Antarctic Science 19 (1), 17–24 (2007) © Antarctic Science Ltd Printed in the UK DOI: 10.1017/S0954102007000041

Distribution of moss-inhabiting diatoms along an altitudinal gradient at sub-Antarctic Îles Kerguelen

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Abstract: Altitudinal gradients provide excellent opportunities to study relationships between species distribution and climatic variables. We studied the species composition of 39 samples of moss-inhabiting diatoms, collected at 50 m intervals from 100–650 m above sea level. The samples contained a total of 130 diatom species, of which 51 occurred in 10 or more samples. Altitude appeared to be the most important variable explaining variation in species composition. Of the 51 common species, 33 showed a significant relationship with altitude. Although the majority of the latter declined with increasing altitude, for nine species the probability of occurrence first increased with increasing elevation, but decreased again at higher altitudes, and four species increased systematically with elevation. As a result, expected species richness per sample decreased from an estimated 43 at 100 m to 25 species per sample at 650 m. Diatom distribution patterns proved to be suitable predictors of the altitudinal position of sample sites. Cross-validation yielded a strong relationship between predicted and observed altitudes.

Received 11 January 2006, accepted 22 June 2006

Key words: climatic gradient, species diversity, transfer function

Introduction

Recent work on sub-Antarctic islands (Van de Vijver *et al.* 2002, 2004, 2005) has shown that the diatom assemblages on the islands are strongly influenced by environmental differences in their habitat. From the specific diatom composition of these assemblages on the various islands, it is also clear that the latitudinal position of the islands plays a major role in determining the regional distribution of the species (Van de Vijver *et al.* 2005). Latitudinal diversity gradients in diatom communities in the southern hemisphere are well documented (Jones 1996, Van de Vijver & Beyens 1999) and show a clear decrease in species number when moving from the sub-Antarctic islands to the Antarctic continent.

In recent years there has been an increasing interest in the use of diatoms for inferring past climatic and environmental parameters such as moisture, trophic conditions, salinity and pH in the Antarctic region (e.g. Roberts & McMinn 1998, Verleyen *et al.* 2003). Although the precise nature of the ecophysiological relationship between diatoms and temperature remains uncertain, the number of studies using diatoms for temperature reconstructions is also growing (Vyverman & Sabbe 1995, Battarbee 2000, Joynt & Wolfe 2001, Bigler & Hall 2003). Most of these studies are concerned with lakes and lake deposits, often including latitudinal climate gradients in the sample sets (e.g. Weckström *et al.* 1997). Anderson (2000) reviewed the principal temperature based reconstructions and is quite critical about the use of temperature as a proxy to determine the diatom composition. But in locations where harsh conditions prevail, such as high altitude and polar sites, temperature can still be an important driving factor.

The sub-Antarctic terrestrial biome is restricted to a small number of islands in the Southern Ocean. These islands contain important records of past environmental and climatic conditions in many deep peat deposits (Van Zinderen Bakker *et al.* 1971, Scott 1985, Selkirk *et al.* 1988, Frenot *et al.* 1997), arising mainly from bryophyte and graminoid dominated vegetation (cf. Aubert de la Rue 1962, Moore 1979, Gremmen 1981, Smith & Steenkamp 2001). Highly diverse diatom assemblages inhabit the moss vegetations, especially in wet and mesic habitats (Van de Vijver & Beyens 1996, 1999, Van de Vijver *et al.* 2001, 2004). Several palynological studies have aimed at elucidating the palaeoclimate of the islands, but because of the small number of vascular plant species (Chown *et al.* 1998), and the often wide ecological amplitude of these species, the resolution of climate reconstructions for these islands based on pollen records is relatively coarse. The species diversity of moss-inhabiting diatoms on sub-Antarctic islands is much larger, with over 200 species on Kerguelen (Van de Vijver *et al.* 2001), suggesting a

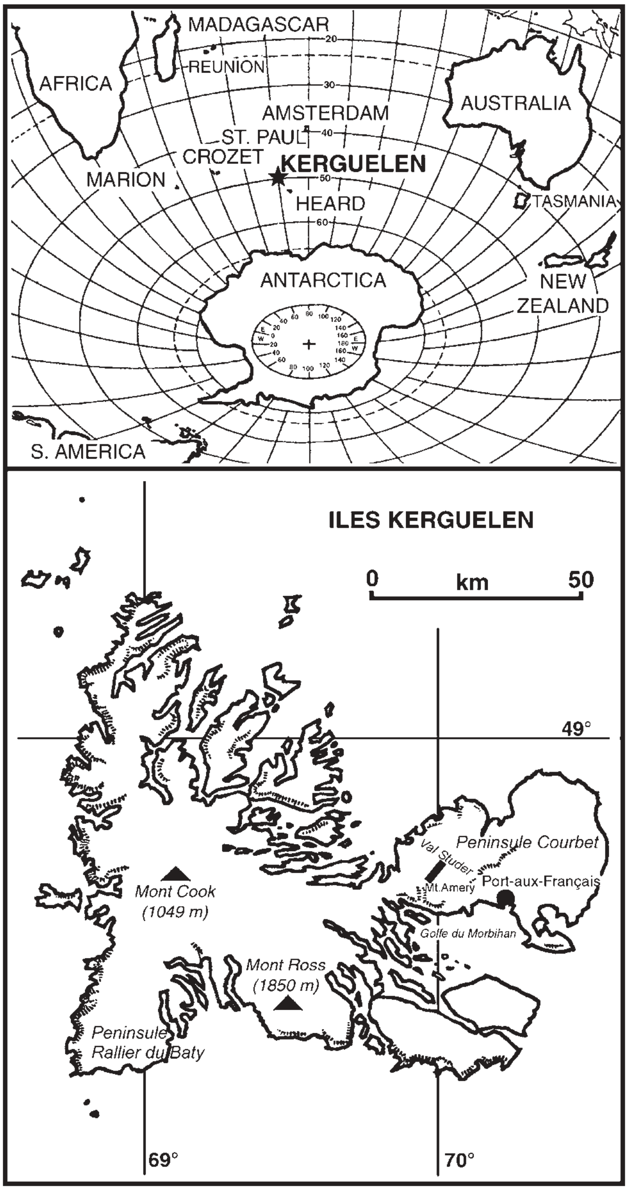

Fig. 1. Geographical position of Iles Kerguelen, and the position of our study area on the main island (the black rectangle between Val Studer and Mount Amery).

possibility for more detailed reconstructions. However, this requires 1) that climate is a significant factor determining species distributions on the islands, and 2) that the relationship between diatom species and assemblages and climate is known.

Altitudinal gradients provide a possibility to study the effect of climate variation on species distribution and assemblage characteristics (Körner 2005), but little study has been made so far on terrestrial diatom assemblages along such gradients. The mountainous areas of Iles Kerguelen are very suitable for the use of altitude as a proxy for climate, notably temperature. Whereas the richest plant communities occur in the coastal areas, the vegetation cover declines rapidly when altitude increases and constitutes what is called “fellfield communities”. These fellfield areas show a homogeneous physiognomy with altitude and very similar habitats, in terms of geological substratum, soil characteristics and vegetation structure, are available for comparisons over a wide range of elevation. In the present study we aimed to quantify the relationship between the distribution of moss-inhabiting diatom species and altitude as a possible proxy for climate, notably temperature on a mountain slope on the sub-Antarctic island of Kerguelen.

Methods

Study area

The French Iles Kerguelen (49ºS, 69ºE) consist of one major island (Grand Terre), surrounded by more than 300 small outlying islands and islets covering a total land area of 7215 km². The main island is mountainous, with the highest peak reaching 1850 m a.s.l. The archipelago is very isolated, *c.* 4000 km from the coasts of South Africa and Australia (Fig 1). The climate is oceanic and cold. Mean annual temperature at the Port-aux-Français weather station is 4.6ºC, with 7.7°C (February) and 2.1ºC (August) for the warmest and coldest month respectively. Wind speed is generally high. Annual rainfall varies from less than 800 mm in the eastern part to more than 3200 mm on the western coast (Frenot *et al*. 1997). No precipitation data are available for our Val Studer study site, but personal observations suggest that rainfall is slightly higher than at Port-aux-Français.

The study area (49°17'S, 70°03'E) was formed by slopes running up from Val Studer to Mount Amery. Val Studer is a valley cutting through the central mountainous area of the Courbet Peninsula in the north-eastern part of the main island. The sampled area ranged from 90–650 m a.s.l. Geologically, the entire region has a quite homogenous structure and consists of almost pure basalt formations. The slopes are covered by very open feldmark vegetation, dominated by the cushion plant *Azorella selago* Hook f. and a number of bryophyte species (Gremmen 1981, Smith & Steenkamp 2001). Vegetation cover is on average some 5%. Locally, seepage water collects and permanently wet habitats occur with dense mats of hygrophilous bryophytes. *Breutelia integrifolia* (Tayl.) Jaeg. is the most common bryophyte in these habitats but at some sites *Philonotis polymorpha* (Müll. Hal.) Kindb., *Bucklandiella orthotrichacea* (Müll. Hal.) Bednarek-Ochyra & Ochyra, *Bryum eatonii* Mitt. and *Brachytheciastrum paradoxum* (Hook. f. & Wilson) Ignatov & Huttunen occur.

Field sampling

On 12–14 January 2004 samples of water-saturated mosses were collected from small (1–5 m^2), isolated seepage areas along an altitudinal gradient from 100 to 650 m a.s.l., at

Table I. Air temperature (°C) data for three climate stations in our study area, measured at 10 cm above the soil surface for the period 21 December 2003–26 January 2004.

Elevation	mean	minimum	maximum
90 m	7.5	-0.4	21.0
371 m	5.3	-1.1	17.7
500 m	4.1	-1.9	15.8

c. 50 m altitude intervals along the gradient. At each altitude three samples were taken, in separate seepage areas, at least 20 m removed from each other, and lacking any visible hydrological connection. Accidentally, no samples were taken at 400 m. Altitudes were established using a GPS. Comparison of the GPS values with barometrically measured heights for a number of sites showed little difference between the two methods.

Each sample consisted of a small handful of bryophytes, taken from the centre of the bryophyte mat. All bryophyte samples are from mats that were 100% saturated with seepage water, with moisture class F = III to IV in the classification of Jung (1936) indicating permanent wet, terrestrial mosses. Whenever possible, samples were taken in stands of the moss *Breutelia integrifolia*. At higher altitudes, however, *Breutelia* was rare and other mosses were dominant in seepage areas.

Air temperature data (measured every 30 minutes at 10 cm above the soil surface) were available from three sites close to our transect, for the period from 21 December to 27 January (Table I). In the text we refer to the temperature of this period as the January temperature.

Sample treatment and counting

Diatom samples were prepared following the method of Van der Werff (1955). Small parts of the samples were cleaned by adding 37% H_2O_2 and heating to 80°C for about 1 hr, after which the reaction was completed by addition of $KMnO_4$. Following digestion and centrifugation, the resulting clean material was diluted with distilled water to avoid excessive concentrations of diatom valves hindering reliable observations. Cleaned diatom valves were mounted in Naphrax®. In each sample, a total of 500 diatom valves were identified and enumerated on random transects across the slides at x1000 under oil immersion objectives using an Olympus BX50 microscope equipped with Differential Interference Contrast (Nomarski) optics. Identification of Antarctic species was based mainly on Van de Vijver *et al.* (2002, 2004). Nomenclature follows the latest taxonomic views (i.c. the genera separated from *Achnanthes s.l., Navicula s.l. and Cymbella s.l.*) based on Krammer (1997), Lange-Bertalot (2001), Bukhtiyarova & Round (1996), and Round & Bukhtiyarova (1996). Samples and slides are stored at the National Botanic Garden (Meise, Belgium).

Data analysis

The variation in species composition of the diatom samples was explored using ordination techniques. First the length of the species variation gradient was established by Detrended Correspondence Analysis (DCA). Because gradient length was relatively short, subsequently Principal Components Analysis (PCA), a method based on a linear relationship between species abundances and ordination axes, was used. To relate patterns of variation in the species data to the value of environmental variables, we used Redundancy Analysis (RDA). These methods are described in detail by Jongman *et al.* (1995) and Ter Braak & Šmilauer (1998). To reduce the heteroscedasticity of the diatom counts, we transformed the abundance data logarithmically, after adding 1 to each abundance figure.

Weighted averaging (WA) regression and calibration models are widely used in palaeoecological studies for quantitative reconstructions of past environmental conditions. In this paper, we investigate the relationship between the abundance of individual species and elevation by means of C^2 (Juggings 2003) version 1.3. WA regression provides a computationally simple and reliable estimate of the optimal altitude of a diatom taxon. Species occurring in more than five samples and present in at least one sample with a relative frequency higher than 1% were included in these regression analyses.

The relationship between species richness and altitude was analysed by linear regression. Because of the limited range of species numbers per sample, no transformations of these data were necessary. As a measure for the change in species composition of the diatom assemblages between altitudinal zones we used the turnover (beta diversity) measure suggested by Wilson & Shmida (1984):

$$\frac{b+c}{2a+b+c}$$

in which a = the number of species in common between the two altitudinal zones, b = the number of species present in the highest of the two zones but not in the lower one, and c = the number of species present in the lower but not in the upper of the two zones in the comparison (cf. Koleff *et al.* 2003). Per altitude we pooled the data from three samples. In case less than three samples were available for the same altitude we did not include these in the analysis. In one case four samples were available for one altitude. To avoid any effect of difference in sampling effort, in this case we left one randomly chosen sample out of the turnover estimates.

Results

In the 39 samples along the altitudinal transect 130 diatom species were recorded. Fifty one of these occurred in 10 or more samples. Figure 2 shows the distribution of the most important taxa along the altitudinal gradient. Species

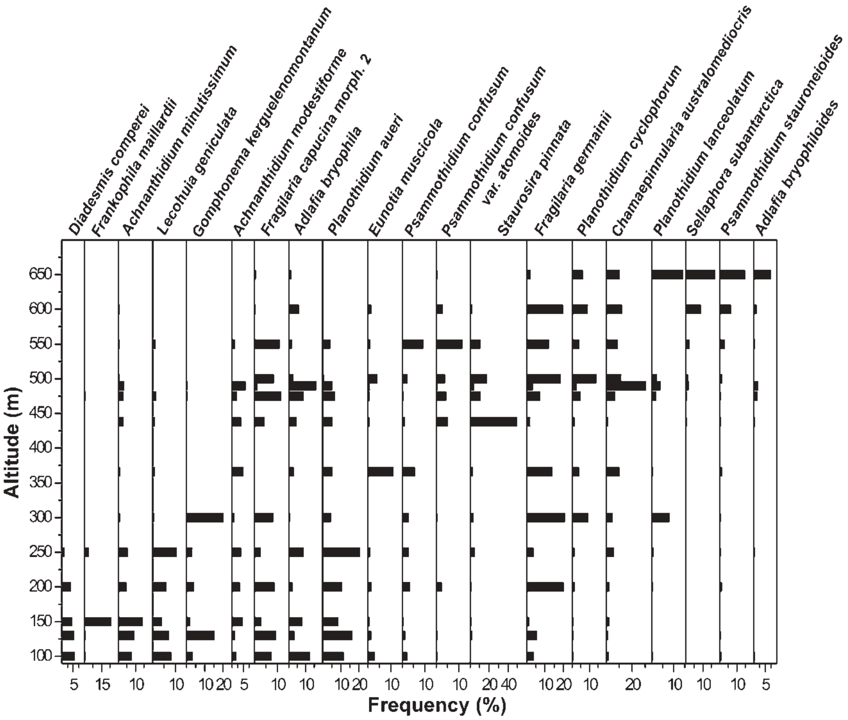

Fig. 2. Distribution of the principal diatom taxa along the altitudinal gradient. Taxa are visually arranged according to their altitudinal preference.

arrangement has been visually determined with species preferring lower altitudes grouped on the left side of the diagram and species typical for higher elevations on the right-hand side. The species number per sample ranged from 17 to 67 species, with an average of 36 (in 500 individuals counted). Species richness declined significantly with altitude. Figure 3 shows the estimated relationship between species richness and altitude (formula used in the model: species number/sample = 43.63–0.0000448*altitude; $P = 0.0002$; $r^2_{adj} = 0.30$), with an estimated mean number of species per sample of 43 at 100 m, and 25 at 650 m. A simple linear regression model with altitude rather than altitude^2 as explanatory variable, explained only slightly less variation, but the distribution of the residuals was not random.

Table II summarizes all ordination results. A Detrended

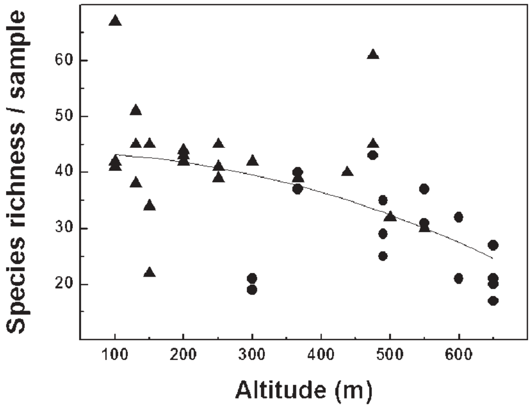

Fig. 3. Relationship between species richness of moss-inhabiting diatoms and altitude. Triangles indicate *Breutelia integrifolia* samples, circles represent samples taken from other moss species.

Table II. Summary of ordination results with all species (130) and with only the 80 most frequent and abundant species. In the RDA, altitude was used as explanatory (environmental) variable.

	axis 1	axis 2	axis 3	axis 4
DCA130 species				
Eigenvalues	0.313	0.132	0.092	0.059
Lengths of gradient (SD.units)	2.989	2.244	1.782	1.284
Cumulative % variance of species	13.8	19.6	23.7	26.3
DCA80 species				
Eigenvalues	0.250	0.097	0.057	0.045
Lengths of gradient (SD.units)	2.540	2.101	1.659	1.254
Cumulative % variance of species	17.1	23.1	27.6	30.7
PCA130 species				
Eigenvalues	0.242	0.121	0.092	0.071
Lengths of gradient (SD.units)	24.2	36.3	45.5	52.5
Cumulative % variance of species	0.263	0.095	0.088	0.072
PCA80 species				
Eigenvalues	26.3	35.8	44.6	51.9
Lengths of gradient (SD.units)	0.204	0.132	0.097	0.073
Cumulative % variance of species	0.936	0.000	0.000	0.000
RDA130 species				
Eigenvalues	20.4	33.6	43.3	50.6
Lengths of gradient (SD.units)	100.0	0.0	0.0	0.0
Cumulative % variance of species	0.224	0.108	0.089	0.076
RDA80 species				
Eigenvalues	0.935	0.000	0.000	0.000
Lengths of gradient (SD.units)	22.4	33.1	42.0	49.6
Cumulative % variance of species	100.0	0.0	0.0	0.0

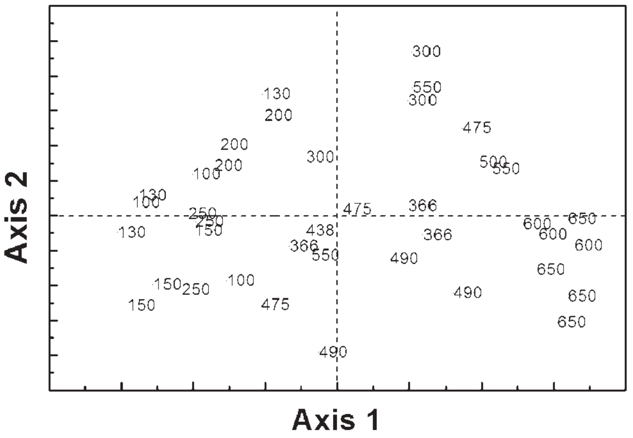

Fig. 4. Ordination diagram showing the position of the samples (as identified by their altitude) on the first two axes of a Principal Components Analysis (PCA), in which only those species occurring with at least 10 valves in the total of the samples, or in at least five samples were included. See Table II for details of the results.

Correspondence Analysis including all samples and all species gave a total gradient length of 2.99 and 2.24 SD units of species turnover for the first and second axis respectively. Therefore a linear model was used for subsequent ordination analyses. In a Principal Component Analysis (Fig. 4) the first ordination axis explained 24.2% of species variation and an additional 12.1% was explained by the second axis. The first axis of the PCA was strongly correlated with altitude (Pearson Product-Moment correlation between the PCA first axis scores and altitude = 0.89), indicating that altitude might be considered to be the most important environmental variable explaining the variation in species composition in our data. In a constrained ordination (RDA), with elevation as the only explanatory environmental variable, the first axis explained 20.4% of the variance of the species data. In contrast, the second axis, i.e. the first unconstrained axis, explained only 13.2 % of species variation (Table II). This again indicates that altitude is the single most influential variable explaining species composition within our dataset. To check the impact of rare species on these results all ordinations were repeated including only those species occurring with ten or more valves in the total data, and/or present in five or more samples. This reduced the total number of species in the analysis from 130 to 80. As can be seen in Table II the results did not differ much from those obtained using all species.

Table III. Correlation (r^2) and RMSE of prediction for the bootstrapped.

Method	Deshrinking	r^2	RMSE	r^2_{boot}	RMSE_{boot}
WAboot	Inverse	0.85	72.6	0.80	91.0
	Classical	0.85	78.9	0.80	88.6

The results of the Weighted Averaging regression analysis present a reliable model to infer altitude based on the Val Studer diatom dataset. The apparent RMSE for the altitude

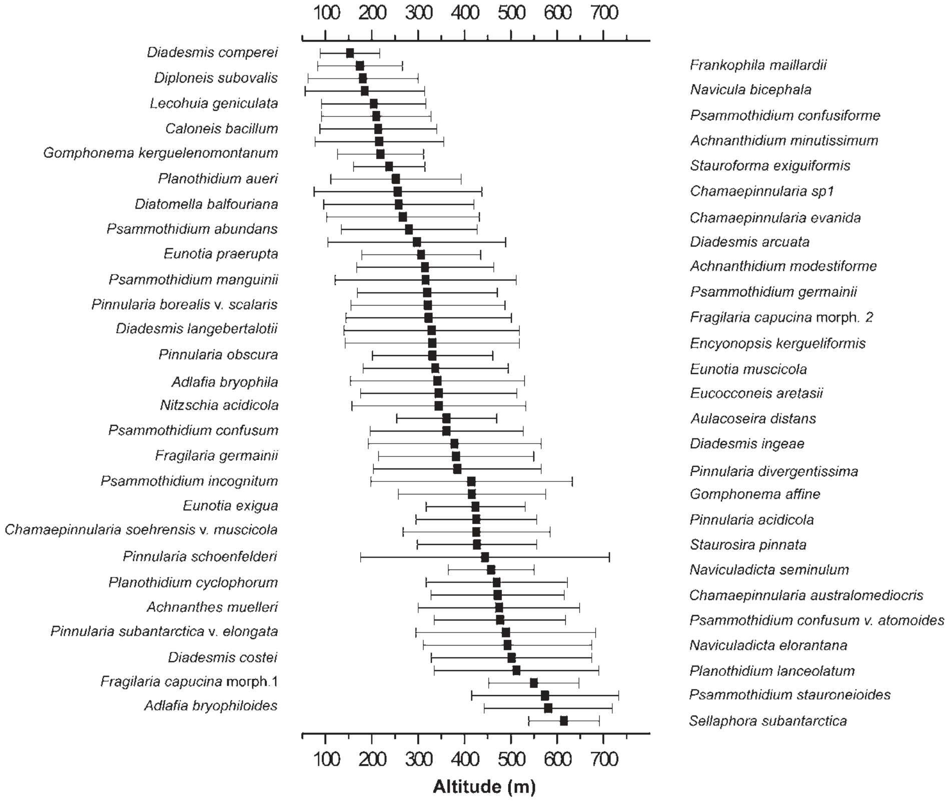

Fig. 5. WA optima and tolerances for altitude in ascending order for the principal diatom taxa used to develop the model.

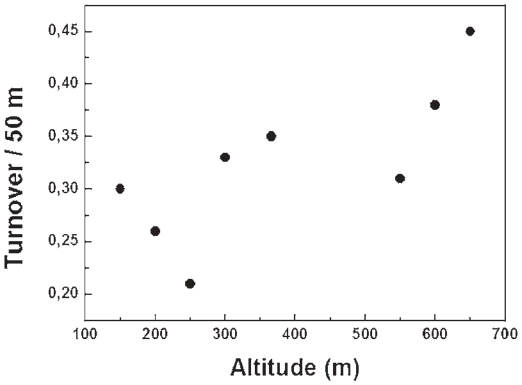

Fig. 6. Species turnover of the diatom flora per 50 m elevation along the altitudinal gradient. Each point indicates turnover between the indicated altitude and 50 m lower. For each altitude, three samples were combined (see text).

calibrations is 72.6 (m) using inverse deshrinking and 78.9 (m) using classical deshrinking. Both methods provide fairly high r^2 indicating a good relationship between inferred and observed altitudes of the samples used in the model (Table III). Figure 5 shows the calculated altitude optima and tolerances for the principal 54 taxa. There is a clear transition between taxa such as *Diadesmis comperei* Le Cohu & Van de Vijver, *Frankophila maillardii* (Le Cohu) Lange-Bertalot and *Lecohuia geniculata* (Germain) Lange-Bertalot that prefer lower altitudes and 'high altitude species' such as *Sellaphora subantarctica* Van de Vijver & Beyens, *Psammothidium stauroneioides* (Manguin) Buhktiyarova and *Adlafia bryophiloides* (Manguin) Van de Vijver.

Species turnover along the altitudinal gradient increased with increasing altitude. The highest turnover was observed above 600 m a.s.l. (Fig. 6). While the number of common species in two adjacent altitudinal zones decreased significantly with increasing altitude, both in absolute numbers ($r^2 = -0.91$, $P < 0.05$) as well as in percentage of the total number of species in the two zones in the comparison ($r^2 = -0.77$, $P < 0.05$), the number of species gained per zone as well as the number of species lost did not show a significant relation with altitude. At the same time there was a negative correlation between the number of species gained and the number of species lost in the comparison of successive 50 m altitudinal zones ($r^2 = -0.85$, $P < 0.05$). When we compare the species occurring at the lower end of our transect, i.e. at 100 m, with those found at 650 m, summing three samples at each altitude, of 75 species found at 100 m only 25 occur at 650 m, while seven species were found at 650 m that did not occur at 100 m. When we added the species found in the two lower zones (100 and 150 m; six samples) and compared these with the two upper zones (600 and 650 m, six samples), we counted 85 species in the lower area, of which 47 were not found in the 600–650 m zone, compared with 17 species which appeared in the 600–650 m zone.

Discussion

Despite our attempts to keep as many variables as possible within our sample population constant, and only vary the altitude, altitude appears to explain only about 20% of the variation in species composition in our diatom data (Table II). On one hand explanation of 20% of species variation by a single variable in ecological data is relatively high. For instance in a set of 100 lakes in northern Sweden, the five best environmental variables together explained 20% of the variation in diatom species composition (Bigler & Hall 2002). For sediment data from a lake in the Swiss Alps sediment age was the best explanatory variable, explaining 17% of species variation (Lotter & Bigler 2000). Rosen *et al*. (2000) showed a maximum of 13% explained species variation in a number of datasets from lakes in northern Sweden. On the other hand, because we tried to keep the type and size of the sampled habitats, as well as moisture conditions constant in our set of samples, and all samples were taken within a period of two weeks, the data were still quite noisy.

The diatom assemblages we studied came from different moss species. We tried to restrict sampling, wherever possible, to *Breutelia integrifolia*, but at higher altitudes this species was quite rare. As a result, there is a correlation between *Breutelia* or non-*Breutelia* and altitude. The effect of moss species on the species composition of the moss-inhabiting diatom assemblage was tested using the samples from 300–650 m. Over this range all sampled moss species were represented in the samples, while all samples from lower altitudes consisted of *Breutelia* only. Constrained ordination with moss species as explanatory variables showed no significant relation between moss species and diatom species composition (Monte Carlo permutation test, 199 permutations; $P < 0.05$). Therefore, the use of different moss species in this study does not seem to influence the diatom composition along the altitudinal gradient.

The weighted averaging model for altitude that has been calculated seems to provide a fairly reliable result but should still be treated with caution. In fact, three categories of species can be detected. A considerable number of species do present bell-shaped curves with their optimum well situated near the middle of the sampled gradient. Good examples of this type of species are *Staurosira pinnata* Ehrenberg and *Fragilaria germainii* Reichardt & Lange-Bertalot. Therefore, the calculated optima for this type of species should be considered to be their true optima. On the other hand, the two other groups of species, i.e. those that prefer lower altitudinal sites and those typical for higher altitudes, might actually be the reason why transfer functions for altitude do not always present the best results.

In addition, the relationship between altitude and abundance of individual species was explored by simple

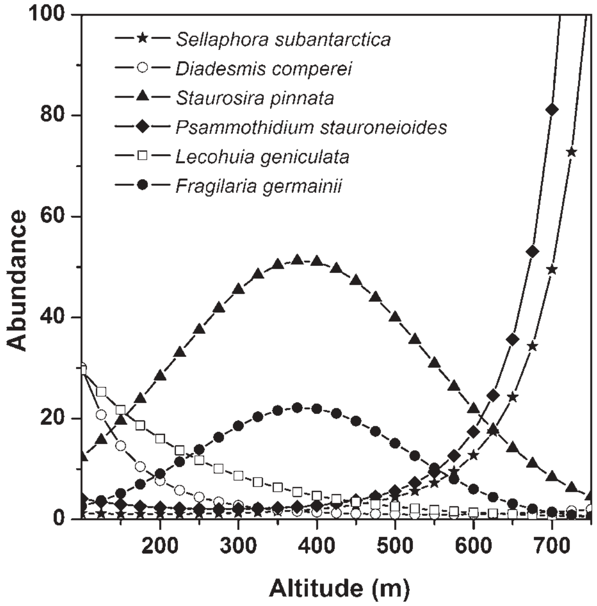

Fig. 7. Relationship between altitude and abundance of individual species, estimated by regression analysis. Regression was performed using log-transformed abundances. For the graphs the estimated log-values were backtransformed to abundance values (number of individuals per 500 valves).

regression analyses, with elevation and elevation² as explanatory variables and ln(abundance) as dependent variable. Significance of regression coefficients was tested with *t*-tests. In cases where the regression coefficient of the quadratic term did not significantly differ from zero, a regression without this term was performed. As can be seen in Fig. 7, species such as *Diadesmis comperei* or *Lecohuia geniculata* do not seem to reach their optimum within the sampled gradient but instead might prefer much lower altitudes. On the other side of the gradient, the same applies for species such as *Sellaphora subantarctica* or *Psammothidium stauroneioides* that have probably optima that are higher than 650 m, the highest altitude that could be sampled in this study.

Nevertheless, even when the calculated optima do not reflect entirely the true optima of the species, there are still interesting observations to make. Based on Fig. 7, it is clear that species that tend to show a more Antarctic distribution such as *Psammothidium stauroneioides*, *Sellaphora subantarctica* and *Chamaepinnularia australomediocris* (Lange-Bertalot & Schmidt) Van de Vijver have their optima on the higher side of the gradient whereas species that can be considered more ubiquitous and/or cosmopolitan such as *Caloneis bacillum* sensu auct. nonnul. of *Achnanthidium minutissimum* (Kützing) Czarnecki tend to prefer lower altitudes. The question whether there are observable similarities in the (sub-)Antarctic region between the distribution of diatoms along an altitudinal and a latitudinal gradient, is still not yet fully understood but it is clear that the same environmental factors controlling the diatom composition at higher latitudes might also play a major role in studying altitudinal gradients.

In this study, we used altitude as the explanatory variable for diatom species distribution. Of course, the causal factor influencing species distribution is not ‘altitude’ as such, but one or more causal variables covarying with altitude. We believe that in the present study temperature is the major factor and that it is the only variable strongly and systematically changing along the gradient that we studied. The studied altitudinal gradient, from 100–650 m a.s.l., represents a temperature gradient of about 4.7°C in mean January temperature (Table I). Assuming a linear relationship between altitude and air temperature, it is possible to convert the species’ altitude optimum into a temperature optimum, with the regression model January temp = 8.263 – 0.00822 x altitude in m ($P = 0.03$, $r^2_{adj} = 0.99$). This assumption of a linear relationship between temperature and altitude for our study site is reasonable, because the topography of the area is very smooth, and the area is very exposed. Therefore the air temperature lapse rate at the surface can be expected to be related to the adiabatic lapse rate, and be considered constant for the altitudinal range of our study. Although it is clear from many studies that temperature affects species distribution and species composition of diatom assemblages (e.g. Vyverman & Sabbe 1995, Lotter *et al*. 1997, Joynt & Wolfe 2001, Bigler & Hall 2003), it is not clear which aspect of temperature is the most influential. We have however insufficient temperature data to clarify this point and more, temperature-specific research will be necessary to clarify this problem.

Acknowledgements

NJMG wishes to thank the French Polar Institute (IPEV) for the invitation to take part in the 2003/2004 summer field season on Kerguelen and the excellent logistic support. This study was part of the IPEV programme 407 RiSCC-4Iles (Dr F. Hennion), and of the RiSCC program of SCAR. It was also supported by the CNRS (Zone Atelier de recherches sur l’environnement antarctique et subantarctique). NJMG is a visiting post-doctoral researcher at the University of Antwerp (Dept. of Biology, Prof Dr L. Beyens). We thank Prof R. Ochyra, Krakow, Poland, for his help with the identification of the bryophytes, and are grateful for useful comments from the referees.

References

Anderson, N.J. 2000. Diatoms, temperature and climatic change. *European Journal of Phycology*, **35**, 307–314.

Aubert de la Rue, E. 1962. Quelques particularités des tourbières de l’Archipel de Kerguelen, leur répartition, leur structure et leur destruction. *TAAF*, **21**, 12–30.

Battarbee, R.W. 2000. Palaeolimnological approaches to climate change, with special regard to the biological record. *Quaternary Science Reviews*, **19**, 107–124.

Bigler, C. & Hall, R.I. 2002. Diatoms as indicators of climatic and limnological change in Swedish Lapland: a 100-lake calibration set and its validation for paleoecological reconstructions. *Journal of Paleolimnology*, **27**, 97–115.

Bigler, C. & Hall, R.I. 2003. Diatoms as quantitative indicators of July temperature: a validation attempt at century-scale with meteorological data from northern Sweden. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **189**, 147–160.

Bukhtiyarova, L. & Round, F.E. 1996. Revision of the genus *Achnanthes* sensu lato. *Psammothidium*, a genus based on *A. marginulatum*. *Diatom Research*, **11**, 1–30.

Chown, S.L., Gremmen, N.J.M. & Gaston, K.J. 1998. Ecological biogeography of Southern Ocean islands: species-area relationships, human impacts, and conservation. *American Naturalist*, **152**, 562–575.

Frenot, Y., Gloaguen, J.C., Van de Vijver, B. & Beyens, L. 1997. Datation of some Holocene peat sediments and glacier fluctuations in the Kerguelen Islands. *Comptes Rendus de l'Académie des Sciences de Paris, Life Sciences*, **320**, 567–573.

Gremmen, N.J.M. 1981. *The vegetation of the Subantarctic islands Marion and Prince Edward.* The Hague: Dr W. Junk, 145 pp.

Jones, V.J. 1996. The diversity, distribution and ecology of diatoms from Antarctic inland waters. *Biodiversity and Conservation*, **5**, 1433–1449.

Jongman, R.H., ter Braak, C.J.F. & van Tongeren, O.F.R. 1995. *Data analysis in community and landscape ecology.* Cambridge: Cambridge University Press, 300 pp.

Joynt III, E.H. & Wolfe, A.P. 2001. Paleoenvironmental inference models from sediment diatom assemblages in Baffin Island lakes (Nunavut, Canada) and reconstructions of summer water temperature. *Canadian Journal of Fisheries and Aquatic Science*, **58**, 1222–1243.

Juggins, S. 2003. *C² User Guide. Software for ecological and paleoecological data analysis and visualization.* University of Newcastle, Newcastle upon Tyne, UK.

Jung, W. 1936. Thekamöben ursprünglucher, lebender deutscher Hochmoore. *Abhandlungen aus dem Landesmuseum der Provinz Westfalen, Museum für Naturkunde*, **7**, 1–87.

Koleff, P., Gaston, K. & Lennon, J.L. 2003. Measuring beta diversity for presence-absence data. *Journal of Animal Ecology*, **72**, 367–382.

Körner, C. 2005. Altitudinal transects - their nature and usefulness. *In* Becker, A. & Gurung, A.B., *eds. Process studies along altitudinal gradients to serve conservation and sustainable development*. Workshop Report: Potsdam/Zürich, 47–48.

Krammer, K. 1997. Die cymbelloiden Diatomeen. Eine Monographie der weltweit bekannten Taxa. Teil 2. *Encyonema* part. *Encyonopsis* and *Cymbellopsis*. *Bibliotheca Diatomologica*, **37**, 1–469.

Lange-Bertalot, H. 2001. Diatoms of the European inland waters and comparable habitats. *Navicula* sensu strictu, 10 genera separated from *Navicula* sensu lato, *Frustulia*. *Diatoms of Europe*, **2**, 1–526.

Lotter, A.F., Birks, H.J.B., Hofmann, W. & Marchetto, A. 1997. Modern diatom, cladocera, chironomid and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. I. Climate. *Journal of Paleolimnology*, **18**, 395–420.

Lotter, A.F. & Bigler, C. 2000. Do diatoms in the Swiss Alps reflect the length of ice-cover? *Aquatic Science*, **62**, 125–141.

Moore, D.M. 1979. Southern oceanic wet heathlands (including Magellanic moorland). *In* Specht, R.L., *ed*. *Ecosystems of the World 9A: Heathlands and related shrublands: descriptive studies*. Amsterdam: Elsevier, 489–497.

Roberts, D. & McMinn, A. 1998. A weighted-averaging regression and calibration model for inferring lakewater salinity from fossil diatom assemblages in saline lakes of the Vestfold Hills: a new tool for interpreting Holocene lake histories in Antarctica. *Journal of Paleolimnology*, **19**, 99–113.

Rosen, P., Hall, R.I., Korsman, T. & Renberg, I. 2000. Diatom transfer-functions for quantifying past air temperature, pH and total organic carbon concentration from lakes in northern Sweden. *Journal of Paleolimnology*, **24**, 109–123.

Round, F.E. & Bukhtiyarova, L. 1996. Four new genera based on *Achnanthes* (*Achnanthidium*) together with a redefinition of *Achnanthidium*. *Diatom Research*, **11**, 345–361.

Scott, L. 1985. Palynological indications of the Quaternary vegetation history of Marion Island (sub-Antarctic). *Journal of Biogeography*, **12**, 413–431.

Selkirk, D.R., Selkirk, P.M., Bergstrom, D.M. & Adamson, D.A. 1988. Ridge top peats and palaeolake deposits on Macquarie Island. *Papers and Proceedings of the Royal Society of Tasmania*, **122**, 83–90.

Smith, V.R. & Steenkamp, M. 2001. Classification of the terrestrial habitats on sub-Antarctic Marion Island based on vegetation and soil chemistry. *Journal of Vegetation Science*, **12**, 181–198.

ter Braak, C.J.F. & Šmilauer, P. 1998. *CANOCO Reference Manual and User's Guide to Canoco for Windows. Software for Canonical Community Ordination (version 4.0).* Centre for Biometry, Wageningen.

Van de Vijver, B. & Beyens, L. 1996. The epiphytic diatom flora of mosses from Stromness Bay area, South Georgia. *Antarctic Science*, **8**, 359–368.

Van de Vijver, B. & Beyens, L. 1999. Biogeography and ecology of freshwater diatoms in Subantarctica: a review. *Journal of Biogeography*, **26**, 993–1000.

Van de Vijver, B., Ledeganck, P. & Beyens, L. 2001. Habitat preferences in freshwater diatom communities from sub-Antarctic Îles Kerguelen. *Antarctic Science*, **13**, 28–36.

Van de Vijver, B., Frenot, Y. & Beyens, L. 2002. Freshwater diatoms from Ile de la Possession (Crozet Archipelago, Subantarctica). *Bibliotheca Diatomologica*, **46**, 412 pp.

Van de Vijver, B., Beyens, L. & Lange-Bertalot, H. 2004. The genus *Stauroneis* in Arctic and Antarctic locations. *Bibliotheca Diatomologica*, **50**, 311 pp.

Van de Vijver, B., Gremmen, N.J.M & Beyens, L. 2005. The genus *Stauroneis* (Bacilariophyceae) in the Antarctic Region. *Journal of Biogeography*, **32**, 1791–1798.

Van der Werff, A. 1955. A new method of cleaning and concentrating diatoms and other organisms. *Verhandlungen der Internationalen Vereinigung für theoretische und Angewandte Limnologie*, **12**, 276–277.

van Zinderen Bakker, E.M., Winterbottom, J.M. & Dyer, R.A. 1971. *Marion and Prince Edward islands: Report on the South African Biological and Geological expedition 1965–1966.* A.A. Balkema. Cape Town, 427 pp.

Verleyen, E., Hodgson, D.A., Vyverman, W., 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. & Sabbe, K. 1995. Diatom-temperature transfer functions based on the altitudinal zonation of diatom assemblages in Papua New Guinea: a possible tool in the reconstruction of regional palaeoclimatic changes. *Journal of Paleolimnology*, **13**, 65–77.

Weckström, J., Korhola A. & Blom, T. 1997. The relationship between diatoms and water temperature in thirty subarctic Fennoscandian lakes. *Arctic and Alpine Research*, **29**, 75–92.

Wilson, M.V. & Shmida, A. 1984. Measuring beta-diversity with presence-absence data. *Journal of Ecology*, **72**, 1055–1064.