Polar Biol (2010) 33:241–255
DOI 10.1007/s00300-009-0700-8

ORIGINAL PAPER

Diatom communities in soils influenced by the wandering albatross (*Diomedea exulans*)

Adéla Moravcová · Louis Beyens · Bart Van de Vijver

Received: 29 December 2008 / Revised: 23 June 2009 / Accepted: 22 July 2009 / Published online: 12 August 2009

Abstract Soil diatom communities within two breeding colonies of the wandering albatross (*Diomedea exulans*) on Île de la Possession (Crozet Archipelago) were investigated. Samples were collected around occupied and abandoned nests and compared with control samples taken from soils lacking any animal influence. A total of 163 diatom taxa has been identified. Differences in the diatom flora were recorded between the two colonies, but the results show that it is almost impossible to identify a single diatom community typical for albatross-influenced areas. Diatom species composition varied markedly between control samples, occupied and abandoned nests. A turnover in the diatom community (shift from eutraphentic to oligotraphentic taxa) was observed when moving away from both occupied and abandoned nests, although no significant differences in diversity have been found. In summary, soil diatom species composition seems to indicate the impact of animal perturbations. However, it is too early to draw sound conclusions and further studies regarding the topic should be performed to confirm the results of the present study.

A. Moravcová
Department of Ecology, Faculty of Science,
Charles University in Prague, Viničná 7,
128 44 Prague 2, Czech Republic

L. Beyens
Unit of Polar Biology, Limnology and Geomorphology,
Department of Biology, Universiteit Antwerpen,
Universiteitsplein 1, 2610 Wilrijk, Belgium

B. Van de Vijver (✉)
Department of Bryophyta and Thallophyta,
National Botanic Garden of Belgium,
Domein van Bouchout, 1860 Meise, Belgium
e-mail: vandevijver@br.fgov.be

Keywords Soil diatoms · Subantarctica · Organic enrichment · Nutrients · Animal impact · Wandering albatross · Perturbed soils

Introduction

During the past few years, there has been a growing interest in the ecology and biogeography of the non-marine diatom communities in the subantarctic and Antarctic regions (Van de Vijver and Beyens 1999a, b; Sabbe et al. 2003; Van de Vijver et al. 2001, 2002a, 2004, 2008; Gremmen et al. 2007). Owing to force-fitting (Tyler 1996), the actual diatom biodiversity has long been underestimated and it is only recently that the typical (often endemic) nature of the non-marine diatom flora is accepted (Sabbe et al. 2003; Van de Vijver et al. 2005, 2007; Vanormelingen et al. 2008).

The terrestrial (soil inhabiting) diatom communities of the subantarctic islands of the southern Indian and Atlantic Oceans have been intensively studied in the past (Van de Vijver and Beyens 1998; Van de Vijver et al. 2002b). On Île de la Possession, Van de Vijver and Beyens (1998) found four different soil community types, characterized by the dominating species and determined by a different moisture content of the soil, by pH and by salinity, whereas in Van de Vijver et al. (2002b) two main environmental factors influenced subantarctic soil diatom communities—moisture and nutrients. One of the most widespread communities on the islands was found in soils influenced by marine mammals and birds, characterized by both high nutrient and salinity conditions and dominated by a typical diatom community with species such as *Diadesmis crozetikerguelensis* Le Cohu and Van de Vijver, *Pinnularia subantarctica* var. *elongata* (Manguin) Van de Vijver and Le Cohu and *Pinnularia parakolbei* Fukushima, Ko-Bayashi and Yoshitake (formerly *Pinnularia kolbei* Manguin). Similar studies were performed in the Maritime Antarctic Region. Fermani et al. (2007) characterized soil microalgal communities from Deception Island (active volcano), where filamentous cyanobacteria and diatoms dominated the algal flora. During this study, several new species were observed indicating the special character of this environment (Van de Vijver and Mataloni 2008).

It is widely accepted that the colonies of marine birds and mammals exert a large impact on the nearby environment under the form of trampling, manuring, salt input and physical disturbance of the vegetation. Several studies on this topic, for example, on Mediterranean and Subantarctic islands (Smith 1978, 1979; Tatur and Myrcha 1984; Joly et al. 1987; Vidal et al. 1998, 2000, 2003; Michel et al. 2006) focus on the role of nesting marine birds on the surrounding soil and vegetation. In his study, on the impact of seabirds and seals on the soil chemistry of Marion Island, Smith (1978) concluded that marine animals provided a major input of nitrogen to the ecosystem. Vidal et al. (2003) observed a higher proportion of alien plant species near king penguin (*Aptenodytes patagonicus* Miller) rookeries due to the physical and chemical impact of these birds. Penguins, however, usually nest in very large colonies exerting very high pressures on the soil and the vegetation due to the overtrampling and toxic levels of overmanuring (Michel et al. 2006). A different situation is found in nesting sites of the wandering albatross (*Diomedea exulans* Linnaeus) (Joly et al. 1987; Vincke et al. 2007), resulting in lower, but still visible effects since their colonies usually are much smaller. Albatross activities, such as manuring of the soil with excrements, regurgitations and food detritus, trampling of vegetation and removal of litter material for nest construction, impose a highly localized perturbation on the immediate vicinity of their nests. Joly et al. (1987) explored how these activities affected the vegetation and the macro-invertebrate communities by comparing species richness and composition between occupied and abandoned nests. Bryophytes and liverworts showed the clearest response to the breeding because they were absent close to the occupied nest. The species richness of vascular plants also seemed to decrease with increased nutrient levels, whereas the macro-invertebrate species richness increased.

In a parallel study, Vincke et al. (2007) already investigated the soil testate amoebae communities in the largest wandering albatross nesting site on Île de la Possession. They observed clear chemical and biological changes induced by the nesting of the albatrosses. Soil samples taken in the vicinity of the occupied nests showed higher moisture and nutrient levels, with a rather low testate amoebae diversity. On the other hand, there seemed to be no significant differences in testacean diversity in soils surrounding abandoned albatross nests and non-influenced areas, suggesting that the recovery to the natural conditions was already apparent.

By analyzing the diatom composition in different albatross colonies, the present study aims to provide data on three research questions. Can we identify a typical albatross-influenced diatom community present on Île de la Possession or are there marked differences in the soil diatom communities between the different albatross colonies analyzed in this study? Secondly, does the nest status (occupied or abandoned) influence the species composition of the soil diatom communities and, in addition, do the diatom communities evolve back to the composition of non-ornitogenic soils, when the bird influence disappears? Thirdly, can we see changes along transects moving away from the albatross nests?

Materials and methods

Sampling site

The material used in this study was collected on Île de la Possession, the largest island of the Crozet Archipelago, situated in the southern Indian Ocean northwards of the Antarctic Convergence (Fig. 1). The archipelago consists of five islands with an oceanic, cold climate [mean annual air temperature 5.3°C, annual precipitation of 2,400 mm per year (Lebouvier and Frenot 2007)]. Île de la Possession (total surface 156 km²) is roughly rectangular in shape with a topography dominated by a series of inland mountains culminating at 934 m (Pic du Mascarin) and deep glacial valleys such as Vallée des Branloires. The vegetation is dominated by grasses and mosses. More details on the topography and vegetation are given in Van de Vijver et al. (2002a). Most of the samples were taken at the principal albatross nesting site on the island, the so-called “Champs des Albatros” at Pointe Basse. A small number of soil samples were taken in the second albatross colony at the opposite site of the island on the Bollard peninsula, close to the permanent French scientific station Base Alfred Faure. Both areas differ in general characteristics: Pointe Basse, located in the northwestern part of the island, is a flat, boggy, open site, largely exposed to seaspray due to the prevailing southwestern wind, whereas Bollard in the southeastern part of the island, is located on the rock cliff well protected from influences of the southwestern wind. Moreover, there is a considerable difference in annual precipitation between the two sites. Pointe Basse has a higher rainfall than the Bollard site (Frenot 1986). The total albatross number at the Pointe Basse nesting site is estimated at 250 breeding pairs, whereas the Bollard nesting site only has about 50 breeding pairs.

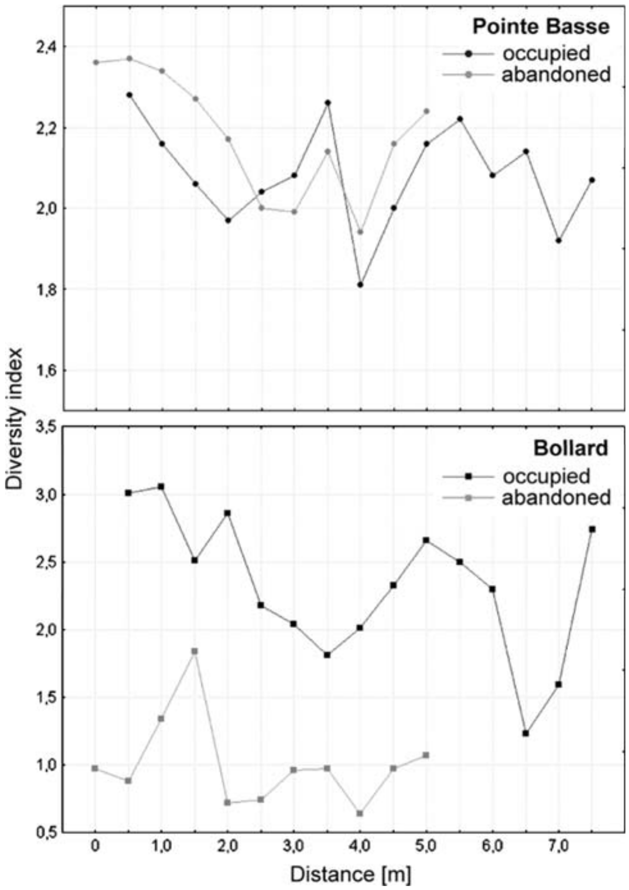

Fig. 1 Mean diversity values from samples around occupied and abandoned nests at Pointe Basse and Bollard are shown. The *x* axis presents the distance from the nest (in m; 0.5–7.5 m within occupied nests, 0–5 m within abandoned nests)

Sampling strategy

Collecting of soil samples was done during the austral summers of 1998–1999 (end of November) and 2004–2005 (beginning of January). In both summers, the sampling was performed under similar weather conditions (temperature around 7°C, sunny conditions, no precipitation). Six nests were chosen randomly (i.e. scattered within the albatros colony) on the nesting ground at Pointe Basse—three occupied at the moment of the sampling (N1/N3/N5) and three abandoned for at least several years (N2/N4/N6) (confirmed by the resident ornithologists, although the exact year of abandoning is unknown). Two more nests were sampled at Bollard, one occupied (N7) and one abandoned (N10). Soil samples (the upper 3 cm of the soil) were collected every 50 cm along the approach routes of the albatrosses towards their nests. At the abandoned nests, a first sample was taken on the nest itself (N2.0/N4.0/N6.0/N10.0). At each nesting area, four control samples (Pointe Basse:C1/C2/C3/C4, Bollard:C5/C6/C7/C8) were collected minimally 500 m from the nearest albatross nests in soils showing similar chemical and vegetational characteristics to soils located far away from any bird colonies (Van de Vijver et al. 2002b). An overview of sampling strategy is shown in Table 1.

All soil samples were stored in 25 ml PVC bottles and fixed immediately with 3% formaldehyde. A complete physicochemical analysis of several soil samples (taken every 100 cm) was carried out in the laboratory. The soil material was treated for chemical analysis following the method of the Dutch Normalisation Institute (Van de Vijver et al. 2002b). Soil moisture was measured in the field using the Eijkelkamp TRIME-FM, but only in January 2005 at Pointe Basse. This device creates an electromagnetic field between two probes and measures moisture by the Time Domain Reflectometry method (Topp 1980). Probes with a length of 11 and 15 cm were used. The value given by the TRIME is total volume percentage.

Although moisture was not measured at Bollard, the soil had a drier outlook than at Pointe Basse (Van de Vijver,

Table 1 Overview of investigated albatross nests at Pointe Basse and Bollard, Île de la Possession

Nesting area	Nest	State of the nest	Sampling date	Total sample length (m)	Sample codes	Number of samples
Pointe Basse	N1	Occupied	November 1999	8.5	N1.1 → N1.17	17
	N2	Abandoned	November 1999	2.5	N2.0 → N2.5	6
	N3	Occupied	January 2005	7.5	N3.1 → N3.15	15
	N4	Abandoned	January 2005	5	N4.0 → N4.10	11
	N5	Occupied	January 2005	7.5	N5.1 → N5.15	15
	N6	Abandoned	January 2005	5	N6.0 → N6.10	11
	CS	Control	January 2005	–	C1-C4	4
Bollard	N7	Occupied	January 2005	7.5	N7.1 → N7.15	15
	N10	Abandoned	January 2005	5	N10.0 → N10.10	11
	CS	Control	January 2005	–	C5–C8	4

The sampling strategy is shown (*CS* control samples)

Table 2 Measured physicochemical variables of all sampling sites on Bollard peninsula

Sample	pH	Conductivity (µS/cm)	PO_4 (mg/L)	NO_2 (mg/L)	NO_3 (mg/L)	SO_4 (mg/L)	NH_4 (mg/L)	Cl^- (mg/L)	TH (mg/L)
C5	4.6	1,122	30	0.11	0.8	49	16	93	50
C6	4.7	1,136	15	0.07	6	65	29	40	200
C7	4.8	876	155	0.06	2.4	65	51	27	200
C8	4.7	959	230	0.09	3.3	80	59	31	50
N7.1	4.5	883	110	0.01	1.7	10	41	51	500
N7.3	4.4	623	15	0.11	3.9	100	20	27	1,500
N7.6	4.4	1,022	12	0.06	5.5	75	26	47	500
N7.9	4.5	982	43	0.03	9.4	60	43	58	0
N7.12	4.7	1,530	35	0.04	5.5	75	61	75	500
N7.15	4.3	526	28	0	2.5	30	29	26	500
N10.0	3.8	753	150	0.04	0.6	80	13	77	500
N10.3	4.3	1,110	110	0.04	2.4	30	6	110	0
N10.6	4.5	622	70	0.04	4	40	11	60	500
N10.9	4.3	1,045	76	0.01	3.2	65	15	89	500

Moisture values were not measured at Bollard

TH total hardness (mg $CaCO_3$/L)

personal observation). Table 2 lists the results of the physicochemical analysis of the Bollard samples. The results of the Pointe Basse samples are given in Vincke et al. (2007). In summary, soil moisture in the Pointe Basse samples reaches the same values in all samples, without a difference between control samples, occupied and abandoned nests). The specific conductance is always rather high with values ranging from 950 to more than 3,400 µS/cm. pH varies between 4.3 and 6.0. Control samples tend to have a lower pH and lower nutrient values than the soil samples in the colony.

Samples for diatom analysis were dried for 24 h at 45°C, after which a constant dry weight is obtained. The weight of the dried material was measured and recorded for further analysis. Diatom slides were prepared following the method described in Van der Werff (1955). A small sample was treated with H_2O_2 and $KMnO_4$ to remove all organic material. To speed up the reaction, samples were heated on a boiling plate for a short period. Following centrifugation, the resulting clean material was diluted with distilled water to avoid excessive concentrations of diatom valves that might obstruct the counting. Cleaned diatom valves were mounted in Naphrax®. In each sample, a total of 500 diatom valves were counted on random transects using Olympus BX51 microscope equipped with Differential Interference Contrast optics. Light micrographs were taken for a later identification of difficult taxa. Samples and slides are stored at the Department of Bryophyta and Thallophyta of the National Botanic Garden of Belgium in Meise. Identifications and taxonomy were based mainly on Van de Vijver et al. (2002a, 2004). The ecological information of the composing subantarctic taxa was based on Van de Vijver and Beyens (1999b, c) and Van de Vijver et al. (2002a, b).

Data analysis

The Shannon Wiener diversity index ($\log_{10}$-based) (Shannon and Weaver 1949) and the evenness of diatom communities were calculated using the Multivariate Statistical Package (MVSP, Kovach Computing Services 2002). To calculate the degree of turnover in species composition along the approach route of the albatrosses towards their nest, Cody's (1975) beta-diversity measure (bc) was used: $bc = (G + L)/2$, where G is the number of species gained and L is the number of species lost along the transect. Low values of bc indicate low species turnover. To assess relationships among environmental parameters and diversity index, the correlation matrix was calculated using STATISTICA software (version 7.0, StatSoft Inc., Tulsa, OK). Significant correlations were set with $P < 0.05$.

To perform multivariate statistical analyses, only diatom taxa occurring in at least one sample with a relative proportion of 1% or more were included in the analyses. To classify the species data, a hierarchic-agglomerative cluster analysis based on minimum variance strategy with the Squared Euclidean Distance as a dissimilarity measure was performed [MVSP, Kovach Computing Services 2002). Species data were ln-transformed to downweight dominant taxa. Correspondence analysis (CA) was done to reveal the structure of species data. Because the total gradient length was smaller than 2 SD, indicating a linear relationship between variables and species abundance data, principal component analysis (PCA) was used in further analyses (ter Braak and Prentice 1988). PCA was performed to visualize possible patterns within the species data. Also species abundance data were log-transformed to downweight dominant taxa. Ordinations were processed using CANOCO and CanoDraw software (ter Braak and Šmilauer 1998, 2002). Acronyms of diatom species were generated ad hoc. All statistical analyses used in this study are described in full detail in Jongman et al. (1995).

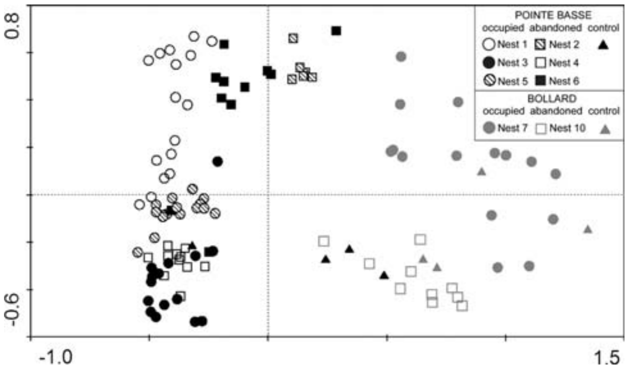

Fig. 2 PCA ordination diagram based on species data. The samples are clearly separated along the first canonical axis to the sites from Pointe Basse (*black symbols*) and Bollard (*gray symbols*). Symbols refer to the state of the nest: *circle* occupied, *square* abandoned, *triangle* control samples

Results

Species composition and diversity

A total of 163 diatom taxa (including species, varieties and formas) belonging to 56 genera have been identified in 108 soil samples. Ninety-eight taxa with a relative abundance ≥1% in at least one sample have been retained for further analysis. A list of all observed diatom taxa is shown in Appendix 1. The principal taxa were *Diadesmis ingeae* Van de Vijver (18% of all counted valves), *Naviculadicta seminulum* Grunow (16%), *Eunotia paludosa* Grunow var. *paludosa* (15%) and *Pinnularia* aff. *divergentissima* Grunow var. *divergentissima* (10%). *Pinnularia* was the most abundant and species-rich genus (30 species and 24% of all counted valves). A small proportion (0.5%) belonged to marine genera such as *Cocconeis*, *Fragilariopsis*, *Thalassionema* and *Thalassiosira*.

The mean species number per sample was 23 ± 9. The lowest species richness has been recorded at the control sites from Pointe Basse (7–10 taxa; with the exception of C4, where 22 taxa have been found), whereas the species richness at the Bollard control samples was much higher (32–42 taxa). The highest number of taxa observed in samples from the occupied nest at Bollard was 55 (N7.2/N7.15), but near the abandoned nest (N10.0/N10.3) only 28 taxa were found. At Pointe Basse, no difference in species number between the occupied and the abandoned nests was observed, 32 being the highest number in both groups (N6.0/N3.13). Furthermore, there were no differences in diversity and evenness between the occupied and the abandoned nests at Pointe Basse (mean diversity 2.08 ± 0.13 and 2.18 ± 0.15, mean evenness 0.69 ± 0.03 and 0.73 ± 0.02, respectively; Fig. 1). The only marked change in diversity occurred at the distance of 4 m from the nest, where a sudden decrease was observed both in the occupied (2.26 → 1.81) and, less pronounced, in the abandoned nests (2.14 → 1.94). On the other hand, we found differences in diversity and evenness between the occupied and the abandoned nests at Bollard (mean diversity 2.32 ± 0.53 and 1.01 ± 0.33, mean evenness 0.66 ± 0.12 and 0.36 ± 0.09, respectively; Fig. 1). Low diversity and evenness values at the abandoned nests were caused by the overall dominance of *Diadesmis ingeae*. At Bollard, no diversity decrease was observed at the distance of 4 m from the nests. Diversity value and evenness were significantly correlated with concentration of ammonium nitrogen and sulfate at Pointe Basse, whereas at Bollard, significant correlations were discovered between concentration of nitrite nitrogen and both diversity and species richness. Turnover values (beta-diversity) were rather similar at all distances at the occupied nests (min 0.26, max 0.37), as well as at the abandoned nests (min 0.2, max 0.34). The exception was the abandoned nest 6, where a high degree of turnover (0.67) at 2 → 2.5 m followed by a marked decrease to 0.09 at 3 → 3.5 m was recorded.

Inter-colonial differences, nest status influence and transect influence

Based on the results from the cluster analysis (not shown) all samples could be grouped into two clusters. A first group comprises all samples from Pointe Basse, whereas the second group includes all Bollard samples and the eight control samples. This clear grouping was confirmed by the results of the PCA shown in Fig. 2. The first two canonical axes explained 40.4% of the variability within the species data ($\lambda_1 = 0.279$, $\lambda_2 = 0.126$). The samples from Pointe Basse are grouped on the left part of the graph while on the right-hand side all Bollard and seven of the eight control samples can be found.

The species composition between both nesting sites differed clearly (Table 3, Appendix 1). *Diadesmis ingeae* prevailed within the Bollard samples (on average 41.8%), whereas at Pointe Basse, the species was less important (on

Table 3 Summary of the main taxa from Pointe Basse and Bollard and their relative abundances in the controls, the occupied and the abandoned nests

Taxon name	Pointe Basse			Bollard		
	O	A	C	O	A	C
Diadesmis ingeae	O	X	X	X	X	X
Eunotia paludosa var. *paludosa*	X	X	X	+	o	o
Chamaepinnularia soehrensis var. *muscicola*	o	O	X	o	o	o
Pinnularia aff. *divergentissima* var. *divergentissima*	X	O	o	X	o	o
Naviculadicta seminulum	X	X	o	o	o	+
Chamaepinnularia australomediocris	o	X	−	X	o	o
Adlafia bryophila	O	+	o	+	o	+
Pinnularia subantarctica var. *elongata*	O	O	o	O	o	o
Stauroneis kriegeri	+	+	o	o	o	o
Pinnularia acidicola var. *acidicola*	o	o	−	+	o	o
Navicula arvensis	o	+	+	o	o	o
Chamaepinnularia sp.1	o	o	−	O	o	O
Frankophila maillardii	o	−	−	+	o	O
Planothidium lanceolatum	o	o	−	+	o	O
Stauroforma exiguiformis	o	o	o	+	o	O
Eunotia muscicola var. *muscicola*	−	−	−	+	o	O
Diadesmis crozetikerguelensis	o	o	o	o	O	o
Orthoseira roseana	−	−	−	−	+	−
Staurosira pinnata	o	o	−	o	o	+
Planothidium aueri	o	o	−	o	o	+
Opephora naveana	o	−	−	o	−	+
Pinnularia carteri	o	o	o	+	o	o
Nitzschia aff. tubicola	o	+	−	o	−	o
Marine species	o	o	−	o	o	o
Pinnularia vatii	o	o	o	o	o	o
Pinnularia angliciformis	o	o	o	o	−	o
Pinnularia microstauron var. *nonfasciata*	o	o	o	o	o	−
Pinnularia parakolbei	o	o	−	o	−	−

O occupied nests, *A* abandoned nests, *C* control sites

Mean percentage abundances are shown as symbols *X* >10%, *O* >5 to 10%, + >2 to 5%, o ≤2%, − absent

average 11.5%). It was the dominant species in the abandoned nest of the Bollard samples76%). The control sites were the only samples at Pointe Basse with rather higher relative abundances of this species (19%). The trend is clearly shown in the symbol plot generated by the PCA ordination of species data (Fig. 3a). Other important taxa abundant at Bollard, but not at Pointe Basse, were *Chamaepinnularia* sp.1, *Diadesmis crozetikerguelensis* Le Cohu and Van de Vijver, *Eunotia muscicola* Krasske var. *muscicola*, *Frankophila maillardii* (Le Cohu) Lange-Bertalot, *Planothidium lanceolatum* (Brébisson) Lange-Bertalot and *Stauroforma exiguiformis* (Lange-Bertalot) Flower, Jones and Round. Control samples at Bollard were characterized by a dominance of *D. ingeae* (31%) and *Chamaepinnularia* sp.1 (9%). Marine taxa were five times more abundant in samples from Bollard (1%) than from Pointe Basse (0.2%). *Chamaepinnularia australomediocris* (Lange-Bertalot and Schmidt) Van de Vijver (13%), *C. soehrensis* var. *muscicola* (Petersen) Lange-Bertalot and Krammer (7%) and *Eunotia paludosa* var. *paludosa* (22%) were the important taxa within the abandoned nests at Pointe Basse. *Naviduladicta seminulum* (29%) and *Pinnularia* aff. *divergentissima* var. *divergentissima* (16 %) were mostly present in the occupied nests in this colony. The control sites at Pointe Basse were dominated by *E. paludosa* var. *paludosa* (36%), *C. soehrensis* var. *muscicola* (31%) and *D. ingeae* (19%) (shown in Table 3; Fig. 3b–f). However, in one of the control samples (C4) there were also higher relative abundances of *N. seminulum* and *Navicula arvensis* Hustedt.

Marked differences in species composition between the control samples, the occupied and the abandoned nests were confirmed by the PCA ordination based on only species data from Pointe Basse (Fig. 4). The first two canonical axes explained 44.9% of the variability within the species data ($\lambda_1 = 0.248$, $\lambda_2 = 0.201$). The first axis separated the samples from the occupied nests (N1/N3/N5) to the left part of the graph and the abandoned nests (N2/N6) with the controls (C1/C2/C3) to the right. The abandoned nest N4 was positioned closer to the group of the occupied nests. The control site C4, characterized by a different species composition compared with the other control samples, was located to the left side as well.

A distinct change in species composition has been observed along the main transects towards the nests. Figure 5 presents the relative abundances of the principal taxa with the increasing distance from the nests. The samples taken close (0.5–4 m) to the occupied nests at Pointe Basse were strongly dominated by *Naviculadicta seminulum.* At more distant sites (4–7.5 m), *Eunotia paludosa* var. *paludosa*, *Chamaepinnularia australomediocris* and *C. soehrensis* var. *muscicola* were of higher importance. A different situation was recorded in the abandoned nests at Pointe Basse. The mean relative abundances of *Naviculadicta seminulum* did not exceed 20%, whereas the other above-mentioned taxa prevailed (especially at 3–5 m from the nests). At the occupied nests from Bollard, samples close to the nests (0–4 m) were dominated by *Chamaepinnularia australomediocris* and *Diadesmis ingeae*. At a distance of 4–6 m, the mean relative abundances of *Chamaepinnularia* sp.1, *Pinnularia* aff. *divergentissima*

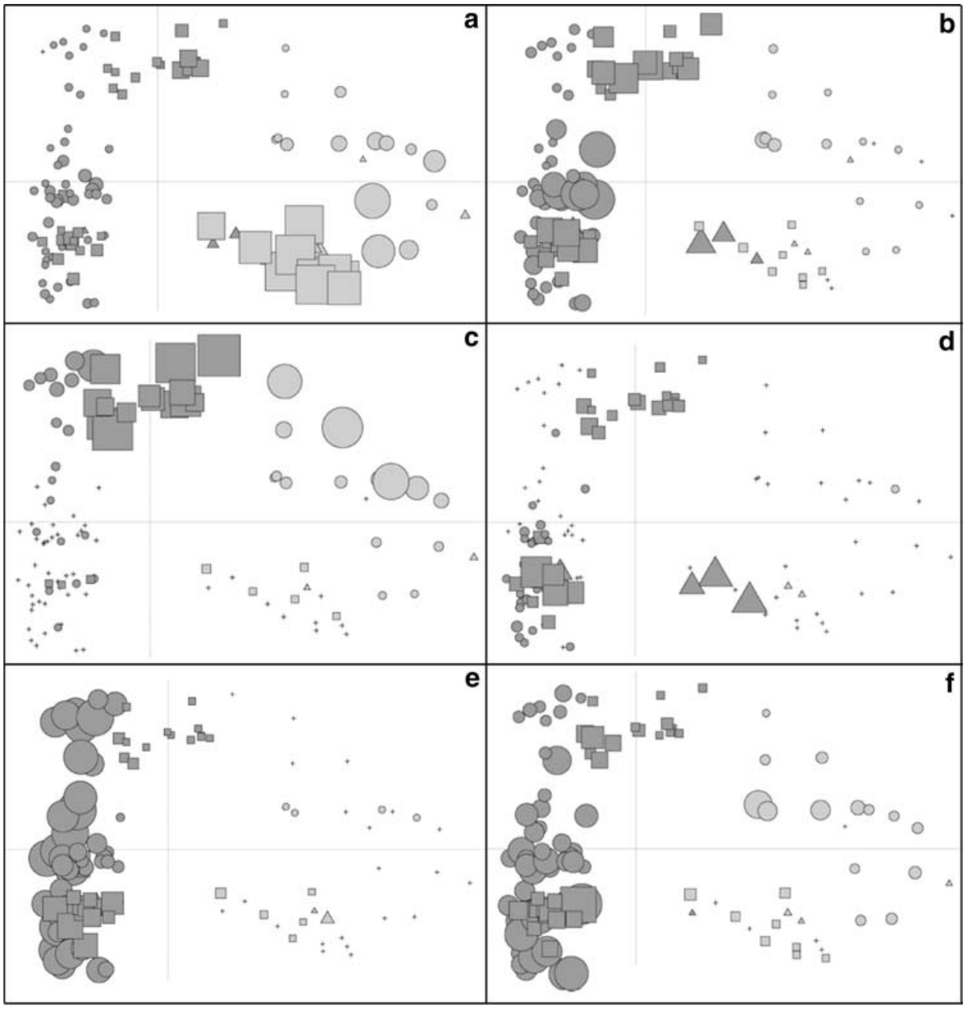

Fig. 3 Symbol plots generated by PCA ordination show the occurrence of some important diatom species within all samples at Pointe Basse (*dark grey symbols*) and Bollard (*light grey symbols*) **a** *Diadesmis ingeae*, **b** *Eunotia paludosa* var. *paludosa*, **c** *Chamaepinnularia australomediocris*, **d** *C. soehrensis* var. *muscicola*, **e** *Navicladicta seminulum*, **f** *Pinnularia* aff. *divergentissima* var. *divergentissima.* Position of samples is the same as in Fig. 2. The species relative abundance values are related to the size of symbols, *cross* indicates species absence in the sample. *Symbols* refer to the state of the nest: *circle* occupied, *square* abandoned, *triangle* control samples

var. *divergentissima* and *P. subantarctica* var. *elongata* (Manguin) Van de Vijver and Le Cohu increased. The most distant sampling sites (6–7.5 m) were strongly dominated by *Diadesmis ingeae* (32–76%). This taxon prevailed also all around the abandoned nest at Bollard, where its mean relative abundances varied between 54–87%.

Discussion

Species composition and diversity

The rather high number of 163 taxa identified in this study is in accordance to the species richness of the diatom flora investigated on Île de la Possession (Van de Vijver and Beyens 1998; Van de Vijver et al. 2002b) and other subantarctic islands (Van de Vijver and Beyens 1996, 1999b; Van de Vijver et al. 2001, 2004, 2008). The relatively high species richness contrasts with the Antarctic inland diatom flora**,** which exhibits much lower numbers of taxa (Sabbe et al. 2003; Gibson et al. 2006; Ohtsuka et al. 2006). However, this is a normal phenomenon related to the typical decrease in species richness when moving southwards (Jones 1996; Van de Vijver and Beyens 1999a).

Many of the dominant taxa identified in this study are considered to be typically subantarctic, such as *Chamaepinnularia australomediocris*, *Chamaepinnularia* sp.1, *Frankophila maillardii*, *Planothidium aueri* (Krasske) Lange-Bertalot. *Diadesmis ingeae*, the most abundant species within the investigated sites, is found on almost all other Antarctic locations and it is one of the most common terrestrial diatoms (Van de Vijver et al. 2002a; Fermani et al. 2007). It usually co-occurs with other subantarctic *Diadesmis* taxa preferring similar soil conditions, such as *D. crozetikerguelensis*, observed mainly near the abandoned nests at Bollard. The distribution of some *Pinnularia* taxa is restricted only to subantarctic islands such as the

Crozet Archipelago, Kerguelen, South Georgia and the Prince Edward Islands (*P. acidicola* var. *acidicola* Van de Vijver and Le Cohu, *P. angliciformis* Van de Vijver and Beyens, *P. vatii* Van de Vijver and Beyens), often being the most abundant and species-rich genus within sub-Antarctic diatom communities (Van de Vijver and Beyens 1996; Van de Vijver et al. 2001, 2002b, 2004). During this study, several fairly large populations of an unusual *Pinnularia,* identified as *P.* aff. *divergentissima* var. *divergentissima,* were found. However, detailed comparison of the type material of the real *P. divergentissima* (Grunow) Cleve and the Crozet specimens revealed a number of taxonomic differences making clear that the Crozet populations represent one single species that cannot be attributed to *P. divergentissima*. On the neighboring islands (Prince Edwards Island, Kerguelen Archipelago, Heard Island), other populations of this *P.* aff. *divergentissima* var. *divergentissima* have been analyzed and they seem to be conspecific. The taxonomical and ecological description of this species will be published elsewhere.

Marine taxa found in our samples were transported to the island by albatrosses hunting for food on the ocean. These birds spend a great amount of time on the sea surface diving for prey and can, therefore, transport frustules of marine diatoms on their feathers (Croll and Holmes 1982; Holmes and Croll 1982) and legs. The highest proportion of marine taxa was found around the occupied nests both at Pointe Basse (0.3%) and at Bollard (1.4%);

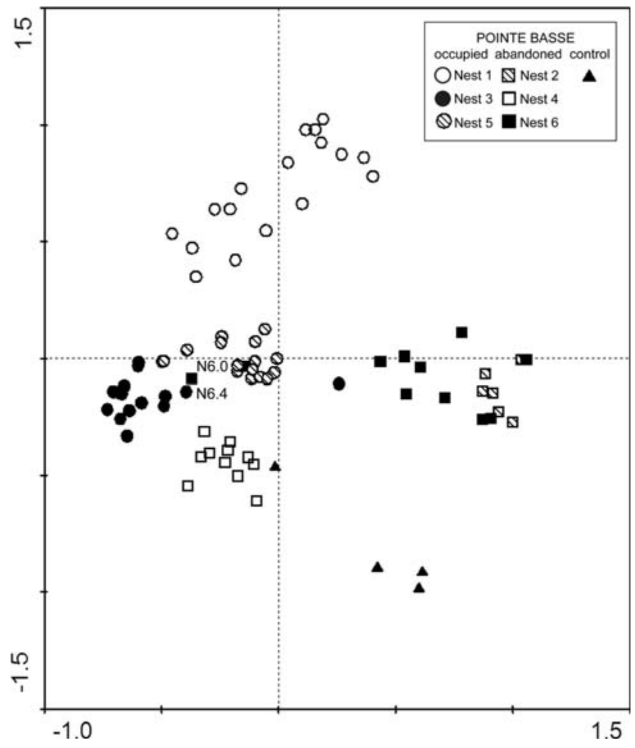

Fig. 4 PCA ordination of species data from Pointe Basse. The first canonical axis represents the intensity of albatross nesting activities and separates the group of the occupied nests and the group of the abandoned nests with the controls to the opposite sides of the *graph*. *Symbols* refer to the state of the nest: *circle* occupied, *square* abandoned, *triangle* control samples

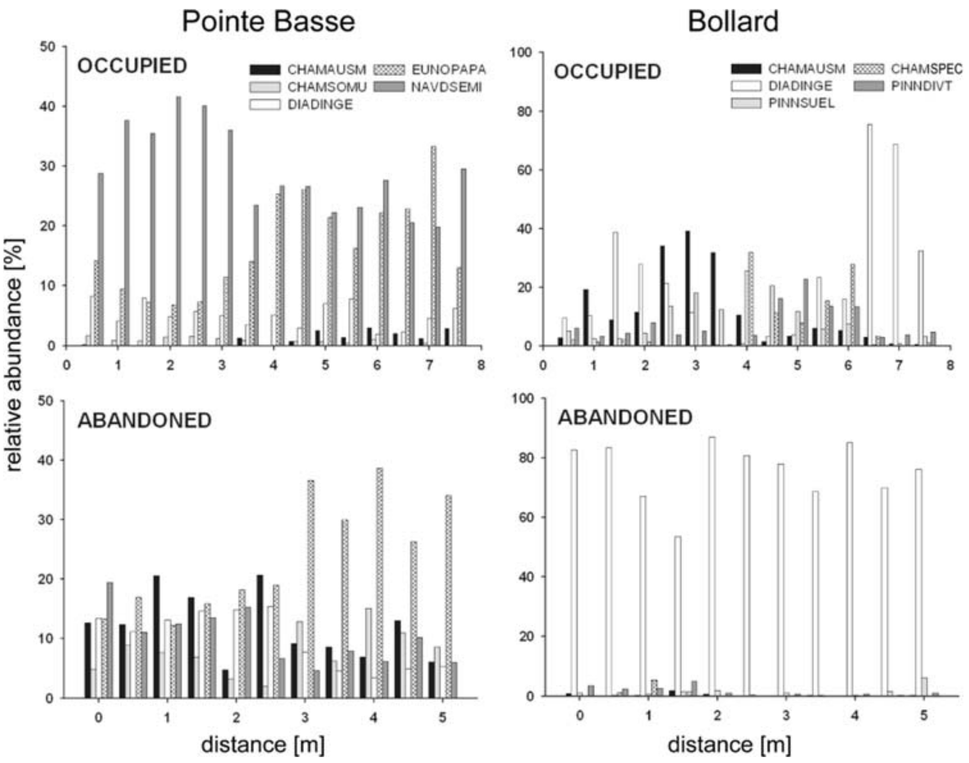

Fig. 5 Mean relative abundances of the most important taxa (separately from Pointe Basse and Bollard) and their changes along the approach routes of albatrosses towards the nests. The *x* axis presents the distance from the nest (in m; 0.5–7.5 m within the occupied nests, 0–5 m within the abandoned nests)

the highest relative abundances (2.6–3.8%) were recorded in the vicinity of the occupied nest N7 at Bollard (N7.1/N7.2/N7.4). It is, however, difficult to explain why these species were more abundant at Bollard since the area is well protected to the sea spray and less influenced by the nesting birds. Both areas are located very close to the sea (<100 m) and are situated on a relatively high cliffs, although the strong winds might blow sea spray up to the nesting sites. To detect whether the albatrosses are the main source of marine taxa around the nesting sites, it will be necessary to examine more closely the amount of diatoms transported on feathers and legs. Because this will imply a quite stressful manipulation of the birds with possible mortality risk, this will be very hard to undertake. Moreover, more nests need to be examined at the Bollard site, to make sure that the amount of marine diatoms found around the nests was a coincidence rather than the general rule.

The lowest diversity was observed around the abandoned nest N10 at Bollard and in the control samples from Pointe Basse. In both cases, it was caused due to the overall dominance of one or a few taxa (*Diadesmis ingeae* in N10, *Chamaepinnularia soehrensis* var. *muscicola*, *D. ingeae* and *Eunotia paludosa* var. *paludosa* in C1/C2/C3/C4). A similar feature was formerly described by Van de Vijver and Beyens (1998), who found communities dominated by *D. ingeae* (formerly *D. contenta*) in drier soils. The species is considered to prefer relatively dry soils (moisture content <40%) and temporarily dry mosses (Van de Vijver et al. 2002c). Moreover, in the latter study, *C. soehrensis* var. *muscicola* and *E. paludosa* var. *paludosa* prevailed in acid, nutrient-poor soils. Similarly, the control sites at Pointe Basse showed very low pH values (median 4.4) and low concentrations of phosphate (median 27 mg/L), nitrate nitrogen (median 3.2 mg/L) and ammonium nitrogen (median 0.2 mg/L).

Inter-colonial differences

The results of the inter-colonial comparison show clearly that it is almost impossible to identify a single diatom community typical for albatross-influenced areas. The samples from Pointe Basse and Bollard were separated by the cluster analysis into two distinct groups. Both nesting areas differ considerably in general environmental characteristics as well as in the number of albatross breeding pairs (see "Materials and methods"). At Pointe Basse, all 250 nests are concentrated on a relatively small area (about 150,000 m^2) compared with Bollard, where around 50 nests are scattered on 200,000 m^2. Consequently, the soil from the albatross colony at Pointe Basse is more influenced by the nesting activities and the subsequent nutrients enrichment by excrements, food detritus, etc. Furthermore, bird activities around their nests (e.g. removing of the moss and the upper soil layers creating shallow basins) provide suitable conditions to keep and enhance the moisture of the soil (Vincke et al. 2007). The mean moisture value in samples around the occupied nests at Pointe Basse was 71 ± 4.9%, whereas it was much lower around the abandoned nests (49.6 ± 7.3%) and at control sites (54.9 ± 11.9%). Furthermore, other taxa usually found in dry- or semi-wet soils, such as *Diadesmis crozetikerguelensis*, *Frankophila maillardii*, *Orthoseira roeseana* (Rabenhost) O'Meara, *Pinnularia borealis* var. *scalaris* (Ehrenberg) Rabenhorst, *P. carteri* Krammer, *Planothidium lanceolatum* (according to Van de Vijver et al. 2002a, b) were of higher importance at Bollard (12.6% altogether) than at Pointe Basse (0.5%). Several abundant taxa preferring wet soils were also observed at Bollard (*Chamaepinnularia australomediocris*, *Pinnularia acidicola* var. *acidicola*, *P.* aff. *divergentissima* var. *divergentissima*, *Stauroforma exiguiformis*, *Staurosira pinnata* Ehrenberg), but usually only in minor abundances, mainly around occupied nests (Table 3). On the other hand, samples at Pointe Basse were dominated by taxa typical for wet soils such as *Adlafia bryophila*, *Chamaepinnularia australomediocris*, *C. soehrensis* var. *muscicola*, *Eunotia paludosa* var. *paludosa*, *Navicula arvensis*, *Nitzschia* aff. *tubicola*, *Pinnularia microstauron* var. *nonfasciata* Krammer, *P.* aff. *divergentissima* var. *divergentissima* and *P. vatii* (Van de Vijver et al. 2002a, b).

The proportion of eutraphentic species (as considered by Krammer and Lange-Bertalot 1986 and Van de Vijver et al. 2002a) was markedly higher at Pointe Basse than at Bollard: *Naviculadicta seminulum*, *P.* aff. *divergentissima* var. *divergentissima*, *P. microstauron* var. *nonfasciata* and *P. subantarctica* var. *elongata* together accounted for 42.3% of all counted valves, whereas at Bollard this is only 10.5%. *Pinnularia parakolbei*, typically recorded from soils affected by animal nutrients input such as penguin rookeries (Van de Vijver and Beyens 1999b; Van de Vijver et al. 2002a) reached its highest abundances at the samples closest to the occupied nests at Pointe Basse (N1.4/N3.2/N3.5/N5.2/N5.4), but it was almost completely absent at Bollard.

The influence of nest status

Although no marked differences in diversity and evenness between occupied and abandoned nests were found, the qualitative species composition itself reflected the nest status (Fig. 4). Diatoms are known to be sensitive to changes in the nutrient status of their environment. Most species have well-defined ecological preferences making them excellent indicators of various environmental stresses such as eutrophication (Kelly et al. 1995; Schönfelder et al. 2002; Poulíčková et al. 2004; Salomoni et al. 2006) and acidification (Coring 1996; Andrén and Jarlman 2006; Sienkiewicz et al. 2006, etc.). This affinity for the nutrient status of their environment is reflected in the species composition around the albatross nests with a clear separation between abandoned and occupied nests, although the results need to be interpreted with caution. *Chamaepinnularia australomediocris*, for instance, usually occurs in soils with low-nutrient concentrations (Van de Vijver et al. 2002a). In the studied samples however, the species reached its highest relative abundances around the abandoned nests at Pointe Basse but also in samples from the vicinity of the occupied nests (up to 4 m) at Bollard. It is possible that the influence of the nesting at Bollard was lower than at Pointe Basse, providing thus suitable environmental conditions for the species. However, this vision is not entirely supported by the physicochemical data (for instance by the very high NH_4–N values at the Bollard sites). Other taxa abundant around the abandoned nests at Pointe Basse as well as close to the occupied nests at Bollard were: *Diadesmis ingeae*, *Pinnularia* aff. *divergentissima* var. *divergentissima*, and *P. subantarctica* var. *elongata* (Table 3; Fig. 5). *Chamaepinnularia soehrensis* var. *muscicola* and *Eunotia paludosa* var. *paludosa* prefer very wet soils (>90%; according to Van de Vijver et al. 2002a, b) with low pH and rather low or moderate conductivity values. The two taxa are known to dominate soil or moss acidophilic communities (Van de Vijver and Beyens 1998, 1999c; Van de Vijver et al. 2004). Therefore, they prevailed at the control sites and around the abandoned nests from Pointe Basse.

The obtained results show that it might even be possible to determine whether a nest has been abandoned only recently or already for a long time, although based on only one result, it is difficult to generalize the result. The increased relative abundances of several eutraphentic taxa (*Naviculadicta seminulum*, *P.* aff. *divergentissima* var. *divergentissima*, *P. subantarctica* var. *elongata*) in the samples of nest N4 indicate, that the nest probably has been abandoned only recently since the effect of nesting activities (especially enhanced nutrient levels) still had a visible influence on the species composition. The same pattern was confirmed by Vincke et al. (2007) in a parallel study of testate amoebae. They found taxa characteristic for both highly and poorly influenced communities around nest N4. They also observed a higher impact of nesting in the samples close to the nest N6 (N6.0/N6.1/N6.2). Similarly in this study, a PCA ordination based on diatom species data separated samples N6.0 and N6.4 as highly affected by the bird nesting (see Fig. 4).

Turn-over along transects

The diversity did not vary markedly along the transect from the nest, apart from one small change. The sudden decrease in diversity at a distance of 4 m from both occupied and abandoned nests at Pointe Basse (Fig. 1) is rather difficult to explain. Most likely, the environmental conditions are unfavorable for both eutraphentic and oligotraphentic species. This is probably the edge of the intensive trampling area around the nest and also the limit of the defecation distance for albatross chicks, which should be followed by a marked change in soil chemistry (Y. Cherel, personal comment). However, no significant differences within the physicochemical data were recorded. Moreover, this trend was not observed in the Bollard samples. This is most probably due to the fact that too many other factors such as microtopography, texture or associated phanerogams have not been investigated here.

Qualitatively, there are, however, changes observed along the transects. Eutraphentic taxa such as *Naviculadicta seminulum* at Pointe Basse, *Pinnularia* aff. *divergentissima* var. *divergentissima*, *P. subantarctica* var. *elongata* and the mesotraphentic *Chamaepinnularia australomediocris* at Bollard, are subsequently replaced by the mesotraphentic *C. australomediocris* and the oligotraphentic species *C. soehrensis* var. *muscicola* and *Eunotia paludosa* var. *paludosa* at Pointe Basse, *Chamaepinnularia* sp.1 and *Diadesmis ingeae* at Bollard when moving away from the nest (Fig. 5). The species turnover is higher around the abandoned nests, when the impact of bird nesting is absent or at least lower due to the absence of a continuous influence.

Based on the results obtained in this study, it is too early to draw sound conclusions on the influence of albatross colonies on the soil diatom composition. Similar studies on the influence of birds on diatoms in the subantarctic region so far do not exist but should be carried out on other islands to confirm the results of the present study.

Acknowledgments The authors wish to thank Dr. Sofie Vincke and Mr. Pieter Ledeganck for sampling and Mrs. Myriam de Haan for the technical assistance with the SEM and sample preparation. Dr. Christine Cocquyt and Dr. Linda Nedbalová are acknowledged for the stimulating discussions. Sampling on Crozet was supported financially and logistically by the French Polar Institute (IPEV) in the framework of the terrestrial program ECOBIO-136 (Ir. Marc Lebouvier and Dr. Y. Frenot) and the program DIVCRO (Prof. Dr. Louis Beyens and Prof. Dr. Ivan Nijs). Ir. Marc Lebouvier and an anonymous reviewer are thanked for their valuable comments that greatly improved the manuscript.

Appendix 1

See Table 4.

Table 4 List of 163 identified diatom taxa with their mean percentage abundances within samples near the abandoned and the occupied nest and at the control sites

Taxon name	Relative abundance (%)					
	Pointe Basse			Bollard		
	O	A	C	O	A	C
Achnanthes muelleri Carlson	o	o	0.1	a	a	a
Achnanthidium minutissumum (Kützing) Czarnecki	o	o	a	0.2	a	0.2
Achnanthidium modestiforme (Lange-Bertalot) Van de Vijver	o	o	a	0.1	a	0.3
Adlafia bryophila (Petersen) Lange-Bertalot	5.3	3.8	0.9	2.2	0.1	4.1
Adlafia bryophiloides (Mangiun) Van de Vijver	o	a	0.1	0.1	a	0.2
Adlafia linearis (Maillard) Van de Vijver	a	a	a	o	a	0.1
Aulacoseira distans (Ehrenberg) Simonsen	a	a	a	o	o	0.3
Caloneis bacillum (Grunow) Cleve	a	a	a	0.1	a	0.3
Caloneis marnieri Manguin	a	a	a	a	a	0.1
Cavinula heterostauron var. *rostrata* (Germain) Van de Vijver	o	a	a	a	a	0.1
Chamaepinnularia aerophila Van de Vijver and Beyens	o	a	a	a	a	a
Chamaepinnularia australomediocris (Lange-Bertalot and Schmidt) Van de Vijver	1.9	12.5	a	9.3	0.3	0.7
Chamaepinnularia evanida (Hustedt) Lange-Bertalot	o	a	a	a	a	a
Chamaepinnularia soehrensis var. *muscicola* (Petersen) Lange-Bertalot and Krammer	0.7	7.5	31.1	0.1	0.1	0.8
Chamaepinnularia sp.1	0.1	0.1	a	4.9	0.7	8.7
Chamaepinnularia sp.2	a	0.2	a	o	a	0.1
Chamaepinnularia sp.3	a	0.2	a	a	a	a
Chamaepinnularia sp.4	a	0.3	a	0.1	a	a
Cyclotella meneghiniana Kützing	a	a	a	o	a	a
Denticula sundayensis Archibald	o	a	a	a	a	a
Diadesmis arcuata (Heiden) Lange-Bertalot	a	a	a	a	o	a
Diadesmis comperei Le Cohu and Van de Vijver	o	o	0.1	0.4	0.4	0.6
Diadesmis costei Le Cohu and Van de Vijver	o	a	a	o	a	0.1
Diadesmis crozetikerguelensis Le Cohu and Van de Vijver	o	o	1.5	0.3	5.5	1.3
Diadesmis ingeae Van de Vijver	5.0	10.7	18.7	18.9	75.6	30.9
Diadesmis langebertalotii Le Cohu and Van de Vijver	o	a	a	0.1	o	0.2
Diadesmis latestriata Van de Vijver, Ledeganck and Beyens	o	a	a	a	a	a
Diadesmis subantarctica Le Cohu and Van de Vijver	a	a	a	0.1	a	a
Diadesmis vidalii Van de Vijver and Ledeganck	o	o	0.1	0.1	o	0.1
Diatomella balfouriana Greville	o	o	a	0.6	o	1.1
Diploneis subovalis Cleve	a	a	a	0.5	o	1.4
Encyonema sp.	o	a	a	o	o	a
Eolimna minima (Grunow) Lange-Bertalot	o	o	a	o	o	0.2
Eunotia muscicola Krasske var. *muscicola*	a	a	a	2.1	0.1	6.6
Eunotia paludosa Grunow var. *paludosa*	16.3	22.0	36.3	4.5	1.4	0.4
Eunotia sp.1	o	a	a	a	a	a
Fragilaria capucina var. *vaucheriae* (Kützing) Lange-Bertalot	a	a	a	0.2	a	0.2
Fragilaria capucina var. *rumpens* (Kützing) Lange-Bertalot	0.1	o	a	0.3	a	a
Fragilaria germanii Reichardt and Lange-Bertalot	o	a	a	0.1	o	0.4
Fragilaria pulchella (Ralfs) Lange-Bertalot	a	a	a	o	a	0.1
Frankophila maillardii (Le Cohu) Lange-Bertalot	o	a	a	4.7	0.6	5.4

Table 4 continued

Taxon name	Relative abundance (%)					
	Pointe Basse			Bollard		
	O	A	C	O	A	C
Frustulia cirisiae Van de Vijver	o	a	a	a	a	a
Frustulia pulchra Germain	a	a	a	o	a	0.1
Frustulia subantarctica Van de Vijver and Beyens	a	a	a	o	a	a
Geissleria paludosa (Hustedt) Lange-Bertalot	a	o	a	o	a	a
Geissleria subantarctica Van de Vijver and Le Cohu	a	a	a	o	a	0.5
Gomphonema affine Kützing var. *affine*	a	a	a	a	a	0.1
Gomphonema exilissimum (Grunow) Lange-Bertalot and Reichardt	a	a	a	a	a	0.4
Gomphonema parvulum Kützing	o	a	a	a	a	a
Gomphonema stonei Reichardt	a	a	a	o	a	a
Gomphonema subantarcticum Van de Vijver and Beyens	o	0.2	a	0.3	a	0.7
Hantzschia amphioxys (Ehrenberg) Grunow	o	a	a	o	o	a
Hantzschia possessionensis Van de Vijver and Beyens	o	o	a	a	o	0.1
Lecohuia geniculata (Germain) Lange-Bertalot	o	a	a	0.1	a	a
Luticola aff. *mutica* (Kützing) Mann	o	o	a	o	o	0.1
Luticola muticopsis (Van Heurck) Mann	o	a	a	o	a	a
Luticola sp.	o	a	a	a	a	a
Luticola suecorum (Carlson) Mann	o	a	a	a	a	a
Mayamaea atomus (Kützing) Lange-Bertalot var. *atomus*	0.2	o	a	0.1	a	a
Mayamaea atomus var. *permitis* (Kützing) Lange-Bertalot	1.2	o	0.1	o	a	a
Mayamaea fossalis (Krasske) Lange-Bertalot var. *fossalis*	a	a	a	a	a	0.4
Muelleria luculenta Spaulding and Kociolek	o	a	a	a	a	a
Navicula arvensis Hustedt	1.3	2.7	2.0	0.3	1.1	0.7
Navicula bicephala Hustedt	1.0	0.2	a	a	a	a
Navicula sp.1	a	o	a	a	a	a
Navicula venetiformis Van de Vijver and Beyens	a	a	a	o	a	a
Naviculadicta elorantana Lange-Bertalot	o	0.2	0.7	0.3	a	a
Naviculadicta seminulum Grunow	29.0	10.9	1.7	4.5	0.9	3.9
Naviculadicta sp.	a	a	0.1	a	a	a
Naviculadicta sp.1	o	a	a	a	a	a
Naviculadicta sp.2	a	a	a	a	0.1	a
Naviculadicta sp.3	o	o	a	a	a	a
Neidium aubertii Manguin	0.2	0.8	a	o	a	0.1
Nitzschia acidoclinata Lange-Bertalot	0.2	0.1	0.1	o	a	a
Nitzschia dissipata (Kützing) Grunow	o	a	a	a	a	a
Nitzschia dissipata var. *media* (Hantzsch) Grunow	a	a	a	o	a	a
Nitzschia frustulum (Kützing) Grunow var. *frustulum*	o	o	a	0.1	a	0.1
Nitzschia palea (Kützing) W. Smith	0.1	0.1	a	0.2	a	0.1
Nitzschia aff. *tubicola* Grunow	o	2.2	a	o	a	0.+
Nitzschia sp.	o	o	a	a	a	a
Opephora naveana Le Cohu	o	a	a	1.2	a	3.1
Orthoseira roeseana (Rabenhorst) O'Meara	a	a	a	a	4.1	a
Pinnularia acidicola var. *acidicola* Van de Vijver and Le Cohu	0.1	0.3	a	5.5	1.8	0.4
Pinnularia acidicola var. *elongata* Van de Vijver and Le Cohu	a	a	a	a	o	a
Pinnularia amae Van de Vijver, Ledeganck and Beyens	o	o	a	a	a	a
Pinnularia angliciformis Van de Vijver and Beyens	1.7	0.1	0.2	0.1	a	0.1

Table 4 continued

Taxon name	Relative abundance (%)					
	Pointe Basse			Bollard		
	O	A	C	O	A	C
Pinnularia borealis var. *scalaris* (Ehrenberg) Rabenhorst	a	o	0.1	0.1	1.1	0.5
Pinnularia bottnica Krammer	0.1	0.1	a	a	a	a
Pinnularia carteri Krammer	o	0.6	2.0	2.5	0.3	0.1
Pinnularia crozetii Van de Vijver and Le Cohu	0.2	0.9	a	a	a	a
Pinnularia aff. *divergentissima* Grunow var. *divergentissima*	15.8	8.3	0.6	11.9	1.5	0.7
Pinnularia divergentissima var. *minor* Krammer	0.1	o	2.2	a	1.1	a
Pinnularia divergentissima var. *subrostrata* Cleve	o	a	a	o	o	a
Pinnularia kerguelensis Heiden and Kolbe	a	o	a	o	a	a
Pinnularia lecohui Van de Vijver	a	a	a	0.2	a	0.2
Pinnularia microstauron (Ehrenberg) Cleve var. *microstauron*	a	a	0.1	o	a	a
Pinnularia microstauron var. *nonfasciata* Krammer	1.7	0.7	0.5	0.1	0.1	a
Pinnularia obscura Krasske	0.8	0.7	a	1.3	a	a
Pinnularia parakolbei Fukushima, Ko-Bayashi and Yoshitake	1.8	0.1	a	o	a	a
Pinnularia rabenhorstii var. *franconica* Krammer	o	a	a	o	a	a
Pinnularia rabenhorstii (Grunow) Krammer var. *rabenhorstii*	o	a	a	a	a	0.1
Pinnularia rabenhorstii var. *raphecurvata* Van de Vijver and Beyens	a	a	a	o	a	a
Pinnularia rabenhorstii var. *subantarctica* Van de Vijver and Le Cohu	o	a	a	a	a	0.1
Pinnularia rhombarea var. *serrata* Van de Vijver and Beyens	o	o	a	o	a	a
Pinnularia similiformis Krammer	a	o	a	a	a	a
Pinnularia subantarctica (Manguin) Van de Vijver and Le Cohu	a	a	a	0.1	a	0.4
Pinnularia subantarctica var. *elongata* (Manguin) Van de Vijver and Le Cohu	8.7	6.2	1.0	7.6	1.3	1.5
Pinnularia subcommutata Krammer	o	a	a	a	a	a
Pinnularia vatii Van de Vijver and Beyens	1.3	2.1	0.2	0.7	0.3	0.1
Pinnularia viridiformis Krammer	a	a	a	o	a	a
Pinnularia viridiformis var. *minor* Krammer	a	a	a	a	a	0.1
Pinnunavis elegans (W. Smith) Okuno	0.1	0.1	a	a	a	a
Pinnunavis genustriata (Hustedt) Lange-Bertalot and Krammer	a	o	a	a	a	a
Planothidium aueri (Krasske) Lange-Bertalot	o	o	a	1.1	0.2	3.2
Planothidium cyclophorum (Heiden) Van de Vijver	o	a	a	0.2	a	0.3
Planothidium delicatulum (Kützing) Round and Bukhtiyarova	a	a	a	0.1	o	a
Planothidium densistriatum Van de Vijver and Beyens	a	a	a	o	a	a
Planothidium lanceolatum (Brébisson) Lange-Bertalot	o	0.3	a	3.7	o	5.2
Planothidium marginostriatum Van de Vijver and Beyens	0.1	o	0.1	a	a	a
Planothidium quadripunctatum (Oppenheim) Sabbe	o	a	a	a	a	a
Planothidium renei (Lange-Bertalot and Schmidt) Van de Vijver	o	0.1	a	0.1	o	0.2
Psammothidium confusum (Manguin) Van de Vijver	o	o	a	0.1	o	0.4
Psammothidium confusum var. *atomoides* (Manguin) Van de Vijver	0.1	a	a	o	o	0.1
Psammothidium confusiforme Van de Vijver and Beyens	0.+	o	a	0.2	o	0.2
Psammothidium germanii (Manguin) Sabbe	o	a	a	o	a	a
Psammothidium incognitum (Krasske) Van de Vijver	a	a	a	o	a	0.1
Psammothidium investians (Carter) Bukhtiyarova	0.2	0.5	a	0.1	a	0.1
Psammothidium manguinii (Hustedt) Van de Vijver	o	o	a	0.1	a	0.3
Psammothidium stauroneioides (Manguin) Bukhtiyarova	o	a	a	o	a	0.1
Psammothidium therezienii (Le Cohu and Maillard) Van de Vijver	a	a	a	a	o	a
Rhopalodia rupestris (W. Smith) Krammer	o	a	a	0.1	a	a

Table 4 continued

Taxon name	Relative abundance (%)					
	Pointe Basse			Bollard		
	O	A	C	O	A	C
Sellaphora subantarctica Van de Vijver and Beyens	0.2	1.3	a	0.1	a	a
Sellaphora tumida Van de Vijver and Beyens	o	o	a	a	a	0.1
Stauroforma exiguiformis (Lange-Bertalot) Flower, Jones and Round	0.1	0.1	0.2	3.4	0.1	6.6
Stauroneis kriegeri Patrick	3.4	2.4	0.1	o	0.1	0.1
Stauroneis pseudomuriella Van de Vijver and Lange-Bertalot	a	a	a	o	a	a
Stauroneis pseudosmithii Van de Vijver and Lange-Bertalot	a	a	a	a	a	0.1
Staurosira circula Van de Vijver and Beyens	a	a	a	o	a	a
Staurosira construens (Ehrenberg) Williams and Round	o	a	a	a	a	a
Staurosira pinnata Ehrenberg	o	o	a	1.6	0.1	3.2
Staurosira venter (Ehrenberg) Cleve and Möller	o	a	a	a	a	0.6
Surirella angusta var. *constricta* Hustedt	a	a	a	a	a	a
Marine species						
Anaulus sp.	o	a	a	a	a	a
Berkeleya sp.	o	a	a	a	a	a
Cocconeis californica var. *kerguelensis* Heiden	o	a	a	a	a	a
Cocconeis costata Gregory	o	o	a	0.2	a	0.3
Cocconeis spp.	o	o	a	0.2	a	a
Coscinodiscus sp.	a	a	a	a	a	a
Fragilariopsis angulata (O'Meara) Hasle	o	o	a	0.1	0.1	0.1
Fragilariopsis kerguelensis (O'Hara) Hustedt	o	o	a	0.4	0.1	0.2
Gomphonemopsis littoralis (Hendey) Medlin	o	a	a	a	a	a
Grammatophora sp.	o	a	a	a	a	a
Licmophora sp.	o	o	a	o	a	a
Navicula perminuta group	o	a	a	0.2	o	0.3
Opephora sp.	o	a	a	a	a	a
Parlibellus sp.	o	a	a	o	a	a
Pseudogomphonema sp.	o	a	a	a	a	a
Rhabdonema sp.	a	a	a	a	a	0.1
Rhoicosphenia sp.	o	a	a	o	a	0.1
Tabularia fasciculata (Agardh) Williams and Round	o	a	a	o	a	a
Thalassionema nitzschioides (Grunow) Mereschkowsky	0.1	o	a	0.3	0.2	0.2
Thalassiosira gracilis var. *expecta* (VanLandingham) Fryxell and Hasle	o	a	a	a	a	a
Thalassiosira sp.	o	o	a	0.2	o	0.1

a absent, *o* <0.1%

References

Andrén CM, Jarlman A (2006) Stream water quality and acidity classified by benthic diatoms. In: Ács É, Kiss KT, Padisák J, Szabó KÉ (eds) 6th International symposium use of algae for monitoring rivers, Hungarian Algological Society, Göd, Hungary

Cody ML (1975) Towards a theory of continental species diversity bird distributions over Mediterranean habitat gradients. In: Cody ML, Diamond JM (eds) Ecology and evolution of communities. Harvard University Press, Cambridge, pp 214–257

Coring E (1996) Use of diatoms for monitoring acidification in small mountain rivers in Germany with special emphasis on "diatom assemblage type analysis" (DATA). In: Whitton BA, Rott E (eds) Use of algae for monitoring rivers II. Institüt für Botanik, Univ. Innsbruck, , pp 7–16

Croll DA, Holmes RW (1982) A note on the occurence of diatoms on the feathers of diving seabirds. Auk 99:765–766

Fermani P, Mataloni G, Van de Vijver B (2007) Soil microalgal communities on an antarctic active volcano (Deception Island, South Shetlands). Polar Biol 30:1381–1393

Frenot Y (1986) Interactions entre la faune lombricienne et les sytèmes édaphiques d'une île subantarctique: l'Ile de la Possession, archipel Crozet. PhD Thesis, Université de Rennes1, 358 p

Gibson JAE, Roberts D, Van de Vijver B (2006) Salinity control of the distribution of diatoms in lakes of the Bunger Hills, East Antarctica. Polar Biol 29:694–704

Gremmen NJM, Van de Vijver B, Frenot Y, Lebouvier M (2007) Distribution of moss-inhabiting diatoms at sub-Antarctic Îles Kerguelen. Antarct Sci 19:17–24

Holmes RW, Croll DA (1982) Initial observations on the composition of dense diatom growths on the body feathers of three species of diving seabirds. In: Holmes RW, Crawford RM, Round FE (eds) 7th Diatom symposium, Philadelphia, pp 265–277

Joly Y, Frenot Y, Vernon P (1987) Environmental modifications of a subantarctic Peat-Bog by the wandering Albatross (*Diomedea exulans*): a preliminary study. Polar Biol 8:61–72

Jones VJ (1996) The diversity, distribution and ecology of diatoms from Antarctic inland waters. Biodivers Conserv 5:1433–1449

Jongman RH, ter Braak CJF, van Tongeren OFR (1995) Data analysis in community and landscape ecology. Pudoc, Wageningen. Cambridge University Press, Cambridge

Kelly MG, Penny CJ, Whitton BA (1995) Comparative performance of benthic diatom indices used to assess river water quality. Hydrobiologia 302:179–188

Kovach Computing Services (2002) Multivariate statistical package, version 3.1. Users manual. Kovach Computing Services, Pentraeth

Krammer K, Lange-Bertalot H (1986) Bacillariophyceae. 1. Teil. In: Ettl H, Gerloff J, Heynig H, Mollenhauer D (eds) Süsswasserflora von Mitteleuropa 2/1. G Fischer Verlag, Stuttgart, pp 1–876

Lebouvier M, Frenot Y (2007) Conservation and management in the French sub-Antarctic islansd and surrounding seas. Pap Proc Roy Soc Tasm 141:23–28

Michel RFM, Schaefer CEGR, Dias LE, Simas FNB, de Sá Mendonça E (2006) Ornithogenic gelisols (Cryosols) from Maritime Antarctica: pedogenesis, vegetation and carbon studies. Soil Sci Soc Am J 70:1370–1376

Ohtsuka T, Kudoh S, Imura S, Ohtani S (2006) Diatoms composing benthic microbial mats in freshwater lakes of Skarvsnes ice-free area, East Antarctica. Polar Biosci 20:113–130

Poulíčková A, Duchoslav M, Dokulil M (2004) Littoral diatom assemblages as bioindicators of lake trophic status: A case study from perialpine lakes in Austria. Eur J Phycol 39:143–152

Sabbe K, Verleyen E, Hodgson DA, Vanhoutte K, Vyverman W (2003) Benthic diatom flora of freshwater and saline lakes in the Larsemann Hills and Rauer Islands, East Antarctica. Antarct Sci 15:227–248

Salomoni SE, Rocha O, Callegaro VL, Lobo EA (2006) Epilithic diatoms as indicators of water quality in the Gravataí river, Rio Grande do Sul, Brazil. Hydrobiologia 559:233–246

Schönfelder I, Gelbrecht J, Schönfelder J, Steinberg CEW (2002) Relationship between littoral diatoms and their chemical environment in Northeastern German lakes and rivers. J Phycol 38:66–82

Shannon CE, Weaver W (1949) The mathematical theory of communication. Urbana University Press, Urbana, IL

Sienkiewicz E, Gąsiorowski M, Hercman H (2006) Is acid rain impacting the Sudetic lakes? Sci Total Environ 369:139–149

Smith VR (1978) Animal-plant-soil nutrient relationships on Marion Island (Subantarctic). Oecologia 32:239–253

Smith VR (1979) The influence of seabird manuring on the phosphorus status on Marion Island (Subantarctic) soils. Oecologia 41:123–126

Tatur A, Myrcha A (1984) Ornithogenic soils on King George Island. Polish Pol Res 5:31–60

ter Braak CJF, Prentice IC (1988) A theory of gradient analysis. Adv Ecol Res 18:271–317

ter Braak CJF, Šmilauer P (1998) CANOCO Reference Manual and Users Guide to Canoco for Windows: Software for Community Ordination (Version 4). Microcomputer Power, Ithaca, NY

ter Braak CJF, Šmilauer P (2002) CANOCO Reference Manual and Users Guide to Canoco for Windows: Software for Canonical Community Ordination (Version 4.5). Microcomputer Power, Ithaca, NY

Topp GC (1980) Electromagnetic determination of soil watercontents: measures in coaxial transmission lines. Water Res 16:574–582

Tyler PA (1996) Endemism in freshwater algae, with special reference to the Australian region. In: Kristiansen J (ed) Biogeography of freshwater algae. Hydrobiologia 336:127–135

Van de Vijver B, Beyens L (1996) Freshwater diatom communities of the Strømness Bay area, South Georgia. Antarct Sci 8:359–368

Van de Vijver B, Beyens L (1998) A preliminary study on the soil diatom assemblages from Ile de la Possession (Crozet, Subantarctica). Eur J Soil Biol 34:133–141

Van de Vijver B, Beyens L (1999a) Biogeography and ecology of freshwater diatoms in Subantarctica: a review. J Biogeogr 26:993–1000

Van de Vijver B, Beyens L (1999b) Freshwater diatoms from Ile de la Possession (Crozet Archipelago, sub-Antarctica): an ecological assessment. Polar Biol 22:178–188

Van de Vijver B, Beyens L (1999c) Moss diatom communities from Ile de la Possession (Crozet, Subantarctica) and their relationship with moisture. Polar Biol 22:219–231

Van de Vijver B, Mataloni G (2008) New and interesting species in the genus *Luticola* D.G. Mann (Bacillariophyta) from Deception Island (South Shetland Islands). Phycologia 47:451–467

Van de Vijver B, Ledeganck P, Beyens L (2001) Habitat preferences in freshwater diatom communities from sub-Antarctic Îles Kerguelen. Antarct Sci 13:28–36

Van de Vijver B, Frenot Y, Beyens L (2002a) Freshwater diatoms from Ile de la Possession (Crozet Archipelago, Subantarctica). Bibl Diatomol 46:1–412

Van de Vijver B, Ledeganck P, Beyens L (2002b) Soil diatom communities from Ile de la Possession (Crozet, sub-Antarctica). Polar Biol 25:721–729

Van de Vijver B, Ledeganck P, Beyens L (2002c) Three new species of *Diadesmis* from soils of Ile de la Possession (Crozet Archipelago, Subantarctic). Cryptogamie Algol 23(4):333–341

Van de Vijver B, Beyens L, Vincke S, Gremmen NJM (2004) Moss-inhabiting diatom communities from Heard Island, sub-Antarctic. Polar Biol 27:532–543

Van de Vijver B, Gremmen NJM, Beyens L (2005) The genus *Stauroneis* (Bacillariophyceae) in the Antarctic region. J Biogeogr 32:1791–1798

Van de Vijver B, Gremmen NJM, Smith V (2008) Diatom communities from the subantarctic Prince Edward Islands: diversity and distribution patterns. Polar Biol 31:795–808

Van der Werff A (1955) A new method of cleaning and concentrating diatoms and other organisms. Verh Internat Verein Theor Angew Limnol 12:276–277

Vanormelingen P, Verleyen E, Vyverman W (2008) The diversity and distribution of diatoms: from cosmopolitanism to narrow endemism. Biodivers Conserv 17:393

Vidal E, Médail F, Tatoni T, Roche P, Vidal P (1998) Impact of gull colonies on the flora of the Riou Archipelago (Mediterranean islands of south-east France. Biol Conserv 84:235–243

Vidal E, Médail F, Tatoni T, Bonnet V (2000) Seabirds drive plant species turnover on small Mediterranean islands at the expense of native taxa. Oecologia 122:427–434

Vidal E, Jouventin P, Frenot Y (2003) Contribution of alien and indigenous species to plant-community assemblages near penguin rookeries at Crozet Archipelago. Polar Biol 26:432–437

Vincke S, Van de Vijver B, Ledeganck P, Nijs I, Beyens L (2007) Testacean communities in perturbed soils: the influence of the wandering albatross. Polar Biol 30:395–406

Vyverman W, Verleyen E, Sabbe K, Vanhoutte K, Sterken M, Hodgson DA, Mann DG, Juggins S, Van de Vijver B, Jones V, Flower R, Roberts D, Chepurnov VA, Kilroy C, Vanormelingen P, De Wever A (2007) Historical processes constrain patterns in global diatom diversity. Ecology 88:1924–1931