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Freshwater Testate Amoebae Communities from Île de la Possession, Crozet Archipelago, Subantarctica

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Abstract

An ecological study of the freshwater testate amoebae (Protozoa, Rhizopoda) on the subantarctic island Île de la Possession (Crozet Archipelago) revealed 85 taxa, belonging to 21 genera. Twenty-two taxa belonged to the genus *Difflugia*, typical for freshwater habitats whereas the genus *Trinema* showed the highest relative abundance. A cluster analysis revealed two communities: a *Difflugiella crenulata* assemblage and a *Trinema lineare–T. enchelys* assemblage. These communities, together with the results of a RDA analysis, represented a clear geographical separation on the island. The *Difflugiella crenulata* assemblage typified locations, with a high specific conductance and neutral to alkaline pH values, on the western part of the island. Aquatic habitats in the larger valleys on the eastern side of Île de la Possession, with a low conductivity and slightly acid pH values, were characterized by the *Trinema* assemblage. Weighted averaging and calibration were used to develop a statistical transfer function to infer the pH of freshwater bodies from the testate amoebae assemblages. The model is usable over a pH range of 5 to 9.

Introduction

A few years ago a series of papers was published describing the nonmarine diatom assemblages in different habitats on the subantarctic island Île de la Possession, belonging to the Crozet Archipelago (Fig. 1) (Van de Vijver and Beyens 1998, 1999a, 1999b; Van de Vijver et al., 2002a, 2002b). During the examination of the raw material, it was clear that a large amount of testate amoebae (Protozoa, Rhizopoda) was present.

These testate amoebae, also known as thecamoebae, are present in a wide range of moist and freshwater habitats, ranging from lakes, pools, rivers, and springs to mosses, peats, and wet soils. Testate amoebae have a short generation time, which makes them suitable indicators of short-lived environmental changes in moisture, pH, trophic status, and climatic changes. Therefore they are used in paleoecological studies (Woodland et al., 1998: Beyens and Meisterfeld, 2001).

Based on both climatological and vegetational characteristics, Stonehouse (1982) described a distinct cold-temperate subantarctic region, comprising the Crozet Archipelago, Kerguelen, Falkland Islands, Macquarie Island, Marion Island, and Prince Edward Island. With the exception of Kerguelen (Richters, 1907; Vanhoffen, 1912; Bonnet, 1981) the testate amoebae fauna of these islands has only been briefly studied. On Île de la Possession, Richters (1907) noted eight species of testate amoebae from moss samples and Smith (1975) recorded nine species from soil samples. Both studies revealed only species of the more common genera, such as *Arcella*, *Assulina*, *Corythion*, *Difflugia*, *Euglypha*, *Nebela*, and *Trinema*.

The major aim of this study is to make a detailed survey of the actual living testate amoebae assemblages in soil, moss, and freshwater habitats on Île de la Possession. The present paper focuses on the aquatic habitats of various parts of the island and tries to link testate amoebae assemblages with their ecological preferences.

Materials and Methods

STUDY SITE

The Crozet Archipelago (45°48′–46°26′S, 50°14′–52°15′E) is a group of small islands located in the southern Indian Ocean, 2400 km north of the Antarctic Continent and 2400 km southeast from the South African coast (Fig. 1). The archipelago, just north of the Antarctic Convergence, consists of five volcanic islands of which Île de la Possession (156 km^2) is the largest. The islands are mainly composed of plagioclase-basalt (Dreux and Rémy, 1963) and their climate is oceanic and cold. More information regarding climate, topography and vegetation of the island is given in Van de Vijver et al. (2002b).

SAMPLING

Field sampling was conducted during the austral summers of 1997–1998 and 2002 at Île de la Possession. Surface sediment and water chemistry samples were collected from water bodies ranging from small pools to lakes (>100 m^2) and from rivers to small brooklets. A distinction was made between the substrates from which the samples were obtained. Next to habitat type (see Van de Vijver and Beyens, 1999a), substrate type was added as a nominal variable, describing five different types: "aufwuchs" (23 samples), "sediment" (18 samples), "gravel" (4 samples), "sapropelium" (10 samples), and "scraping samples" (11 samples). All samples were taken with a 50-ml PVC bottle. Three percent formaldehyde was added to fix the samples.

Specific conductance and pH were measured with a WTW Multiline P4. Water chemistry analysis (turbidity, total hardness, color, NH_4^+, NO_2^-, NO_3^-, PO_4^{3+}, SiO_2, SO_4^{2-}, Cl^{-1}) was performed in the laboratory using a Palintest interface spectrophotometer. Detailed results of the physicochemical analysis are published in Van de Vijver and Beyens (1999a).

SLIDE PREPARATION AND COUNTING

The samples were passed over a sieve with a mesh diameter of 595 μm and concentrated by centrifugation (5 min at 2500 rpm). Rose bengal was added to distinguish dead from living tests. In each sample 150 tests were counted using a Leitz Wetzlar® microscope. One hundred and fifty individuals should record most taxa present (Fig. 2) (Woodland, 1998), as long as an increase of 10% in sample size does not exceed a 10% increase of taxa (Müller-Dombois and Ellenberg, 1974).

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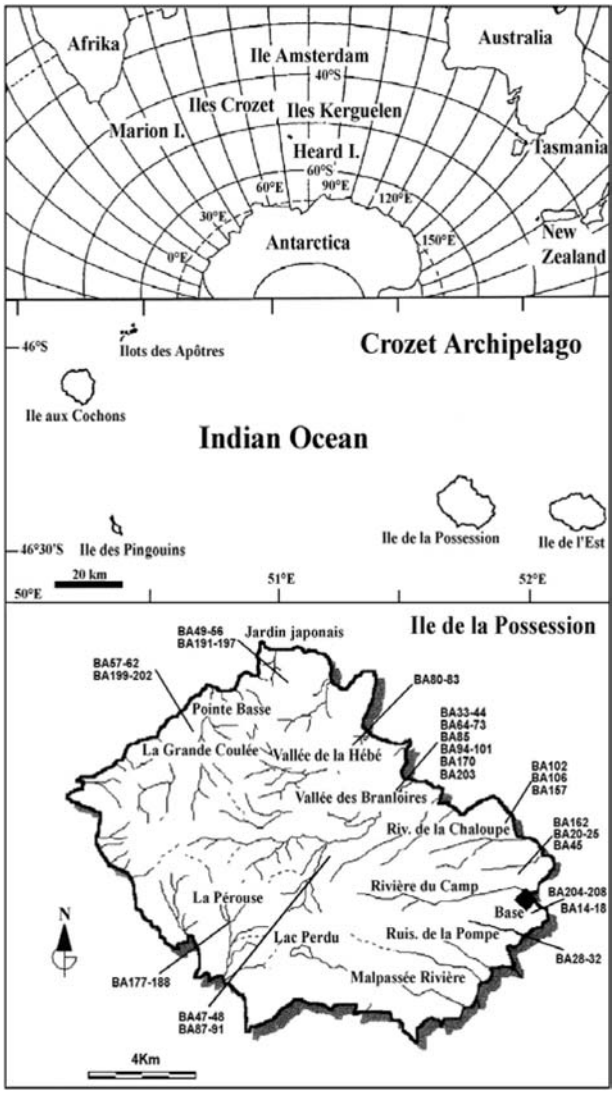

FIGURE 1. Sketch map of Antarctica, the Crozet Archipelago, and Île de la Possession showing the locations of the different sampling sites (only first and last sample numbers are shown).

Morphological identifications of the testate amoebae are mainly based on Deflandre (1928, 1929, 1936), Grospietsch (1964), Decloître (1960, 1962, 1978, 1979, 1981), Ogden and Hedley(1980), Ogden (1983), and Hoogenraad and de Groot (1940).

Samples are stored at the University of Antwerp (UA), Department of Biology, Polar Ecology, Limnology and Paleobiology Unit.

COMMUNITY ANALYSIS

The data set was first screened to remove rare taxa. If a taxon was not present in at least one site with a relative abundance of 2%, it was considered a "rare" taxon and removed from further statistical analysis (Jongman et al., 1995).

A hierarchic-agglomerative cluster analysis, based on a minimum variance strategy with the Squared Euclidian Distance as a dissimilarity measure, was carried out to classify the species data. Species abundances data were square root transformed. Clustering was performed with the Multivariate Statistical Package (MVSP) (Kovach Computing Services, 1993).

Ordination techniques were performed to explore the relationships between the freshwater testate fauna and the measured environmental

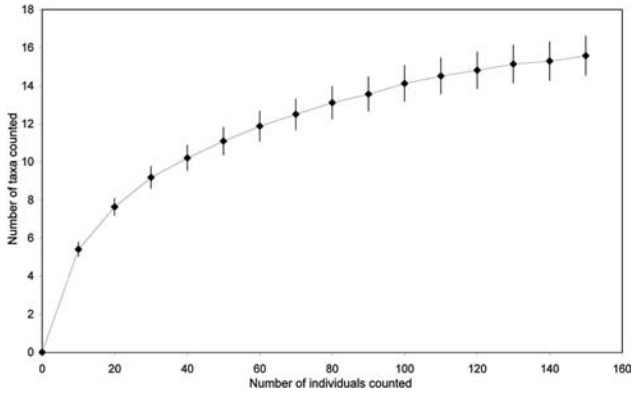

FIGURE 2. Cumulative species diversity for samples, shown as the mean, ± 2 standard errors. Standard errors are based on all samples.

variables. A correspondence analysis (CA) revealed that the total gradient length was smaller than 2 standard deviations (SD), thereby indicating a linear relationship between the variables and the species abundance data. Therefore a Redundancy Analysis (RDA) was used to detect patterns of variation in the species data which can be explained by environmental variables (Jongman et al., 1995). All environmental variables, except for pH, "habitat type," and "substrate type," were log-transformed since they had skewed distributions. Si and NO_2^- were removed from the original data set since their values were below the limit of detection (NO_2^-) or unreliable (Si). Since not all of the other environmental variables influenced the distributions of testate amoebae independently, a RDA analysis with forward selection and unrestricted Monte Carlo tests (999 permutations, $P < 0.05$) was carried out. Groups of significantly ($P < 0.05$) correlated environmental variables were identified (Hall and Smol, 1992) by making a Pearson correlation matrix with Bonferroni-adjusted probabilities (Wilkinson, 1988). The matrix of all Pearson product-moment correlations between the environmental variables is given in Van de Vijver and Beyens (1999a).

The statistical techniques used in this study are described in detail in Jongman et al. (1995). Ordination analysis was performed using the computerprogram CANOCO version 4.0 (ter Braak, 1998).

pH TRANSFER FUNCTION

Weighted average (WA) regression and calibration (Line and Birks, 1990), using the program WACALIB (version 3.0), were used to determine the optima and tolerances of the most common species for pH. The optima were calculated for pH, using simple weighted averaging with classical deshrinking. Bootstrap estimates were used afterwards to obtain valid r^2 correlation values for the transfer function. Species abundances data were square-root transformed to reduce the influence of dominant taxa such as *Trinema lineare* and to give more emphasis to subdominant species. This is a quite common technique, used frequently in the past (e.g., Cumming and Smol, 1993). A minimum occurrence in two samples was needed for taxa to be included in the analysis.

Results and Discussion

SPECIES COMPOSITION

In total 91 samples have been analyzed, from which 25 samples were withdrawn from further analysis since they contained little (<10 tests per slide) or no thecamoebae. In the remaining 66 samples a total of 85 taxa (including species, varieties and forms) belonging to 21 genera was recorded. Thirty-six percent of all counted testate amoebae were still alive at the moment of sampling.

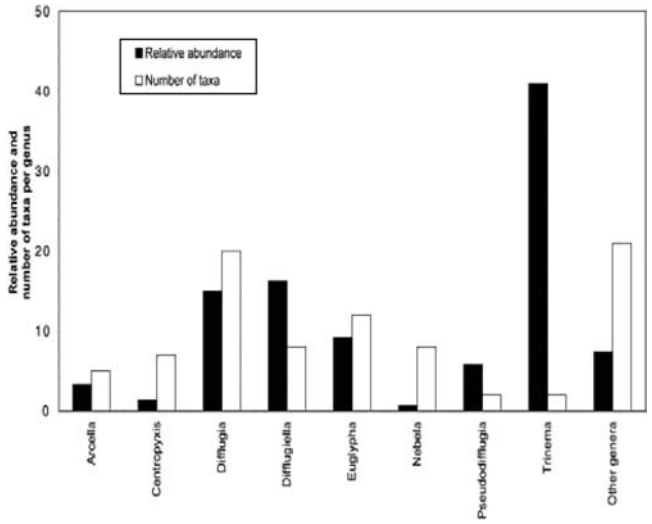

FIGURE 3. Relative abundance of the main Testacea genera observed in this study (black bars) and the number of taxa occurring in the different genera (white bars).

The number of taxa found in aquatic habitats is clearly superior to the number of taxa encountered in terrestrial habitats on Île de la Possession (Richters, 1907; Smith, 1975). Beyens et al. (1995) came to the same conclusion comparing the aquatic habitats of South Georgia with soil and moss samples. A taxonomical list of all observed testate amoebae taxa is given in Appendix 1. Several unidentified species are included in this list. Identification using scanning electron microscopy (SEM) and description of possible new taxa will be the subject of a future publication.

Diversity analysis of the samples revealed a mean Shannon-Wiener index of 0.85 ± 0.02 and a mean evenness number of 0.72 ± 0.01. The average number of taxa per sample was 15.5 ± 0.5. The highest number of taxa (25 taxa) was found in BW143, a sediment sample from a lake in Vallée des Branloires. The lowest number of taxa (7 taxa) was observed in W502, taken from Rivière du Camp. In general all river samples from Île de la Possession contained very few thecamoebae taxa as well as thecamoebae individuals. The same observation has been made by Schönborn (1981, 1982, 1992), who stated that testate amoebae contribute insignificantly to the flow of energy and the cycling of nutrients in running waters.

The number of taxa per genus and the relative abundance of the different genera are represented in Figure 3.

The dominating taxa in the aquatic habitats were cosmopolitan and merely ubiquitous species; they were also found in mosses and soils. The overall dominance of the genus *Trinema* is entirely explained by the occurrence of *Trinema lineare* Penard and *T. enchelys* Leidy. *Trinema lineare* was found in all but one sample with a mean relative abundance of 24%. *Trinema enchelys* was less dominant, but nevertheless present in 63 samples with a mean relative abundance of 17%. These two species have been commonly reported from subantarctic locations (Kerguelen Islands: Bonnet [1981], Marion island: Grospietsch [1969], and South Georgia: Smith [1982]). Other important species were: *Difflugiella crenulata* Playfair (10%), *Pseudodifflugia fulva* Penard (5.6%), *Difflugia globulus* Hopkinson (4.3%), *Difflugiella oviformis* Bonnet & Thomas (4%), *Difflugia pristis* Penard (3.74%), *Euglypha rotunda* Wailes (3.73%), and *Arcella arenaria* Greeff (3.1%).

The major part of the observed taxa belonged to the genus *Difflugia* (20 taxa). This dominance is commonly observed in aquatic habitats from temperate and boreal zones in the Northern Hemisphere (Schönborn, 1966; Chardez, 1985; Beyens et al., 1986) and also in subantarctic aquatic habitats (Beyens et al., 1995). Genera such as *Difflugia* and

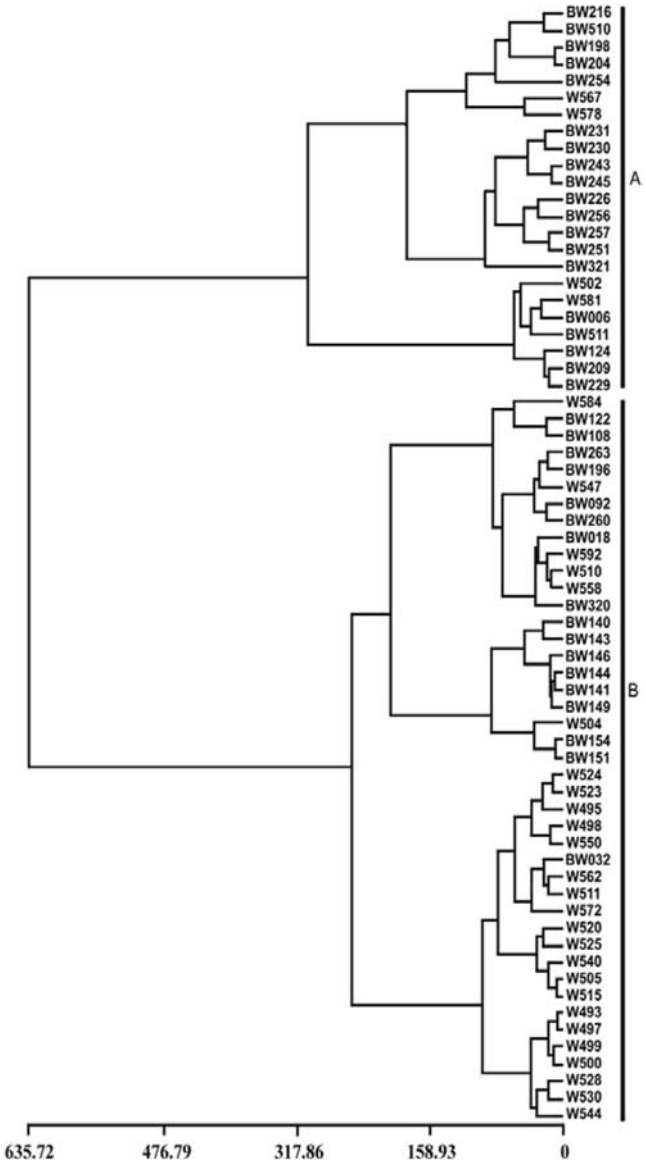

FIGURE 4. Cluster dendrogram showing all samples used for analysis (66). Letters indicated on the right refer to the different assemblages: (A) Difflugiella crenulata *assemblage; (B)* Trinema *assemblage. Lower axis shows the linkage distance.*

Arcella are more abundant in aquatic environments, while the genus *Nebela*, for instance, is more bound to terrestrial mosses (Beyens et al., 1995). This explains the extremely low relative abundance (0.6%) of the genus *Nebela* in this study compared to the dominance of *Nebela* in moss habitats in the Antarctic (Smith and Wilkinson, 1986).

COMMUNITY ANALYSIS

A cluster analysis (Fig. 4) revealed two major sample groups, named after the dominant species:

(A) *Difflugiella crenulata* assemblage
(B) *Trinema lineare–Trinema enchelys* assemblage.

Table 1 lists the main characteristics of the two assemblages. Assemblage (A) can be separated from assemblage (B) by the higher abundance of *Difflugiella crenulata* Playfair (24% in [A] and 3.1% in [B]). Other typical taxa in assemblage (A), although far less dominant, are *Trinema enchelys* (12%), *Difflugia pristis* (10%), and *Trinema*

TABLE 1

Some characteristics of the different assemblages (mean numbers ± standard errors)

	Diffugiella crenulata assemblage	*Trinema* assemblage
Number of samples	23	43
Number of taxa	15 ± 1	15.9 ± 0.5
pH	7.3 ± 0.3	6.42 ± 0.12
Conductivity (μS cm^{-1})	492 ± 120	127 ± 19
Cl^- (mg L^{-1})	195 ± 128	24 ± 5
Hardness ($CaCO_3$ mg L^{-1})	39 ± 10	5.9 ± 1.3
NH_4^+ (mg L^{-1})	17 ± 7	20 ± 3
Diversity index	0.83 ± 0.04	0.86 ± 0.02
Eveness number	0.72 ± 0.02	0.72 ± 0.01
Habitat type:		
River	2	3
Brooklet	0	4
Pool	8	17
Lake	13	19
Substrate type:		
Aufwuchs	12	10
Sediment	3	20
Sapropelium	1	9
Gravel	1	3
Scraping sample	6	1
Geographic location:		
La Pérouse	10	1
Baie Américaine	1	22
Riviére du Camp	2	12
Pointe Basse (+ Jardin Japonais)	9	5
Other	1	3
Characteristics taxa in the assemblages: taxon present in *n* (%) of samples * frequency of taxon in these samples (%)		
Assulina muscorum	13 * 0.2	47 * 1.3
Centropyxis aerophila	48 * 2.1	23 * 0.4
Corythion dubium	22 * 0.3	74 * 1.8
Cyphoderia sp 1	0 * 0	12 * 0.3
Difflugia sp 3	22 * 0.3	9 * 1
Difflugia pristis	78 * 10	9 * 0.4
Difflugiella crenulata	87 * 24	63 * 3.1
Difflugiella oviformis v. *fusca*	4 * 0.02	49 * 1.3
Difflugia sp 6	35 * 4	16 * 0.4
Euglypha laevis	48 * 1.2	56 * 4
Euglypha rotunda	74 * 2.4	93 * 4
Euglypha tuberculata	17 * 0.3	61 * 3
Nebela tubulata	4 * 0.02	21 * 0.2
Phryganella paradoxa	26 * 1	40 * 1
Pseudodifflugia fulva	78 * 7.4	77 * 4.7
Trinema enchelys	87 * 12	100 * 19
Trinema lineare	96 * 9	100 * 32

lineare (9%). In assemblage (B) on the other hand, *Trinema lineare* is the most dominant taxon, with a relative abundance of 32%. Next to *Trinema enchelys* (19%), the relatively high abundances of *Pseudodifflugia fulva* Penard (4.7%) and *Euglypha laevis* Perty (4%) typify the second assemblage. Diversity analysis revealed no remarkable differences between the two assemblages.

The two assemblages, as revealed by the cluster analysis, represent a clear geographical separation. The majority of the samples taken from "La Pérouse" and "Jardin Japonais" (western side of Île de la Possession) are characterized by the taxon *Difflugiella crenulata* (assemblage A). *Difflugiella crenulata* is typically found in stagnant waters with waterplants and submerged mosses, although it is also found in

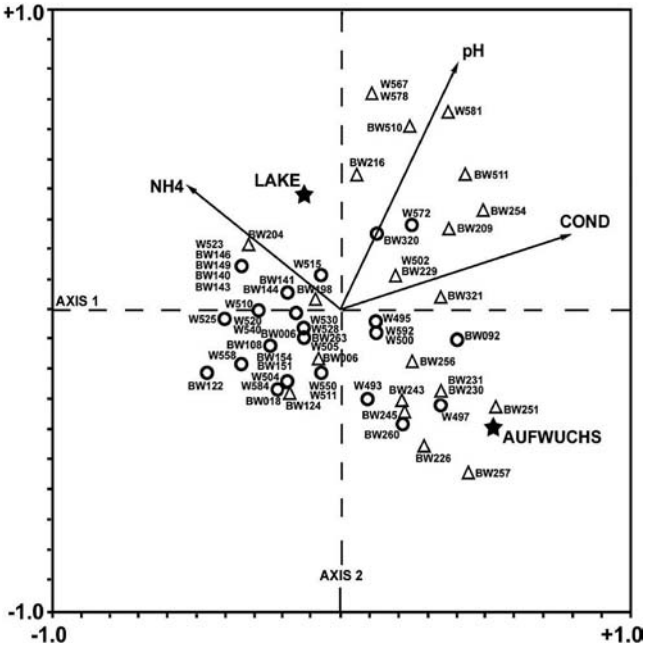

FIGURE 5. Redundancy Analysis (RDA) ordination diagram showing the relationship between sites and environmental variables. Only RDA axes 1 and 2 are shown. Arrows indicate environmental variables as detected by forward selection. Continuous variables are represented by arrows, categorical variables are indicated with a star. Samples labelled with and open circle belong to the Trinema *assemblage; samples with an open triangle belong to the* Difflugiella crenulata *assemblage.*

Sphagnum (Grospietsch, 1964). On the other hand most samples from the eastern side of the island, "Baie Américaine" and "Rivière du Camp," can be found in the *Trinema* assemblage (B) (Table 1).

In the RDA ordination diagram (Fig. 5), axis 1 is relatively strongly correlated to the specific conductance of the samples (interset correlation 0.59), while axis 2 is related to the pH (interset correlation 0.64) of the samples.

The *Difflugiella crenulata* assemblage (labelled with Δ in Fig. 5) seems to be situated almost entirely on the right side of the RDA diagram. Samples of this assemblage are characterized by higher specific conductance values and neutral to slightly alkaline pH values. In Jardin Japonais and the coastal part of La Grande Coulée, these high specific conductance and pH values can be explained by any form of salinity input (wind, sea spray, animal transport) (Van de Vijver and Beyens, 1999a). Since Jardin Japonais was initially formed by subsidence from nearby Cap Vertical, some of the lakes and pools formed by this event are situated below sea level (Van de Vijver and Beyens, 1999a). The direct infiltration of seawater influences the pH and specific conductance in this area.

Van de Vijver and Beyens (1999a) assumed that the presence of large animal colonies, occupying the small lakes and pools by the coastline, were the cause of the high measured pH and specific conductance values in the area. This hypothesis is supported by the elevated chloride concentrations in the *Difflugiella crenulata* assemblage (Table 1). No specific ecological data of the taxon *Difflugiella crenulata* were found. Trappeniers et al. (1999) reported a *Difflugiella crenulata–Cryptodifflugia compressa* assemblage in the Zackenberg area (Northeast Greenland). That assemblage had also slightly elevated pH values, although no high specific conductance values were measured.

The area of La Pérouse on the other hand shows very high specific conductance values, but the pH values are circumneutral. The locations sampled in this area are situated high above sea level, so direct infiltra-

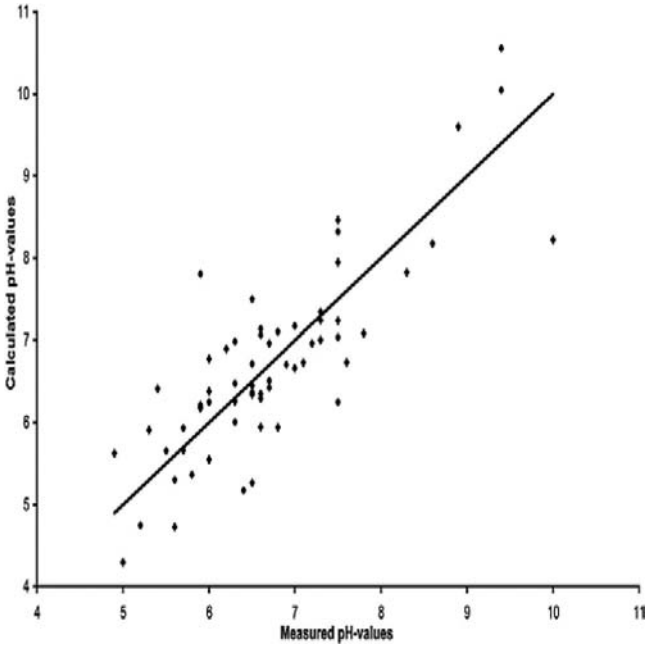

FIGURE 6. Plot of observed versus inferred pH values. Linear regression equation is $y = 0.9999x + 0.0006$*, where* x *and* y *are the observed and the calculated pH values, respectively. The dark diamonds represent the different samples.*

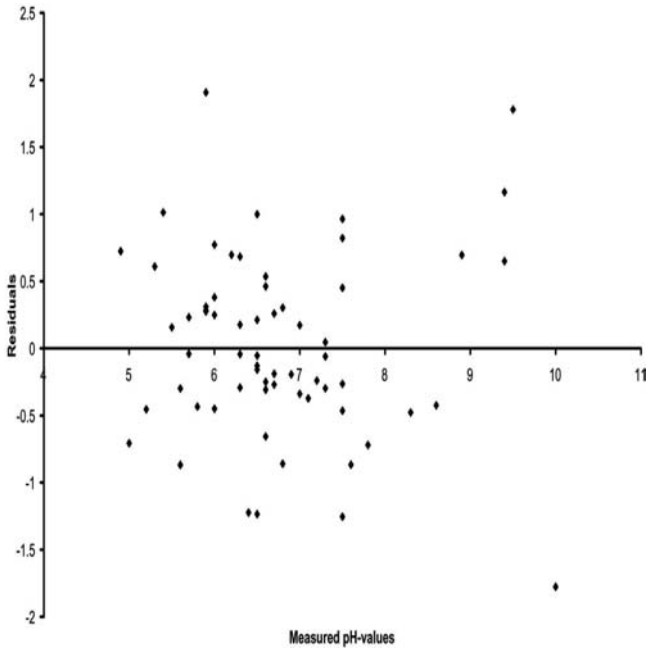

FIGURE 7. Plot of the observed pH values versus the residulas. Linear regression equation is $y = 0.0002x - 0.0001$ *where* x *represents the observed pH values and* y *the residuals. The dark diamonds represent the different samples.*

tion of seawater is not possible. A possible explanation for the elevated specific conductance values can be the phenomenon of sea spray. Since Île de la Possession is continually exposed to very strong winds, prevailing from the west with a mean wind speed of 11 m s^{-1} (Smith, 1978), the influence of sea spray in the coastal pools and lakes on the west coast is great. The higher nutrient values in La Pérouse are also caused by large colonies of skuas (*Catharacta lonnbergi*) in this area.

The majority of the samples from the *Trinema* assemblage are situated on the left side of de RDA-diagram (Fig. 5). These samples have a lower specific conductance and slightly acid pH values. *Trinema lineare* and *T. enchelys* are common species in all moist habitats (Decloître, 1981) and have possibly broad ecological ranges. As has been mentioned before, most samples from the *Trinema* assemblage are taken from larger valleys on Île de la Possession (Vallée des Branloires and Vallée du Camp). Frenot (1986) reported very low pH values, due to the large amounts of peat, in the large valleys. Consequently the pools and lakes in these valleys also have lower pH values (Van de Vijver and Beyens, 1999a).

Unlike Van de Vijver and Beyens (1999a), who reported a clear disparity between lake/pool and stream communities for the diatom flora of Île de la Possession, this kind of distinction could not be made for the testate amoebae fauna (Table 1). It is obvious that these heterotrophic organisms do not interact with the environment in the same way diatoms do.

DEVELOPMENT OF A TESTATE AMOEBAE-BASED pH TRANSFER FUNCTION

The results of the cluster and the RDA analysis showed that pH is one of the principal factors influencing the freshwater testate amoebae communities on Île de la Possession. Therefore pH can be inferred from the amoebae communities using weighted averaging regression and calibration.

When the calibration is performed, it is clear that a linear relationship between inferred and observed pH is revealed (Fig. 6, $r^2 = 0.71$, $RMSR_{boot} = 0.42$, $n = 66$). This signifies that the amoebae-predicted values for pH compare quite well with the effective measurements in the field. The plot of the residuals indicates that a significant under- or overestimation of the pH values is not observed (Fig. 7, $r^2 = 0.00$, $n = 66$).

The optima and tolerances of all species occurring in at least two samples with respect to pH are shown in Figure 8. The calculated optima and tolerances of these testate amoebae species improve and

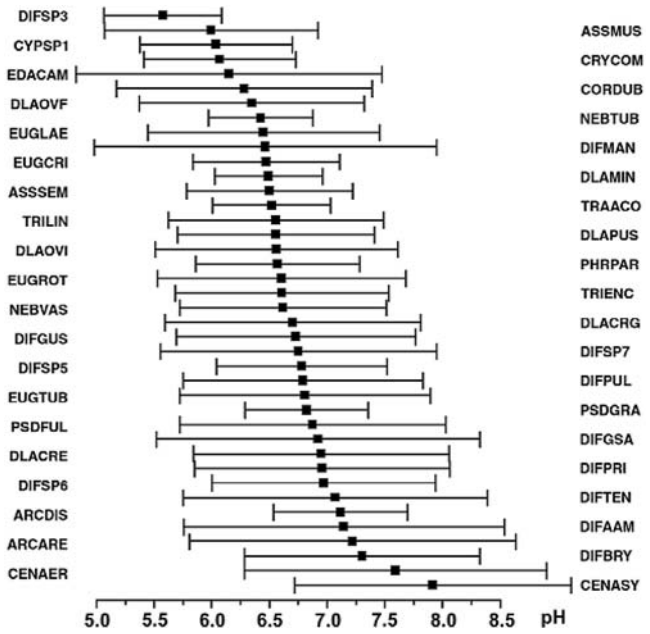

FIGURE 8. Weighted Average (WA) optima and tolerances for pH illustrated in ascending order for the principal testate amoebae species used to develop the model. Codes are explained in Appendix 1.

extend significantly our knowledge of the ecology of testate amoebae, more specific the species occurring in the subantarctic region. The obtained data will be useful afterwards in paleoecological interpretations of peat cores.

Acknowledgments

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APPENDIX 1

List of all observed testate amoebae taxa. Codes used in Figure 8 are added

Arcella arenaria Greeff	ARCARE
Arcella discoides Ehrenberg	ARCDIS
Arcella rotundata v. *aplanata* Deflandre	
Arcella sp 1	
Arcella vulgaris Ehrenberg	
Assulina muscorum Greeff	ASSMUS
Assulina seminulum Penard	ASSSEM
Assulina sp 1	
Centropyxis aculeate Stein	
Centropyxis aerophila Deflandre	CENAER
Centropyxis aerophila v. *sphagnicola* Deflandre	CENASY
Centropyxis aerophila v. *sylvatica* Deflandre	CENASY
Centropyxis cassis Deflandre	
Centropyxis hirsuta Deflandre	
Centropyxis platystoma (Penard) Deflandre	
Corythion dubium Taranek	CORDUB
Cryptodifflugia compressa Penard	CRYCOM
Cyclopyxis aff. *arcelloides*	
Cyclopyxis sp 1	
Cyphoderia ampulla Ehrenberg	
Cyphoderia sp 1	
Difflugia aff. *ampullula*	DIFAAM
Difflugia aff.*angulostoma*	
Difflugia ampullula Playfair	DIFAMP
Difflugia angulostoma Gauthier-Lièvre & Thomas	
Difflugia bacillifera Penard	
Difflugia bryophila Jung	DIFBRY
Difflugia globulosa Dujardin	DIFGSA
Difflugia globulus Hopkinson	DIFGUS
Difflugia longicollis Gassowsky	
Difflugia lucida Penard	
Difflugia manicata Penard	DIFMAN
Difflugia microstoma Thomas	
Difflugia pristis Penard	DIFPRI
Difflugia pulex Penard	DIFPUL
Difflugia sp 1	
Difflugia sp 2	
Difflugia sp 3	DIFSP3
Difflugia sp 4	
Difflugia sp 5	DIFSP5
Difflugia sp 6	DIFSP6
Difflugia sp 7	DIFSP7
Difflugia tenuis (Penard) Chardez	DIFTEN
Difflugiella crenulata Playfair	DLACRE
Difflugiella crenulata v. *globulosa* Playfair	DLACRG
Difflugiella minuta Playfair	DLAMIN
Difflugiella oviformis (Penard) Bonnet & Thomas	DLAOVI
Difflugiella oviformis v. *fusca* (Penard) Bonnet & Thomas	DLAOVF
Difflugiella pusilla Playfair	DLAPUS
Difflugiella sacculus (Penard) Deflandre	
Difflugiella sp 2	
Edaphonobiotus campascoides Schönborn, Foissner & Meisterfeld	EDACAM
Euglypha acanthophora (Ehrenberg) Perty	
Euglypha acuminata Ehrenberg	
Euglypha ciliata (Ehrenberg) Penard	
Euglypha ciliata v. *glabra* Wailes	
Euglypha compressa Carter	
Euglypha cristata Leidy	EUGCRI
Euglypha cuspidata Bonnet	
Euglypha laevis Perty	EUGLAE
Euglypha rotunda Wailes	EUGROT
Euglypha strigosa Leidy	
Euglypha strigosa v. *glabra* Wailes	
Euglypha tuberculata Dujardin	EUGTUB
Frenzelina reniformis Penard	
Hyalosphenia sp 1	
Nebela dentistoma Penard	
Nebela minor Penard	
Nebela sp 1	
Nebela sp 3	
Nebela sp 4	
Nebela tincta Awerinzew	
Nebela tubalata Brown	NEBTUB
Nebela vas Certes	NEBVAS
Paraquadrula irregularis Deflandre	
Phryganella paradoxa Penard	PHRPAR
Plagiopyxis callida Penard	
Plagiopyxis declivis Thomas	
Protoplagiopyxis sp 1	
Pseudodifflugia fulva Penard	PSDFUL
Pseudodifflugia gracilis Schlumberger	PSDGRA
Tracheleuglypha acolla Bonnet & Thomas	TRAACO
Tracheleuglypha sp 1	
Trinema enchelys Leidy	TRIENC
Trinema lineare Penard	TRILIN