Freshwater diatom communities from Ile Amsterdam (TAAF, southern Indian Ocean)

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Abstract: Diatom and water chemistry samples were collected during the austral summer of 2007 from lakes, streams and bogponds on Ile Amsterdam (TAAF), a small island located in the southern Indian Ocean. A diverse diatom flora of 104 taxa was found, dominated by several *Pinnularia* taxa, *Frustulia lebouvieri*, *Kobayasiella subantarctica*, *Eunotia paludosa*, *E. muscicola* and *Planothidium subantarcticum*. Biogeographically, the Ile Amsterdam freshwater diatom flora is composed of cosmopolitan, sub–Antarctic and endemic elements. The biogeographical analysis showed that almost 17% of all observed taxa can be considered endemic to Ile Amsterdam with an additional 14% showing an exclusive sub–Antarctic distribution. The flora can be considered as typical for oceanic islands based on its disharmonic composition with several genera lacking and other being overrepresented.

Canonical Component Analysis was used to classify the samples based on their chemical characteristics, revealing that, specific conductance, sulphate and pH were the main factors dividing the samples into four different groups. The geological history of the island in combination with the climate and the specific environmental features of the main habitat in the Caldera most likely shaped the composition of the actual diatom communities.

Key words: Bacillariophyta, biogeography, ecology, Ile Amsterdam, southern Indian Ocean, sub–Antarctic region

Introduction

Diatoms (Bacillariophyceae) are one of the most abundant and species–rich algal groups in freshwater and terrestrial ecosystems in the (sub–)Antarctic region (Jones 1996; Van de Vijver & Beyens 1999a; Sabbe et al. 2003). The past few years, there has been an increasing effort in revising the freshwater and limno–terrestrial diatom flora of the entire (sub–) Antarctic region. Especially the diatom flora on the islands in the southern Indian Ocean has been the subject of intensive taxonomic studies (a.o. Romero & Van de Vijver 2011; Van de Vijver et al. 2002a, 2002b, 2011, 2013; Witkowski et al. 2012) followed by detailed ecological surveys of the diatom communities inhabiting these islands [e.g., Iles Kerguelen (Van de Vijver et al. 2001); Iles Crozet (Van de Vijver & Beyens 1999b; Van de Vijver et al. 2002a), Heard Island (Van de Vijver et al. 2004a) and the Prince Edward Islands (Van de Vijver et al. 2008a)].

The results of these studies clearly indicated the presence of a highly specific diatom flora on all investigated islands containing a large number of species with a very restricted, even sometimes endemic distribution, contrary to the generally accepted ideas about the cosmopolitan nature of micro–organisms worldwide (Finlay & Clarke 1999).

Just north of the sub–Antarctic islands in the southern Indian Ocean, two small volcanic islands can be found, Ile Amsterdam (77°30'E, 37°50'S) and Ile Saint Paul (77°31' E, 38°41'S). The first results of a survey on the terrestrial and freshwater diatoms of Ile Amsterdam have been published in 1999 (Van de Vijver & Beyens 1999c) reporting 90 taxa from 24 samples. Based on these results, two sampling campaigns have been undertaken in 1999 and 2007 in order to investigate in–depth the diatom flora of both islands. A new *Luticola* species was published based on material collected in 1999 from Ile Saint Paul (Van de Vijver et al. 2002b). In 2008, a paper describing three *Eunotia* Ehrenberg species was published (Van de Vijver et al. 2008b) followed by the description of a new genus, *Microfissurata* Lange–Bertalot, Cantonati et Van de Vijver, based on two species of which one was found on Ile Amsterdam (i.e. *Microfissurata australis* Van

DE VIJVER et LANGE–BERTALOT; CANTONATI et al. 2009). Several years later, 23 different *Pinnularia* EHRENBERG taxa have been observed during a taxonomic analysis of aquatic, moss and soil samples, of which twelve did not correspond to any other currently known species and were described as new species (VAN DE VIJVER et al. 2012). Special attention was further given to the different lava tube diatom communities that are present on the island. As a result of this, several unknown taxa were found and described as new for science (VAN DE VIJVER & COX 2013; LOWE et al. 2013). Despite this growing interest and the handful of taxonomic papers, little is known on the ecology and composition of the diatom communities of Ile Amsterdam.

The present paper focusses on the ecological preferences of the freshwater diatom flora of Ile Amsterdam, its biogeographical position within the southern Indian Ocean Province, and the different diatom communities on the island in relation to several habitat characteristics.

MATERIAL AND METHODS

Study Site. Ile Amsterdam is an entirely volcanic island located in the southern Indian Ocean, halfway between the African continent and Australia (Fig. 1) and is one of the most remote and isolated oceanic islands in the world. The island, with a total surface of 55 km², presents the shape of a small cone culminating at 881m (Mont de la Dives) and is geologically spoken, very young, with its main part arisen during the period 400–200 kyr BP (GIRET 1987, DOUCET 2003). Ile Amsterdam has a temperate oceanic climate with a mean annual temperature of 14.0°C with minimum and maximum temperatures of 11.2 °C in August and 17.4 °C in February respectively (LEBOUVIER & FRENOT 2007). Strong westerly winds are frequent, especially in winter. Relative humidity is generally high (> 80%) due to the frequency of low cloud ceilings. Precipitation, falling primarily as rain, is usually high with an annual average of 1114 mm distributed over more than 220 days at the meteorological station (Martin de Viviès, 27 m a. s. l.); a dry period occurs in summer (c. 70 mm in February). According to a one year record (FRENOT & VALLEIX 1990) in the Caldera at 700 m a.s.l. the mean temperature is lower by 7 °C while the precipitation is almost twice as high.

Permanent waterbodies are restricted to the higher plateau (Caldera, Plateau des Tourbières) in the centre and the west–southwestern part of the island (Falaises d'Entrecasteaux, Grandes Ravines). Almost all other areas lack (semi–permanent) waterbodies due to the steepness of the slope and the permeability of the lava tunnels, holes and fissures. Due to frequent fog and clouds, and high relative humidity in the upper areas (from 500 m a.s.l.), extensive peat formations have been developed, especially in the volcanic caldera (HEGER et al. 2009).

Ile Amsterdam is not truly sub–Antarctic. Nevertheless, on the higher central plateau, the vegetation has a typical sub–Antarctic character consisting of mosses, small ferns [e.g., *Blechnum penna–marina* (POIRET) KUHN], grasses, sedges (e.g., *Uncinia brevicaulis* THOUARS) and *Lycopodium* ssp. (TREHEN et al. 1990). The rather species–poor vegetation

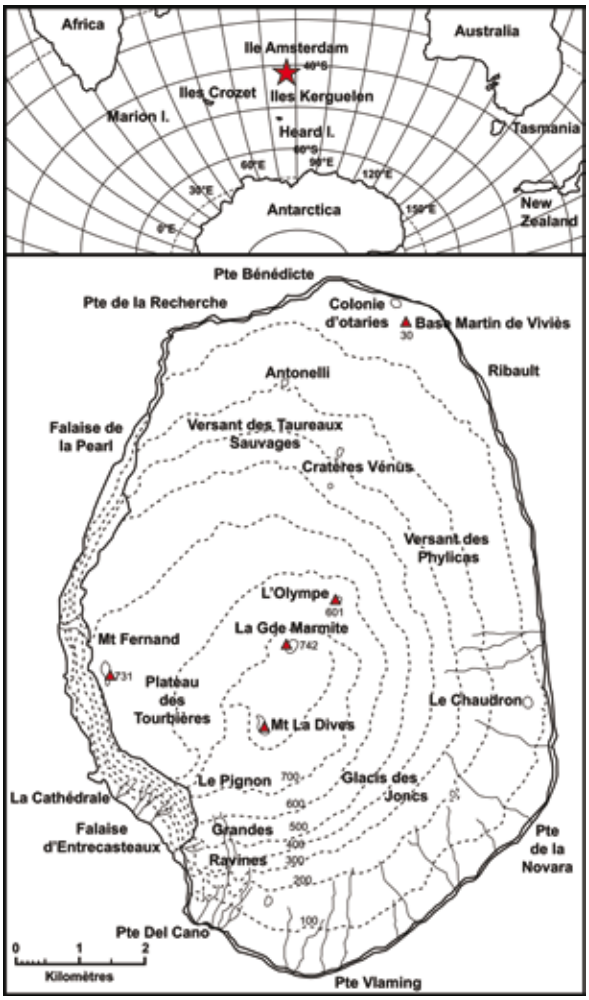

Fig. 1. (a) Location of Ile Amsterdam in the southern hemisphere; (b) Ile Amsterdam with the main topographic indications used in the text.

is dominated by both native (43) and introduced (56) species, reflecting the isolation of the island (FRENOT et al. 2001). The vegetation differs however in two aspects from the other islands in the southern Indian Ocean. The lower part of the island used to be covered by dense *Phylica arborea* THOUARS forests, a native tree restricted to the Tristan da Cunha archipelago and Ile Amsterdam, patches of which are still present on the island. Secondly, the native flora includes also several (endemic) *Sphagnum* species, forming extensive peatlands above 500 m a.s.l. However, *Sphagnum* peatlands are absent on the other sub–Antarctic islands (FLATBERG et al. 2011). Although the diversity of the lichen flora is rather poor (77 species), recently a new lichen species, *Caloplaca amsterdamensis* APTROOT et ERTZ was described (APTROOT et al. 2011).

The endemic fauna is composed of a few marine bird species such as the rare Amsterdam albatross (*Diomedea amsterdamensis* ROUX et al.) and several large fur seal colonies (*Arctocephalus tropicalis* GRAY). Fires, past human activities and the introduction of cattle (*Bos taurus* Linnaeus) have caused serious ecological damage and altered significantly the biodiversity of the island (MICOL & JOUVENTIN 1995) although it is unclear what the effects are on the micro–flora and –fauna of the island.

Table 1. Physico–chemical characteristics (when available) of samples collected on Ile Amsterdam, temperature in °C, conductivity in µS.cm^{-1}, altitude in m.a.s.l., other variables in mg.l^{-1}

sample	NO^{2-} +$N0^{3-}$	NH_4^+	PO_4^{3-}	SO_4^{2-}	Cl^-	pH	cond	T	altitude	Na^+	K^+	Ca^{2+}	Mg^{2+}
W001	2.3	0.25	0.01	8	34	5.56	136	10.2	750	17.0	0.6	1.0	1.73
W003	2.1	0.12	0.09	2	103	4.67	73	12.0	711	4.6	0.4	0.2	0.39
W004	2.1	0.22	0.01	4	18	5.91	64	14.3	717	3.6	0.1	0.2	0.35
W005						5.91	64	14.3	710				
W006						5.86	63	14.3	710				
W007	1.0	0.05	0.13	2	153	5.15	68	11.8	714	5.6	0.4	0.3	0.45
W009	3.8	1.10	0.05	13	24	4.80	66	15.0	711	4.1	0.3	0.2	0.39
W010						4.50	115	14.6	709				
W011	1.4	0.27	0.01	4	13	5.08	86	13.8	710	5.5	0.5	0.3	0.55
W012	1.3	0.12	0.01	4	22	5.57	80	13.8	700	12.9	1.0	0.8	1.14
W013						5.57	80	13.8	700				
W016						5.54	84	17.2	701				
W017	10.2	0.54	0.17	14	49	5.39	56	14.5	706	6.5	0.4	0.5	0.59
W018						5.39	56	14.5	706				
W019	1.05	0.05	0.01	2	19	5.03	62	15.5	710	6.7	0.1	0.4	0.53
W020						5.03	62	15.5	710				
W022	2.3	0.05	0.01	2	12	5.84	40	14.8	713	6.1	0.1	0.5	0.43
W023						5.84	40	14.8	713				
W025	2.9	0.26	0.01	2	13	5.58	50	13.9	716	4.4	0.1	0.2	0.28
W027	1.7	0.12	0.01	2	19	5.48	57	13.6	715	6.4	0.3	0.5	0.58
W028						5.48	57	13.6	715				
W030						5.24	56	13.2	715				
W031	5.3	15.2	1.58	56	247	6.90	1057	19.5	10	126	33.8	6.0	9.96
W032						6.90	1057	19.5	10				
W033	0.31	0.09	0.06	10	63	5.81	239	17.0	220	35.5	1.3	4.1	4.62
W034						5.81	239	17.0	220				
W035	0.29	0.05	0.01	6	42	4.14	167	17.1	386	24.2	1.8	1.6	2.48
W036						4.35	138		398				
W037	2.0	0.05	0.20	20	63	7.82	627	13.0	20	41.0	4.2	22.2	12.6
W038						7.82	627	13.0	20				
W039	2.1	0.05	0.07	19	61	7.94	1126	12.0	73	42.1	4.1	20.7	12.8
W040						7.94	1126	12.0	73				
W041	0.21	0.05	0.08	21	34	8.49	316	12.0	132	25.5	3.2	20.2	12.2
W042						8.58	325	11.0	78				
W043	0.07	0.05	0.06	22	33	8.58	325	11.0	78	25.4	3.2	20.3	12.3
W044						7.83	293	13.0	69				
W045	0.28	0.20	0.11	17	39	7.83	293	13.0	69	19.1	2.0	9.5	6.15

Table 1 Cont.

sample	NO^{2-} +$N0^{3-}$	NH_4^+	PO_4^{3-}	SO_4^{2-}	Cl^-	pH	cond	T	altitude	Na^+	K^+	Ca^{2+}	Mg^{2+}
W046						6.18	444	14.0	600				
W047	0.02	0.05	0.01	7	28	6.18	444	14.0	600	16.2	0.4	1.1	1.60
W048	0.13	0.05	0.01	5	17	5.40	67	8.5	739	10.3	0.4	0.7	0.95
W049						5.40	67	8.5	739				
W050	0.60	0.05	0.0	6	17	6.70	69	14.0	570	11.4	0.1	0.7	0.98
W051						6.70	69	14.0	570				
W052						6.76	54	17.0	757				
W053						6.10	68	16.0	758				
W056						6.44	68	15.0	759				
W058						6.03	46	16.0	748				
W059	0.02	0.05	0.08	7	27	6.80	46	14.0	742	9.8	12.5	0.6	0.76
W060						6.80	46	14.0	742				
W062	0.02	0.05	0.01	6	15	6.59	46	16.0	749	8.8	0.1	0.7	0.76
W063						6.59	46	16.0	749				
W064						6.13	88	13.0	711				
W065	0.02	0.05	0.04	7	27	6.13	88	13.0	711	12.2	7.9	1.1	1.21
W067	0.02	0.05	0.01	7	17	6.47	62	15.0	720	12.1	0.1	1.0	1.06
W068						6.47	62	15.0	720				
W069	0.02	0.05	0.01	7	20	5.75	81	15.0	706	14.0	0.4	1.0	1.35
W070						5.75	81	15.0	706				
W072						5.94	74	13.0	676				
W074						5.47	43	14.0	697				
W076	0.02	0.05	0.01	5	14	5.06	55	13.0	717	9.6	0.4	0.6	0.93
W078						5.02	47	12.0	717				
W080						4.98	78	15.0	717				
W082	0.02	0.05	0.01	6	17	5.22	48	15.0	724	9.1	0.4	0.4	0.76
W084						4.93	57	15.0	724				
W085						5.22	47	14.0	725				
W087						5.30	76	15.0	724				
W089						5.39	44	15.0	727				
W091						5.79	57	16.0	725				
W093						5.78	76	14.0	725				
W095	0.02	0.05	0.01	10	13	5.58	45	15.0	724	8.0	0.1	0.7	0.62
W097	0.02	0.05	0.01	7	19	4.98	67	13.0	739	10.3	0.4	0.6	0.78
W098						4.98	67	13.0	739				
W100						4.76	62	13.0	743				
W101	0.02	0.05	0.01	8	18	4.71	69	13.0	738	7.4	0.4	0.5	0.66

Table 1 Cont.

sample	NO^{2-} $+NO^{3-}$	NH_4^+	PO_4^{3-}	SO_4^{2-}	Cl^-	pH	cond	T	altitude	Na^+	K^+	Ca^{2+}	Mg^{2+}
W104						5.32	83	11.0	804				
W108						5.13	50	13.0	738				
W111	0.02	0.05	0.01	8	19	5.19	73	12.0	745	12.0	0.5	0.8	1.12
W113	0.02	0.05	0.01	8	18	4.89	71	13	742	12.6	0.1	0.8	1.09
W116	0.02	0.05	0.01	7	18	5.54	55	15.0	726	11.1	0.1	0.8	0.94
W118	0.02	0.05	0.01	5	15	5.42	60	14.0	707	9.9	0.1	0.7	0.86
W119						5.42	60	14.0	707				
W121						7.15	329	15.0					
W122						7.15	329	15.0					
W123	0.18	0.05	0.01	5	17	5.03	62	12.0	675	7.6	0.1	0.6	0.71
W124	0.27	0.05	0.02	17	143	6.21	487	14.0	131	77.6	1.9	7.0	9.64
W125	0.02	0.05	0.01	21	171	6.05	595	13.0	135	58.7	1.1	4.5	7.84
W126							240	14.0	121				
W127	0.02	0.05	0.01	10	63	6.38	240	14.0	121	40.0	1.0	3.1	4.72
W128	0.02	0.05	0.01	9	55	6.14	223	13.0	121	36.9	1.0	2.6	4.04
W129	0.02	0.05	0.01	12	96	6.36	358	14.0	163	52.5	1.7	5.7	6.24
W130	0.02	0.05	0.35	137	1062	6.44	3440	17.0	78	632	23.0	30.2	63.9
W131						6.44	3440	17.0	78				
W132						8.46	235	16.0	59				
W133						8.46	235	16.0	59				

In 1949, a scientific and meteorological station, Martin–de–Viviès, was established on the north–eastern coast. Since 2006 the island gained the status of Nature Reserve and a management plan is currently in place to provide greater protection for the environment and its biota (Lebouvier & Frenot 2007).

Sampling. A total of 133 diatom samples were collected during November and December 2007. Sampling locations were chosen in order to represent a maximum variability of habitat types ranging from small streams, lakes, bogponds and temporary pools from all over the island. The samples were collected in PVC bottles and fixed with 3% formaldehyde. Each sample was geographically localized using GPS and was accompanied by a detailed site description. In situ, pH, specific conductance, water temperature and oxygen have been measured for all samples using a WTW 340i Multimeter. For 46 of them, water has been collected 20 cm below the surface, filtered in situ and deep–frozen to be subsequently analysed in the laboratory at the University of Antwerp. Table 1 lists all samples together with their chemical characteristics. In the frozen water samples NO_2^-+NO_3^-N, NH_4^+–N, PO_4^{3-}–P, SO_4^{2-}, Cl^-, Na^+, K^+, Mg^{2+}, Ca^{2+}, Fe^{2+} were analysed at the Laboratory for Ecosystem Management (University of Antwerp, Belgium) using a continuous flow analysis (CFA–SKALAR).

Slide preparation and counting. A selection of 95 samples (out of 133) was further surveyed for diatoms, including all 46 samples with full chemical analysis. Diatom samples were prepared following the method described in Van der Werff (1955). Small quantities of the samples were cleaned by adding 37% H_2O_2 and heating to 80 °C for about 1 h. 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 that may hinder reliable observations. Cleaned diatom valves were mounted in Naphrax®. Samples and slides are stored at the National Botanic Garden of Belgium (BR), Department of Bryophytes and Thallophytes. In each sample, 400 diatom valves were identified and enumerated on random transects at 1 000× magnification using an Olympus BX51 microscope equipped with Differential Interference Contrast (Nomarski) optics. Slides have been scanned after doing the 400 valves counts in order to find rare species. Identifications of Antarctic and sub–Antarctic species are based on descriptions by Bourrelly & Manguin (1954), Le Cohu & Maillard (1983, 1986), Schmidt et al. (1990), Oppenheim (1994), Van de Vijver et al. (2002a, 2004b, 2008b, 2011, 2012) and Le Cohu (2005).

Nomenclature follows VAN DE VIJVER et al. 2002a.

Data analysis. For a pair wise comparison of the diatom flora of Ile Amsterdam with those of the other sub–Antarctic islands of the southern Indian Ocean Province (Prince Edward Islands, Iles Crozet, Iles Kerguelen, Heard Island) the Community Coefficient of SØRENSEN (1948) is used. This index has the following formula: 2c/(a+b+2c) where a and b are the numbers of species exclusively observed in each of the two sites and c is the number of species shared by these sites.

To evaluate the extent to which our sampling effort represented the diatom flora in the waterbodies of Ile Amsterdam, we calculated the incidence–based species richness estimator (ICE, CHAO et al. 2000) and the mean Chao2 richness estimator (CHAO 1984), both using the EstimateS program version 8.2 (COLWELL 2009). Shannon–Wiener diversity index (log10–based) and Hill's evenness index were calculated using the statistical package MVSP. Ordination was used to show the patterns in species composition. The statistical analysis was performed using CANOCO version 4.5 (TER BRAAK & ŠMILAUER 2002). Square root–transformed abundance data were used in the ordinations.

Principal Components Analysis (PCA) was used to determine the main directions of variation in the water chemistry dataset. Fe was removed from the original data set since most of its values were below the limit of detection. All environmental variables, except for pH and temperature, were log–transformed since they had skewed distributions. After this transformation, no skewed distributions were shown. Detrended Correspondence Analysis (DCA) was carried out to estimate gradient length. The results showed that two samples (W031, W032), subject to excessive marine influence (sampled from a pool in the middle of a large fur seal colony) were considered to be outliers. A DCA with the outliers omitted showed gradient lengths for the first four axes of 4.5, 3.8, 2.3, and 2.9, suggesting that methods based on unimodal models (Canonical Correspondence Analysis) would be appropriate for a subsequent ordination (TER BRAAK & PRENTICE 1988). A CCA with 46 samples (for which physic–chemical data were available) was used to detect patterns of variation in the species data that can be explained by environmental variables. All other samples were added as passive samples. Since not all of the 13 environmental variables influence the diatom distributions independently, we used Canonical Correspondence Analysis (CCA) with forward selection and unrestricted Monte Carlo permutation tests (999 permutations, $P \leq 0.05$). All statistical and numerical techniques used in this study are described in full detail in JONGMAN et al. (1995).

RESULTS

Water chemistry

The major patterns of variation within the chemistry data are revealed based on a Principal Component Analysis (Fig. 2). Based on its extreme high conductivity value, sample W130 was removed from the analysis. Small angles between biplot arrows indicate generally high positive correlations. Environmental variables that explain most of the variation, are represented by the longest arrows aligned along the axes and hence are more important. PCA axis 1 accounts for 64% of the variance (λ_1=0.643) in the data set and reflects two, strongly negatively correlated main gradients: on one hand altitude and on the other pH and specific

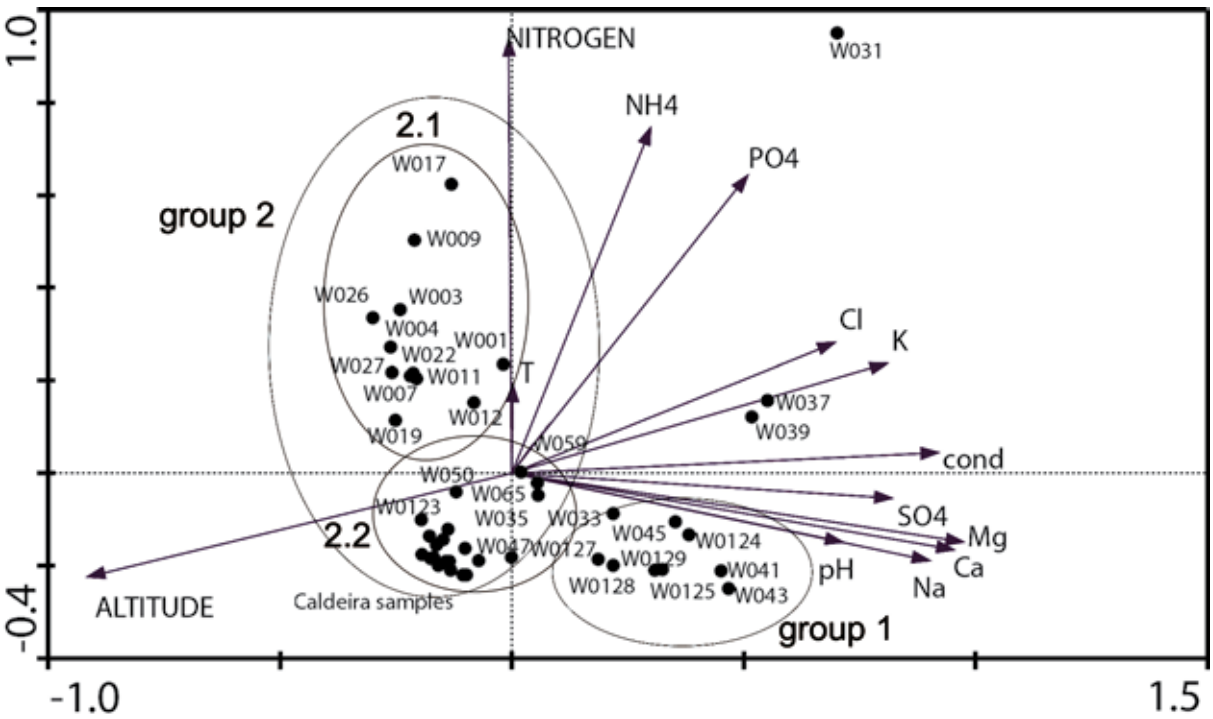

Fig. 2. A correlation biplot of samples and environmental variables resulting from the Principal Components Analysis of the water chemistry dataset.

conductance, the latter being highly linked to Cl^-, Na^+, Ca^{2+}, K^+, Mg^{2+} and SO_4^{2-}. Axis 2 seems less important and accounts for only 17% of the variance (λ_2=0.165) and is most likely reflecting a nitrogen gradient. Sample W031, situated in the upper left part of the diagram, is set somewhat apart from the other samples without being considered a complete outlier. This sample has the highest ammonium (NH_4^+–N) and phosphate (PO_4^{3-}–P) load most likely caused by animal influence as the sample was taken from a pool in the fur seal colony close to the sea. Two major groups of samples can be recognized. A first group contains all samples collected at Pointe Del Cano and Pointe d'Entrecasteaux showing high amounts of the above mentioned ions, whereas the second group is composed of all samples taken from the Caldera region in the centre of the island. The latter group can be subdivided into two parts. A first subgroup (2.1) contains only samples from the lowest plateau in the Caldera, immediately in the vicinity of the Museau de Tanche crater. These samples are characterized by elevated nitrogen values (1.0–10.2 mg/l) and are separated from all other samples in the Caldera region forming subgroup 2.2, characterized by low nitrogen values (<0.8 mg.l^{-1}).

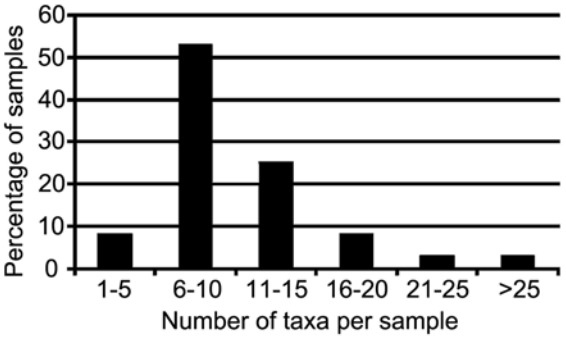

Fig. 3. Frequency distribution of diatom taxa in studied samples.

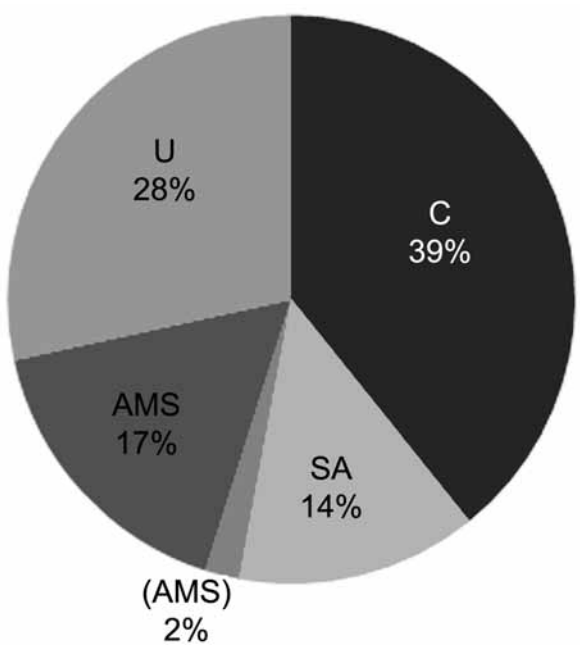

Fig. 4. Distribution of the species according to their biogeographical distribution [Distribution: (C) cosmopolitan, (AMS) Ile Amsterdam, (SA) subantarctic region, (U) unknown, ((AMS)) – Ile Amsterdam but yet undescribed].

Species composition and the similarity analysis. A total of 98 diatom taxa (including species, varieties and forms) belonging to 33 genera has been found during the analysis of 95 freshwater samples. Six additional taxa were observed outside the counts bringing the total number of diatoms in our samples up to 104. Table 6 provides a full list of all species observed in this study together with the biogeographical distribution of the taxa.

Using species richness estimators, it is possible to evaluate how well the sampling effort reflected the true diatom species richness. The expected total number of taxa in all samples is 110 (ICE) or 113 (Chao2), suggesting that the counting protocol scored between 87 and 89% of the total taxa present in the samples overall.

Species richness per sample ranged from 1 to 27. Two samples were entirely monospecific, composed of only *Eunotia paludosa* Grunow (W007 & W009). The distribution of species numbers per sample (Fig. 3) showed that most samples contained between 6 and 10 taxa per sample with an average number of taxa per sample of 11 ± 5. Table 2 lists all genera arranged according to their species number. The most species rich genera include *Pinnularia* (20 species), *Nitzschia* (11 species), *Diadesmis* (9 species), *Luticola* (6 species) and *Eunotia* (5 species). The five most abundant species made up 66.2% of all the diatoms counted: *Frustulia lebouvieri* Van de Vijver et Gremmen (30.8%), *Eunotia paludosa* (9.8%), *Kobayasiella subantarctica* Van de Vijver et Vanhoutte (9.7%), *Planothidium subantarcticum* Van de Vijver et C.E.Wetzel (8.6%) and *Eunotia muscicola* Krasske (7.3%). On the other side of the abundance scale, 83 taxa (more than 85% of all counted taxa) had a total relative abundance of less than 1%.

Detailed scanning electron microscopy analysis observations revealed the presence of several recently described species, mostly within the genus *Pinnularia* such as *P. australogibba* Van de Vijver, Chattová et Metzeltin or *P. amsterdamensis* Chattová, Metzeltin et Van de Vijver. Additionally, three recently described species were found during a survey of lava tube sample W033: *Mayamaea cavernicola* Van de Vijver, *Sellaphora barae* Van de Vijver and *Orthoseira verleyenii* Van de Vijver. A large number of taxa (12%) could at present only be identified up to the genus level, mostly within the genera *Amphora*, *Diadesmis* and *Luticola*.

Based on the biogeographic distribution of the

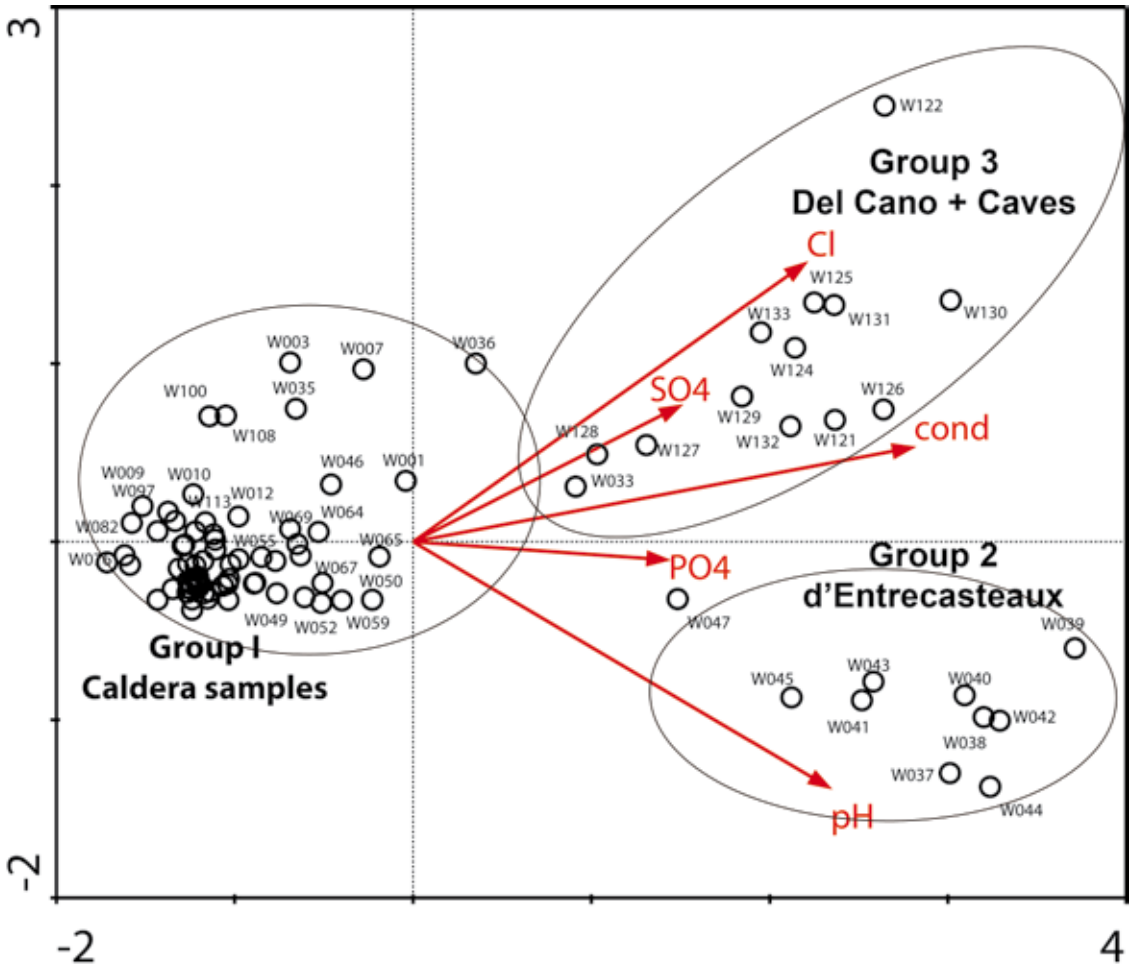

Fig. 5. Canonical Correspondence Analysis (CCA) correlation biplot of samples versus environmental variables based on species relative abundance data. The different groups (except group 4) are indicated on the diagram. The CCA–analysis was based on 46 samples for which a complete set of physic–chemical data were available. The other samples were added as passive samples.

taxa, it is clear that the Amsterdam freshwater diatom flora is composed of cosmopolitan, sub–Antarctic and endemic elements (Fig. 4). Almost 17% of all recorded taxa can be considered endemic to Ile Amsterdam, most of them belonging to the genus *Pinnularia*. An additional 14% of the taxa show an exclusive sub–Antarctic distribution such as *Achnanthes naviformis* VAN DE VIJVER et BEYENS, *Frustulia lebouvieri* and *Kobayasiella subantarctica*.

A similarity analysis based on presence/absence data was performed between the Ile Amsterdam diatom flora with the floras from the other islands in the southern Indian Ocean Province (Prince Edward Islands, Iles Crozet, Iles Kerguelen and Heard Island). Based on this presence/absence list of the Ile Amsterdam taxa, the Ile Amsterdam diatom flora shows a low affinity with the diatom floras of the true sub–Antarctic islands in the southern Indian Ocean with SØRENSEN similarity coefficients ranging between 0.28 and 0.29 (Table 3). The low similarity values are most likely the consequence of both a low total number of species on Ile Amsterdam and a low number of shared species. Typical shared sub–Antarctic taxa include *Achnanthes muelleri* CARLSON, *Achnanthes naviformis*, *Chamaepinnularia aerophila* VAN DE VIJVER et BEYENS, *Diadesmis vidalii* VAN DE VIJVER, LEDEGANCK et BEYENS and *Diadesmis crozetikerguelensis* LE COHU et VAN DE VIJVER.

Diatom community analysis. The initial dataset of 95 samples and 98 diatom taxa was used in the multivariate analysis. After a first analysis, two samples were removed from the analysis as outliers (W031 & W032). The original set of 13 environmental variables was reduced to five. Potassium (K^+), Sodium (Na^+), Magnesium (Mg^{2+}) and Calcium (Ca^{2+}) were highly correlated to specific conductance and therefore removed from the analysis. Forward selection with Monte Carlo unrestricted permutations (999 permutations) identified specific conductance, Cl^-, SO_4^{2-}, $PO_4^{2-}$and pH as the environmental variables that explain significant variation in the diatom data ($P<0.05$). The CCA restrained to these five selected variables explained only 28.7% of the species variance. This is low but typical for noisy data sets with many blank values (STEVENSON et al. 1991). The first two

Table 2. Genera ordered by decreasing percentual portion (%) calculated on the number of the taxa (n).

	n	%
Pinnularia	21	20.2
Nitzschia	10	9.6
Diadesmis	9	8.7
Luticola	6	5.8
Eunotia	5	4.8
Achnanthes	4	3.8
Navicula	4	3.8
Stauroneis	4	3.8
Gomphonema	3	2.9
Mayamaea	3	2.9
Pinuavis	3	2.9
Planothidium	3	2.9
Psammothidium	3	2.9
Sellaphora	3	2.9
Amphora	2	1.9
Frustulia	2	1.9
Hantzschia	2	1.9
Orthoseira	2	1.9
Achnanthidium	1	1.0
Caloneis	1	1.0
Chamaepinularia	1	1.0
Craticula	1	1.0
Denticula	1	1.0
Karayevia	1	1.0
Kobayasiella	1	1.0
Lecohuia	1	1.0
Melosira	1	1.0
Opephora	1	1.0
Placoneis	1	1.0
Pseudostaurosira	1	1.0
Rhopalodia	1	1.0
Stauroforma	1	1.0
Tryblionella	1	1.0
Total	104	

axes account for 79.6% of the cumulative variance. The first two axes (λ_1 = 0.709, λ_2 = 0.228) were highly significant ($p<0.001$) (ter Braak & Šmilauer 2002). CCA axis 1 is strongly correlated with specific conductance (inter–set correlation = 0.88) and to a lesser extent with pH (0.73) and Cl^- (0.68) whereas CCA axis 2 is correlated with Cl^- (0.52) and negatively with pH (–0.46). The CCA diagram (Fig. 5) shows three main groups of samples. Table 4 lists the relevant (measured) ecological parameters, together with mean species diversity, mean evenness and mean number of taxa. Samples W031 and W032, considered outliers and not taken into account in the CCA, were added as a fourth group since both were taken from the same pool in the fur seal colony. The dominant and subdominant species observed in each group are shown in Table 5.

The first group, situated in the left part of the diagram, is composed exclusively of high–altitude very acid lakes with low specific conductance, nutrient and ion values. These lakes are characterized by *Eunotia muscicola*, *Frustulia lebouvieri* and *Kobayasiella subantarctica*. Additionally, *Pinnularia vixconspicua* Chattová, Van de Vijver et Metzeltin and *E. lecohui* Van de Vijver, though in general rather rare on the island, show a remarkable abundance in these lakes. The second group, found in the lower right part of the diagram, contains all samples collected from streams and pools in the vicinity of Falaise d'Entrecasteaux, located in the southern part of the island. These samples have higher pH values (8.2±0.4) and a higher conductivity, SO_4^{2-}, Mg^{2+}, Ca^{2+} and K^+ values. Dominant taxa include *Planothidium subantarcticum, Navicula gregaria* Donkin, *Navicula veneta* Kützing and *Sellaphora seminulum* (Grunow) D.G.Mann. The third group is composed of samples from two localities: all samples from the Del Cano region in the southern part of the island together with four samples taken in small cave pools located in the Grand Tunnel near the scientific base in the northern part of Ile Amsterdam. The samples are characterized by a slightly acid pH, higher specific conductance values and higher Cl^- and Na^+ values, possibly the result of increased sea–spray input. The samples are dominated by *Planothidium subantarcticum*, *Karayevia oblongella* (Østrup) M.Aboal, *Achnanthidium* cf. *minutissimum* (Kützing) Czarnecki, *Melosira* sp. and several *Diadesmis* taxa. The last group (not represented in the Canoco Analysis) is based on only two samples (W031 and W032) that were left out as outliers. Both samples, showing very high specific conductance, SO_4^{2-}, N and PO_4^{2-} concentrations, were taken from a large rocky pool in the middle of a large fur seal colony and are dominated by *Pinnularia subacoricola* Metzeltin, Lange–Bertalot et García–Rodríguez, *Nitzschia palea* (Kützing) W.Smith and *Luticola* sp1 with *Mayamaea permitis* (Hustedt) K.Bruder et Medlin and *Pinnularia australogibba* var. *subcapitata* Van de Vijver, Chattová et Metzeltin often being subdominant.

Discussion

Species composition and general biogeography

The low similarity values based on presence/absence data between Ile Amsterdam and the other islands are not surprising considering the low number of species observed at the sites, the differences in the microhabitat diversity, the rather large distance between the islands, the very isolated position of Ile Amsterdam and the relative young geological age. Similar results can be found in the species composition of other organisms such as higher plants, mosses and lichens (Aptroot et al. 2011). The sub–Antarctic islands, grouped by Stonehouse (1982) in the so–called "cold–temperate sub–Antarctic Region" whereas Ile Amsterdam is located in the "warm–temperate sub–Antarctic Region", show a higher diversity of microhabitats such as different types of bogponds, animal wallows, fellfields and lakes, where different diatom floras could develop (Van de Vijver et al. 2008). On Ile Amsterdam, the number of stagnant waterbodies is limited to the acid, *Sphagnum*–dominated, pools and lakes in the caldera region, showing a rather uniform diatom composition.

It is however true that based on relative abundance data, the situation is somewhat different. Within the five most abundant taxa, three are typical sub–Antarctic taxa and two can even be considered to have a worldwide distribution. The three sub–Antarctic taxa are confined only to the southern Indian Ocean islands and absent on all other studied Antarctic localities (Kopalová & Van de Vijver 2013; Kopalová et al. 2013). *Frustulia lebouvieri* was so far only found on the Prince Edward Islands, the most northerly situated sub–Antarctic Islands (Van de Vijver et al. 2008a) whereas the other two species are absent from the most southern sub–Antarctic island (Heard Island; Van de Vijver et al. 2004). Both cosmopolitan taxa belong to the most common taxa in the southern hemisphere and are present, usually in large abundances, on merely every analysed Antarctic locality (Kellogg & Kellogg 2002). This may indicate that these 5 taxa probably a rather broad environmental tolerances, easily capable of adapting to prevailing environmental conditions. It also might indicate that their dispersal to and colonisation of Ile Amsterdam was therefore facilitated. Their overall dominance on Ile Amsterdam is not necessarily related to possible anthropogenic impact although the only way to clearly demonstrate this will be the analysis of Holocene sediment and peat to identify the evolution of the diatom communities on the island. Hypotheses on the human impact is therefore at the moment high speculative and therefore not relevant.

A typical feature of oceanic islands is the fact that the flora and fauna on these islands are usually disharmonic (Gillespie 2007). Some genera tend to be overrepresented whereas others are missing or show only a reduced diversity. The diatom flora of Ile Amsterdam proved to be a good example of this rule. As can be seen in Table 2, *Pinnularia* accounts for more than 20% of all recorded taxa whereas other typical species–rich genera such as *Navicula*, *Nitzschia* or *Eunotia* are less abundantly present on the island or even completely absent as is the case for *Fragilaria*. One of the reasons might be the highly specific nature of the Ile Amsterdam environment dominated by the acid *Sphagnum*–dominated peatland area in the upper Caldera. However, in comparable northern hemisphere environments, genera such as *Neidium*, *Brachysira*, *Eunotia* and *Frustulia* co–dominate bogponds and heathland fens, often represented by a high number of taxa (e.g., Fránková et al. 2009; Lange–Bertalot et al. 2011; Poulíčková et al. 2013). The main reason for this disharmony is most likely the reduced dispersion and colonisation success of these genera followed by an increased speciation of the successful genera. Vyverman et al. (2007) already stated that the effect of isolation was particularly high on Ile Amsterdam reducing the genus diversity compared to the other islands, contradicting that way the ongoing discussion on the possible ubiquity of diatoms (Finlay & Clarke 1999). The effect is apparently even more striking based on species level. Only a very low number of taxa are shared with the other islands. Most remarkably is the fact that more than 75% of these shared taxa show a cosmopolitan, even worldwide, distribution. Typical examples such as *Navicula gregaria* or *Amphora veneta* are widespread in the world and seem to be present on every continent (Kellogg & Kellogg 2002; Metzeltin et al. 2009; Hofmann et al. 2011). Whether these taxa are also genetically similar is an open question. Recent results on the cosmopolitan *Pinnularia borealis* Ehrenberg showed the presence of several genetically different lineages including a typical Antarctic lineage (Souffreau et al. 2013). Only a minority of the shared species have a restricted sub–Antarctic distribution, confirming previous biogeographic results on the sub–Antarctic flora (Van de Vijver et al. 2005, 2011). The low similarity also indicates the presence of a highly specific diatom flora on Ile Amsterdam. It is clear from the large number of cf. and sp. taxa in the species list (Table 6) that a large part of the observed species show some affinity with known taxa but at the same time sufficient differences to be separated as independent taxa. Several have been described recently (Van de Vijver et al. 2012; Van de Vijver & Cox 2013; Lowe et al. 2013) whereas some others still await a formal description. Additional morphological analysis will be necessary to reveal their true taxonomic status and it is likely that some of them will need a formal description as new taxa.

It is possible that the geographic isolation combined with the special environmental and climatic conditions resulted in an increased speciation rate, as is often seen on oceanic islands (Fleischer et al.

Table 3. Similarity analysis (Sørensen index) between Ile Amsterdam and other sub–Antarctic localities.

	Amsterdam Island	Prince Edward Islands	Kerguelen	Crozet	Heard Island
Number of taxa	104	196	210	220	191
Index of Sørensen	–	0.29	0.29	0.28	0.28

Table 4. Water chemistry and diversity features in the different sample groups identified by the CCA analysis (mean and standard deviation).

	1	2	3	4
number of samples (#with physico–chemical data)	70(31)	9(6)	14(8)	2(1)
number of taxa	9±3	15±5	18±6	16±2
number of genera	5±2	12±2	13±2	10±2
diversity	1.3±0.4	1.5±0.2	1.74±0.6	2±0.1
Evenness	0.58±0.17	0.55±0.07	0.59±0.17	0.73±0.08
pH	5.5±0.6	8.1±0.3	6.7±0.9	6.9
specific conductance	74±68	562±326	312±113	1057
$(NO_2^-+NO_3^-)N$	0.9±1.9	0.9±0.9	0.11±0.1	5.3
NH_4^+–N	0.1±0.11	0.08±0.1	0.06±0.01	15.2
PO_4^{3-}P	0.02±0.03	0.1±0.1	0.02±0.01	1.58
SO_4^{2-}	6±2.5	19.8±1.7	13±4.3	56
Cl^-	23±17	46±13.2	99±44	247
Na^+	10±3	31±9	50±15	126
K^+	1±0.1	3.3±0.8	1.3±0.3	33.8
Ca^{2+}	0.7±0.2	19±5	4.5±1.4	6.0
Mg^{2+}	0.9±0.3	11.2±2.5	6.2±1.9	9.96

2008, Buckley et al. 2009). Important genera such as *Pinnularia* and *Eunotia* show more than 60% of taxa that are only found on Ile Amsterdam (Van de Vijver et al. 2009, 2012). Some of these taxa present affinities with cosmopolitan taxa for instance *P. australogibba* is strongly related to *P. gibba* Ehrenberg but differs in several important details to justify a separation as an independent species. Molecular research should make clear how long these taxa have been separated. The analysis of the *Pinnularia borealis* populations in Souffreau et al. (2013) already discussed this phenomenon. Rapid speciation has been shown before within diatoms. Theriot et al. (2006) reported, although sometimes contested, on the rapid morphological evolution of the endemic *Stephanodiscus yellowstonensis* Theriot et Stoermer that evolved within several thousands of years from *S. niagarae* Ehrenberg. Similar results can be seen in other organisms on Ile Amsterdam. Among the seventeen native phanerogamic species reported from Ile Amsterdam, six are endemic to Ile Amsterdam and Ile Saint–Paul (Tréhen et al. 1990; Galley et al. 2007). A lot of these species are nowadays mainly present in the Caldera region, which is quite isolated from the rest of the island. Typical examples of higher plants in the Caldera region include *Plantago stauntoni* Reichardt (Rønsted et al. 2002) and *P. pentasperma* Hemsley. Recently, several new *Sphagnum* taxa have been described from Ile Amsterdam (Flatberg et al. 2011) with all reported species showing a restricted distribution to Ile Amsterdam and/or the neighbouring Ile Saint–Paul. The same applies for the Hepaticae and Anthocerotae flora of the island (Grolle 2002; Váňa et al. 2010), despite the fact that the island is rather

understudied for these groups.

Freshwater diatom communities

Both chemistry data and diatom distributions indicate that specific conductance and pH are the major factors separating the freshwater diatom communities on Ile Amsterdam. The presence of $PO4^{3-}$–P as one of the determining factors is yet unclear. A possible explanation is the presence of marine mammals at lower altitude in combination with soil erosion, high winds and seaspray. This may cause a higher phosphorus load in the investigated samples. As can be seen, the samples from the fur seal colony show high levels of phosphorus whereas in the caldera, phosphorus levels are always quite low. The waterbodies in the region near Falaises d'Entrecasteaux and Pointe Del Cano all have a slightly acid to clearly alkaline pH whereas in the Caldera the waterbodies are strictly acidic. d'Entrecasteaux and Del Cano present a similar habitat on very steep cliffs, the latter more or less taken in the small ravines that were cut out by the rivers. The similar physicochemical characteristics of the small brooks confirm this. Subsequently, the diatom communities also present a high similarity. They are dominated by taxa preferring circumneutral to alkaline conditions such as *Planothidium subantarcticum*, *Sellaphora seminulum*, *Amphora veneta*, several *Nitzschia* taxa and *Rhopalodia rupestris* (LEVKOV 2009; HOFMANN et al. 2011; VAN DE VIJVER et al. 2013). Rivers on Ile de la Possession (Crozet Archipelago) and Iles Kerguelen on the contrary have very high frequencies of various *Fragilaria* taxa, such as *Fragilaria capucina* DESMAZIÈRES, *Frankophila maillardii* (R.LE COHU) LANGE–BERTALOT and *Fragilaria germainii* E.REICHARDT et LANGE–BERTALOT (VAN DE VIJVER & BEYENS 1999b) whereas lotic waters on Ile Amsterdam completely lack any *Fragilaria* taxa. The acid diatom community in the Caldera regions differs considerably from similar communities on sub–Antarctic islands. On Ile de la Possession, acid pools such as bogponds and peatland lakes are dominated by *Chamaepinnularia soehrensis* var. *muscicola* (J.B.PETERSEN) LANGE–BERTALOT et KRAMMER, *Eunotia paludosa* and *E. muscicola* (VAN DE VIJVER & BEYENS 1999b), the latter two also present in relatively large numbers on Ile Amsterdam. On the contrary, *Frustulia lebouvieri* and most of the *Pinnularia* taxa that dominate the Ile Amsterdam peatlands, play a less important role on the sub–Antarctic islands. On the Prince Edward Islands, lakes and ponds are dominated by *Aulacoseira principissa* VAN DE VIJVER, *Psammothidium abundans* (MANGUIN) BUKHTIYAROVA et ROUND and *Eunotia paludosa* (VAN DE VIJVER et al. 2008b). Moving southwards, the acid diatom communities change even more with *Stauroforma exiguiformis* (LANGE–BERTALOT) FLOWER, JONES et ROUND and *Aulacoseira principissa* as dominant taxa on Iles Kerguelen (VAN DE VIJVER et al. 2001). A major habitat difference between the Caldera region and the sub–Antarctic islands is the overall dominance of *Sphagnum* taxa as peat forming mosses on Ile Amsterdam whereas on the sub–Antarctic Islands, *Sphagnum* taxa are completely lacking (FLATBERG et al. 2011). On these islands, the peatland moss vegetation is mostly composed of *Rhacomitrium* and *Sanionia* (VAN DE VIJVER et al. 2004a).

The PCA analysis indicated altitude as a contributor to the variation in the sample diversity. This is probably a rather artificial contribution as in the analysis most samples originate either from the Caldera region (at an altitude of 700 m) or from the southern part of the island (at almost sea–level). Intermediate samples are not numerous in the analysis. On the other hand, there is a striking difference between the physic–chemical composition of the Caldera region and the southern part of the island and as such can altitude be used to indicate the nature of the samples. It is however unclear whether the geological history of the island influenced the chemistry of the waterbodies and subsequently the shaping of their diatom communities on Ile Amsterdam. But based on this history it is possible to develop a plausible hypothesis. Ile Amsterdam has been shaped by two consecutive volcanic episodes. The volcanism on Ile Amsterdam is characterized by the formation of a mostly subalkaline tholeiitic basalt with a high concentration of magnesium (DOUCET et al. 2004). This geochemical composition probably resulted in the formation of the alkaline and slightly acid diatom communities found in the d'Entrecasteaux and Del Cano areas and probably might represent the original habitat for diatom communities on the island. All sampled streams in these areas seep out of the bedrock in the steep cliffs that form the southern shore of Ile Amsterdam and then run for several tens of meters on the lowland area towards the ocean. Most likely, the water originates from the upper Caldera region penetrating the porous underlying basaltic bedrock only to reappear almost at sea level as small but fast–flowing streams (VAN DE VIJVER, pers. obs.). The high levels of Na^+ and Cl^- most likely result from seaspray that is deposited continuously in the streams and on the lowlands in combination with soil erosion and strong winds. Whether this is also the case for Ca^{2+} is unclear. There is no indication of calcareous rocks on the entirely volcanic island. A possible source of the Ca^{2+} may be the huge colony of the yellow–nose albatross nearby but this is highly speculative and needs to be tested before it can be put forward as an hypothesis. Precipitation at sea level is rather limited (FRENOT & VALLEIX 1990) making it a less probable source for the continuous streams in the d'Entrecasteaux and Del Cano areas. The large Caldera that was formed during the last volcanic phase (DOUCET et al. 2003) constantly receives year round a large amount of precipitation (LEBOUVIER & FRENOT 2007) enabling the development of thick peat layers, almost exclusively

Table 5. List of diatom species and their abundance in the four groups (1 to 4) of samples identified by the CCA analysis [(X) >10%, (O) 5–10%, (+) 2–5%, (o) 2–0.5 %, (·) < 0.5%)].

Taxon name	**1**	**2**	**3**	**4**
Frustulia lebouvieri	X		.	
Kobayasiella subantarctica	X		.	
Eunotia muscicola var. *muscicola*	X		+	
Eunotia paludosa var. *paludosa*	X		o	
Eunotia lecohui	O			
Pinnularia vixconspicua	O		.	+
Pinnularia perminor	+		.	
Planothidium subantarcticum	o	X	X	.
Navicula gregaria	.	X	o	
Navicula veneta		O	.	.
Nitzschia frustulum	.	O	o	
Sellaphora seminulum	.	O	o	o
Amphora veneta	.	+		
Tryblionella debilis		o	o	
Karayevia oblongella	o	+	X	.
Achnanthidium cf. *minutissimum*	.	.	O	
Melosira sp	.	.	O	
Nitzschia sp1			O	
Planothidium pericavum		.	+	
Diadesmis contenta		.	+	
Diadesmis crozetikerguelensis		.	+	
Diadesmis sp1	.	o	+	
Diadesmis sp2	.	o	+	+
Diadesmis vidalii			+	
Psammothidium investians	.		+	
Achnanthes coarctata			o	
Pinnularia subacoricola			.	X
Nitzschia palea		.		X
Luticola sp1			.	X
Mayamaea permitis			.	O
Pinnularia australogibba var. *subcapitata*		.		+
Craticula submolesta	.			+

Table 6. Taxonomical list of all diatom taxa observed in this study. Unidentified species are given provisional letter codes or numbers [Distribution: (C) cosmopolitan, (AMS) Ile Amsterdam, (SA) Subantarctic region, (U) unknown, ((AMS)) Ile Amsterdam but yet undescribed].

Taxon name	**Distribution**
Achnanthes coarctata (BRÉBISSON) GRUNOW	C
Achnanthes cf. *islandica* OESTRUP	U
Achnanthes muelleri CARLSON	SA
Achnanthes naviformis VAN DE VIJVER et BEYENS	SA
Achnanthidium cf. *minutissimum* (KÜTZING) CZARNECKI	U
Amphora sp.	(AMS)
Amphora veneta KÜTZING	C
Caloneis aff. *bacillum* (GRUNOW) P.T.CLEVE	U
Chamaepinularia aerophila VAN DE VIJVER et BEYENS	SA
Craticula submolesta (HUSTEDT) LANGE–BERTALOT	C
Denticula sundaysensis ARCHIBALD	C
Diadesmis aff. *comperei* LE COHU et VAN DE VIJVER	U
Diadesmis aff. *ingeae* VAN DE VIJVER	U
Diadesmis contenta (GRUNOW) D.G.MANN	C
Diadesmis crozetikerguelensis LE COHU et VAN DE VIJVER	SA
Diadesmis gallica W.SMITH	C
Diadesmis sp1	U
Diadesmis sp2	U
Diadesmis subantarctica LE COHU et VAN DE VIJVER	SA
Diadesmis vidalii VAN DE VIJVER, LEDEGANCK et BEYENS	SA
Eunotia cocquytiae VAN DE VIJVER	AMS
Eunotia lecohui VAN DE VIJVER	AMS
Eunotia muscicola KRASSKE var. *muscicola*	C
Eunotia paludosa GRUNOW var. *paludosa*	C
Eunotia pugilistica VAN DE VIJVER	AMS
Frustulia aff. *vulgaris* (THWAITES) DE TONI	U
Frustulia lebouvieri VAN DE VIJVER et GREMMEN	SA
Gomphonema cf. *exilissimum* GRUNOW	U
Gomphonema cf. *montanum* SCHUMANN	U
Gomphonema parvulum KÜTZING	C
Hantzschia amphioxys (EHRENBERG) GRUNOW	C
Hantzschia possessionensis VAN DE VIJVER et BEYENS	SA
Karayevia oblongella (OESTRUP) M.ABOAL	C
Kobayasiella subantarctica VAN DE VIJVER et VANHOUTTE	SA
Lecohuia sp	U
Luticola beyensii VAN DE VIJVER, LEDEGANCK et LEBOUVIER	SA
Luticola cf. *cohnii* (HILSE) D.G.MANN	U

Table 6 Cont.

Taxon name	Distribution
Luticola sp1	U
Luticola sp2	U
Luticola sp3	U
Luticola sp4	U
Mayamaea cavernicola Van de Vijver	AMS
Mayamaea cf. *agrestis* (Hustedt) Lange–Bertalot	U
Mayamaea permitis (Hustedt) K.Bruder et Medlin	C
Melosira sp	(AMS)
Navicula arvensis Hustedt	C
Navicula cf. *tenelloides* Hustedt	U
Navicula gregaria Donkin	C
Navicula veneta Kützing	C
Nitzschia acidoclinata Lange–Bertalot	C
Nitzschia cf. *liebetruthii* Rabenhorst	U
Nitzschia cf. *pseudofonticola* Hustedt	U
Nitzschia cf. *pusilla* Grunow	U
Nitzschia communis Rabenhorst	C
Nitzschia commutata Grunow	C
Nitzschia frustulum (Kützing) Grunow	C
Nitzschia inconspicua Grunow	C
Nitzschia palea (Kützing) W. Smith	C
Nitzschia sp1	U
Opephora naveana Le Cohu	C
Orthoseira roeseana (Rabenhorst) O'Meara	C
Orthoseira verleyenii Van de Vijver	AMS
Pinnularia acidicola var. *acidicola* Van de Vijver et Le Cohu	SA
Pinnularia amsterdamensis Chattová, Van de Vijver et Metzeltin	AMS
Pinnularia australogibba Van de Vijver, Chattová et Metzeltin	AMS
Pinnularia australogibba var. *subcapitata* Van de Vijver, Chattová et Metzeltin	AMS
Pinnularia borealis s.l. Ehrenberg	C
Pinnularia borealis var. *subislandica* Krammer	C
Pinnularia bottnica Krammer	C
Pinnularia cf. *obscuriformis* Krammer	U
Pinnularia microstauron (Ehrenberg) Cleve	C
Pinnularia myriamiae Van de Vijver, Chattová et Metzeltin	AMS
Pinnularia perminor Kulikovskiy, Lange–Bertalot et Metzeltin	C
Pinnularia pseudohilseana Van de Vijver, Chattová et Metzeltin	AMS
Pinnularia rabenhorstii var. *subantarctica* Van de Vijver et Le Cohu	SA

Table 6 Cont.

Taxon name	Distribution
Pinnularia robrechtii VAN DE VIJVER	AMS
Pinnularia sinistra KRAMMER	C
Pinnularia sp [cf. *divergentissima* (GRUNOW) CLEVE]	U
Pinnularia subacoricola METZELTIN, LANGE–BERTALOT et GARCÍA–RODRÍGUEZ	C
Pinnularia subsinistra VAN DE VIJVER, CHATTOVÁ et METZELTIN	AMS
Pinnularia vixconspicua CHATTOVÁ, METZELTIN et VAN DE VIJVER	AMS
Pinnularia vlaminghii VAN DE VIJVER, CHATTOVÁ et METZELTIN	AMS
Pinnularia whinamiae VAN DE VIJVER	AMS
Pinnunavis elegans (W. SMITH) OKUNO	C
Pinnunavis gebhardii (KRASSKE) VAN DE VIJVER	SA
Pinnunavis sp	U
Placoneis cf. *anglica* (RALFS) R.LOWE	U
Planothidium delicatulum (KÜTZING) ROUND et BUKHTIYAROVA	C
Planothidium pericavum (CARTER) LANGE–BERTALOT	C
Planothidium subantarcticum VAN DE VIJVER et C.E.WETZEL	SA
Psammothidium abundans (MANGUIN) BUKHTIYAROVA et ROUND	C
Psammothidium staroneioides (MANGUIN) BUKHTIYAROVA	C
Psamnothidium investians (CARTER) BUKHTIYAROVA	C
Pseudostaurosira trainorii E.A.MORALES	C
Rhopalodia rupestris (W. SMITH) KRAMMER	C
Sellaphora barae VAN DE VIJVER	AMS
*Sellaphora seminulum (*GRUNOW) D.G.MANN	C
Sellaphora sp1	U
Stauroforma exiguiformis (LANGE–BERTALOT) FLOWER, JONES et ROUND	C
Stauroneis bertrandii VAN DE VIJVER et LANGE–BERTALOT	AMS
Stauroneis pseudomuriella VAN DE VIJVER et LANGE–BERTALOT	SA
Stauroneis cf. *thermicola* (J.B.PETERSEN) LUND	U
Stauroneis kriegeri PATRICK	C
Tryblionella debilis (ARNOTT) GRUNOW	C

composed of *Sphagnum* mosses. *Sphagnum* is well known for acidifying its environment (CLYMO 1963, 1964; MUNSON & GHERINI 1993) and this activity in the isolated Caldera region in combination with the flat geomorphology of the Caldera most likely created the highly acid and oligotrophic habitat where the acid diatom community could develop. Other regions on Ile Amsterdam where *Sphagnum* could be found (e.g., near the Pignon area), the *Sphagnum* vegetation is often found on more or less steep slopes where peat formation is less likely.

CONCLUSION

The freshwater diatom flora on Ile Amsterdam is unique in many aspects. This study showed the presence of a rather species poor diatom flora although for some genera such as *Pinnularia* a remarkable high diversity was found. The latter unbalanced diversity is most likely the result of the biogeographical isolation and the oceanic nature of the island. The combination of the subalkaline volcanism that shaped the island and the acidifying properties of *Sphagnum* most likely resulted

in the actual composition of these quite contrasting diatom communities that were observed in this study.

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