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Freshwater diatom communities of the Strømness Bay area, South Georgia

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Abstract: Modern diatom samples were collected from 43 sites across the Strømness Bay area of South Georgia. From 115 taxa belonging to 22 six diatom assemblages were distinguished. A CCA-analysis indicated that the assemblages are linked to pH and conductivity ranges, and habitat structure. The *Eunotia paludosa* var. *paludosa* - *Eunotia subarcuatoides* assemblage occurs in small acid water bodies. Samples of the *Fragilaria germainii* - *Pinnularia* aff. *anglica* assemblage are found in pools with a relatively high conductivity. The *Fragilaria neoproducta* assemblage and the *Achnanthes subatomoides* - *Navicula vitabunda* assemblage are mainly found in larger pools and lakes. This relationship between the assemblages and pH was comparable with results found in the testate amoebae fauna of South Georgia.

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Introduction

Diatoms are commonly observed in maritime Antarctic freshwater habitats (e.g. South Shetland Islands, South Orkney Islands (Jones *et al.* 1993, Oppenheim & Greenwood 1990) and Antarctic Peninsula (Hansson & Håkansson 1992)) but the subantarctic diatom flora of South Georgia (53°30'–55°S, 35°30'–38°30'E) has been poorly studied. Although there have been some floristic studies by Reinsch (1890), Carlson (1913), Fukushima (1965) and Kobayashi (1963, 1965), little work has been done on the ecology of the various taxa and the different diatom communities of the island. The purpose of this study was to investigate the aquatic diatom communities of Strømness Bay area and to provide an assessment of their relationship to particular ecological parameters. Since diatom flora composition is strongly related to water chemistry, the determination of the different assemblages will also offer a chemical and physical

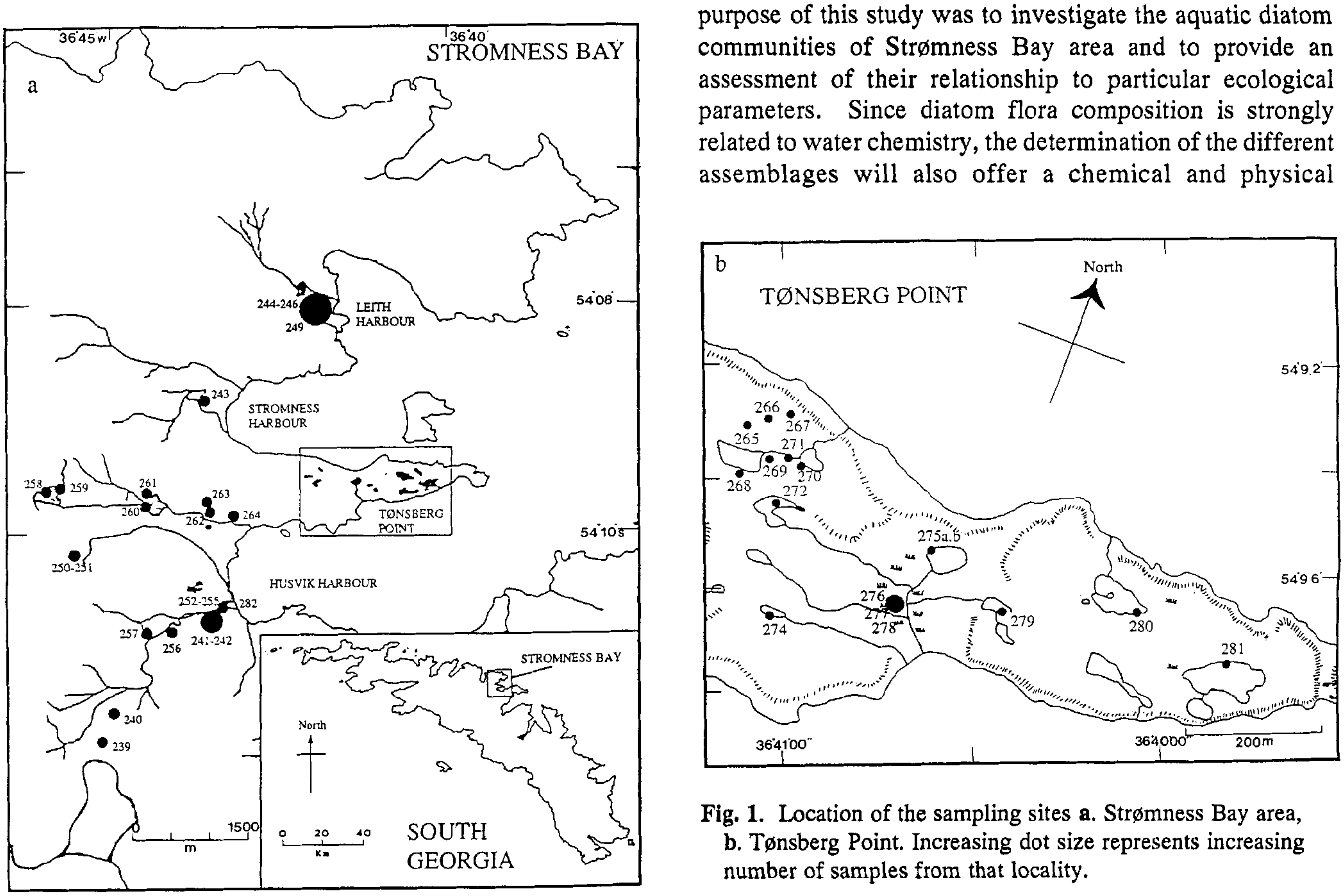

Fig. 1. Location of the sampling sites **a.** Strømness Bay area, **b.** Tønsberg Point. Increasing dot size represents increasing number of samples from that locality.

Table I. List of all sites and parameter values (m = mosses, s = sediment).

Site	Sample no.	Sampling date	Water body	Temperature °C	pH	Conductivity µS
S239	W365(m)	02.12.92	stream	2.4	8.2	27
S240	W366(m)	02.12.92	stream	3.1	7.7	30
S242	W367(m)	04.12.92	pool	23.3	6.1	93
S243	W374(s)	08.12.92	lake	10.3	7.6	110
S244	W368(s)	08.12.92	pool	11.7	7.3	30
S245	W369(s)	08.12.92	pool	11.3	9.7	69
S246	W370(m)	08.12.92	pool	9.0	5.6	43
S249	W373(m)	09.12.92	stream	9.6	7.3	70
S252	W375(m)	16.12.92	pool	14.8	4.5	42
S253B	W377(s)	16.12.92	stream	7.7	6.6	71
S254	W378(s)	16.12.92	pool	16.8	5.0	46
S255	W379(s)	16.12.92	pool	17.3	5.9	62
S256	W380(m+s)	20.12.92	pool	4.0	7.3	62
S258	W381(m)	22.12.92	lake	5.8	7.6	63
S259	W383(m)	22.12.92	stream	3.6	7.6	26
S260	W384(s) W386(m)	23.12.92	lake	5.0	7.4	39
S261	W387(m)	23.12.92	pool	9.7	6.6	51
S262	W388(m) W389(s)	24.12.92	lake	8.8	5.7	22
S263	W390(m) W391(s)	24.12.92	pool	9.8	4.2	13
S264	W392(m)	24.12.92	pool	8.0	4.0	40
S265	W393(m)	26.12.92	pool	16.6	5.6	40
S266	W395(m)	26.12.92	pool	23.1	4.3	133
S267	W396(m)	26.12.92	pool	22.2	4.2	124
S268	W397(m) W398(s)	31.12.92	lake	11.9	7.5	52
S269	W399(m)	31.12.92	pool	10.8	4.6	54
S270	W400(s)	31.12.92	lake	10.3	5.5	33
S271	W401(s) W402(m)	01.01.93	pool	9.0	6.6	41
S272	W403(s)	01.01.93	lake	10.3	7.2	56
S274	W405(s)	01.01.93	lake	10.4	6.5	41
S275A	W406(s)	05.01.93	lake	10.3	7.8	59
S275B	W407(m)	05.01.93	pool	10.4	8.1	73
S275C	W408(s)	05.01.93	stream	5.5	6.9	101
S276	W409(s)	05.01.93	pool	11.2	7.9	260
S277	W410(s)	05.01.93	pool	11.2	6.6	334
S278	W411(s)	05.01.93	pool	12.6	3.9	489
S279	W412(m)	06.01.93	lake	9.6	6.2	26
S280	W414(s)	06.01.93	lake	9.4	5.7	33
S281	W416(s)	06.01.93	lake	9.7	6.2	35

classification of the water bodies in this small part of South Georgia.

Material and methods

Thirty seven samples were collected from water bodies ranging from small pools to lakes > 100 m long, six samples were collected from small streams in the Strømness Bay area, situated on the north-eastern side of South Georgia (Fig. 1). Table I lists the main characteristics of every sample. Water temperature, pH and conductivity were measured with a Hanna water tester. The water bodies were classified in three groups : small streams (water type value 1), ponds (water type value 2) and lakes (>100m long) (water type value 3). Sediment samples were obtained by scraping the bottom with a 50 ml PVC-bottle. For the other samples, a few moss plants were taken. 3% formalin was used to fix the material for further diatom analysis. The samples were oxidized using H_2O_2 and $KMnO_4$ (Van der Werff 1955). Cleaned diatom valves were mounted in Naphrax. At least 500 valves were counted on random transects across each slide.

The Shannon-Wiener index was calculated for diversity. A hierarchic-agglomerative cluster analysis (Kovach Computing Services 1993), based on minimum variance strategy with the Squarred Euclidian Distance as dissimilarity measure, was used to classify the samples. Assemblages were named after the dominant taxa appearing in each cluster. To discover principal patterns in the distribution of diatom taxa within the Strømness Bay area, Detrended Correspondence Analysis (DCA) and Canonical Correspondence Analysis (CCA) were carried out on the log normal-transformed abundance data (ter Braak 1987). CCA was used to determine the relationship between the diatom distributions and four measured ecological variables (i.e. water type, pH, conductivity and temperature). No other variables were adequately quantified. TWINSPAN (Hill 1979) was used to determine

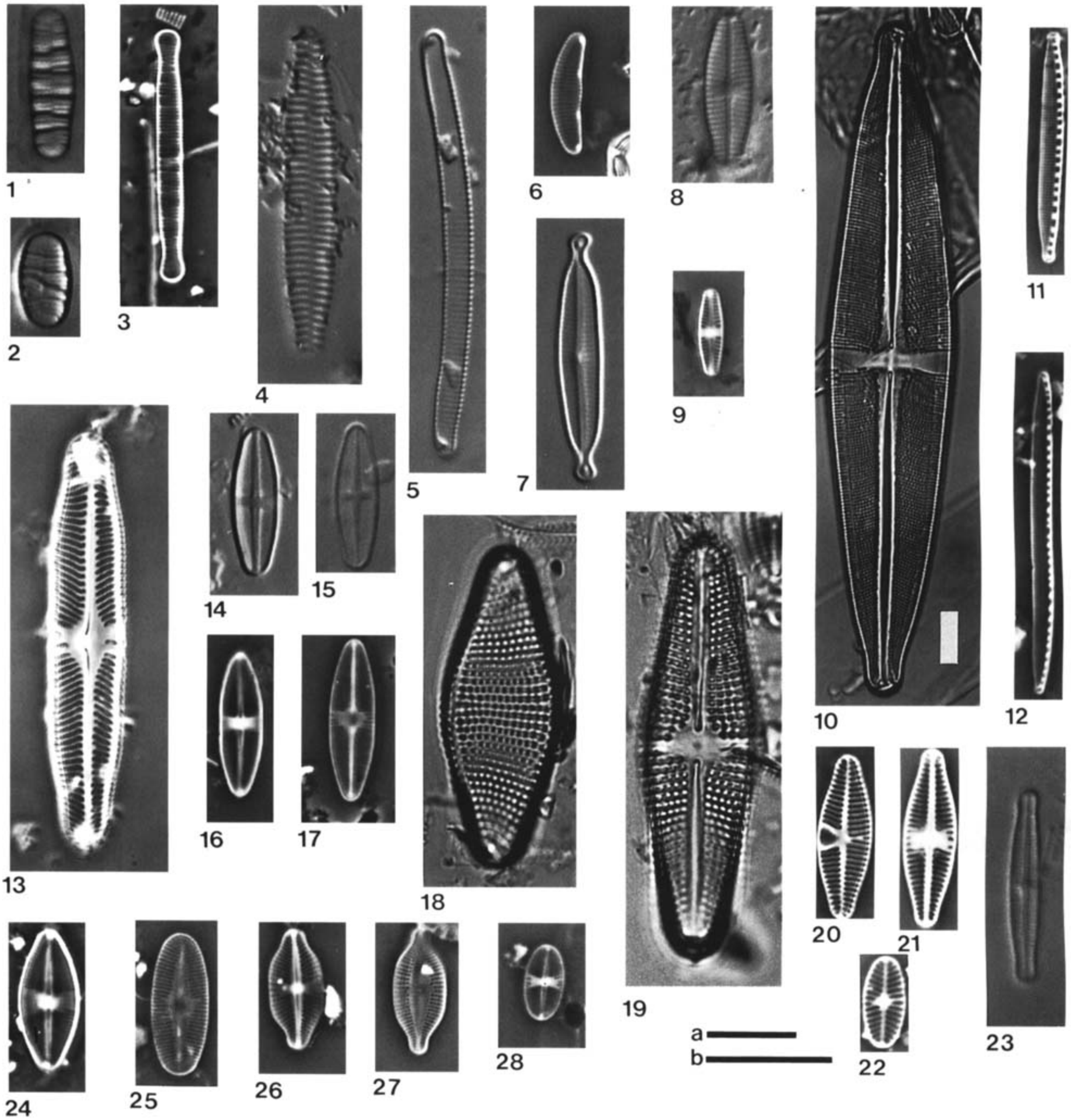

Fig. 2. Light microscopic photographs of selected taxa : 1, 2 *Diatoma* sp., 3 *Fragilaria germainii*, 4 *F. neoproducta*, 5 *Eunotia paludosa* var. *paludosa*, 6 *E. subarcuatoides*, 7 *Cymbella microcephala*, 8 *Navicula vitabunda*, 9 *N. australomediocris*, 10 *Stauroneis phoenicenteron*, 11 *Nitzschia perminuta* , 12 *N. acidoclinata*, 13 *Pinnularia* aff. *anglica*, 14 *Achnanthes confusa* raphid valve, 15 *A. confusa* araphid valve, 16 *A. incognita* raphid valve, 17 *A. incognita* araphid valve, 18 *A. muelleri* araphid valve, 19 *A. muelleri* raphid valve, 20 *A. lanceolata* var. *lanceolata* araphid valve, 21 *A. lanceolata* var. *lanceolata* raphid valve, 22 *A. quadripunctata* raphid valve, 23 *A. minutissima* var. *minutissima* raphid valve, 24 *A. ninkei* raphid valve, 25 *A. helvetica* araphid valve, 26 *A. manguinii* var. *elliptica* raphid valve, 27 *A. manguinii* var. *elliptica* araphid valve, 28 *A. subatomoides* raphid valve. Scale bar a represents 10µm for photographs 3, 6, 9, 11-13, 16-17, 20-22, 24-28, scale bar b represents 10µm for photographs 1-2, 4-5, 7-8, 14-15, 18-19 ,23. The white scale bar in photograph 10 represents 10µm.

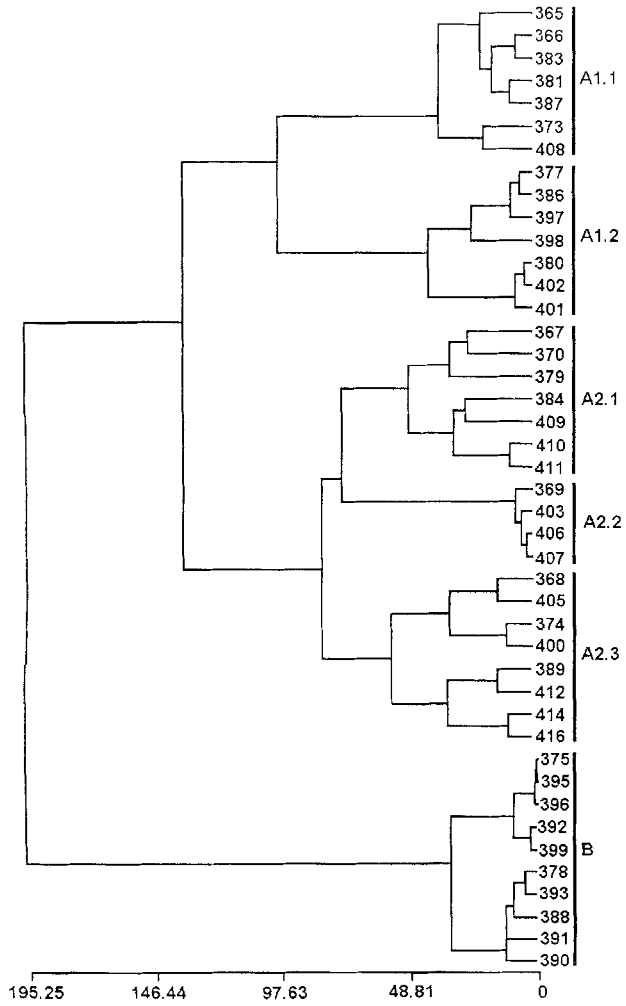

Fig. 3. Cluster dendrogram based on species composition. The different clusters are marked on the right side.

the main indicator species in the different assemblages.

Results and discussion

In all 43 samples a well-preserved diatom flora was found comprising 115 taxa, belonging to 22 genera (Appendix I, Fig. 2). Earlier studies on diatom communities of South Georgia reported 19 (Reinsch 1890), 45 (Carlson 1913) and 49 (Fukushima 1965) taxa respectively. The most recorded genera were *Achnanthes* (33% of all counted valves), *Fragilaria* (19%), *Eunotia* (18%), *Pinnularia* (11%) and *Navicula* (6%). This dominance of *Achnanthes* is commonly observed in Antarctic freshwater lakes (Oppenheim 1994) and is explained by their preference of oligotrophic, circumneutral and electrolyte-poor water (Lange-Bertalot & Krammer 1989). The dominance may also be related to the overall presence of stones and submerged bryophytes, as these habitats are quite suitable for the attached species of *Achnanthes* (V. Jones pers. comm., Björck *et al.* 1991). The

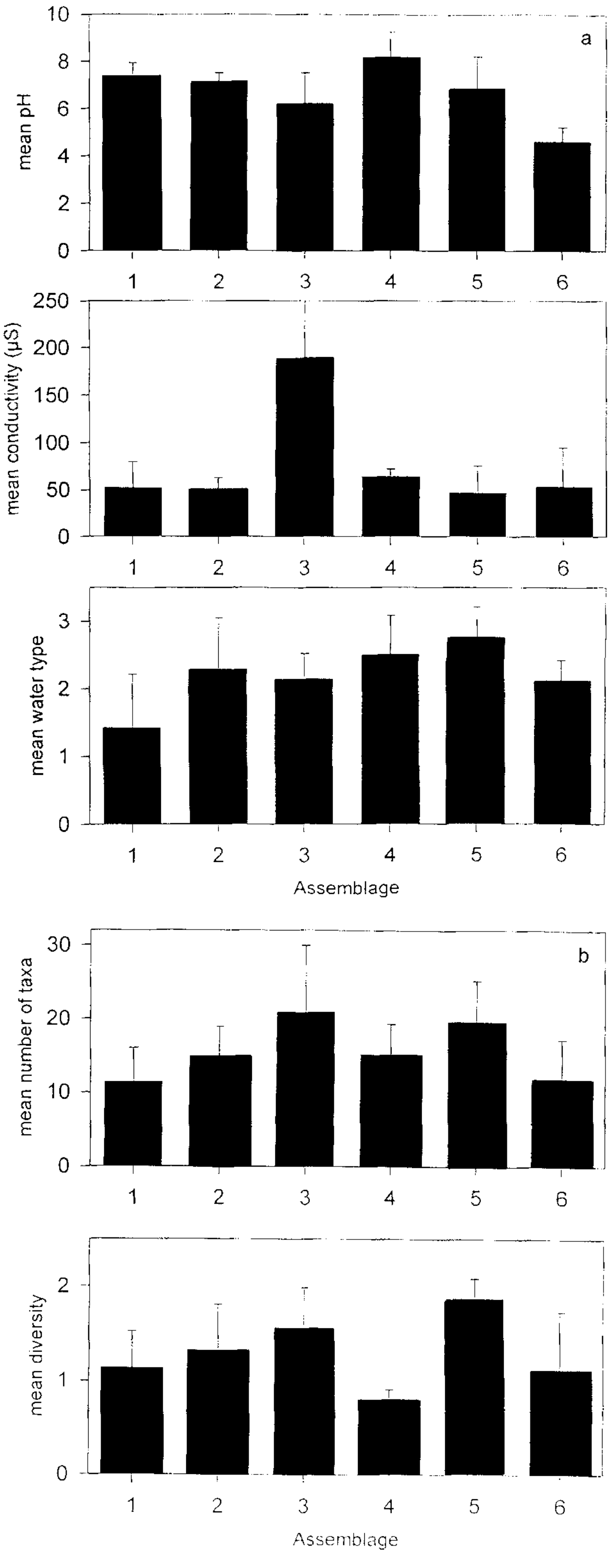

Fig. 4. Histographs reflecting the mean ecological parameters for each assemblage **a.** physicochemical variables, **b.** mean diversity and mean number of taxa. Standard deviation is shown as error bars. The numbers of the assemblages are resp. 1 = A1.1, 2 = A1.2, 3 = A2.1, 4 = A2.2, 5 = A2.3, 6 = B. The different values are represented in Table II.

Table II. Main characteristics of the different assemblages (dominant species show very high abundances in each sample of the assemblage, subdominant species are always present in the assemblage but never show high abundances). Species data presented as: present in n% of samples # dominant or subdominant in n% of these samples.

	A1.1	A1.2	A2.1	A2.2	A2.3	
number of samples	7	7	7	4	8	10
samples with mosses	6	4	2	1	1	8
mean pH	7.4±0.5	7.1±0.5	6.2±1.3	8.2±1.1	6.8±1.4	4.6±0.6
mean conductivity	52.6±27.8	51.1±12.0	188.6±175.7	64.3±8.1	47.1±28.7	52.7±42.3
mean diversity	1.11 ± 0.41	1.31 ± 0.49	1.56 ± 0.42	0.81 ± 0.10	1.87 ± 0.21	1.12 ± 0.61
mean number of taxa	11.4 ± 4.7	14.9 ± 4.1	20.9 ± 9.1	15 ± 4.3	19.6 ± 5.5	11.9 ± 5.3
mean water type	1.4 ± 0.8	2.3 ± 0.8	2.1 ± 0.4	2.5 ± 0.6	2.8 ± 0.5	2.1 ± 0.3
Achnanthes confusa	28.6 # 0	100 # 85.7	57.1 # 14.3	0	37.5 # 25	50 # 20
A. incognita	71.4 # 28.6	71.4 # 42.9	28.6 # 0	25 # 0	37.5 # 0	70 # 0
A. lanc. lanceolata	100 # 85.7	42.9 # 14.3	71.4 # 0	75 # 0	12.5 # 0	30 # 0
A. min. minutissima	42.9 # 14.3	57.1 # 57.1	14.3 # 0	25 # 0	37.5 # 0	50 # 10
A. subatomoides	28.6 # 0	14.3 # 0	28.6 # 0	75 # 25	100 # 62.5	70 # 10
Aulacoseira sp.	0	0	0	0	75 ± 12.5	30 ± 0
Eunotia pal. paludosa	28.6 ± 0	14.3 ± 0	42.9 ± 0	0	37.5 ± 0	80 ± 80
E. subarcuatoides	0	14.3 ± 0	14.3 ± 0	0	50 ± 12.5	80 ± 80
Fragilaria pin. pinnata	28.6 ± 14.3	85.7 ± 0	57.1 ± 14.3	0	37.5 ± 0	10 ± 0
F. germainii	57.1 # 14.3	85.7 # 28.6	100 # 28.6	100 # 25	62.5 # 12.5	40 # 0
F. neoproducta	14.3 # 0	0	0	100 # 100	12.5 # 12.5	0
Gomphonema parv. parvulum	57.1 ± 28.6	71.4 ± 28.6	57.1 ± 0	75 ± 0	62.5 ± 0	20 ± 0
Navicula minima	42.9 ± 14.3	0	57.1 ± 0	75 ± 25	37.5 ± 0	20 ± 0
N. pseudoscutiformis	0	28.6 ± 0	28.6 ± 0	50 ± 0	62.5 ± 25	20 ± 0
N. vitabunda	0	14.3 ± 0	14.3 ± 0	75 ± 0	87.5 ± 50	10 ± 0
Pinnularia aff. anglica	14.3 ± 0	42.9 ± 0	85.7 ± 42.9	50 ± 0	87.5 ± 0	60 ± 50
P. microstauron	14.3 ± 0	0	28.6 ± 14.3	0	62.5 ± 0	20 ± 0
P. sinistra	28.6 ± 0	28.6 ± 0	71.43 ± 14.3	0	75 ± 12.5	10 ± 0
Stauroneis anceps	0	14.3 ± 0	14.3 ± 14.3	75 ± 25	50 ± 0	0

most diverse diatom flora was observed at site W384 (m) with 34 taxa; by contrast at site W396 (m) only four diatom taxa were found.

The following taxa, found in this study, are only reported from the Antarctic (within the Polar Front): *Achnanthes confusa, A. ninkei, A. manguinii, Navicula australomediocris. Navicula megacuspidata* Carlson (absent from this study) is also known only from South Georgia. Beyens *et al.* (1995) found a new testate amoeba taxon belonging to the genus *Microcorycia*. If these last two species are really endemic, it is quite possible they evolved after the deglaciation. Their presence alone is not considered an indication of the presence of glacial refugia. Wilkinson (1990) suggested a lack of glacial refugia on basis of the absence of endemic testate amoebae species, belonging to the genus *Nebela*, in South Georgia. *Achnanthes muelleri*, another diatom species found in the study, has only been observed on South Georgia and the Falkland Islands. This opens the way to the speculation that *A. muelleri* reached South Georgia from the Falklands.

According to the cluster dendrogram (Fig. 3), six assemblages can be distinguished, forming two major sample groups.

The first group includes five assemblages, grouping 33 samples:

A1.1 *Achnanthes lanceolata* var. *lanceolata* assemblage
A1.2 *Achnanthes minutissima* var. *minutissima* - *Achnanthes confusa* assemblage

A2.1 *Fragilaria germainii* - *Pinnularia* aff. *anglica* assemblage
A2.2 *Fragilaria neoproducta* assemblage
A2.3 *Achnanthes subatomoides* - *Navicula vitabunda* assemblage

The second group consists of one assemblage with 10 samples:

B *Eunotia paludosa* var. *paludosa* - *Eunotia subarcuatoides* assemblage

Table II lists the mean parameters and the dominant or subdominant species of each cluster. In Fig. 4a & b the relevant ecological parameters are shown on histographs together with mean species diversity and mean number of taxa found in each assemblage.

Cluster A1.1 consists of seven samples and is mostly dominated by *Achnanthes lanceolata* var. *lanceolata*. Other important taxa are *A. muelleri* and a *Diatoma* species, which is thought to be new. The description will be published elsewhere. The samples are characterized by a circumneutral pH and a low conductivity. Cluster A1.2 shows a dominance of two other *Achnanthes* species, *A. minutissima* var.

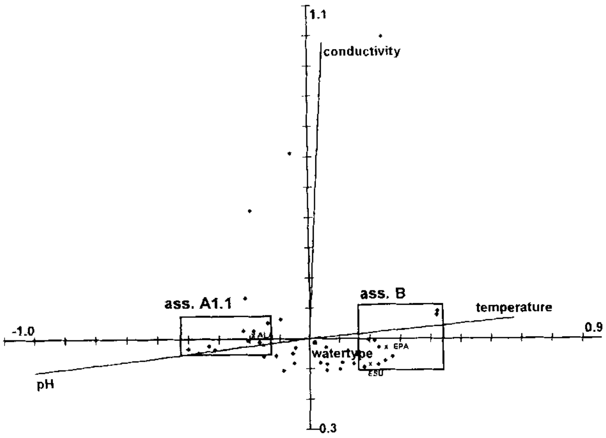

Fig. 5. CCA-analysis: sites plotting the first axis against the second, environmental variables are added. Two characteristic diatom assemblages, together with their main species are plotted on the diagram, i.e. ass. A1.1 (ALA = *Achnanthes lanceolata* var. *lanceolata*) and ass. B (EPA = *Eunotia paludosa* var. *paludosa*, ESU = *Eunotia subarcuatoides*).

minutissima and *A. confusa*. *A. incognita* plays a subdominant role in this cluster. The mean pH is nearly the same as for the first cluster, i.e. 7.1.

Cluster A2.1 is very heterogenous, with no clearly dominant species. *Fragilaria germainii* and *Pinnularia aff. anglica* are present in most of the samples. Three samples (409, 410, 411) have a high conductivity. In cluster A2.2 the diatom flora is dominated by *Fragilaria neoproducta*. The mean pH is alkaline (i.e. 8.2). The last cluster is dominated by *Achnanthes subatomoides* and *Navicula vitabunda*. Most of the eight samples were taken from large lakes (mean water type value = 2.75) with low conductivity and pH.

Cluster B is distinguished by the dominance of *Eunotia paludosa* var. *paludosa* and *E. subarcuatoides*. The mean pH of this group is very low (4.6), with most samples coming from small water bodies.

These results are supported by the ordination- and the TWINSPAN-analysis. Two main groups of sites could be distinguished in the TWINSPAN-diagram. Group 1 consists for the greater part of samples from circumneutral to slightly alkaline water bodies. The other group represents more acid conditions. Three of the assemblages defined in Fig. 3 match TWINSPAN groups (Table III). The *Achnanthes minutissima* var. *minutissima* - *Achnanthes confusa* assemblage closely resembles group 011 and the *Fragilaria neoproducta* assemblage matches group 0010. Moreover the indicator species given by TWINSPAN for the first division are *Eunotia paludosa* var. *paludosa* and *E. subarcuatoides*. In the agglomerative dendrogram, these two species are also characteristic for a major group (i.e. the *Eunotia paludosa* var. *paludosa* - *Eunotia subarcuatoides* assemblage). The TWINSPAN analysis also confirms the distribution of the diatom taxa for each group of assemblages. In Group 1 high frequencies of *Achnanthes confusa, A. minutissima* var. *minutissima, A. lanceolata* var. *lanceolata, A. incognita, Fragilaria germainii* and *F. neoproducta* were found. Those species were also characteristic for the different assemblages of the first group in the agglomerative clustering. The second group was represented by *Eunotia paludosa* var. *paludosa, E. subarcuatoides* and *Pinnularia* aff. *anglica*.

Axes 1 and 2 of the DCA-analysis show relative high eigenvalues ($\lambda_1 = 0.700$, $\lambda_2 = 0.569$). Together they account for 15.6 % of the cumulative variance in the diatom data. This low proportion of variance is not unusual for data sets containing a large number of taxa and many zero values (Hall & Smol 1992). A possible relationship between the diatom assemblages and the ecological variables was explored by the CCA analysis. The first two axes (Fig. 5) account for 62.1% of the variance. Axis 1 is strongly correlated with the pH (interset correlation = -0.85), whilst the second axis is related to the conductivity (0.73). A clear pH gradient separates the samples to the right of axis 2, containing species with an affinity for acid water (e.g. *Eunotia paludosa* var. *paludosa* and *E. subarcuatoides*) from the sample group on the left side with mostly diatoms typical of circumneutral water bodies.

Table III. Result of the TWINSPAN analysis. The numbers refer to the samples. The groups 0010*, 011* and 101* are found back in the agglomerative cluster analysis (assemblages A2.2, A1.2 and B respectively).

0							**1**			
365, 366, 367, 368, 369, 370, 373, 374, 377, 379, 380, 381, 383, 384, 386, 387, 397, 398, 400, 401, 402, 403, 405, 406, 407, 408							375, 378, 388, 389, 390, 391, 392, 393, 395, 396, 399, 409, 410, 411, 412, 414, 416			
00			**01**				**10**			**11**
367, 368, 369, 370, 403, 405, 406, 407, 408			365, 366, 373, 374, 377, 379, 380, 381, 383, 384, 386, 387, 397, 398, 400, 401, 402				375, 378, 388, 389, 390, 391, 392, 393, 395, 396, 399, 412, 414, 416			409, 410, 411
000	**001**		**010**		**011***		**100**	**101**		
367, 370	368, 369, 403, 405, 406, 407, 408		365, 366, 373, 380, 381, 383, 402		374, 377, 379, 384, 386, 387, 397, 398, 400, 401		389, 412, 414, 414	375, 378, 388, 390, 391, 392, 393, 395, 396, 399		
	0010*	**0011**	**0100**	**0101**	**0110**	**0111**		**1010**	**1011**	
	369, 403, 406, 407, 408	368, 405	373	365, 366, 380, 381, 383, 402	374, 377, 379, 386, 387, 397, 398, 400, 401	384		378, 390, 391	375, 388, 392, 393, 395, 396, 399	

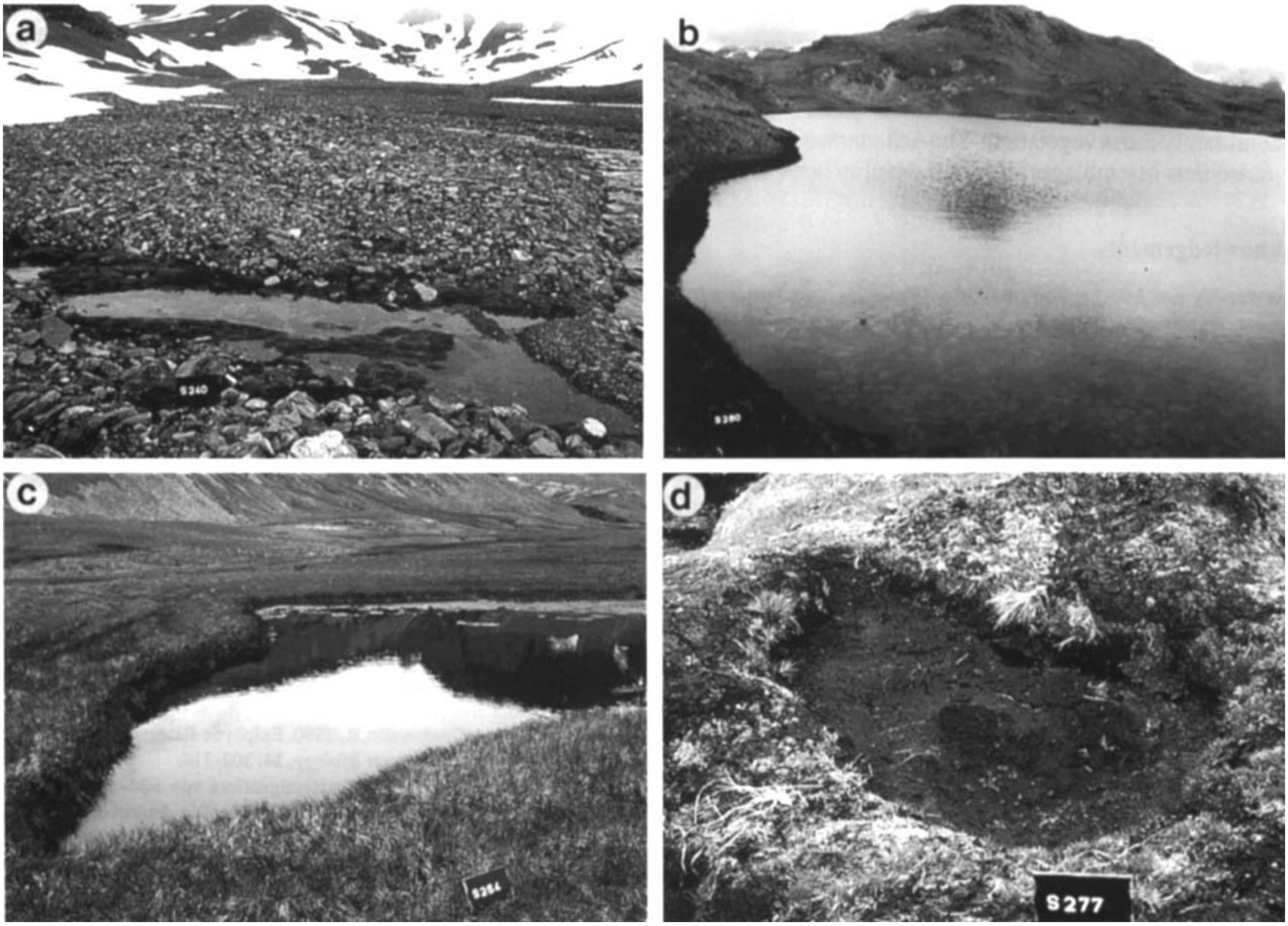

Fig. 6. Characteristic habitats of some diatom assemblages : **a.** site 240, a small stream in which the *Achnanthes lanceolata* var. *lanceolata* assemblage was found, **b.** site 280, a lake harbouring the *Achnanthes subatomoides-Navicula vitabunda* assemblage, **c.** site 254 with the *Eunotia paludosa* var. *paludosa-Eunotia subarcuatoides* assemblage, **d.** site 277 an elephant seal pool with the *Fragilaria germainii-Pinnularia* aff. *anglica* assemblage.

The major factor in differentiating the assemblages is thus clearly the pH. This strong relationship between diatoms and pH is often seen in soft water throughout the whole world (Charles & Smol 1988, Tolonen *et al.* 1986). The *Eunotia paludosa* var. *paludosa* – *E. subarcuatoides* assemblage is characteristic of acid water bodies. The same clustering of testate amoebae fauna (Beyens *et al.* 1995) belonging to the *Nebela collaris* assemblage also show a strong pH relationship but no conductivity relationship in contrast to the diatom assemblages.

The *Fragilaria germainii - Pinnularia* aff. *anglica* assemblage contains samples with a diatom flora typical of brackish water. A relative high number of marine and brackish species is found in these samples e.g. *Cocconeis imperatrix* and *Rhabdonema arcuatum* var. *robusta*. A possible explanation could be the former presence of elephant seals (*Mirounga leonina*) in the three pools (Fig.6d). The skin and the excrement of these marine mammals may contain enough salt to give the water a higher conductivity. Marine diatom valves could be left on the elephant seals and end up in the pools. Foged (1951,1953) reported the presence of marine and brackish water diatoms near heron (*Ardea cinerea*) and cormorant (*Phalacrocorax carbo sinensis*) colonies. Birds transported the diatoms, together with food and nesting material. This transport of diatoms by birds and insects has also been discussed by Wutrich & Matthey (1980). Seaspray might also be involved in transporting marine diatoms in the freshwater pools (Sterrenburg personal communication) but in this case the pools influenced were no more likely to get sea spray than the unaffected pools.

Habitat plays a minor but still important role in characterizing the different assemblages and this was also evident in the testate amoebae fauna (Beyens *et al.* 1995). Metcalfe (1988) has already pointed this out in his study on the Mexican diatom assemblages. The *Fragilaria neoproducta* assemblage and the *Achnanthes subatomoides - Navicula vitabunda* assemblage seem to occur mainly in larger water bodies (Fig. 6b). This is expressed in the presence of many planktonic species like *Aulacoseira alpigena* and *Fragilaria construens f. subsalina*. The *Eunotia paludosa* var. *paludosa* - *Eunotia subarcuatoides* assemblage is characteristic of small ponds with an predominantly moss vegetation. The *Achnanthes lanceolata* var. *lanceolata* assemblages is found in small streams (Fig. 6a).

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Appendix I. List of taxa and their presence in the six assemblages, expressed as number of samples in which they occur in the assemblages.

Assemblage (number of samples)	A1.1 7	A1.2 7	A2.1 7	A2.2 4	A2.3 8	B 10
Achnanthes biasolettiana Grunow		1				
Achnanthes confusa Manguin	2	7	4		3	5
Achnanthes helvetica (Hustedt) Lange-Bertalot	1	2	1		4	1
Achnanthes incognita Krasske	5	5	2	1	3	7
Achnanthes investians Carter					1	
Achnanthes lanceolata var. *lanceolata* Grunow	7	3	5	3	1	3
Achnanthes manguinii var. *elliptica* Hustedt					1	
Achnanthes minutissima var. *gracillima* (Meister) Lange-Bertalot		1				
Achnanthes minutissima var. *minutissima* Kützing	3	4	1	1	3	5
Achnanthes modestiformis Lange-Bertalot		1	1		1	
Achnanthes mülleri Carlson	3					
Achnanthes ninkei Guermeer & Manguin					1	
Achnanthes oblongella Oestrup		1			1	
Achnanthes quadripunctata Oppenheim				1		
Achnanthes subatomoides (Hustedt) Lange-Bertalot & Archibald	2	1	2	3	8	7
Amphora veneta Kützing			2	1		
Aulacoseira alpigena (Grunow) Krammer		2			4	1
Aulacoseira sp1					6	3
Brachysira sp1	2					
Cocconeis costata Gregory			2			
Cocconeis imperatrix M. Peragallo			1			
Cocconeis scutellum Ehrenberg			1			
Cocconeis sp1			1			
Cyclotella stelligera Cleve & Grunow		1			1	
Cymbella cistula (Ehrenberg) Kirchner	2	3	1	1	1	
Cymbella cuspidata Kützing			1			
Cymbella microcephala Grunow		2		1	1	
Cymbella silesiaca Bleisch		1	1			
Denticula kuetzingii Grunow		1				
Diatoma sp1	2	1	3			
Diploneis subovalis Cleve		3	2			
Eunotia exigua (Brébisson) Rabenhorst			2		3	3
Eunotia muscicola var. *muscicola* Krasske		3				
Eunotia muscicola var. *tridentula* Nörpel & Lange-Bertalot			1			
Eunotia paludosa var. *paludosa* Grunow	2	1	3		3	8
Eunotia praerupta Ehrenberg		2	2		1	
Eunotia pyramidata var. *ventralis* Krasske		1				
Eunotia sp1						1
Eunotia subarcuatoides Alles et al.		1	1		4	8
Fragilaria bicapitata Mayer	1					
Fragilaria capucina s.l. Desmazières				1	1	1
Fragilaria capucina var. *capucina* Desmazières	1	1	2	2	1	
Fragilaria capucina var. *gracilis* (Oestrup) Hustedt		1	1			
Fragilaria construens f. *subsalina* (Hustedt) Hustedt	1	2	1	1	5	1
Fragilaria construens f. *venter* (Ehrenberg) Hustedt					1	
Fragilaria elliptica Schumann	1	1	3	1	4	
Fragilaria exigua Grunow		3	1		5	
Fragilaria germainii Reichardt & Lange-Bertalot	4	6	7	4	5	4
Fragilaria nanana Lange-Bertalot		1	1			
Fragilaria neoproducta Lange-Bertalot	1			4	1	
Fragilaria pinnata var. *pinnata* Ehrenberg	2	6	4		3	1
Fragilaria sp1			1			
Fragilaria sp2			1			
Fragilaria sp3			1			
Fragilaria sp4			1			
Gomphonema affine Kützing						1
Gomphonema gracile Ehrenberg					2	1
Gomphonema parallellistriatum Lange-Bertalot & Reichardt	3			1		1
Gomphonema parvulum var. *excillissimum* Grunow	2	2	1	1		
Gomphonema parvulum var. *parvulius* Lange-Bertalot & Reichardt		1	1			

Appendix I. (cont.) List of taxa and their presence in the six assemblages, expressed as number of samples in which they occur in the assemblages.

Assemblage (number of samples)	A1.1 7	A1.2 7	A2.1 7	A2.2 4	A2.3 8	B 10
Gomphonema parvulum var. *parvulum* (Kützing) Kützing	4	5	4	3	5	2
Gomphonema sp1	1					
Gomphonema sp2	1					
Hantzschia amphioxys (Ehrenberg) W. Smith			4		2	3
Navicula arvensis Hustedt					2	4
Navicula atomus var. *atomus* (Kützing) Grunow			1			
Navicula atomus var. *permitits* (Hustedt) Lange-Bertalot	1	1				
Navicula australomediocris Lange-Bertalot & R. Smith	1					
Navicula bryophila Petersen	2					
Navicula contenta Grunow	2					
Navicula cuspidata (Kützing) Kützing				1		
Navicula difficillima Hustedt					4	
Navicula gregaria Donkin	1				1	
Navicula joubaudii Germain				1	2	
Navicula minima Grunow	3		4	3	3	2
Navicula mutica var. *mutica* Kützing			3			1
Navicula pseudoscutiformis Kützing		2	2	2	5	2
Navicula rhynchocephala Kützing				1	2	
Navicula seminulum Grunow	1			3	2	
Navicula sp1	1		1			
Navicula sp2			1			
Navicula sp3			1			
Navicula sp4			2			
Navicula vitabunda Hustedt		1	1	3	7	1
Nitzschia acidoclinata Lange-Bertalot	1	1	3	1	1	
Nitzschia frustulum var. *frustulum* (Kützing) Grunow	3	2	1	3	2	
Nitzschia gracilis Hantzsch	1		3	2	1	1
Nitzschia homburgensis Lange-Bertalot			1			
Nitzschia inconspicua Grunow	1	1				
Nitzschia kerguelensis (O'Meara) Hasle			1			1
Nitzschia palea (Kützing) W. Smith			3			
Nitzschia perminuta (Grunow) M. Peragallo	1		1			
Nitzschia sp1			1			
Nitzschia sp2			1			
Nitzschia subacicularis Hustedt				1		
Pinnularia aff. *anglica* Krammer	1	3	6	2	7	6
Pinnularia borealis var. *scalaris* (Ehrenberg) Rabenhorst	2	2	3		2	
Pinnularia brebissonii (Kützing) Rabenhorst			1			
Pinnularia divergens var. *decrescens* (Grunow) Krammer			1			
Pinnularia krookii (Grunow) Cleve	1		3			
Pinnularia lagerstedtii (Cleve) Cleve-Euler					3	2
Pinnularia microstauron (Ehrenberg) W. Smith	1		2		5	2
Pinnularia schoenfelderi Krammer	1					1
Pinnularia silvatica Petersen		1	3		3	5
Pinnularia sinistra Krammer	2	2	5		6	1
Pinnularia sp1			2			
Pinnularia subcapitata var. *elongata* Krammer					1	
Pinnularia viridiformis Krammer		4	6		1	2
Rhabdonema arcuatum var. *robusta* (Grunow) Hustedt			1		2	
Stauroneis anceps Ehrenberg		1	1	3	4	
Stauroneis phoenicenteron (Nitzsch) Ehrenberg		2	4	1	2	
Surirella angusta Kützing			1			
Synedra rumpens f. *familiaris* (Kützing) Grunow		3	1	3	3	1
Tabellaria flocculosa (Roth) Kützing		1				
Thalassiosira gracilis var. *expecta* (Van Landingham) Fryxell & Hasle			1			