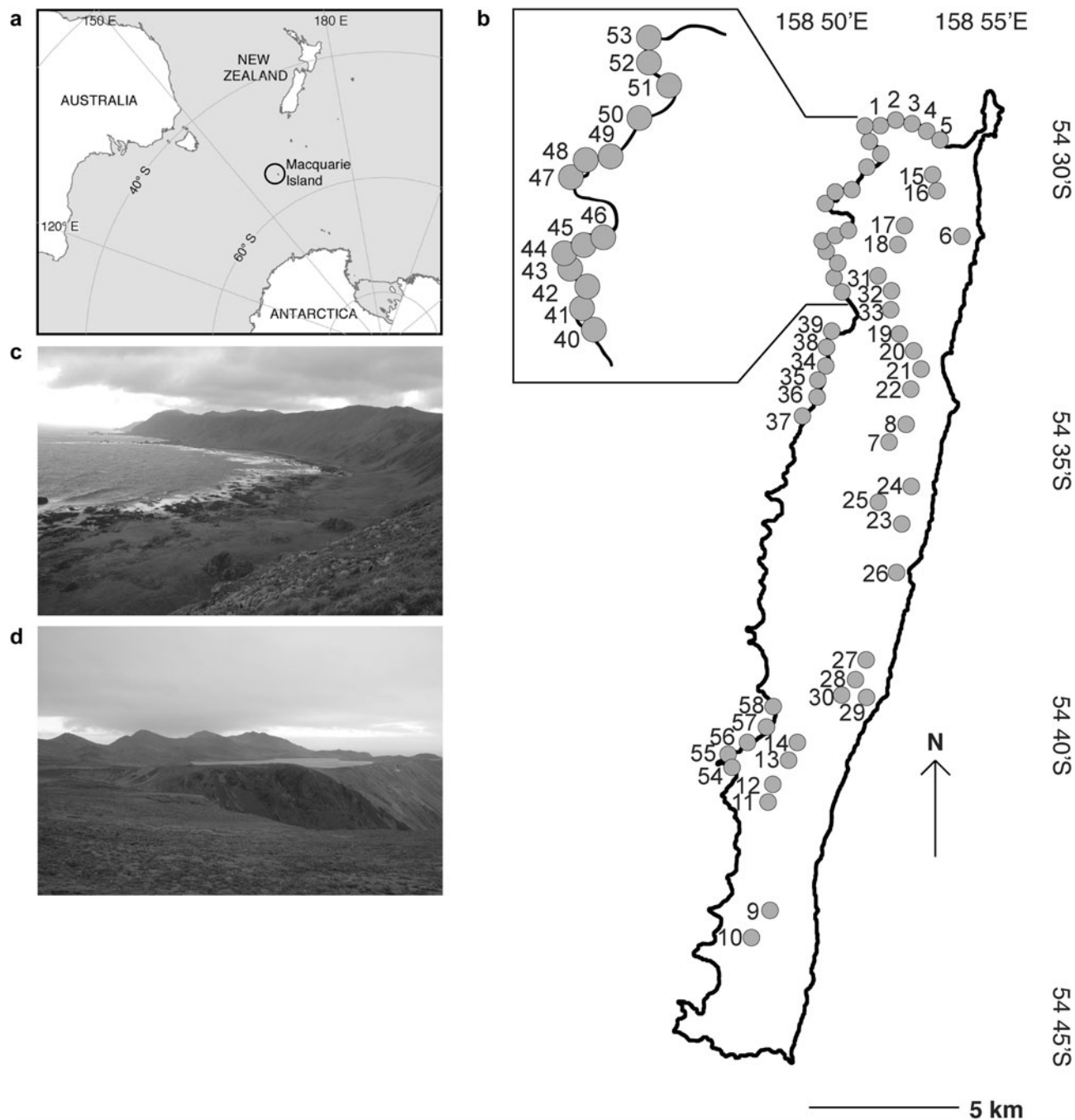


Fig. 1. **a.** Location of Macquarie Island, situated south of New Zealand and Australia, and north of Antarctica, **b.** Location of sampling sites, **c.** looking north from the south-west coast of Macquarie Island, illustrating the coastal terrace and plateau that characterizes the island, and **d.** looking south down the western side of the plateau. Please note: detailed topographic maps are available from <http://aadc-maps.aad.gov.au/aadc/mapcat/>

present new data from lakes and ponds on Macquarie Island and quantify the relationships between surface sediment diatom assemblages and present day environmental conditions. These relationships are then used to develop diatom-based transfer functions that will be applied to future studies of environmental change on the island.

Study area

Macquarie Island (54°30'S, 158°57'E) is located just north of the Polar Front, 1500 km south-east of Tasmania, 1200 km south-west of New Zealand and 1300 km from the Antarctic continent (Fig. 1). It is 34 km long, 5 km at its widest and has an area of 120 km².

The island experiences a cool, wet and windy oceanic climate with small annual and diurnal variations in temperature. The weather is dominated by westerly to north-westerly winds, with a mean annual wind speed of $\sim 30 \text{ km hr}^{-1}$, reaching gale forces of up to 170 km hr^{-1} . Mean annual precipitation is 920 mm and it rains > 300 days per year (BOM 2007, www.bom.gov.au/weather/tas/macquarie/). Due to almost constant cloud cover, light levels are generally low, with a mean annual average of 2.2 hours of sunshine per day (BOM 2007). Mean temperature ranges between 4.9°C in winter and 8.8°C in summer, with a daily variation of $\sim 3.5^\circ\text{C}$ (BOM 2007). Since continuous meteorological observations began in 1949, mean surface air temperature has increased by 0.3°C degrees (Tweedie & Bergstrom 2000).

Geologically, Macquarie Island is a rare example of uplifted oceanic crust that is part of the Macquarie Ridge Complex, which runs south from New Zealand (Davis 1988). Faulting, uplift, sea level changes, erosion and periglacial processes have been the major factors shaping Macquarie Island and its lakes. While the occurrence of past glacial activity has been debated, it is now believed that glaciation did not play a significant role in shaping the current landscape (Selkirk *et al.* 1990), although it is still debatable if permanent snow and ice accumulated in some areas during the Last Glacial Maximum (McGlone 2002).

The island consists of a steep sided (generally $20\text{--}40^\circ$) narrow plateau, rising directly from the coast or raised beach terraces and averages 250–300 m above sea level, with its highest point at 433 m. Macquarie Island is extensively vegetated with tussock grasslands, herbs and sedges, areas of peat, mosses, liverworts and lichens, and there are no trees (Fig. 1).

The island is also home to abundant wildlife, providing a vital refuge and important breeding ground in a region of sparse landmasses. In recognition of its geological and wildlife attributes, Macquarie Island has been designated as a Sanctuary (1933), a Tasmanian State Reserve (1978), World Heritage Area (1997) and United Nations Educational, Scientific and Cultural Organization Biosphere Reserve (the only Biosphere Reserve in the sub-Antarctic biogeographic region). The adjacent seas are designated as a Marine Park and form the second largest Marine Protected Area in the world. Nevertheless, human impacts on the island have been significant since its discovery in 1810. Early interest in the island was purely commercial, based on exploitation of penguin and seal resources (Davis 1988). During this period a number of alien vertebrate species were introduced including cats (*Felis catus*, 1820s), European rabbits (*Oryzolagus cuniculus*, 1870s), weka (*Gallirallus australis scotti*, 1870s), house mice (*Mus musculus*, 1890s) and ship rats (*Rattus rattus*, 1900) (Copson & Whinam 2001). In 1919 the commercial exploitation of penguins and seals was terminated (Brothers & Copson 1988), but introduced species continue to threaten its fragile habitats

and conservation status. Cats and weka have recently been eradicated (2000 and 1989 respectively, PWS 2007), but this has intensified damage by rabbits, particularly through vegetation disturbance and erosion.

The island is characterized by abundant shallow and deep ponds and lakes. Oceanic spray is the principal source of ions to the lakes, with geochemical weathering playing a minor role (Buckney & Tyler 1974). The ion chemistry of the lakes is influenced by the prevailing westerly winds and distance from the ocean, and seasonal variation in chemical composition is small (Buckney & Tyler 1974, Bryden 1988).

Methods

Data collection

Fifty-eight sites in 50 ponds and lakes on the coastal terrace and plateau were sampled during a six week period from February–April 2006. These sites include most ponds and lakes on Macquarie Island. The largest four lakes were sampled at two locations (at the western and eastern sides) to try and account for spatial variability in nutrients and conductivity. At each site, surface sediment samples (top 1 cm) were collected from *c.* 1 m water depth using a hand-operated gravity corer (Glew 1991). While there are a few deep lakes on Macquarie Island, most are shallow and only 1–2 m deep. Consequently, samples were collected from *c.* 1 m depth throughout the sampling campaign. At each site, surface water conductivity, dissolved oxygen, pH, temperature and turbidity were measured using a Hydrolab Datasonde 4a. Duplicate water samples were collected for soluble reactive phosphate (SRP), nitrate/nitrite and silicate analyses. Sample tubes were rinsed several times in lake water at each site prior to collection. Samples for nutrient analysis were frozen as soon as possible after collection and analysed using an Alpkem Autoanalyzer (Continuous Flow Solution Analyzer) at the Commonwealth Scientific and Industrial Research Organization Marine and Atmospheric Laboratories, Hobart, in May 2006. The autoanalyser uses the principles of colorimetric analysis in a continuous flow system with all manipulations of the samples automated. Each analytical channel was calibrated using standards of known concentration (Eriksen 1997).

Diatom analysis

Diatom samples were prepared using standard methods (Battarbee *et al.* 2001). At least 400 frustules were counted per sample, using phase contrast and oil immersion at 1000 \times magnification on a Zeiss Z20 light microscope. The relative abundance of all species (including unidentified forms) was recorded as a percentage of the total number of frustules counted (Battarbee *et al.* 2001). Taxonomy was principally based on sub-Antarctic (e.g. Van de Vijver *et al.* 2002b), Antarctic (i.e. Roberts & McMinn 1999) and Australian taxonomic literature (e.g. Vyverman *et al.* 1995, Hodgson

Table I. Environmental data recorded from Macquarie Island lakes.

Site no.	Type	Easting	Northing	Temp (°C)	pH	SpCond ($\mu\text{S cm}^{-1}$)	DO (mg L^{-1})	Turb (NTU)	Si ($\mu\text{g Si L}^{-1}$)	SRP ($\mu\text{g P L}^{-1}$)	N ($\mu\text{g N L}^{-1}$)
1	c	493055	3961062	10.83	5.74	522	10.23	146	31.11	294.2	262.8
2	c	493067	3961112	10.24	6.26	608	4.73	58	107.9	1951	3545
3	c	493259	3960999	9.28	7.07	559	10.17	32	177.1	380.6	1514
4	c	493516	3960937	9.30	7.40	555	10.40	391	414.8	260.6	4636
5	c	493873	3960714	9.70	7.40	406	10.66	7	364.6	24.30	7.45
6	i	495374	3956986	13.48	9.95	255	12.33	9	11.75	188.6	33.59
7	i	492867	3949922	8.44	6.47	164	11.11	6	2.15	0.00	0.98
8	i	492954	3950051	8.47	6.48	164	11.09	7	2.88	0.22	1.88
9	i	488472	3933817	7.39	7.46	224	11.35	9	65.90	1.99	5.80
10	i	488566	3933546	7.35	7.21	223	11.50	16	73.21	3.97	4.91
11	i	488549	3938611	6.93	6.35	215	11.52	10	5.65	1.40	7.65
12	i	488395	3938844	6.74	6.52	215	11.55	9	3.15	0.64	3.29
13	i	488468	3939570	7.45	7.10	265	11.27	9	8.91	2.27	0.72
14	i	488857	3940204	7.87	7.08	265	11.33	10	11.81	3.34	5.61
15	i	494279	3958913	4.86	6.59	183	12.07	12	24.14	4.81	30.08
16	i	494218	3958818	5.86	6.98	179	11.66	7	69.55	24.49	15.48
17	i	492881	3957684	5.44	6.83	179	12.06	9	192.8	0.67	0.15
18	i	492767	3957255	5.49	7.01	179	11.80	8	92.31	0.04	4.75
19	i	493436	3953044	7.03	8.72	280	12.16	276	820.5	93.13	14.72
20	i	493432	3952816	7.10	8.75	278	11.81	16	648.4	163.1	125.6
21	i	493247	3952211	6.64	6.84	164	11.69	31	7.03	0.73	9.51
22	i	493101	3951912	6.40	6.79	164	11.61	7	2.80	0.28	1.27
23	i	492954	3948077	7.50	7.33	146	11.81	7	14.08	4.56	2.25
24	i	493025	3948123	8.16	7.40	139	11.70	6	68.15	2.94	9.68
25	i	493029	3947950	7.79	6.85	116	11.54	9	9.19	5.35	8.57
26	i	493223	3946260	8.29	7.26	209	11.34	9	1525	61.84	21.11
27	i	491799	3942967	11.74	6.28	0	10.36	84	4.11	0.00	3.75
28	i	491696	3942835	10.82	6.44	0	10.85	18	2.74	1.35	2.41
29	i	491658	3941607	7.13	5.99	120	11.82	21	31.06	7.82	23.81
30	i	491625	3941880	7.34	7.50	156	11.86	7	4.66	3.39	8.06
31	i	492356	3955702	4.58	7.56	248	13.02	21	12.26	120.0	7.98
32	i	492314	3955758	4.50	7.39	247	13.01	20	5.90	18.06	15.58
33	i	492432	3955812	4.49	7.36	248	13.02	30	16.89	13.07	13.51
34	c	490852	3953408	6.83	7.57	909	11.78	8	201.9	155.4	68.74
35	c	490986	3952954	7.48	6.27	528	7.26	974	918.2	78.06	41.74

c = coastal lake, i = inland lake, Temp = Temperature, SpCond = specific conductivity, DO = dissolved oxygen, Si = silicate, SRP = soluble reactive phosphate, N = nitrate/nitrite.

et al. 1997). All taxa were photographed and are archived, including taxonomic data, with the first author. A final species list (of 129 species) was developed including only those species occurring with $\geq 1\%$ relative abundance.

Statistical analyses

Multivariate statistical analyses were used to identify major environmental gradients in the dataset, explore diatom-environment relationships and identify environmental variables that explained independent portions of the variance in the diatom data. Simple Weighted Averaging (WA) was used to determine species' ecological preferences (i.e. optima and tolerances) for these environmental variables and, together with Weighted Averaging Partial Least Squares (WAPLS), was used to develop transfer functions.

Prior to statistical analyses, each environmental variable was checked for skewness, and nutrients and turbidity were $\log(x + 1)$ transformed. Principal Component Analysis (PCA) was performed on the environmental data to determine the major environmental gradients. Detrended Correspondence Analysis (DCA) with detrending by segments and downweighting of rare species was performed on the species data (untransformed) to establish whether species distribution was unimodal or linear. As gradient lengths were greater than 2 standard deviation units, unimodal ordination techniques were used. Species data were $\log(x + 1)$ transformed for subsequent analyses.

A series of Canonical Correspondence Analyses (CCA) were performed with scaling focused on inter-species distances, biplot scaling and downweighting of rare species. Variance Inflation Factors (VIFs) were identified and any environmental variables with VIFs > 20 were removed. CCAs with forward selection and Monte Carlo

Table I. (Continued) Environmental data recorded from Macquarie Island lakes.

Site no.	Type	Easting	Northing	Temp (°C)	pH	SpCond ($\mu\text{S cm}^{-1}$)	DO (mg L^{-1})	Turb (NTU)	Si ($\mu\text{g Si L}^{-1}$)	SRP ($\mu\text{g P L}^{-1}$)	N ($\mu\text{g N L}^{-1}$)
36	c	490935	3952984	7.48	7.03	625	12.25	26	1596	239.8	3327
37	c	490859	3953144	8.57	6.73	1136	9.17	214	73.93	1029	181.1
38	c	490756	3953694	6.33	7.47	1482	11.91	9	169.8	526.9	635.8
39	c	490752	3953720	5.45	7.82	1528	12.24	95	43.33	496.8	206.6
40	c	491753	3955051	6.24	6.08	552	8.13	21	86.41	205.4	119.1
41	c	491599	3955369	5.79	7.19	495	11.12	7	1090	17.20	153.6
42	c	491182	3956333	5.61	7.23	525	11.95	8	499.5	150.6	33.64
43	c	491137	3956586	5.29	6.61	2	10.97	12	72.08	916.7	1186
44	c	490767	3957116	6.32	7.25	1502	12.14	20	72.27	1461	6461
45	c	490982	3957320	6.02	6.66	1244	10.75	9	504.7	9890	160.2
46	c	491353	3958630	8.03	7.32	693	11.48	21	2459	1250	188.2
47	c	491553	3958564	8.73	7.46	698	12.03	28	291.2	1558	5240
48	c	491557	3958671	8.89	8.12	603	14.43	30	2706	217.4	28.51
49	c	491956	3959447	13.13	8.13	732	13.59	1042	441.2	415.2	84.78
50	c	491979	3959468	10.01	7.85	1265	11.21	2724	1064	774.2	624.6
51	c	492008	3959442	8.16	7.28	1094	9.55	247	989.1	671.5	1947
52	c	492158	3959475	7.78	7.41	710	11.98	81	695.8	570.7	125.6
53	c	492711	3960308	9.41	9.13	769	18.08	10	1975	369.1	1839
54	c	487570	3939965	6.75	6.77	1176	11.51	6	99.53	807.8	1052
55	c	487545	3939906	6.93	5.50	1478	10.44	10	78.74	101.2	116.5
56	c	488208	3940384	7.61	6.61	646	10.97	36	96.16	2249	1936
57	c	488376	3940530	7.31	6.69	1571	8.71	83	120.0	2806	8578
58	c	489012	3941269	8.76	8.36	749	14.66	16	285.6	611.9	3523
All sites	mean			7.65	7.15	527.4	11.43	121.6	370.1	538.1	831.1
	median			7.42	7.15	343.0	11.55	16.00	82.58	110.6	33.62
	min			4.49	5.50	0.00	4.73	6.00	2.15	0.00	0.15
	max			13.48	9.95	1571	18.08	2724	2706	9890	8578
Coastal sites	mean			7.94	7.15	845.4	11.15	212.4	590.9	1016	1594
	median			7.70	7.24	704.0	11.17	27.00	288.4	511.8	443.7
	min			5.29	5.50	2.00	4.73	6.00	31.11	17.20	7.45
	max			13.13	9.13	1571	18.08	2724	2706	9890	8578
Inland sites	mean			7.33	7.16	186.6	11.72	24.39	133.5	26.00	13.67
	median			7.24	7.05	181.0	11.68	9.00	12.04	3.37	7.81
	min			4.49	5.99	0.00	10.36	6.00	2.15	0.00	0.15
	max			13.48	9.95	280.0	13.02	276.0	1526	188.6	125.6

c = coastal lake, i = inland lake, Temp = Temperature, SpCond = specific conductivity, DO = dissolved oxygen, Si = silicate, SRP = soluble reactive phosphate, N = nitrate/nitrite.

permutation tests ($p < 0.05$) were used to identify which environmental variables explained independent portions of the variance in the diatom data. Variance partitioning was used to determine the amount of variation explained by each variable and the interaction between them. All ordinations were performed using the software program R (R Development Core Team 2006).

Species ecological preferences (i.e. optima and tolerances) were determined using simple WA. Transfer functions were developed using simple WA with inverse and classical deshrinking, and with/without tolerance downweighting, and WAPLS to determine which model led to the best performing transfer functions. Performance was assessed using leave-one-out cross validation (i.e. jackknifing). The transfer function for each environmental variable with the best correlation (r^2), best predicted correlation (r_{jack}^2), lowest root mean squared error (RMSE) and lowest root mean squared error of prediction (RMSE_p) was identified

and used. Species ecological preferences and transfer functions were determined using the software program C2 version 1.4 (Juggins 2003).

Results

Limnology

Table I outlines the environmental data measured at each lake. The lakes were all freshwater and conductivity

Table II. Principal Component Analysis results of the environmental data.

Axes	1	2	3	4	Total variance
Eigenvalues	0.312	0.169	0.123	0.058	1.000
Cumulative % variance of environmental data	31.2	48.1	60.4	66.2	
Sum of all eigenvalues					1.000

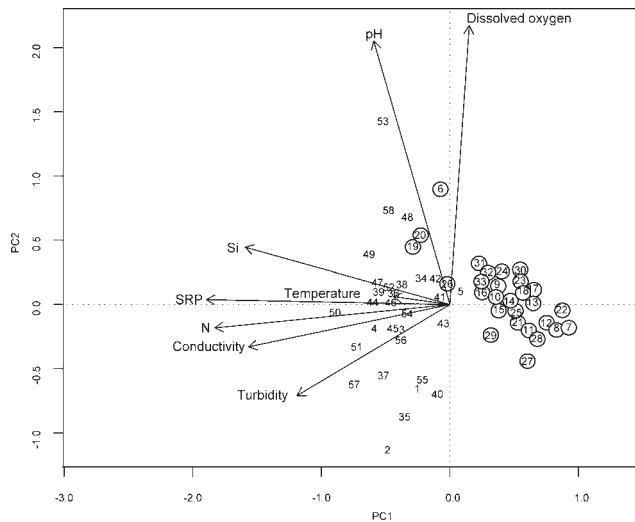


Fig. 2. Principal Components Analysis of the environmental variables in the Macquarie Island dataset. Circled sites are inland sites. N = nitrate/nitrite, Si = silicate, SRP = soluble reactive phosphate.

varied from 0–1571 $\mu\text{S cm}^{-1}$ (mean 343 $\mu\text{S cm}^{-1}$). The nutrient status of sites varied from oligotrophic to highly eutrophic (i.e. SRP ranged from 0–9890 $\mu\text{g P L}^{-1}$, mean 538.1 $\mu\text{g P L}^{-1}$; nitrate/nitrite from 0.15–8578 $\mu\text{g N L}^{-1}$, mean 831.1 $\mu\text{g N L}^{-1}$; and silicate from 2.15–2706 μg

Si L^{-1} , mean 370.1 $\mu\text{g Si L}^{-1}$). Sites ranged from acidic to alkaline (i.e. pH 5.5–9.95, mean 7.15). Dissolved oxygen ranged from 4.73–18.08 mg L^{-1} (mean 11.43 mg L^{-1}), temperature ranged from 4.49–13.48°C (mean 7.65°C) and turbidity ranged from 6–2724 NTU (mean 121.6 NTU).

PCA of the environmental data indicated that nearly 50% of the variation in the environmental data was captured by the first two principal components (Table II). Variation along the first axis was explained by conductivity, nutrients and turbidity, with high nutrient and conductivity sites on the left hand side, and low nutrient and conductivity sites on the right hand side of the biplot. Variation along the second axis was explained by pH and dissolved oxygen (Fig. 2). The distribution of coastal and inland sites in Fig. 2 clearly illustrates the oceanic source and importance of conductivity and nutrients to the lakes.

Exploring diatom-environment relationships

In total, 208 diatom species were identified from 34 genera. Only those species occurring with a maximum relative abundance $\geq 1\%$ were included in the statistical analyses (129 taxa). These taxa represent 96.5–100% (mean 99.1%) of the total diatom count for each sample site. These taxa are listed in the Supplementary material (including their number

Table III. Abundant and common species in the dataset. Species in bold are both.

Species	Code	N	Max	Mean	Mean (adj)	Med	Med (adj)
Species occurring with $\geq 50\%$ maximum relative abundance							
<i>Aulacoseira distans</i> (Ehrenberg) Simonsen	CEN17	15	75.2	3.21	12.64	0	4.36
<i>Cocconeis pediculus</i> Ehrenberg	COC8	12	50.0	2.32	11.43	0	2.73
<i>Cyclotella meneghiniana</i> Kützing	CEN15	5	52.9	0.96	8.07	0	0.44
<i>Eunotia paludosa</i> Grunow	UNK57b	6	56.3	1.33	13.07	0	3.09
<i>Fragilaria capucina</i> Desmazieres	FRA8	33	97.9	25.07	44.82	1.8	39.46
<i>Navicula</i> sp. 1	NAV63	13	52.7	1.75	7.93	0	3
<i>Planothidium delicatulum</i> (Kützing)	ACH26	17	81.3	5.42	18.83	0	6.70
Round & Bukhtiyarova							
<i>Planothidium quadripunctatum</i> (Oppenheim) Sabbe	PLA _{hau}	24	70.4	6.12	15.06	0	3.28
<i>Psammothidium abundans</i> (Manguin)	ACH _{sub2}	24	95.1	8.9	21.88	0	12.7
Bukhtiyarova & Round							
<i>Stauroneis</i> sp. 1	ACH _{sub}	31	62.5	3.72	7.08	0.17	2.94
<i>Stauroneis venter</i> (Ehrenberg) Cleve & Moller	CEN16	5	50	1.12	13.27	0	4.59
Unknown sp. 1	NAV32c	15	74.3	3.51	13.8	0	1.71
Species occurring at ≥ 15 sites							
<i>Diatomella</i> cf. <i>balfouriana</i> Greville	UNK37b	15	11.74	0.71	2.78	0	1.67
<i>Encyonema</i> sp. 1	AMP18a	15	6.98	0.51	2.33	0	1.69
<i>Gomphonema angustatum</i> C.A. Agardh	GOMang	15	6.1	0.45	2.05	0	1.47
<i>Opephora marina</i> (Gregory) Petit	OPE3	24	17.9	1.59	3.92	0	2.84
<i>Pinnularia subantarctica</i> var. <i>elongata</i> (Manguin) Van de Vijver & Le Cohu	NAV55	15	2.94	0.26	1.16	0	0.86
<i>Planothidium lanceolatum</i> (Brebisson) Lange-Bertalot	PLA _{fre3}	52	27.9	1.56	3.8	0	0.99
<i>Planothidium renei</i> (Lange-Bertalot & Schmidt) Van de Vijver	ACH25	17	28.8	0.87	3.01	0	0.99

Code = species code used in ordination plots, N = number of occurrences, Max = maximum relative abundance, Mean (adj) = non-zero mean, Med = median, Med (adj) = non-zero median. All species abundances are % relative abundance.

Table VIII. Variance partitioning results. Note: SRP = soluble reactive phosphate.

Environmental variable	Covariable	\sum Canonical eigenvalues	% Variance explained	% Interaction	P Value
Conductivity	none	0.423	8.3	0	<0.005
	SRP	0.147	2.9	5.4	0.01
	silicate	0.271	5.3	3.0	0.005
	temperature	0.422	8.3	0	<0.005
	pH	0.421	8.2	0.1	<0.005
	Total interaction				8.5
SRP	none	0.529	10.3	0	<0.005
	conductivity	0.251	4.9	5.4	<0.005
	Silicate	0.293	5.7	4.6	0.005
	temperature	0.522	10.2	0.1	<0.005
	pH	0.519	10.2	0.1	<0.005
	Total interaction		10.2		
Silicate	none	0.380	7.4	0	<0.005
	conductivity	0.227	4.4	3.0	<0.005
	SRP	0.143	2.8	4.6	0.005
	temperature	0.374	7.3	0.1	<0.005
	pH	0.344	6.7	0.7	<0.005
	Total interaction		8.5		
Temperature	none	0.136	2.7	0	0.043
	conductivity	0.135	2.6	0.1	0.023
	SRP	0.128	2.5	0.2	0.002
	silicate	0.130	2.5	0.2	0.033
	pH	0.140	2.7	0	0.005
	Total interaction				0.5
pH	none	0.206	4.0	0	<0.005
	conductivity	0.205	4.0	0	<0.005
	SRP	0.196	3.8	0.2	<0.005
	silicate	0.171	3.3	0.7	<0.005
	temperature	0.210	4.1	0.1	<0.005
	Total interaction				1.0

silicate and temperature as the environmental variables that explained independent portions of the variance in diatom species distribution.

CCA of these variables indicated that they explain 21.7% of the variance in the species data and axes 1–4 explain 10.9%, 4.4%, 2.7% and 2.0% respectively (Table VII).

Variance partitioning indicated that there was a lot of interaction between conductivity, SRP and silicate, and that most of the interaction was due to silicate (Table VIII).

Species optima and tolerances

Simple WA was used to determine species optima and tolerances for conductivity, pH, silicate, SRP and temperature. Species optima and tolerances are provided in the Supplementary material (www.journals.cambridge.org/jin_ANS). There were clear transitions in the abundance and occurrence of the most abundant diatoms along the major environmental gradients (Fig. 4):

Aulacoseira distans, *Eunotia paludosa*, *Navicula* sp. 1 and Unknown sp. 1 were most abundant at low conductivity sites, while *Planothidium delicatulum* and *Planothidium quadripunctatum* were most abundant at higher conductivity sites.

Aulacoseira distans was the most abundant at acidic sites, while *Cocconeis pediculus* was most abundant at alkaline sites.

Eunotia paludosa, *Stauroneis* sp. 1 and Unknown sp. 1 were most abundant at low silicate sites, while *Fragilaria capucina* and *Planothidium delicatulum* were most abundant at high silicate concentrations.

Eunotia paludosa, *Navicula* sp. 1, *Stauroneis* sp. 1 and Unknown sp. 1 were most abundant at low SRP sites, while *Cyclotella meneghiniana* and *Planothidium delicatulum* were most abundant at high SRP sites.

Staurosira venter and *Psammothidium abundans* were most abundant at cooler sites, while *Cocconeis pediculus* and Unknown sp. 1 were most abundant at warmer sites (Fig. 4).

Table IX. Transfer function results. Note: SRP, silicate and temperature were $\log_{(x+1)}$ transformed. SRP = soluble reactive phosphate.

Variable	r^2	r_p^2	RMSE	RMSE _p	Model
Conductivity	0.82	0.66	0.11	0.14	WA _{ela}
SRP	0.90	0.80	0.40	0.50	WA _{ela}
Silicate	0.91	0.61	0.25	0.53	WAPLS-2
pH	0.70	0.29	0.44	0.68	WA _{inv}
Temperature	0.56	0.23	0.06	0.08	WA _{inv}

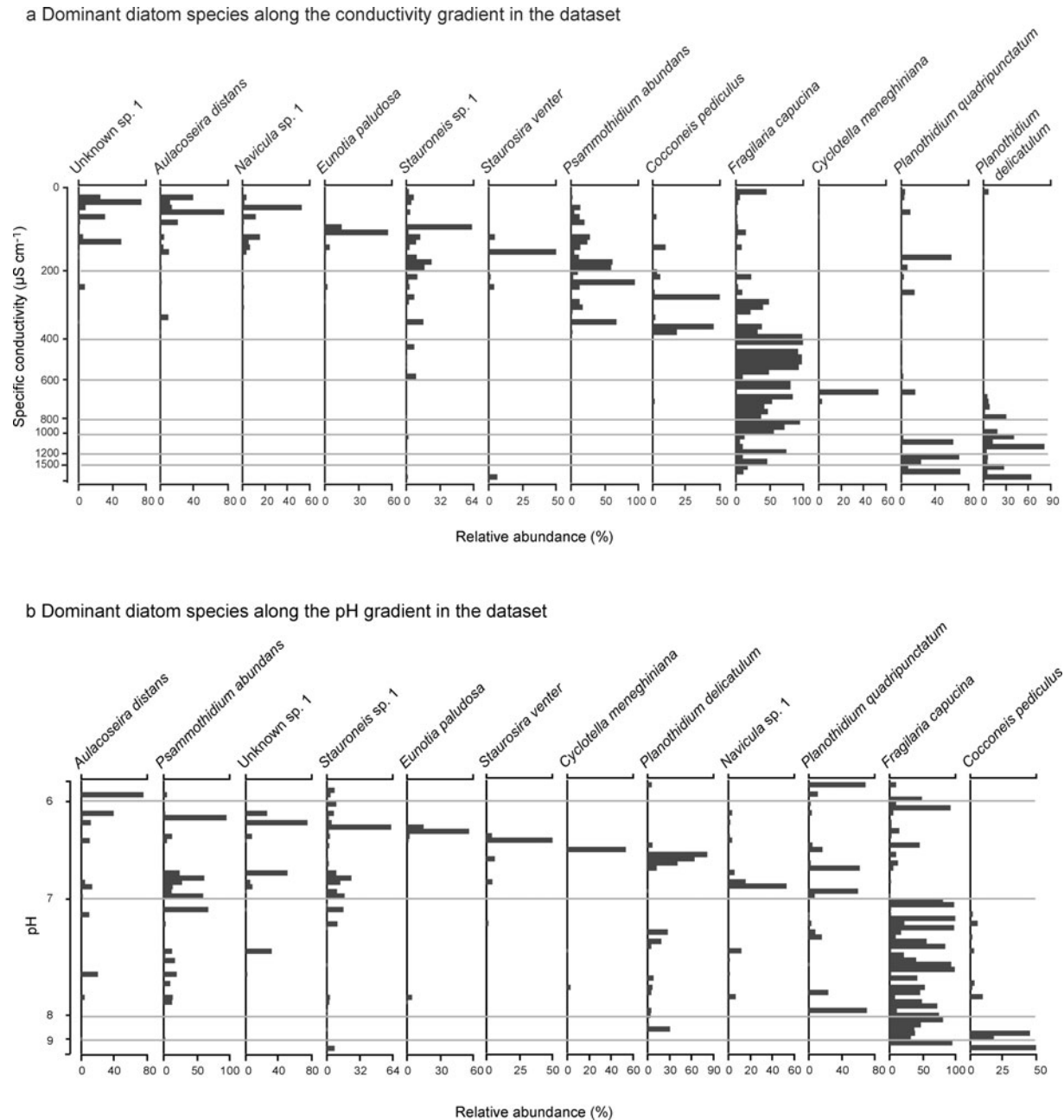


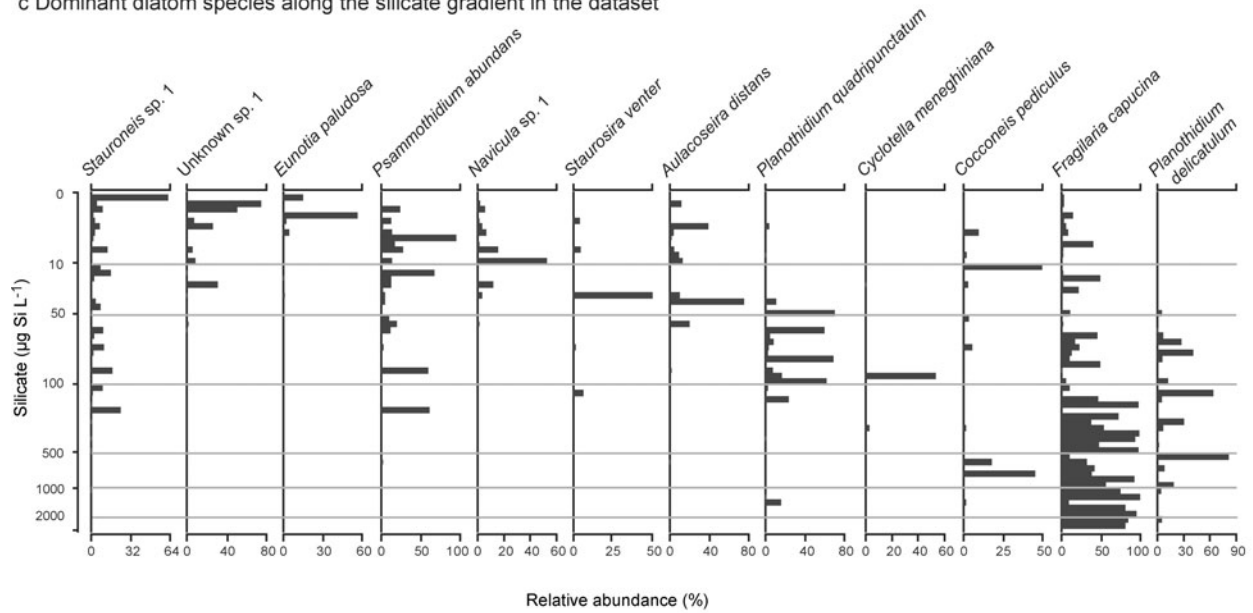
Fig. 4. Abundant diatom species distribution along the **a.** conductivity, **b.** pH, **c.** silicate, **d.** soluble reactive phosphate and **e.** temperature gradients in the dataset, illustrating the strong environmental gradients in the dataset. Grey lines represent different zones within the environmental gradients. Species abundances are represented as % relative abundance. (Continued)

Diatom-based transfer functions

As pH, SRP, conductivity, silicate and temperature explained independent portions of the variance in the diatom data, transfer functions for these were developed. Both simple WA and WAPLS were used to determine which model led to the best performing transfer function for each environmental variable (Table IX). Statistically robust transfer functions for SRP (WA_{cla} $r^2 = 0.90$, $r^2p = 0.80$,

$RMSEp = 0.50 \log \mu g P L^{-1}$), conductivity (WA_{cla} , $r^2 = 0.82$, $r^2p = 0.66$, $RMSEp = 0.14$ ppt) and silicate ($WAPLS-2$, $r^2 = 0.91$, $r^2p = 0.61$, $RMSEp = 0.53 \log \mu g Si L^{-1}$) were developed. The pH and temperature transfer functions had relatively poor predictive performances (WA_{inv} , $r^2 = 0.70$, $r^2p = 0.29$, $RMSEp = 0.68$, and $WAPLS-2$, $r^2 = 0.56$, $r^2p = 0.23$, $RMSEp = 0.08 \log ^\circ C$ respectively).

c Dominant diatom species along the silicate gradient in the dataset



d Dominant diatom species along the soluble phosphate gradient in the dataset

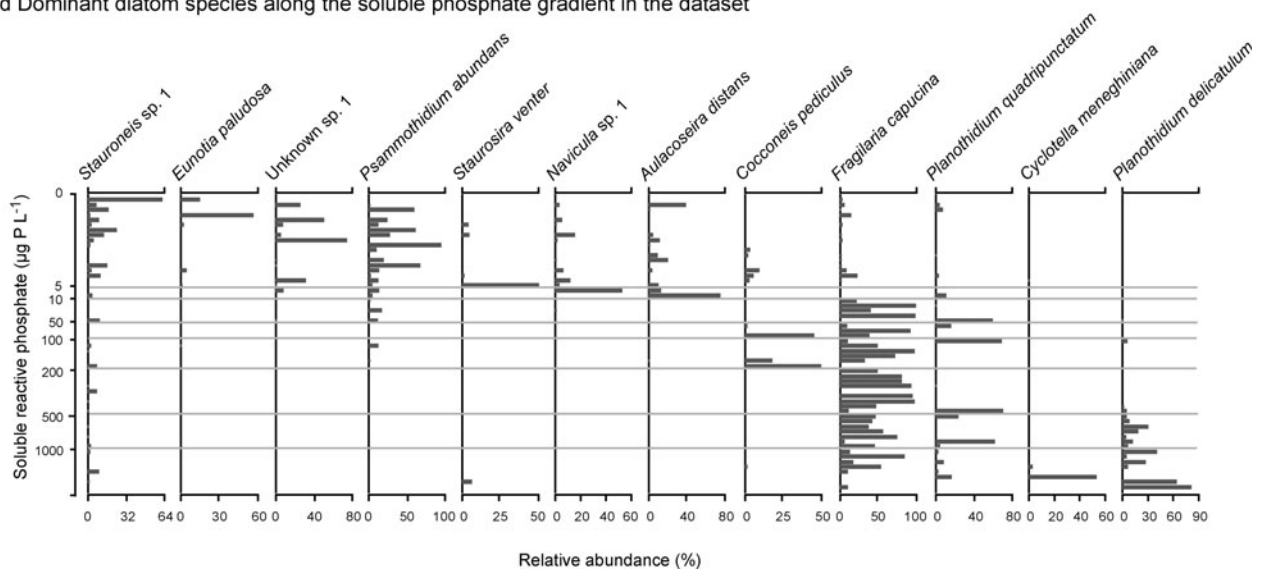


Fig. 4. Abundant diatom species distribution along the **a.** conductivity, **b.** pH, **c.** silicate, **d.** soluble reactive phosphate and **e.** temperature gradients in the dataset, illustrating the strong environmental gradients in the dataset. Grey lines represent different zones within the environmental gradients. Species abundances are represented as % relative abundance. (Continued)

Discussion

The aims of this study were to investigate diatom assemblages in surface sediment samples from lakes on Macquarie Island, relate them to present-day environmental conditions and develop transfer functions for selected environmental variables. This has revealed new insights into the major limnological patterns on the island and the ecological preferences of diatoms on Macquarie Island across a range of environmental variables.

Limnology

The lakes analysed in this study are all freshwater. There is a wide range of nutrient concentrations ranging from mostly oligotrophic lakes on the plateau to eutrophic lakes on the coastal terrace. There are similar wide ranges in dissolved oxygen, pH, temperature and turbidity. Eutrophic lakes and ponds commonly occur along the coastlines of sub-Antarctic and maritime Antarctic islands (e.g. Jones *et al.* 1993, Van de Vijver & Beyens 1999). These lakes and

e Dominant diatom species along the temperature gradient in the dataset

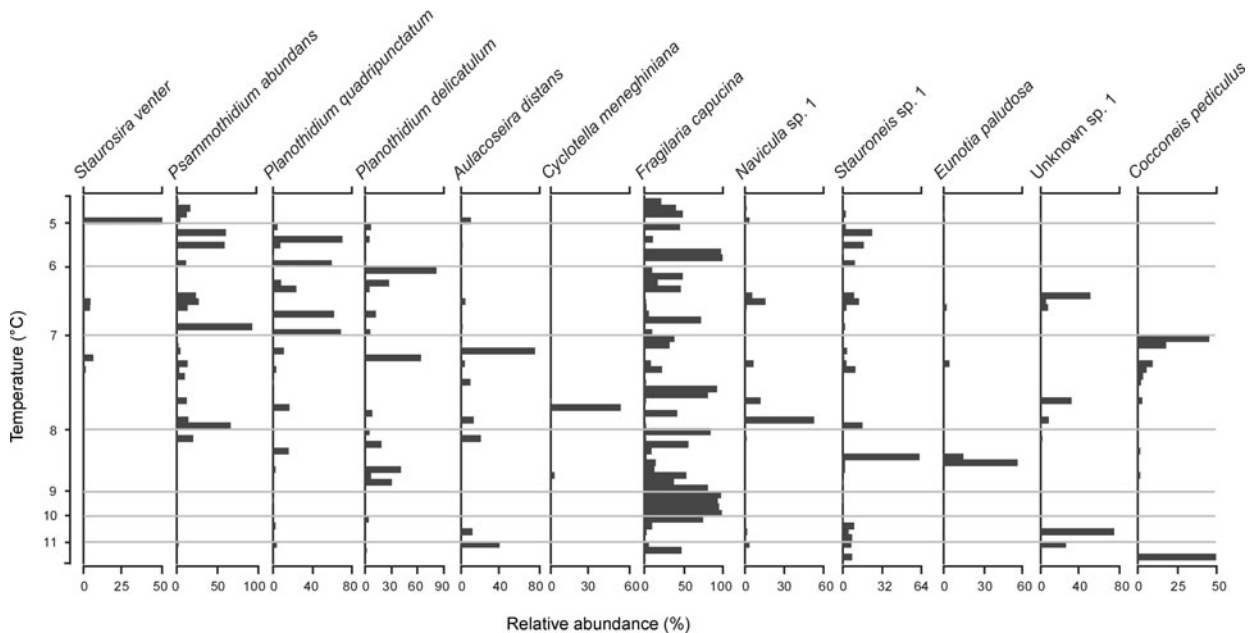


Fig. 4. Abundant diatom species distribution along the **a.** conductivity, **b.** pH, **c.** silicate, **d.** soluble reactive phosphate and **e.** temperature gradients in the dataset, illustrating the strong environmental gradients in the dataset. Grey lines represent different zones within the environmental gradients. Species abundances are represented as % relative abundance.

ponds can be highly eutrophic, reaching greater than $1000 \mu\text{g P L}^{-1}$ and $1000 \mu\text{g N L}^{-1}$ (e.g. Ile de la Possession, Van de Vijver & Beyens 1999, and this study, Table I). Seals, penguins and seabirds are considered to contribute significant amounts of nutrients and the highest SRP and nitrate/nitrite values recorded in this study were near seal or penguin colonies.

PCA of the environmental data shows that in addition to the influence of conductivity detected by Buckney & Tyler (1974), the lakes are also organized along gradients of nutrients and turbidity, and to a lesser extent, pH and dissolved oxygen (Fig. 2). CCA with geographical and physical factors plotted as passive variables demonstrates the influence of distance from the west coast and the importance of the prevailing weather characteristics on conductivity, nutrients, pH and temperature (Fig. 5). With increasing distance from the west coast, these environmental variables decrease. All of the passive variables are highly correlated with each other, which is not surprising due to the westerly weather patterns that dominate the climate of Macquarie Island and the absence of lakes on the eastern coastal terrace.

Ecological preferences of diatom communities on Macquarie Island

The frequency distribution of selected taxa in the dataset provides examples of how individual species abundances

respond to selected environmental variables (Fig. 6). This, together with clear transitions in species abundance and occurrence (Fig. 4), highlights the large limnological gradients in the lakes on Macquarie Island and allows potential indicator species to be identified.

Diatom taxa characteristic of higher nutrient and conductivity concentrations include *Planothidium delicatulum* and *Cyclotella meneghiniana* (Figs 4, 5 & 7). These are both cosmopolitan species and *Planothidium delicatulum* has previously been found on the Antarctic continent, and Macquarie, Kerguelen, South Orkney and South Shetland islands (Van de Vijver *et al.* 2002b). *Cyclotella meneghiniana* has previously been found on Ile de la Possession by Van de Vijver & Beyens (1999) when nutrient enrichment was sufficient and is common in eutrophic systems elsewhere (Weckström & Juggins 2006). This appears to be the case in this study as well, as *Cyclotella meneghiniana* was most abundant at a coastal site with high SRP and nitrate/nitrite (i.e. $\text{SRP} > 2000 \mu\text{g P L}^{-1}$, nitrate/nitrite $> 1900 \mu\text{g N L}^{-1}$, Table I). Planktonic species are generally absent from Antarctic diatom assemblages (Jones *et al.* 1993), apart from some brackish to marine lakes in the Vestfold Hills, East Antarctica, where the diatom flora includes planktonic marine and sea ice diatoms (Verleyen *et al.* 2003). The general absence of planktonic diatom taxa in sub-Antarctic lakes is in contrast to lakes in temperate regions in the Southern Hemisphere,

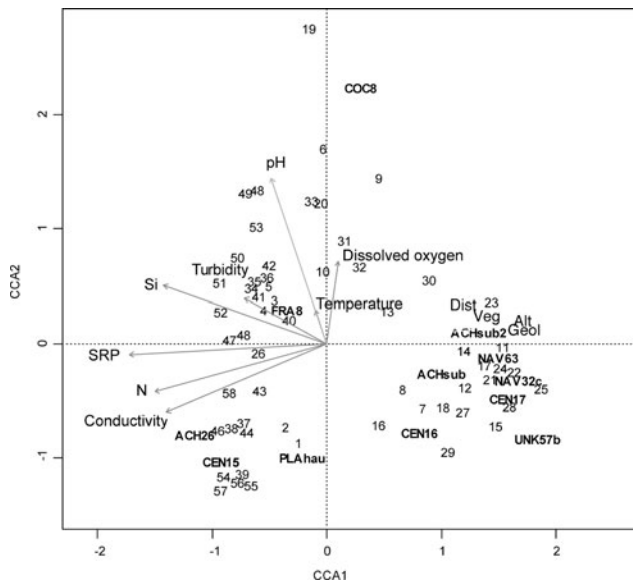


Fig. 5. Canonical Correspondence Analysis with passive geographical variables added, illustrating the influence of distance from the west coast and the importance of the prevailing weather characteristics on nutrients, pH, conductivity and temperature in Macquarie Island lakes and ponds. Alt = altitude, Dist = distance from west coast, Geol = geology, N = nitrate/nitrite, Si = silicate, SRP = soluble reactive phosphate, Veg = surrounding vegetation cover type.

where planktonic diatoms often dominate (Van de Vijver & Beyens 1999).

Aulacoseira distans, like *Cyclotella meneghiniana*, is a tychoplanktonic species that featured widely in this dataset, but only in inland lakes. It has also been identified on King George Island, South Georgia, Iles Kerguelen and Crozet, and Ile de la Possession (Van de Vijver *et al.* 2002b). This is a heavily silicified species that needs water turbulence and/or high water levels to maintain suspension in the water column. A high or increasing abundance of *Aulacoseira distans* in diatom assemblages may indicate increased mixing intensity or lake level (Köster *et al.* 2004).

Psammothidium abundans is a benthic diatom associated with prostrate microbial mats (Verleyen *et al.* 2003). Diatom communities characteristic of low nutrient and conductivity conditions on Macquarie Island include *Eunotia paludosa*, which is characteristic of freshwaters elsewhere and is acidophilous, and *Navicula* sp. 1 and Unknown sp. 1, which have both been found elsewhere in the sub-Antarctic, but have yet to be fully identified and described (Bart Van de Vijver personal communication 2007).

Evaluation of transfer functions

Based on the dataset, statistically robust transfer functions for conductivity, SRP and silicate were developed (Table IX).

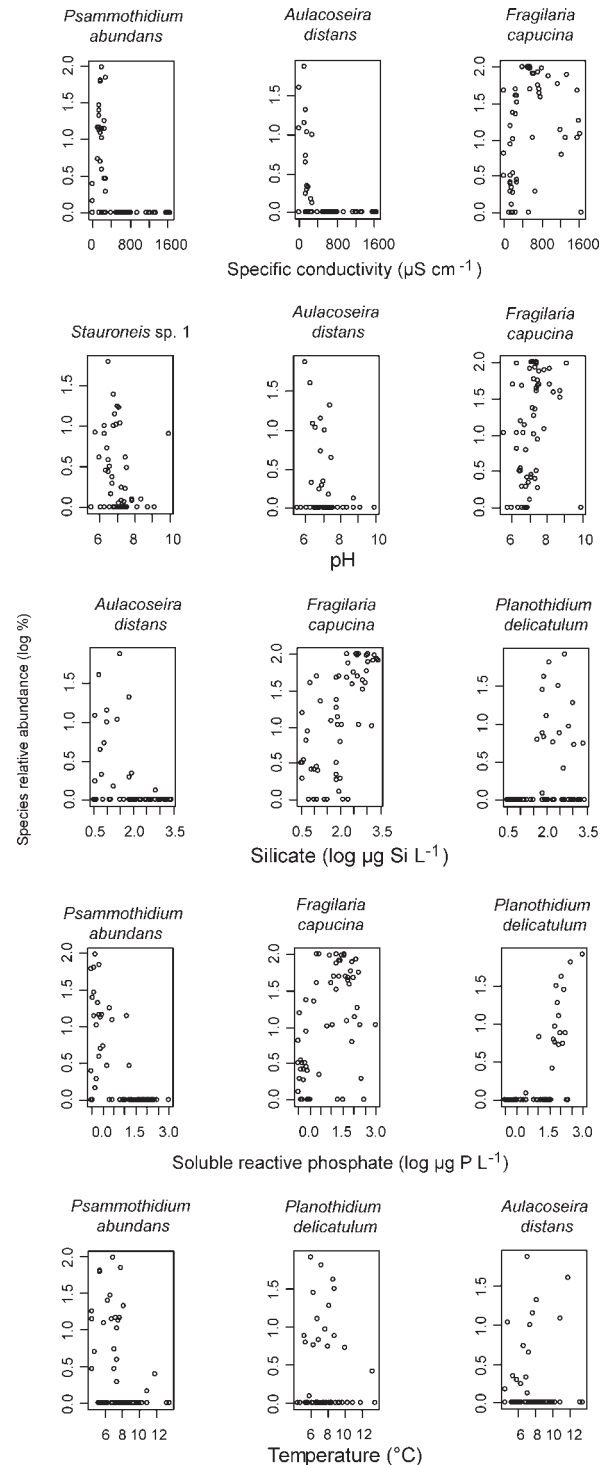


Fig. 6. Frequency distribution of selected abundant diatom taxa in the Macquarie Island reference dataset along the conductivity, pH, silicate, soluble reactive phosphate and temperature gradients.

The best performing transfer function models used simple WA for conductivity and SRP, and WAPLS-2 components for silicate. The WAPLS model for silicate may have

performed better than simple WA due to a reduction in the 'edge effect' (i.e. the underestimation of optima at the high end and overestimation at the low end of the gradient, Birks 1998) and the presence of more than one important environmental variable in the dataset (Verleyen *et al.* 2003). The distribution of species occurrence in the dataset illustrates the clear transitions in the dataset between species and changes in the concentration of each variable (Fig. 4).

The transfer functions for pH and temperature had relatively poor predictive performance (Table IX). This is surprising as there is a long, relatively well-populated pH gradient in the dataset. However, the diatoms seem to be pre-adapted to wide pH gradients and do not show the limited tolerances that are necessary to develop strong transfer functions. This is illustrated in the plot of diatom species occurrences along the pH gradient in the dataset: while some species only occur at low and high pH, most occur throughout the pH gradient (Fig. 4). Similarly, the diatom-temperature transfer function performed poorly, probably due to the uneven distribution of lakes along the temperature gradient, with generally higher temperatures recorded in lakes located on the coastal terrace and lower temperatures recorded in lakes on the plateau. The influence of temperature is confounded by the influence of distance from the west coast and the importance of this in controlling the supply of nutrients and ions (conductivity) to the lakes. As indicated by a plot of the occurrence of dominant diatom species along the temperature gradient, the diatoms do not show quite as clear transitions as they do with other environmental variables, although some species appear to be more abundant at either end of the temperature gradient (Fig. 4). However, temperature can still be an important driving factor and diatom-temperature transfer functions have previously been developed for high latitude locations (e.g. Pienitz *et al.* 1995, Wolfe 2003, Gremmen *et al.* 2007).

Further sampling is planned to increase the number of samples in the dataset over a more evenly distributed altitudinal gradient to try and improve the performance of the diatom-temperature transfer function. Analyses of microfossil invertebrates are also underway to investigate the potential for developing an invertebrate-temperature transfer function.

Potential applications of this dataset to climate change studies

Understanding past rates and magnitudes of climate changes provides a fundamental basis for understanding recently observed rates of global warming and assessing the implications of this for the future.

The prevailing westerly winds are a dominant feature of Macquarie Island climate, and their latitudinal position shifts over time (Lamy *et al.* 2001). Toggweiler *et al.* (2006) demonstrated that warm climates, like the present, tend to have poleward-shifted westerlies, while cold climates like during the Last Glacial Maximum (LGM) have

equatorward-shifted westerlies. Recent observations tend to support this as recent increases in global temperatures have coincided with poleward shifted westerlies (Shindell & Schmidt 2004) and Marshall & Connolly (2006) have shown that in the northern Antarctic Peninsula region, the current rising temperature trend is probably due to increased westerly wind strength, driven by increased greenhouse gas concentrations. Consequently, it is possible that poleward displacement of the southern westerlies could be involved in past periods of higher temperature and precipitation on both the sub-Antarctic islands and Antarctic Peninsula, while during periods where the westerlies move equatorward, these regions can be expected to adopt a more cold, dry Antarctic-like climate regime.

Recent examinations of global ocean temperature changes have shown warming in the upper 1000 m since the 1950s (Gillie 2002). Warming in the Southern Ocean has been concentrated within the Antarctic Circumpolar Current (ACC) and has caused an average 8% increase in rainfall over the Southern Ocean and South Pacific since the late 1970s (Wong *et al.* 1999).

These changes are likely to occur at greater magnitude on longer glacial-interglacial timescales and involve movement of the fronts within the ACC, including the Polar Frontal Zone (PFZ). Marine core records from the Southern Ocean show that during the LGM the PFZ moved at least as far north as 52°S, accompanied by a northward extension of sea ice extent and a major reduction in biological production (Crosta *et al.* 1998). As Macquarie Island is located at 54°S, it is ideally placed to respond to changes in the position of the westerlies, provide information on migration of the PFZ poleward and equatorward, and respond to warming of the Southern Ocean. These factors control the climate of Macquarie Island by influencing wind, precipitation and temperature regimes, and this study shows that records of these changes are likely to be preserved in lake sediments on the island. The nutrient and conductivity transfer functions developed in this study may be applied to sub-fossil diatom assemblages in lake sediments on Macquarie Island to reconstruct nutrient and conductivity trends. Increased wind and rainfall can be expected to result in an increase in nutrients (from surface runoff) and conductivity (from sea spray) of the lakes (see the close association between nutrients, conductivity and turbidity, Figs 2 & 4). These transfer functions can be applied over long time periods (i.e. glacial-interglacial timescales) to investigate nutrient and conductivity changes as a consequence of poleward and equatorward shifts in the westerlies and PFZ. Over shorter time periods, high resolution studies may allow sub-decadal patterns in wind and rainfall to be reconstructed. Applying quantitative reconstruction techniques to sediments from Macquarie Island lakes therefore has the potential to provide valuable insights into long-term ecological change, contributing to understanding changes in the Southern Ocean and climate change.

Potential applications of this dataset to human impact studies

While Macquarie Island lakes respond to changes in climate, they are also vulnerable to direct human impacts. The greatest current threat is the rapidly expanding rabbit population. Rabbits were introduced in 1878 and with the recent removal of feral cats by 2001, the rabbit population has experienced a rapid increase in numbers. The major impact of this has been an increase in grazing pressure and burrowing, resulting in large areas of vegetation being destroyed, causing slope instability, erosion and loss of habitat (PWS 2007).

Diatom-inferred nutrient and conductivity trends will enable changes in lake water chemistry to be tracked and diatom analyses will record any changes in biodiversity as a result of these human impacts. With additional geochemical analyses, it should be possible to track changing feral animal populations. Similar work has been undertaken on Signy Island where seal hairs were used to track an expanding seal population following the decline and cessation of the whaling industry (Hodgson & Johnston 1997) and on King George Island and Hope Bay where faecally derived elements have been used to track changes in penguin populations (Zale 1994, Sun *et al.* 2000). In the northern high latitudes, changes in nutrient inputs to lakes have been used to track the impact of changing seabird populations (Wagner & Melles 2001). A similar approach could be used to reconstruct past animal populations on Macquarie Island.

Conclusions

Climate changes, in particular increasing wind, temperature and rainfall, and problems associated with feral animals, means that establishing baseline conditions before human arrival on Macquarie Island is a critical step in developing appropriate management strategies and targets to maintain the island's conservation and World Heritage status. This study has demonstrated that diatom-based palaeolimnological methods provide powerful tools to reconstruct past environments on Macquarie Island. Currently, the management and conservation strategies of Macquarie Island are focused on the present and future. What palaeolimnology can offer is an accurate reconstruction of past natural variability, a definition of baseline environmental conditions on the island prior to human contact and provides a way to track the nature and direction of subsequent environmental change. The success of future management efforts (such as the removal of non native species) can then be judged against these natural baselines.

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References

- BATTARBEE, R.W., JONES, V.J., FLOWER, R.J., CAMERON, N.G., BENNION, H., CARVALHO, L. & JUGGINS, S. 2001. Diatoms. In SMOLM, J.P., BIRKS, H.J.B. & LAST, W.M., eds. *Tracking environmental change using lake sediments: terrestrial, algal and siliceous indicators*. Dordrecht: Kluwer, 155–202.
- BIRKS, H.J.B. 1998. Numerical tools in palaeolimnology - progress, potentialities, and problems. *Journal of Paleolimnology*, **20**, 307–322.
- BROTHERS, N.P. & COPSON, G.R. 1988. Macquarie Island flora and fauna management - interpreting progress and predictions for the future. *Papers and Proceedings of the Royal Society of Tasmania*, **122**, 129–136.
- BRYDEN, M.M. 1988. Southern elephant seals as subjects for physiological research. *Papers and Proceedings of the Royal Society of Tasmania*, **122**, 153–158.
- BUCKNEY, R.T. & TYLER, P.A. 1974. Reconnaissance limnology of sub-Antarctic islands II: additional features of the chemistry of Macquarie Island lakes and tarns. *Australian Journal of Marine and Freshwater*, **25**, 89–95.
- COPSON, G. & WHINHAM, J. 2001. Review of ecological restoration programmes on subantarctic Macquarie Island: pest management progress and future directions. *Ecological Management and Restoration*, **2**, 129–138.
- CROSTA, X., PICHON, J.J. & BURCKLE, L.H. 1998. Reappraisal of Antarctic seasonal sea ice at Last Glacial Maximum. *Geophysical Research Letters*, **25**, 2703–2706.
- DAVIS, B.W. 1988. Heritage conservation in Antarctic and subantarctic jurisdictions: the case of Macquarie Island. *Papers and Proceedings of the Royal Society of Tasmania*, **122**, 9–14.
- ERIKSEN, R. 1997. *A practical manual for the determination of salinity, dissolved oxygen, and nutrients in seawater*. Antarctic Cooperative Research Centre Report, No. 11. Hobart, TAS: Antarctic CRC, 83 pp.
- GILLIE, S.T. 2002. Warming of the Southern Ocean since the 1950s. *Science*, **295**, 1275–1277.
- GLEW, J.R. 1991. Miniature gravity corer for recovering short gravity cores. *Journal of Paleolimnology*, **5**, 285–287.
- GREMMEN, N.J.M., VAN DE VIJVER, B., FRENOT, Y. & LEBOUVIER, M. 2007. Distribution of moss-inhabiting diatoms along the altitudinal gradient at sub-Antarctic Iles Kerguelen. *Antarctic Science*, **19**, 17–24.
- HODGSON, D.A. & JOHNSTON, N.M. 1997. Inferring seal populations from lake sediments. *Nature*, **387**, 30–31.
- HODGSON, D.A., VYVERMAN, W.G. & TYLER, P.A. 1997. *Diatoms of meromictic lakes adjacent to the Gordon River, and of the Gordon River estuary in south-west Tasmania*. Biolothea Diatomologica, Band 35. Berlin: Cramer, 172 pp.
- HODGSON, D.A., ROBERTS, D., MCMINN, A., VERLEYEN, E., TERRY, B., CORBETT, C. & VYVERMAN, W. 2006. Recent rapid salinity rise in three East Antarctic lakes. *Journal of Paleolimnology*, **36**, 385–406.
- JONES, V.J. & BIRKS, H.J.B. 2004. Lake-sediment records of recent environmental change on Svalbard: results of diatom analysis. *Journal of Paleolimnology*, **31**, 445–466.

- JONES, V.J. & JUGGINS, S. 1995. The construction of a diatom-based chlorophyll *a* transfer function and its application at three lakes on Signy Island (maritime Antarctic) subject to differing degrees of nutrient enrichment. *Freshwater Biology*, **34**, 433–445.
- JONES, V.J., JUGGINS, S. & ELLIS-EVANS, J.C. 1993. The relationship between water chemistry and surface sediment diatom assemblages in maritime Antarctic lakes. *Antarctic Science*, **5**, 339–348.
- JUGGINS, S. 2003. *C2 User Guide. Software for ecological and palaeoecological data analysis and visualisation*. Newcastle-upon-Tyne, UK: University of Newcastle.
- KÖSTER, D., RACCA, J.M.J. & PIENITZ, R. 2004. Diatom-based inference models and reconstructions revisited: methods and transformations. *Journal of Paleolimnology*, **32**, 233–246.
- KUMKE, T., KIENEL, U., WECKSTROM, J., KORHOLA, A. & HUBBERTEN, H.W. 2004. Inferred Holocene paleotemperatures from diatoms at Lake Lama, Central Siberia. *Arctic Antarctic and Alpine Research*, **36**, 624–634.
- LAMY, F., HEBBELN, D., RÖHL, U. & WEFER, G. 2001. Holocene rainfall variability in southern Chile: a marine record of latitudinal shifts in the southern westerlies. *Earth and Planetary Science Letters*, **185**, 369–382.
- LIM, D.S.S., SMOL, J.P. & DOUGLAS, M.S.V. 2007. Diatom assemblages and their relationship to lakewater nitrogen levels and other limnological variables from 36 lakes and ponds on Banks Island, N.W.T., Canadian Arctic. *Journal of Paleolimnology*, **18**, 313–333.
- MARSHALL, G.J. & CONNOLLEY, W.M. 2006. The effect of changing Southern Hemisphere winter sea surface temperatures on Southern Annular Mode strength. *Geophysical Research Letters*, **33**, 10.1029/2006GL026627.
- MCGLONE, M.S. 2002. The Late Quaternary peat, vegetation and climate history of the Southern Ocean islands of New Zealand. *Quaternary Science Reviews*, **21**, 683–707.
- PIENITZ, R., SMOL, J.P. & BIRKS, H.J.B. 1995. Assessment of fresh-water diatoms as quantitative indicators of past climatic-change in the Yukon and Northwest-Territories, Canada. *Journal of Paleolimnology*, **13**, 21–49.
- PWS. 2007. *Plan for the eradication of rabbits and rodents on Subantarctic Macquarie Island*. Parks and Wildlife Service. Department of Tourism, Arts and the Environment, Tasmania, March 2007, 30 pp.
- R DEVELOPMENT CORE TEAM. 2006. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing. Vienna, Austria (available from <http://www.R-project.org>).
- RINTOUL, S.R., HUGHES, C.W. & OLBERS, D. 2001. The Antarctic Circumpolar Current system. In SIEDLER, G., CHURCH, J. & GOULD, J., eds. *Ocean, circulation and climate: observing and modeling the global ocean*. London: Academic Press, 271–302.
- ROBERTS, D. & McMINN, A. 1999. *Diatoms of the saline lakes of the Vestfold Hills, Antarctica*. Bibliotheca Diatomologica, Band 44. Berlin: Cramer, 83 pp.
- SABBE, K., HODGSON, D.A., VERLEYEN, E., TATON, A., WILMOTTE, A., VANHOUTTE, K. & VYVERMAN, W.G. 2004. Salinity, depth and the structure and composition of microbial mats in continental Antarctic lakes. *Freshwater Biology*, **49**, 296–319.
- SELKIRK, P.M., SEPELT, R.D. & SELKIRK, D.R. 1990. *Subantarctic Macquarie Island: environment and biology*. Studies in Polar Research. Cambridge: Cambridge University Press, 285 pp.
- SHINDELL, D.T. & SCHMIDT, G.A. 2004. Southern Hemisphere climate response to ozone changes and greenhouse gas increases. *Geophysical Research Letters*, **31**, 10.1029/2004GL020724.
- STOEMER, E.F. & SMOL, J.P. 1999. *The diatoms: applications for the environmental and earth sciences*. Cambridge: Cambridge University Press, 469 pp.
- SUN, L.G., XIE, Z.Q. & ZHAO, J.L. 2000. Palaeoecology - a 3000-year record of penguin populations. *Nature*, **407**, 858.
- TOGGWEILER, J.R., RUSSELL, J.L. & CARSON, S.R. 2006. Midlatitude westerlies, atmospheric CO₂, and climate change during the ice ages. *Paleoceanography*, **21**, A2005–A2005.
- TWEEDIE, C.E. & BERGSTROM, D.M. 2000. A climate change scenario for surface air temperature at Subantarctic Macquarie Island. In DAVISON, W., HOWARD-WILLIAMS, C. & BROADY, P., eds. *Antarctic ecosystems: models for wider understanding*. Christchurch: Caxton Press, 272–281.
- VAN DE VIJVER, B. & BEYENS, L. 1999. Moss diatom communities from Ile de la Possession (Crozet, Subantarctica) and their relationship with moisture. *Polar Biology*, **22**, 219–231.
- VAN DE VIJVER, B., BEYENS, L., VINCKE, S. & GREMMEN, N.J.M. 2004. Moss-inhabiting diatom communities from Heard Island, sub-Antarctica. *Polar Biology*, **27**, 532–543.
- VAN DE VIJVER, B., LEDEGANCK, P. & BEYENS, L. 2002a. Soil diatom communities from Ile de la Possession (Crozet, sub-Antarctica). *Polar Biology*, **25**, 721–729.
- VAN DE VIJVER, B., FRENOT, Y. & BEYENS, L. 2002b. *Freshwater diatoms from Ile de la Possession (Crozet Archipelago, Subantarctica)*. Bibliotheca Diatomologica, Band 46. Berlin: Cramer, 412 pp.
- VERLEYEN, E., HODGSON, D.A., VYVERMAN, W.G., ROBERTS, D., McMINN, A., VANHOUTTE, K. & SABBE, K. 2003. Modelling diatom responses to climate induced fluctuations in the moisture balance in continental Antarctic lakes. *Journal of Paleolimnology*, **30**, 195–215.
- VYVERMAN, W., VYVERMAN, R., HODGSON, D.A. & TYLER, P.A. 1995. *Diatoms from Tasmanian mountain lakes: a reference dataset (TASDIAT) for environmental reconstructions and a systematic autoecological study*. Bibliotheca Diatomologica, Band 33. Berlin: Cramer, 192 pp.
- WAGNER, B. & MELLES, M. 2001. A Holocene seabird record from Raffles Sø, East Greenland, in response to climatic and oceanic changes. *Boreas*, **30**, 228–39.
- WECKSTRÖM, K. & JUGGINS, S. 2006. Coastal diatom-environment relationships from the Gulf of Finland, Baltic Sea. *Journal of Phycology*, **42**, 21–35.
- WOLFE, A.P. 2003. Diatom community responses to late-Holocene climatic variability, Baffin Island, Canada: a comparison of numerical approaches. *Holocene*, **13**, 29–37.
- WONG, A.P.S., BINDOFF, N.L. & CHURCH, J.L. 1999. Large scale freshening of intermediate waters in the Pacific and Indian Oceans. *Nature*, **400**, 440–443.
- ZALE, R. 1994. Changes in the size of the Hope Bay Adelie penguin rookery as inferred from Lake Boeckella sediments. *Ecography*, **17**, 297–304.