

Biogeographic study of the planktonic communities of the Prince Edward Islands (Southern Ocean)

P.W.Froneman and E.A.Pakhomov

Southern Ocean Group, Department of Zoology and Entomology, Rhodes University, PO Box 94, Grahamstown, 6140, South Africa

Abstract. Microphytoplankton and zooplankton composition and distribution in the vicinity of the Prince Edward Islands and at the Sub-antarctic Front (SAF) were investigated in late austral summer (April/May) 1996. Samples were collected for analysis of chlorophyll *a* concentration (Chl *a*), microphytoplankton and zooplankton abundance. Generally, the highest Chl *a* concentrations (up to 2.0 µg l⁻¹) and zooplankton densities (up to 192 ind. m⁻³) were recorded at stations within the inter-island area while the lowest values (<0.4 µg l⁻¹) were observed at stations upstream of the islands. High Chl *a* and zooplankton biomass values were also associated with the SAF. Microphytoplankton were dominated by chain-forming species of the genera *Chaetoceros* (mainly *C.neglectus*), *Fragilariopsis* spp. and the large diatom *Dactyliosolen antarcticus*. The zooplankton assemblages were always dominated by mesozooplankton which at times contributed up to 98% of total zooplankton abundance and up to 95% of total biomass. Among mesozooplankton, copepods, mainly *Clausocalanus brevipes* and *Metridia lucens* numerically dominated. Among the macrozooplankton euphausiids, mainly *Euphausia vallentini*, *E.longirostris* and *Stylocheiron maximum*, and chaetognaths (*Sagitta gazellae*) accounted for the bulk of abundance and biomass. Cluster and ordination analysis did not identify any distinct biogeographic regions among either the microphytoplankton or zooplankton.

Introduction

Biogeographic studies of the planktonic communities in the open waters of the Southern Ocean are well documented (Hansen and Lowery, 1985; Pakhomov *et al.*, 1994; Froneman *et al.*, 1995a,b; Pakhomov and McQuaid, 1996). The results of these studies have shown that distinct plankton communities are associated with specific water masses separated by the oceanic frontal systems (Pakhomov *et al.*, 1994; Froneman *et al.*, 1995a,b). For example, it is well established that in the Southern Ocean, the planktonic communities composition differs markedly north and south of the Antarctic Polar Front (APF) due to the high nutrient concentrations and abundances of large microphytoplankton associated with the continuous upwelling in the region of the front (El-Sayed, 1988; Froneman *et al.*, 1995b). The differences in the community structure associated with the different water masses are thought to reflect the specific physiological requirements of the individual species (Froneman *et al.*, 1995b). Although in addition to physico-chemical parameters, biological processes such as herbivory and carnivory have also been shown to be important in determining the distribution of plankton in the Southern Ocean. The frontal systems proper are thought to represent important boundaries to the distribution of planktonic species due to their strong physico-chemical gradients (Deacon, 1982; Froneman *et al.*, 1995a,b).

Biogeographic studies in the vicinity of oceanic islands in the Southern Ocean have largely been restricted to the waters surrounding South Georgia (Hardy and Gunther, 1935; Theriot and Fryxell, 1985; Priddle *et al.*, 1986; Dodge and Priddle,

1987; Atkinson, 1989; Froneman *et al.*, 1997a). Several distinct microphytoplankton communities associated with distinct water masses have been identified in the vicinity of South Georgia during these investigations. Furthermore, the studies in the vicinity of the island have shown that under anomalous oceanographic conditions, Sub-antarctic Surface Waters may be advected southwards towards the island resulting in changes in the plankton community structure (Atkinson and Peck, 1988; Froneman *et al.*, 1997a). In the immediate vicinity of the island, however, small micro-scale processes including grazing by zooplankton may be important in imposing biogeographical patterns on microphytoplankton (Froneman *et al.*, 1997a).

The Prince Edward Islands (47°S; 38°E) are situated in the Sub-antarctic waters of the West Wind drift between the Sub-antarctic Front (SAF) and the APF. Meanders in the position of the SAF periodically result in the interchange of Antarctic and subantarctic surface waters which according to Boden and Parker (1986) are reflected in the changes in the phytoplankton and zooplankton species composition around the islands. Although considerable data on the species composition of the planktonic communities in the inshore waters are available (Grindley and Lane, 1979; Miller, 1982; Boden and Parker, 1986; Boden and Reid, 1989; Perissinotto and Boden, 1989; Pakhomov and Froneman, *in press*), we are unaware of any study that has undertaken numerical analysis of the planktonic communities in the off-shore waters of the Prince Edward Islands.

In this paper we present data on the first biogeographic study of the planktonic communities in the inshore and off-shore waters surrounding the Prince Edward Islands in late austral summer 1996.

Method

Samples for the analysis of chlorophyll *a* (Chl *a*), microphytoplankton and zooplankton abundance were obtained during voyage 81 of the research vessel mv SA 'Agulhas' conducted in late austral summer (April/May) 1996 to the region of the Prince Edward Islands. In the upstream region (west) of the islands, samples were collected along the 37°E meridian between 47°S and 44°30'S. This was followed by an intensive inter-island survey (Figure 1).

Water samples for the identification and enumeration of microphytoplankton were taken using a shipboard pump (Iwaki Magnet Pump), made from polyvinylidene fluoride and ceramic materials, and operated at a flow rate of ~4 l min⁻¹ (Allanson *et al.*, 1981). The pump outlet was ~5 m below the sea surface and the seawater supplied to the laboratory through PVC piping. Previous studies have shown that the collection of water samples using the shipboard pump does not significantly alter microphytoplankton community structure as a result of diatom cell rupture or breakage (Allanson *et al.*, 1981). For the taxonomic analysis of the microphytoplankton standing stock, a 20 µm mesh filtration unit (Berman and Kimor, 1983) was connected to the pump outlet and a constant volume of 20 l of seawater was filtered at each station. The phytoplankton retained by the filter were preserved in 2% buffered formalin and enumerated and identified using a Nikon TMS inverted microscope operated at 400× magnification. A minimum of

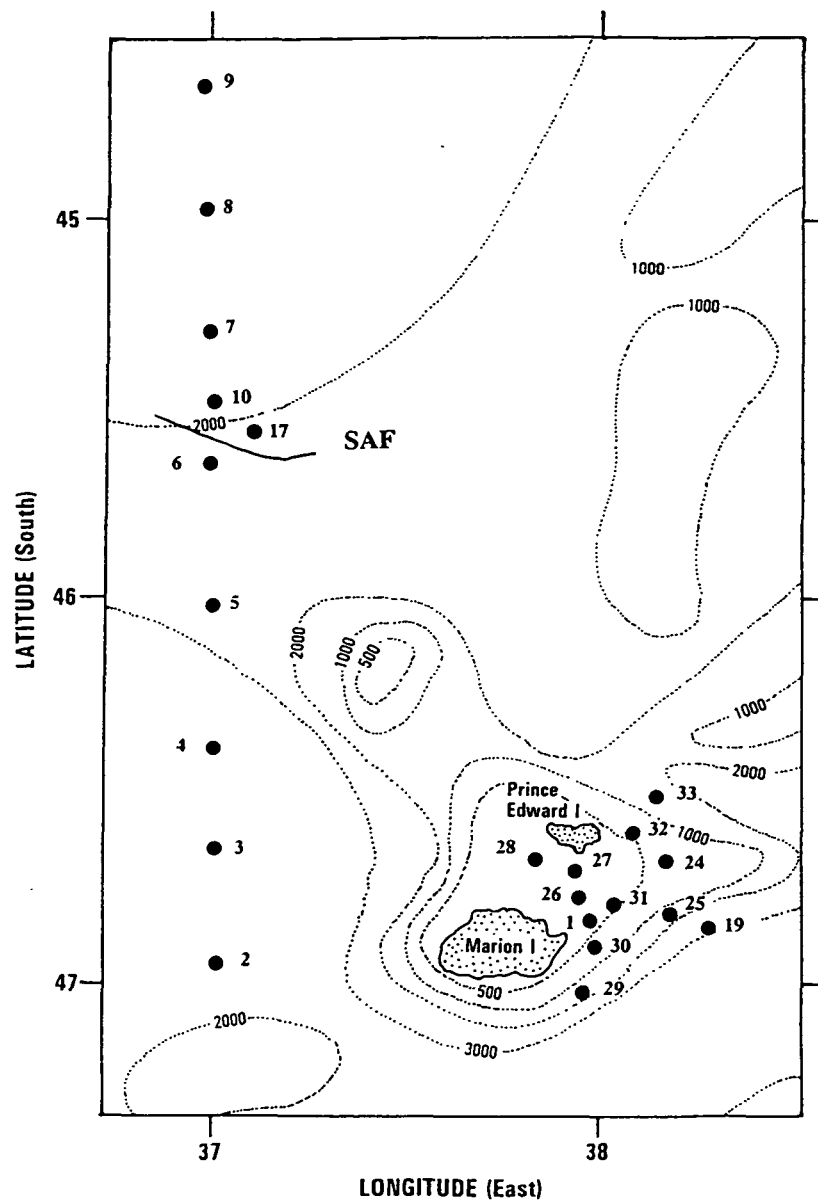


Fig. 1. Cruise track and spatial distribution of stations in the waters surrounding the Prince Edward Islands in austral autumn (April/May) 1996. SAF = Sub-antarctic Front.

500 cells or 100 fields was counted for each sample. Densities were then expressed as cells l^{-1} . Microphytoplankton species were identified using the works of Priddle and Fryxell (1985) and Tomas (1996).

In addition to the microphytoplankton sample, Chl *a* concentrations were

determined at each station. A 250 ml water sample obtained from the shipboard pump was gently filtered (~ 710 mmHg) through a serial filtration unit and fractionated into the pico- (<2.0 μm), nano- (2.0 – 20.0 μm) and microphytoplankton (>20 μm) size fractions. Chl *a* concentrations were then determined fluorometrically after extraction in 90% acetone for 24 h (Holm-Hansen and Riemann, 1978).

Zooplankton samples were collected using a Bongo net with a mesh size of 300 μm . The net was fitted with a Universal Underwater Unit (U³) which monitored temperature and depth continuously during the tow. The volume of water filtered during each tow was calculated with an electronic flow meter. Towing speed varied from 1.5–3.0 knots and the net was towed obliquely between 300 and 0 m (or between the bottom and 0 m within the inter-island region). The samples were fixed in 4–6% buffered formalin and examined in a 1/8 sub-sample for the taxonomic identification. The zooplankton species composition was identified using the keys of Boltvoskoy (1981) and Razouls (1994). The data were then expressed as ind. m^{-3} . The dry weight of the meso- and macrozooplankton at each station was determined from a 1/4 sub-sample after oven drying for 24 h at 60°C.

Numerical analysis

All data collected along the transect were log-transformed (Legendre and Legendre, 1983) before comparing stations using the Bray–Curtis measure of similarity. The analysis was carried out employing the Plymouth Routines in Multivariate Ecological Research (Primer, Clarke and Warwick, 1994) computer package according to the procedure described by Field *et al.* (1982). Groupings in the dendrogram were not attempted below the 50% similarity level. Significance levels and sources of error between the groupings were tested using the similarity programs SIMPER and ANOSIM (Clarke and Warwick, 1994).

Relationships between Chl *a*, zooplankton abundance and dry weights of meso- and macrozooplankton in the various regions sampled were tested using Pearson correlation analysis and analysis of variance (ANOVA). The analyses were carried out using the computer package Stratigraphics Version 5.0 (Statistical Graphics Corporation).

Results

Chlorophyll a distribution

Total Chl *a* concentration were generally highest at stations in the vicinity of the SAF and between the islands (Figure 2). Chl *a* concentrations within these regions ranged from 1.2 to 2.0 $\mu\text{g l}^{-1}$ and between 0.5 and 1.5 $\mu\text{g l}^{-1}$, respectively. At these stations, total Chl *a* was generally dominated by microphytoplankton which comprised up to 69% of the total in the vicinity of the SAF and up to 61% in the waters in the vicinity of the islands. An exception was found at station MS1 located within the inter-island region where the lowest Chl *a* concentration (0.13 $\mu\text{g l}^{-1}$) during the entire investigation was recorded (Figure 2). At this station, nanophytoplankton (2–20 μm) formed the most important contributor to total

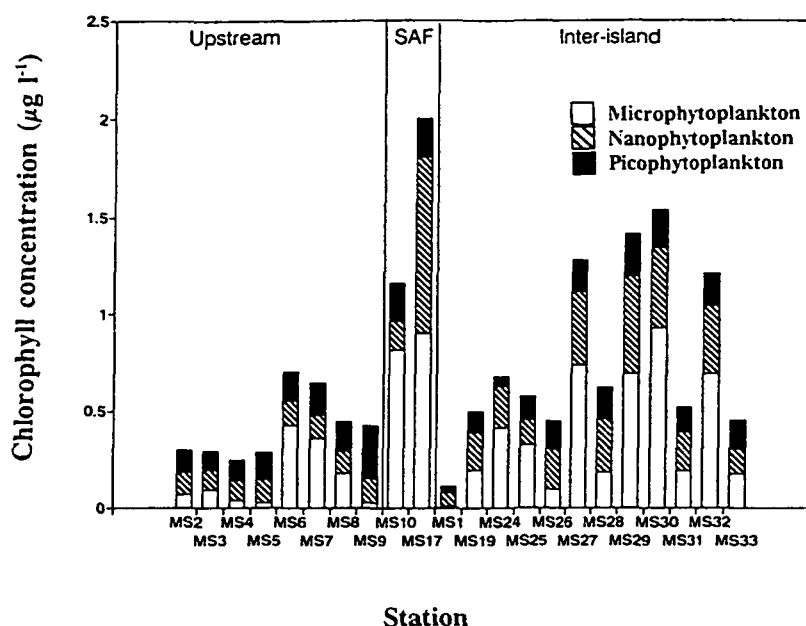


Fig. 2. Size fractionated chlorophyll *a* concentrations along the transect conducted in the upstream and inter-island region of the Prince Edward Islands in austral autumn (April/May) 1996. SAF = Sub-antarctic Front.

chlorophyll. At stations in the upstream region of the islands, total Chl *a* concentrations were lower, ranging from 0.25 to 0.65 $\mu\text{g l}^{-1}$ (Figure 2). At these stations, although highly variable, nano- and picophytoplankton generally dominated total Chl *a* concentrations. Exceptions were stations MS6 and MS7 where microphytoplankton dominated total Chl *a* (Figure 2).

Microphytoplankton abundance and species composition

Microphytoplankton abundance varied considerably along the transect with densities ranging from 10^3 to 10^5 cells l^{-1} . No distinct patterns in microphytoplankton abundance were evident during the survey (Table I). Throughout the investigation, microphytoplankton species composition was dominated by chain-forming species of the genus *Chaetoceros* (Table I). An exception was at station MS2 where *Dactyliosolen antarcticus* was the most abundant species. The single most common microphytoplankton species was *Chaetoceros neglectus* which at times contributed up to 99% of the total microphytoplankton cells counted (Table I). In particular at stations downstream of the island, this species totally dominated the total cell counts (Table I). Generally, the second most common species throughout the survey was *Dactyliosolen antarcticus* which comprised between 5 and 47% of the total. Also well represented among the microphytoplankton were *Chaetoceros atlanticus* and *Fragilariopsis* spp. (Table I).

Table I. Microphytoplankton species composition and species richness and abundance along a transect conducted in austral autumn (April/May) 1996 in the vicinity of the Prince Edward Islands. Only those species contributing >5% of the total are shown

Station	No. species	Abundance (cells l ⁻¹)	Species composition and % contribution
MS2	11	39 405	<i>Dactyliosolen antarcticus</i> (47); <i>Chaetoceros neglectus</i> (38); <i>Rhizosolenia chunii</i> (5)
MS3	21	63 205	<i>Chaetoceros neglectus</i> (94)
MS4	21	5967	<i>Chaetoceros neglectus</i> (27); <i>Dactyliosolen antarcticus</i> (25); <i>Chaetoceros atlanticus</i> (18); <i>C. criophilum</i> (8)
MS5	20	3036	<i>Chaetoceros atlanticus</i> (21); <i>C. neglectus</i> (19); <i>Dactyliosolen antarcticus</i> (19); <i>Fragilariopsis</i> spp. (8)
MS6	22	234 990	<i>Chaetoceros neglectus</i> (96)
MS7	20	3209	<i>Chaetoceros neglectus</i> (76); <i>Fragilariopsis</i> spp. (5); <i>Dactyliosolen antarcticus</i> (5)
MS9	21	104 540	<i>Chaetoceros neglectus</i> (25); <i>Pseudonitzschia seriata</i> (25); <i>Dactyliosolen antarcticus</i> (11); <i>Thalassiosira</i> spp. (9)
MS10	24	57 345	<i>Chaetoceros neglectus</i> (87); <i>Fragilariopsis</i> spp. (7)
MS17	22	8106	<i>Chaetoceros atlanticus</i> (15); <i>Pseudonitzschia seriata</i> (12); <i>Chaetoceros neglectus</i> (11); <i>Dactyliosolen antarcticus</i> (11); <i>Thalassiosira</i> spp. (8)
MS19	20	2925	<i>Chaetoceros neglectus</i> (60); <i>Pseudonitzschia seriata</i> (11); <i>Chaetoceros atlanticus</i> (5); <i>Thalassiosira</i> spp. (5)
MS21	19	113 716	<i>Chaetoceros neglectus</i> (99)
MS22	24	104 700	<i>Chaetoceros neglectus</i> (96)
MS24	22	99 060	<i>Chaetoceros neglectus</i> (95)
MS25	17	51 519	<i>Chaetoceros neglectus</i> (91); <i>Dactyliosolen antarcticus</i> (5)
MS26	23	54 446	<i>Chaetoceros neglectus</i> (98)
MS27	25	150 758	<i>Chaetoceros neglectus</i> (93)
MS28	23	33 827	<i>Chaetoceros neglectus</i> (86); <i>Dactyliosolen antarcticus</i> (5); <i>Fragilariopsis</i> spp. (5)
MS29	22	200 516	<i>Chaetoceros neglectus</i> (94)
MS30	17	188 664	<i>Chaetoceros neglectus</i> (98)
MS32	17	123 827	<i>Chaetoceros neglectus</i> (96)
MS33	20	34 428	<i>Chaetoceros neglectus</i> (97)

Zooplankton community structure, distribution and abundance

The 10 most abundant zooplankton species contributing >95% of the total zooplankton at each station are shown in Table II. Although highly variable, the highest zooplankton abundances (up to 192 ind. m⁻³) were generally recorded at stations in the inter-island region and in the vicinity of the SAF (Figure 2). An exception was found at station MS17 in the vicinity of the SAF where the lowest zooplankton abundances along the entire transect were recorded. The low densities at this station were an artifact caused by unfavourable weather conditions which resulted in only the upper 10 m of the water column being sampled. Upstream of the islands, total zooplankton abundances were generally <80 ind. m⁻³ (Figure 2). During the entire investigation, the mesozooplankton size fraction comprising copepods was the most important contributor to zooplankton standing stock (Table III). Densities of copepods ranged from 19 to 158 ind. m⁻³. Among the copepods, *Clausocalanus brevipes* was identified as the single most abundant species comprising at times up to 87% of total. Exceptions were found

at stations MS 10, 17 and 29 where *Metridia lucens* and *M. gerlachei* numerically dominated (Table II). *Metridia lucens* was identified as the second most abundant copepod, although its contribution was generally <20% of the total. Also well represented among the copepods were *Oithona* spp. (mainly *Oithona frigida* and *O. similis*) and *Pleuromamma* spp. The chaetognath *Eukrohnia hamata*, ostracods and the pteropods *Limacina* spp. were also well represented among the mesozooplankton community (Table II). The contributions of these species were, however, generally <10% of the total zooplankton counts.

The macrozooplankton always contributed <2% of total zooplankton counts and, as a consequence, are not shown in Table II. The macrozooplankton fraction was dominated by the chaetognath *Sagitta gazellae* and euphausiid species. Among the euphausiids, *Euphausia vallentini*, *Thysanoessa* spp., *Stylocheiron maximum* and *Nematoscelis megalops* were numerically the most abundant although their densities were always <<1 ind. m⁻³. Pearson correlation analysis showed that total zooplankton abundance was significantly correlated to total Chl *a* concentrations ($r^2 = 0.48$; $P < 0.05$).

Zooplankton biomass

Total zooplankton biomass throughout the investigation showed no clear spatial patterns (Table II). At stations upstream of the islands, total zooplankton biomass ranged from 0.76 to 5.69 mg DW m⁻³, while at stations in the vicinity of

Table II. Dry weight of meso- and macrozooplankton at stations along the grid survey conducted in the vicinity of the Prince Edward Islands in late austral summer (April/May) 1996. Results expressed are mg DW m⁻³. Data were collected over the depths 300–0 m or between the bottom and 0 m at shallow water stations

Station	Mesozooplankton	Macrozooplankton
MS1	0.66	0.04
MS2	2.12	0.25
MS3	4.32	0.28
MS4	1.16	0.32
MS5	1.96	0.56
MS6	3.04	0.84
MS7	0.60	0.16
MS8	1.32	0.18
MS9	3.56	0.65
MS10	4.24	1.45
MS17	3.61	0.48
MS19	2.76	0.28
MS24	2.16	0.24
MS25	1.68	0.08
MS26	1.56	0.20
MS27	4.88	0.33
MS28	3.28	0.44
MS29	7.75	0.64
MS30	1.60	0.08
MS31	2.40	0.40
MS32	2.48	0.40
MS33	2.96	0.32

Table III. Mean abundances of the most abundant zooplankton species along a transect conducted in the waters surrounding the Prince Edward Islands in austral autumn (April/May) 1996. Results expressed are ind. m³. + = present but in low abundances; - = absent. Data were collected over the depths 300-0 m or between the bottom and 0 m at shallow water stations

Species	MS1	MS2	MS3	MS4	MS5	MS6	MS7	MS8	MS9	MS10	MS17
Copepoda											
<i>Aetideus armatus</i>	0.1	0.4	1.5	+	0.1	0.1	0.5	0.9	0.5	3.0	+
<i>Calanus similimus</i>	0.1	0.1	+	+	+	+	0.1	+	+	2.2	1.2
<i>Clausocalanus brevipes</i>	111.1	17.9	15.1	17.1	44.3	29.4	22.4	16.7	23.7	40.5	4.5
<i>C. laiceps</i>	0.1	+	+	+	+	+	+	+	+	+	4.5
<i>Metridia gerlachei</i>	3.5	+	+	+	+	1.3	+	+	-	+	0.6
<i>M. lucens</i>	+	9.9	3.4	3.6	10.1	13.4	0.5	5.0	8.5	+	+
<i>Oithona antarcticus</i>	+	+	+	1.5	+	+	+	+	+	12.7	8.1
<i>O. frigida</i>	+	7.6	3.6	3.3	3.1	9.2	5.2	3.4	2.5	0.5	0.1
<i>O. similis</i>	1.3	0.7	1.6	3.0	0.3	0.8	0.5	1.9	+	0.1	0.5
<i>Pleuromamma</i> spp.	-	4.5	4.7	4.2	2.8	5.4			19.9	+	+
<i>Rhincalanus gigas</i>	+	-	3.3	1.9	-	+	0.9	1.2	-	4.7	-
Ostracoda	2.1	+	+	+	4.7	+	+	5.5	1.8	+	0.3
Pteropoda											
<i>Limacina</i> spp.	2.1	4.5	10.4	4.2	6.6	4.8	4.7	5.3	5.5	28.1	+
Chaetognatha											
<i>Eukrohnia hamata</i>	0.8	3.9	8.5	8.1	2.1	5.4	12.2	4.2	2.6	3.7	0.3
<i>Sagitta gazellae</i>	1.3	1.0	1.9	1.4	2.6	2.2	1.4	7.8	0.4	12.6	0.9

Table III continued

Species	MS19	MS24	MS25	MS26	MS27	MS28	MS29	MS30	MS31	MS32	MS33
Copepoda											
<i>Aetideus armatus</i>	1.1	+	+	+	+	+	+	3.0	1.7	0.7	1.4
<i>Calanus similimus</i>	1.3	0.1	+	3.4	1.5	0.1	+	1.6	+	+	+
<i>Clausocalanus brevipes</i>	17.9	3.8	12.7	13.5	111.5	36.8	45.4	3.2	13.2	4.1	15.2
<i>C. laticeps</i>	+	+	2.3	+	+	+	1.6	1.7	+	1.4	
<i>Metridia gerlachei</i>	+	5.6	—	—	—	—	—	—	+	—	—
<i>M. lucens</i>	5.6	8.5	7.7	6.5	40.3	35.4	+	6.3	18.2	38.5	23.9
<i>Oithona antarcticus</i>	+	+	+	—	—	1.5	+	+	—	+	—
<i>O. frigida</i>	+	+	1.3	1.3	7.4	4.9	9.8	5.4	31.1	7.9	25.3
<i>O. similis</i>	+	1.4	1.2	1.7	3.7	1.4	2.4	+	0.1	+	+
<i>Pleuromamma</i> spp.	2.4	+	2.9	1.3	5.2	18.7	2.0	+	+	19.9	1.4
<i>Rhincalanus gigas</i>	+	1.4	+	—	—	—	2.9	+	2.9	—	5.6
Ostracoda	4.2	2.1	6.4	3.4	7.4	+	5.4	3.0	5.6	9.1	5.1
Pteropoda											
<i>Limacina</i> spp.	1.8	4.6	3.4	0.5	1.5	6.2	5.4	1.9	14.9	2.9	3.5
Chaetognatha											
<i>Eukrohnia hamata</i>	3.4	5.3	5.7	5.9	2.4	1.2	4.9	3.2	13.2	4.1	15.2
<i>Sagitta gazellae</i>	0.8	1.2	1.4	4.0	2.8	3.9	3.7	2.0	3.7	1.4	0.3

the islands, biomass values ranged from 1.76 to 8.39 mg DW m⁻³ (Table III). The mesozooplankton site fraction formed the most important contributor to total biomass throughout the investigation, contributing between 74 and 94% of total at stations upstream of the islands and between 80 and 95% at stations in the vicinity of the islands. Analysis of variance indicated that the total zooplankton biomass levels were not significantly different between stations upstream and downstream of the islands ($P > 0.05\%$). However, the relative contribution of the macrozooplankton to total zooplankton stock was significantly higher at stations upstream of the islands than at stations in the vicinity of the islands ($F = 11.8$; $P < 0.001$).

Numerical analysis

The results of the numerical analyses conducted with the microphytoplankton and zooplankton abundance data are shown in Figures 4 and 5. Three groupings of microphytoplankton, designated groups 1 to 3, were identified with the cluster analysis (Figure 4). Each grouping identified, however, comprised a combination of stations found in the upstream and in the vicinity of the islands and, as a consequence, the groupings do not reflect spatial variations in community structure. Rather, the groupings identified reflected differences in the relative contributions of the most important species. For example, Group 1 stations differed from Group 2 in that the *Pseudonitzschia seriata* group was well represented in Group

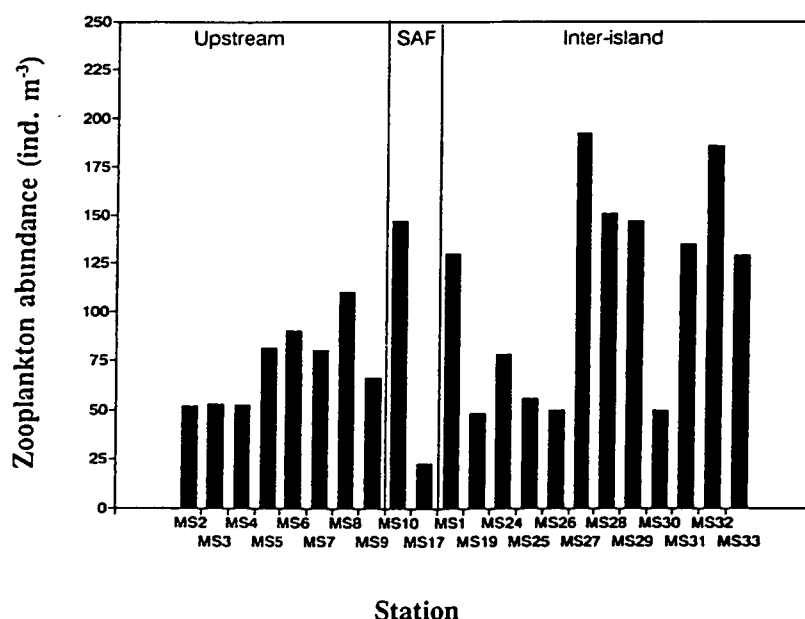


Fig. 3. Zooplankton abundance along the transect conducted in the upstream and inter-island region of the Prince Edward Islands in austral autumn (April/May) 1996. SAF = Sub-antarctic Front.

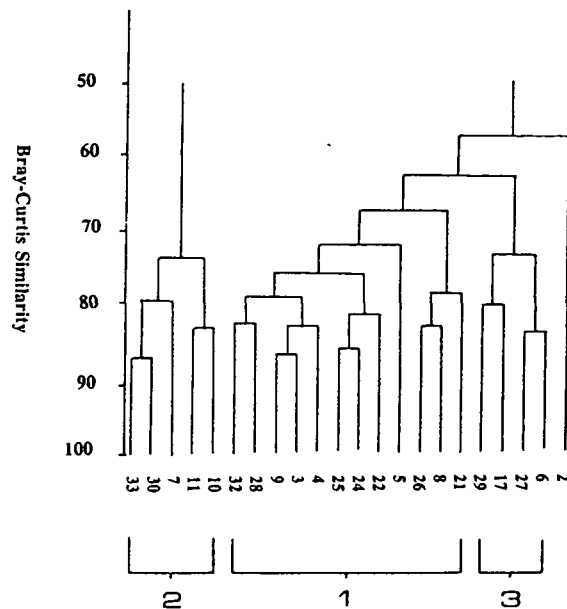


Fig. 4. Dendrogram showing the classification of the 22 stations where microphytoplankton samples were collected from the waters surrounding the Prince Edward Islands in austral summer (April/May) 1996.

2 but almost absent from Group 1 stations. Similarly Group 3 differed from Groups 1 and 2 in that *Chaetoceros atlanticus* was well represented in Group 3 but was present in only low numbers in Groups 1 and 2. Station 2 was identified as an outlier with the hierarchical cluster analysis (Figure 4). At this station *Dactyliosolen antarctica* was identified as the most abundant microphytoplankton species (Table I).

Three groupings of zooplankton stations, designated Groups 1 to 3, were obtained with the hierarchical cluster analysis (Figure 5). Although the ANOSIM showed a high degree of species overlap, the SIMPER program identified these groupings as being significantly different from one another ($P < 0.05$). The first grouping of stations identified (Group 1) was composed of all those stations found upstream of the island. An exception was station 8 which was located upstream of the island but was allocated into those stations found within the inter-island group (Figure 5). The remaining two groups of stations, Groups 2 and 3, were composed of stations found in the vicinity of the islands. Differences between the two groups were generally associated with overall densities of zooplankton rather than species composition. For example, Group 2 was characterized by extremely low abundances ($<5 \text{ ind. m}^{-3}$) of *Oithona frigida* and *Metridia lucens*, while the abundances of these two species in Group 3 were $>30 \text{ ind. m}^{-3}$. Collectively, these two species accounted for $>20\%$ of the total differences between the two groups. Station 17, which was characterized by the lowest zooplankton abundances along the entire transect, was identified as an outlier

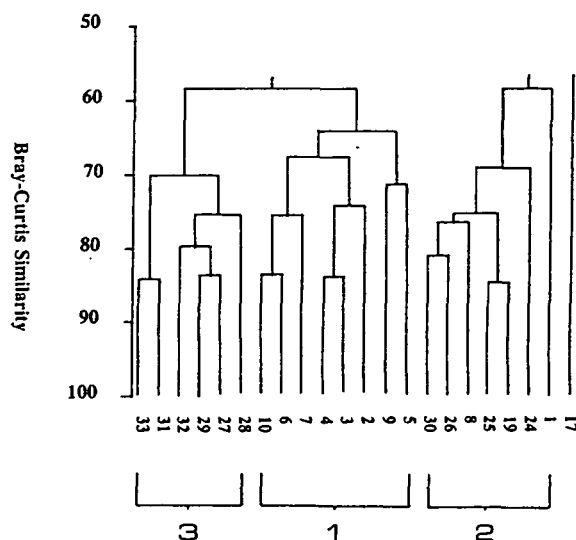


Fig. 5. Dendrogram showing the classification of the 22 stations where zooplankton samples were collected from the waters surrounding the Prince Edward Islands in austral summer (April/May) 1996.

with the hierarchical cluster analysis (Figure 5). The low zooplankton abundances at this station were an artifact caused by unfavourable weather conditions which resulted in only the surface (<10 m) zooplankton community being sampled.

Discussion

The planktonic communities in the inshore waters of the Prince Edward Islands have been the subject of extensive investigations in the past (Grindley and Lane, 1979; Miller, 1982; Allanson *et al.*, 1985; Boden and Parker, 1986; Perissinotto, 1989). These studies have largely addressed the species composition and the grazing impact of herbivorous zooplankton on phytoplankton production. The origins of these communities are, however, unknown. Boden and Parker (1986) suggested that the plankton community in the waters surrounding the islands was derived from the region north of the islands. Subsequently, Perissinotto (1989) hypothesized that the zooplankton communities were derived from the area upstream of the islands which were advected to the inter-island by the Antarctic Circumpolar current. Throughout this investigation both the zooplankton and microphytoplankton assemblages upstream of the islands were always similar to those found around the islands (Tables I and II). This result provides clear evidence of the importance of the upstream communities in determining the species composition of the plankton communities of the Prince Edward Islands.

Although the numerical analyses employed identified three distinct microphytoplankton associations along the survey, these associations showed no distinct spatial patterns (Figure 4). Rather, the differences between the groupings identified reflect changes in the relative abundances of the dominants. Unfortunately,

as no physico-chemical data were collected during the survey, it is impossible to speculate on the reasons for the changes in community structure. Boden *et al.* (1988) examining the distribution of diatoms in the Sub-antarctic waters suggested that environmental gradients may be expected to be associated with variations in species abundance rather than species limits. Also, according to Perissinotto and Boden (1989), shifts in the dominants in the waters surrounding the islands are a feature of the environment. It is possible that the changes in the microphytoplankton community in the waters surrounding the islands may have resulted from the mesoscale patchiness which may be driven by both physical and biological parameters.

Although no spatial segregation of microphytoplankton assemblages was found, two major groupings of stations were identified using the zooplankton data (Figure 5). These groupings broadly corresponded to the region upstream of the islands and in the vicinity of the islands. As was found in the microphytoplankton, the differences between the groups reflect changes in relative abundances of species rather than species composition. The elevated zooplankton within the inter-island region appears to be related to the high chlorophyll concentrations found in the region. Indeed, during this investigation, total zooplankton abundance was significantly correlated to chlorophyll (Chl *a*) concentration ($r^2 = 0.48$; $P < 0.05$). It is possible that the high abundances of zooplankton recorded at stations in the inter-island region may also have resulted from the shallow water depth within the region which would prevent the migration of zooplankton species to depth (Perissinotto and McQuaid, 1992). The zooplankton species composition and numerical abundance of copepods throughout this investigation agree well with previous investigations, although our abundances of copepods appear to be among the lower range reported in the literature for the Prince Edward Islands (Grindley and Lane, 1979; Boden and Parker, 1986; Perissinotto, 1989; Perissinotto and Boden, 1989). The low abundances of copepods during this investigation may have resulted from the mesh size employed which may have undersampled the contribution of the smaller copepods, particularly *Oithona* spp., during the investigation. The low abundances of copepods during this investigation may also have resulted from high rates of predation by chaetognaths. A study conducted in parallel to this investigation showed that chaetognaths were able to control copepod standing stock, consuming at times in excess of 100% of their daily production in the region upstream of the islands (Froneman and Pakhomov, in press).

During this investigation, elevated Chl *a* concentrations were generally recorded in the immediate waters surrounding the islands (Figure 2). The enhanced Chl *a* levels observed during this study within the inter-island region are consistent with previous studies conducted in the waters surrounding the Prince Edward Islands (Perissinotto and Duncombe Rae, 1990; Perissinotto *et al.*, 1990). Perissinotto and Duncombe Rae (1990) suggested that the elevated chlorophyll concentrations found within the inter-island region were the result of elevated phytoplankton production rates associated with the anticyclonic eddies in the region. This would serve to generate water column stability which together with the high nutrient concentrations generally recorded in the water surrounding the island (Allanson *et al.*, 1985; Ismail, 1990), would promote phytoplankton growth.

This is supported by preliminary results of a size fractionated primary production study that was conducted in parallel to this investigation. This showed that the highest production rates were recorded in the inter-island region (R.K.Laubscher, personal communication). It is worth noting that the high Chl *a* concentrations recorded in the vicinity of the islands were almost entirely dominated by a single microphytoplankton species, *Chaetoceros neglectus*, suggesting an algal bloom.

The high Chl *a* concentrations and zooplankton biomass generally recorded at stations in the vicinity of the SAF when compared to waters away from the frontal region during this investigation (Figures 2 and 3) are consistent with recent studies (Froneman *et al.*, 1995a,b; Pakhomov and McQuaid, 1996). The elevated Chl *a* concentrations in the vicinity of the front may have been the result of elevated primary production resulting from increased water column stability (Jacques, 1989; Laubscher *et al.*, 1993). Lutjeharms and Valentine (1984) using oceanographic data collected during 61 crossings of the SAF, showed that the front exhibited latitudinal shifts in excess of 2° and may even at times lie to the south of the islands. Subsequently, Nagata *et al.* (1988) also showed that the SAF exhibits marked meridional shifts over short periods. It is not unreasonable to suggest that the elevated plankton biomass associated with the front may be transported to the island ecosystem proper. This would serve to increase food availability, particularly macrozooplankton (highest biomass along the entire transect was associated with the front) (Table III), to the top predators. Furthermore, meridional shifts in the position of the SAF suggest that Sub-antarctic Zone surface waters and Polar Front Zone waters may be introduced into the area, thus providing a possible mechanism to allow the introduction of sub-antarctic zone species to the island. A similar process has been suggested to result in the introduction of sub-antarctic phytoplankton species in the waters surrounding South Georgia (Froneman *et al.*, 1997a). Further investigations are, however, required to assess the impact of the meridional shifts in the position of the SAF on the Prince Edward archipelago pelagic ecosystem.

A feature of this investigation was the virtual absence of macrozooplankton at stations found in the vicinity of the islands (Table II). Indeed, analysis of variance test showed that the relative contribution of macrozooplankton to total zooplankton biomass upstream of the island was significantly higher than at downstream stations ($F = 11.79$; $P < 0.001$). The absence of macrozooplankton in the vicinity of the islands is thought to result from the predation impact of the high densities of predators, particularly seabirds and seals (Perissinotto and McQuaid, 1992). According to Perissinotto (1989), the depleted macrozooplankton stocks within the islands are replenished from upstream macrozooplankton which are advected to the island during the night. During the day, the prey are trapped at shallow water depths by the bottom topography and are, thus, vulnerable to predation by top predators (Perissinotto and McQuaid, 1992). These facts suggest that biological factors promote mesoscale changes in the size structure of the macrozooplankton community in the vicinity of the islands. The mesozooplankton community structure appears, however, to be unaffected by the larger predators possibly because they are too small to be efficiently fed on.

In conclusion, the results of this investigation suggest that there are no distinct

biogeographical patterns in microphytoplankton community in the waters surrounding the Prince Edward Islands. The elevated total Chl *a* concentration in the vicinity of the islands reflects an increase in the contribution of the larger microphytoplankton to total resulting from increased nutrient availability and water column stability. The shift in the size composition of the phytoplankton assemblages may affect the partitioning of carbon between the classical food web dominated by large zooplankton and the microbial loop (Froneman *et al.*, 1997b). This has important implications for the biologically mediated carbon flux, the biological pump (Longhurst, 1991). The virtual absence of macrozooplankton within the inter-island region supports the previously suggested hypothesis of Perissinotto and McQuaid (1992) that the land based top predators may be responsible for this absence. There is some evidence that the SAF is highly productive and that shifts in the meridional position of the front may transport the productive waters to the vicinity of the islands.

Acknowledgements

We would like to thank the Department of Environmental Affairs and Tourism for providing funds and facilities for this study. We acknowledge the assistance of the master and crew of the S.A. 'Agulhas'. We would also like to thank S.Plon, L.Gurney, P.Illgner and N.Mzinzi for their valuable assistance at sea. Finally, we would like to thank V.Meaton for the identification and enumeration of the microphytoplankton samples.

References

- Allanson, B.R., Hart, H.C. and Lutjeharms, J.R.E. (1981) Observations on the nutrients, chlorophyll and primary production of the Southern Ocean south of Africa. *S. Afr. J. Antarct. Res.*, **10**, 3–13.
- Allanson, B.R., Boden, B.P., Parker, L. and Duncombe Rae, C. (1985) A contribution to the Oceanology of the Prince Edward Islands. In Siegfried, W.R., Condy, P.R. and Laws, R.M. (eds), *Antarctic Nutrient Cycles and Food Webs*. Springer-Verlag, Berlin, pp. 38–45.
- Atkinson, A. (1989) Distribution of six major copepod species around South Georgia in early summer. *Polar Biol.*, **9**, 353–363.
- Atkinson, A. and Peck, J.M. (1988) A summer winter comparison of the zooplankton in the oceanic area around South Georgia. *Polar Biol.*, **8**, 463–473.
- Berman, T. and Kimor, B. (1983) A large scale filtration apparatus for net plankton sampling. *J. Plankton Res.*, **5**, 111–116.
- Boden, B.P. and Parker, L.D. (1986) The plankton of the Prince Edward Islands. *Polar Biol.*, **5**, 81–93.
- Boden, B.P. and Reid, F.M.H. (1989) Marine plankton diatoms between Cape Town and the Prince Edward Islands (SW Indian Ocean). *J. S. Afr. Antarct. Res.*, **19**, 1–49.
- Boden, B.P., Duncombe Rae, C.M. and Lutjeharms, J.R.E. (1988) The distribution of the diatoms of the south-west Indian Ocean surface waters between Cape Town and the Prince Edward Island archipelago. *S. Afr. J. Sci.*, **84**, 911–918.
- Boltovskoy, D. (1981) Atlas del zooplankton del Atlantico Sudoccidental. Publicacion especial del INIDEP Mar del Plata, Argentina. pp. 1–936.
- Clarke, K.R. and Warwick, R.M. (1994) Change in marine communities: an approach to statistical analysis and interpretation. Environmental Research Council, Cambridge.
- Deacon, G.E.R. (1982) Physical and biological zonation in the Southern Ocean. *Deep-Sea Res.*, **29**, 1–15.
- Dodge, J.D. and Priddle, J. (1987) Species composition and ecology of dinoflagellates from the Southern Ocean near South Georgia. *J. Plankton Res.*, **9**, 685–697.

- El-Sayed, S.Z. (1988) Productivity in the Southern Ocean: a closer look. *Comp. Biochem. Physiol.*, **90**, 489–498.
- Field, J.G., Clarke, K.R. and Warwick, R.M. (1982) A practical strategy for analyzing multispecies distribution patterns. *Mar. Ecol. Prog. Ser.*, **8**, 37–52.
- Froneman, P.W., Perissinotto, R., McQuaid, C.D. and Laubscher, R.K. (1995a) Summer distribution of netphytoplankton in the Atlantic sector of the Southern Ocean. *Polar Biol.*, **15**, 77–84.
- Froneman, P.W., McQuaid, C.D. and Perissinotto, R. (1995b) Biogeographic structure of the microphytoplankton assemblages of the south Atlantic and Southern Ocean during austral summer. *J. Plankton Res.*, **17**, 1791–1802.
- Froneman, P.W., Pakhomov, E.A. and Laubscher, R.K. (1997a) Microphytoplankton assemblages in the waters surrounding South Georgia, Antarctica during austral summer 1994. *Polar Biol.*, **17**, 515–522.
- Froneman, P.W., Pakhomov, E.A., Perissinotto, R., Laubscher, R.K. and McQuaid, C.D. (1997b) Dynamics of the plankton communities of the Lazarev Sea (Southern Ocean) during seasonal ice melt. *Mar. Ecol. Prog. Ser.*, **149**, 201–214.
- Froneman, P.W. and Pakhomov, E.A. (1998) Trophic importance of the chaetognaths *Eukrohnia hamata* and *Sagitta gazellae* in the pelagic system of the Prince Edward Islands (Southern Ocean). *Polar Biol.* (in press).
- Grindley, J.R. and Lane, S.B. (1979) Zooplankton around Marion and Prince Edward Islands. *CNFRA*, **44**, 111–125.
- Hansen, R.B. and Lowery, H.K. (1985) Spatial distribution, structure, biomass, and physiology of microbial assemblages across the Southern Ocean frontal zones during late austral winter. *Appl. Environ. Microbiol.*, **49**, 1029–1039.
- Hardy, A.C. and Gunther, E.R. (1935) The plankton of the South Georgia whaling grounds and adjacent waters, 1926–1927. *Discovery Reports*. Cambridge University Press, Cambridge.
- Holm-Hansen, O. and Riemann, B. (1978) Chlorophyll-a determination: improvements in methodology. *Oikos*, **30**, 438–447.
- Ismail, M.E. (1990) Surface nutrients in the vicinity of the Prince Edward Islands during April/May 1989. *S. Afr. J. Antarct. Res.*, **20**, 33–36.
- Jacques, G. (1989) Primary production in the open Antarctic ocean during the austral summer. A review. *Vie Milieu*, **39**, 1–17.
- Laubscher, R.K., Perissinotto, R. and McQuaid, C.D. (1993) Phytoplankton production and biomass at frontal zones in the Atlantic sector of the Southern Ocean. *Polar Biol.*, **13**, 471–481.
- Legendre, L. and Legendre, P. (1983) *Numerical Ecology*. Elsevier Scientific Publishing Company, Amsterdam.
- Longhurst, A.R. (1991) Role of the marine biosphere in the global carbon cycle. *Limnol. Oceanogr.*, **36**(8), 1507–1526.
- Lutjeharms, J.R.E. and Valentine, H.R. (1984) Southern Ocean thermal fronts south of Africa. *Deep-Sea Res.*, **31**, 1461–1475.
- Miller, D.G.M. (1982) Results of a combined hydro-acoustic and midwater trawling survey of the Prince Edward Island group. *S. Afr. J. Antarct. Res.*, **12**, 3–10.
- Nagata, Y., Michida, Y. and Umimura, Y. (1988) Variation of positions and structures of the oceanic fronts in the Indian sector of the Southern Ocean in the period from 1965 to 1987. In Sahrhage, D. (ed.), *Antarctic Ocean and Resources Variability*. Springer Verlag, Berlin, pp. 92–98.
- Pakhomov, E.A. and McQuaid, C.D. (1996) Distribution of surface zooplankton and seabirds across the Southern Ocean. *Polar Biol.*, **16**, 271–286.
- Pakhomov, E.A., Perissinotto, R. and McQuaid, C.D. (1994) Comparative structure of the macrozooplankton/micronekton communities of the Subtropical and Antarctic Polar Fronts. *Mar. Ecol. Prog. Ser.*, **111**, 155–169.
- Perissinotto, R. (1989) The structure and diurnal variations of the zooplankton of the Prince Edward Islands: implications for the biomass build-up of higher trophic levels. *Polar Biol.*, **9**, 505–510.
- Perissinotto, R. and Boden, B.P. (1989) Zooplankton-phytoplankton relationships at the Prince Edward Islands during April/May 1985 and 1986. *S. Afr. J. Antarct. Res.*, **19**, 26–30.
- Perissinotto, R. and McQuaid, C.D. (1992) Land-based predator impact on vertically migrating zooplankton and micronekton advected to a Southern Ocean archipelago. *Mar. Ecol. Prog. Ser.*, **15**, 15–27.
- Perissinotto, R. and Duncombe Rae, C.M. (1990) Occurrence of anticyclonic eddies on the Prince Edward Plateau (Southern Ocean): effects on phytoplankton biomass and production. *Deep-Sea Res.*, **37**, 777–793.
- Perissinotto, R., Duncombe Rae, C.M., Boden, B.P. and Allanson, B.R. (1990) Vertical stability as a

Biogeographic study of planktonic communities of the Prince Edward Islands

- controlling factor of the marine phytoplankton at the Prince Edward Archipelago (Southern Ocean). *Mar. Ecol. Prog. Ser.*, **60**, 205–209.
- Perissinotto, R., Duncombe Rae, C.M., Boden, B.P. and Allanson, B.R. (1990) Vertical stability as a controlling factor of the marine phytoplankton production at the Prince Edward Archipelago (Southern Ocean). *Mar. Ecol. Prog. Ser.*, **60**, 205–209.
- Priddle, J. and Fryxell, G. (1985) *Handbook of the Common Plankton Diatoms of the Southern Ocean*. University Press, Cambridge.
- Priddle, J., Heywood, R.B. and Theriot, E. (1986) Some environmental factors influencing phytoplankton in the Southern Ocean around South Georgia. *Polar Biol.*, **5**, 65–79.
- Razouls, C. (1994) Manuel d'identification des principales especes de copepods pelagiques antarctiques et subantarctiques. *Ann. Inst. Oceanogr.*, **70**, 3–204.
- Theriot, E. and Fryxell, G. (1985) Multivariate statistical analysis of net diatom species distribution in the southwestern Atlantic and Indian Ocean. *Polar Biol.*, **5**, 23–30.
- Tomas, C.R. (1996) *Identifying Marine Diatoms and Dinoflagellates*. Academic Press, San Diego, 598 pp.

Received on April 28, 1997; accepted on November 18, 1997