ZOOPLANKTON COMMUNITY STRUCTURE OF PRYDZ BAY, ANTARCTICA, JANUARY–FEBRUARY 1993

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Abstract: Previous large scale surveys around Prydz Bay have identified the continental shelf edge as an area of rapid transition between three major zooplankton communities. One of these is dominated by the Antarctic krill *Euphausia superba*. This community was located mainly along the continental shelf edge, usually between the offshore main oceanic community dominated by copepods and chaetognaths, and the neritic community dominated by *E. crystallorophias*. A survey in January–March 1991 found similar community compositions but the krill community was restricted to the western part of the area. This study reports on the results of a repeat survey in January–February 1993 which extended the survey area to the west. Using the same multivariate analyses, the characteristic shelf and oceanic assemblages were again similar to previous surveys, but the krill community was restricted to three scattered sites. A number of hypotheses are presented to explain the apparent absence of krill: 1) there has been a genuine decline in krill numbers since the earlier surveys; 2) the overall distribution pattern of krill has changed and they were outside the survey area; and 3) the krill biomass had not declined or moved geographically but remained in the survey area but dispersed, thus not forming a distinctive community.

1. Introduction

The basis of the BIOMASS (Biological Investigations of Marine Antarctic Systems and Stocks) program was an attempt to understand the structure and dynamic functioning of the Antarctic marine ecosystem (Hempel, 1983; El-Sayed, 1994). The main focus and emphasis of the program was the assessment of the stocks of the Antarctic krill *Euphausia superba* which was perceived as the central key component of the Antarctic marine ecosystem. Research undertaken as part of BIOMASS, and later, have shown that krill are not the only important or dominant taxon in that ecosystem. For example, copepods collectively can form a significant component of the zooplankton biomass, at times exceeding that of the krill (Everson, 1984; Yamada and Kawamura, 1986; Smith and Schnack-Schiel, 1990; Conover and Huntley, 1991). They can also consume at least three times, perhaps as much as eight times, the primary production eaten by krill (Conover and Huntley, 1991). Consequently, copepods and other zooplankton such as *Euphausia crystallorophias* form important alternative pathways in the Antarctic food web as food for fish and birds (Williams, 1985, 1989; Green and Williams, 1986; Foster *et al.*, 1987; Kellermann, 1987; Hubold and Ekau, 1990; Boysen-Ennen *et al.*, 1991). A

thorough understanding of the structure of ecosystems, notably at the community level, remains a fundamental foundation to studies of species interactions, biological ocean fluxes, the effects of local and global change on biota, implementation of ecosystem monitoring strategies, and to protect and manage the ecosystem, especially in relation to harvestable resources.

Various studies have sought to define the structure of Antarctic zooplankton communities, in relation to species composition and associations, as well as their distribution patterns. These studies have ranged from early descriptive studies of individual species distributions (HARDY and GUNTHER, 1935) to more intensive surveys that have often employed the use of multivariate analytical techniques (e.g. BOYSEN-ENNEN and PIATKOWSKI, 1988; HUBOLD et al., 1988; PIATKOWSKI, 1989a,b; ATKINSON et al., 1990; SIEGEL and PIATKOWSKI, 1990).

Four large scale surveys were undertaken by Australia in the Prydz Bay region during the 1980's, which identified three zooplankton communities in the shelf edge area of Prydz Bay. A neritic community was located in the southern part of the Prydz Bay continental shelf, dominated by E. crystallorophias, gammarids and larvae of the fish Pleuragramma antarcticum. A main oceanic community was prevalent in the region north of the shelf edge to approximately 62–63°S, with the major components being copepods, chaetognaths, siphonophores and the euphausiid Thysanoessa macrura. The third community was characterized by the high abundance and dominance of the Antarctic krill E. superba and also by the paucity of zooplankton. This community was mainly located along the continental shelf edge, usually between the main oceanic and neritic communities. Higher abundances of krill along the shelf edge have been observed in other studies using hydroacoustics techniques (HIGGIN-BOTTOM et al., 1988; BIBIK and YAKOLEV, 1991,) research scale nets (PAKHOMOV, 1989, 1993) and commercial trawls (ICHII, 1990).

The continental shelf edge of Prydz Bay was thus identified as an area of particular interest because of the dominance of krill but also as an area of rapid transition between three major communities. In January to March 1991, the Prydz Bay–continental shelf area was the subject of a more intensive mesoscale survey (as defined by HAURY et al., 1977), to define more accurately the distributions and boundaries of the three main zooplankton communities in that area (HOSIE and COCHRAN, 1994). The species composition of the communities defined in 1991 were much the same as previously defined in the macroscale surveys. However, rather than clarifying the distribution patterns of the communities, the 1991 survey found that the krill dominated community distribution was significantly different from those previously observed. That community did not separate the copepod and E. crystallorophias dominated communities in Prydz Bay and apparently was displaced to the west. The 1990/91 season was notably different from previous surveys: the persistence of pack-ice in the region; the absence of a large polynya which normally forms in the south of Prydz Bay near the Amery Ice Shelf (SMITH et al., 1984; STRETEN and PIKE, 1984); shallower mixed layer, with associated very high chlorophyll concentrations in the neritic zone. These were all considered a function of the quite calm weather conditions that occurred during that season and may have directly or indirectly affected the distribution of the zooplankton communities, although no

cause-and-effect could be proven (Hosie and Cochran, 1994). Since the distribution patterns in this survey were apparently anomalous it was deemed necessary to repeat the survey.

The same transects were thus resurveyed in January–February 1993 with an additional five transects extending west of the 1991 survey area. The prime objective of the 1993 survey was the same as that of 1991, of more accurately defining the distributions and boundaries of the three main zooplankton in that area. The species composition and affinities, and distribution patterns of the communities were defined by the same multi- and uni-variate analytical techniques used in the previous study of the zooplankton community ecology of the Prydz Bay region (Hosie, 1994a; Hosie and Cochran, 1994). The patterns defined in the present study were compared with various environmental parameters to determine the factors that might govern the zooplankton distributions and in particular, those that may have caused the change in distribution patterns in 1991, notably wind. We accepted Mills' (1969) definition of a community for the purposes of this study: a community is a group of organisms occurring in a particular environment, presumably interacting with each other and with the environment, and separable from other groups by means of ecological surveys.

2. Methods

2.1. Sampling procedures

The Prydz Bay continental shelf study area was defined for the present purpose as being from 60° to 78° E and south from 65° S to the Antarctic coast or Amery Ice Shelf. Sampling sites were located at 30 nautical mile intervals along 13 longitudinal transects which were 1.5° of longitude apart (Fig. 1). Much of the sample area and sampling sites duplicated that of the January–February 1991 survey (Hosie and Cochran, 1994), with the addition of another 5 transects extending west of the 1991 survey area. Sampling commenced on 16 January in the north-east corner of the grid at station 2–then progressed westward to finish at station 120 on 7 February 1993. Heavy pack-ice (9–10/10 cover) persisted through much of the area, north of Davis, around Cape Darnley and west of Mawson (Fig . 1). This caused the cancellation or adjustment in position of sampling sites and some course alteration especially along transects 70°30' E and 72° E. This also occurred in 1991. Zooplankton were collected at each sampling site in a 0–200 m downward oblique haul using a Rectangular Midwater Trawl (RMT 8) with a nominal mouth area of 8 m^2 and mesh size of 4.5 mm (Baker *et al.*, 1973). The last 1.8 m of the net had a mesh of 1.5 mm and the cod end mesh was 0.85 mm. Siegel (1986) noted that an RMT 8 with 4.5 mm mesh may undersample krill less than 20 mm in length. Small zooplankton, especially copepods, also would have been undersampled, although the finer meshes at the end of the net and cod end did retain substantial numbers of copepods to permit relative comparison of abundances between sample sites.

An electro-mechanical net release and real time depth sensor was mounted above the net. The net was thus opened just below the surface and then closed at 200 m, or within 20 m of the sea-floor in shallower water. The net was equipped with a
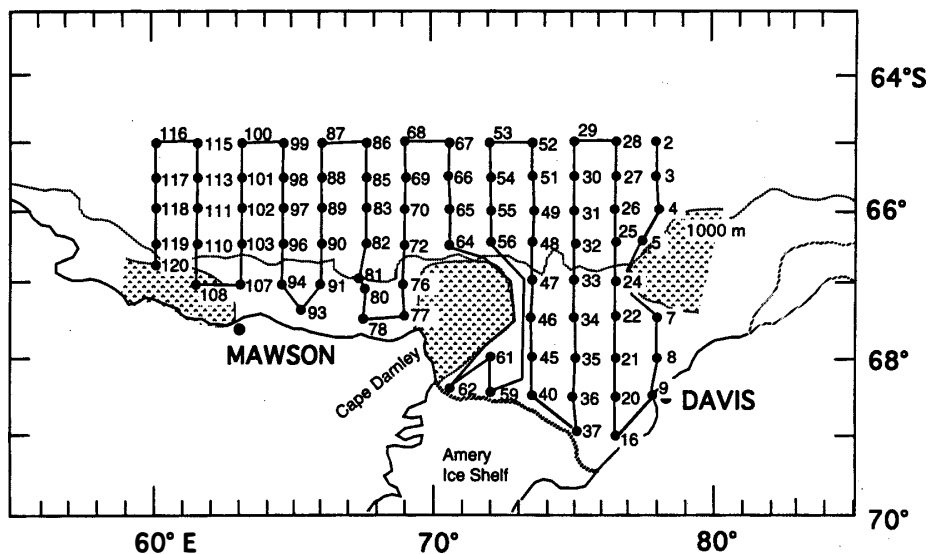
Fig. 1.   Cruise track of RSV AURORA AUSTRALIS, 16 January to 7 February 1993, showing net sampling sites and the 1000 m water depth contour.

flowmeter and in calculating the volume filtered, the effects of towing speed and trajectory were taken into account (ROE et al., 1980; POMMERANZ et al., 1982).

Basic sorting of taxa was carried out on board ship. In particular, specimens of E. superba were removed, as well as large and fragile zooplankton (jellyfish, salps, etc.). All specimens were preserved in Steedman's solution (STEEDMAN, 1976) for later examination in the Antarctic Division laboratories where specimens were identified to species level where possible and counted. All krill from each site were individually wet weighed, or a subsample of circa 200 individuals were weighed when catches were large. Other zooplankton were wet weighed altogether as individual species groups, or other identifiable taxa. For the purposes of this study, macrozooplankton where defined as all species collected by the RMT 8. Unlike the previous macroscale surveys (HOSIE, 1994a,b), ichthyoplankton were not included in the present analyses. Ichthyoplankton is the subject of another more detailed study on fish ecology in Prydz Bay (WILLIAMS, 1992). Euphausiid larvae were also not included in the analyses. They were collected by other more efficient means and are also the subject of a separate more detailed study.

At each sampling site water samples were collected for phytoplankton pigment analysis, at depths of 0, 10, 25, 50, 100, and 200 m, using a General Oceanics rosette sampler with 5 l Niskin bottles. The chlorophyll a (Chl a) level in each bottle was determined by HPLC analysis (WRIGHT and SHEARER, 1984; WRIGHT, 1987; WRIGHT et al., 1991). A Neil Brown Mark 3 CTD was mounted on the rosette which provided continuous profiles of conductivity/salinity and temperature. However, during the early transects we discovered that there was a fault in the water tight integrity of all three CTDs on board, caused during factory upgrading and calibration of the CTDs to WOCE (World Ocean Circulation Experiment) standard. The fault resulted in the flooding of all three units before discovered. Although the units were cleaned and the fault repaired on board, data from the first three transects and part of the fourth

(stations 2 to 46) are unusable. Stations 20 and 46 were revisited for phytoplankton and geological studies. Temperature data collected from subsequent transects (stations 47 to 120) were deemed suitable, to at least the second decimal point, for comparison with the biological data, though perhaps not so by normal physical oceanographic standards, and seem quite comparable to previous oceanographic surveys in the region (Smith *et al.*, 1984; Nunes Vaz and Lennon, 1996). There is doubt about the validity of the salinity data, in particular the degree of variation in calibration during the voyage. Post cruise calibrations were different from original calibrations pre-flooding and it is not known whether the change in calibration was constant after flooding or varied with time. Thus some caution is required in the interpretation of the salinity data itself and in correlations with the zooplankton data.

A hydroacoustic survey was conducted along the 13 transects in association with the net sampling, with the objective of determining the distribution and biomass of krill in the region. Data were collected using a Simrad EK 500 echosounder operating at a frequency of 120 kHz. The results of that survey are the subject of a more detailed study (Pauly and Higginbottom, 1994).

2.2. Data analyses

Complete details of the multivariate data analysis techniques, as modified from Field *et al.* (1982) and Kruskal and Wish (1978), have been described previously in Hosie (1994 a,b) and Hosie and Cochran (1994). One of these references should be consulted to gain a thorough understanding of the analytical methodologies employed in this paper. In summary, a species by sampling site matrix, expressed as density values of number of individuals 1000 m^{-3}, was analysed by cluster analysis and non-metric multidimensional scaling (NMDS) ordination. Sampling sites were first compared to define areas with similar species composition. Groupings of sampling sites derived from the cluster and NMDS analyses were tested using multivariate and univariate statistical tests to establish the validity of observed patterns. Indicator species characterizing each group were then defined using Field's information statistic $(2\Delta I_i)$ (Field *et al.*, 1982) and by analysis of variance with student Newman-Keuls (SNK) multiple range test (Zar, 1984). New NMDS ordination scores were compared by multiple regression analysis with various environmental parameters to determine which of these may best explain the zooplankton distributions. Inverse analysis of the data set was then carried out to define species affinities. The data set was reduced to a subset of common dominant species to avoid spurious associations amongst rare species, caused by their chance occurrence at one site. Following the example of Field *et al.* (1982), and as used in previous analyses, dominant species were defined as those comprising >4% of the total number of individuals for any given sampling site. Table 1 lists the 22 species so defined. A flow chart summarizing the numerical analyses is shown in Fig. 2. Multivariate analyses were carried out using BIO$\sum$TAT II (Pimental, R.A. and Smith, J.D., 1985 Sigma Soft, Placentia, California). Additions and variations to the previous methodology are described below.

As mentioned above (Section 2.1), there is some concern that some of the smaller zooplankton, in particular copepods, may be undersampled by the 4.5 mm mesh of the RMT 8. The four most abundant copepod species in the region are

Table 1. Dominant species used in the inverse cluster analysis and ordination of species, and also in the ANOVA/SNK analyses to define species indicators. Dominant species were defined as those with a >4% numerical dominance for any given sampling site in the normal RMT 8 data set or as >1% in the adjusted RMT 8 data set.

Taxa	>4%, normal data	>1%, adjusted data
Calanoides acutus	●	●
Calanus propinquus	●	●
Clio pyramidata	●	●
Clione antarctica	●	●
Callianira cristata	●	
Cyllopus lucasii	●	●
Euchaeta antarctica	●	●
Eukrohnia hamata	●	●
Euphausia crystallorophias	●	●
Euphausia superba	●	●
Hyperia macrocephala	●	
Ihlea racovitzai	●	
Limacina helicina	●	●
Metridia gerlachei	●	●
Pleurobrachia pileus	●	
Rhincalanus gigas	●	●
Sagitta gazellae	●	●
Sagitta marri	●	
Salpa thompsoni	●	●
Siphonophora (Nectophores)	●	●
Solmundella bitentaculata	●	●
Thysanoessa macrura	●	●

Calanus propinquus, Calanoides acutus, Rhincalanus gigas and *Metridia gerlachei* (ZMIJEWSKA, 1983; YAMADA and KAWAMURA, 1986; HOSIE, 1994a,b; HOSIE and COCHRAN, 1994). The first three species have been traditionally viewed as herbivores, the latter an omnivore although possibly feeding mainly on phytoplankton during summer months and collectively are important consumers of primary production (CONOVER and HUNTLEY, 1991; HUNTLEY and ESCRITOR, 1992). The previous classification of these species as a dominant group of the Main Ocean Community, which extends over most of the survey area, was based on underestimated abundances (HOSIE, 1994a,b; HOSIE and COCHRAN, 1994). A recent study compared the abundances of the four copepods species collected simultaneously by RMT 1 (nominal 1 m² mouth area, 300 μm mesh) and RMT 8 nets at selected sampling sites during the current survey (BEAUMONT, 1995). Her results showed that the density estimates from the RMT 1 were consistently higher than those derived from the RMT 8 and that the RMT 1 to RMT 8 density ratio was different for each species increasing indirectly with the size of the species as shown below.

We assumed the density estimates of the copepods derived from the RMT 1 more accurately represent the true abundance of these species, whereas the RMT 8 with its
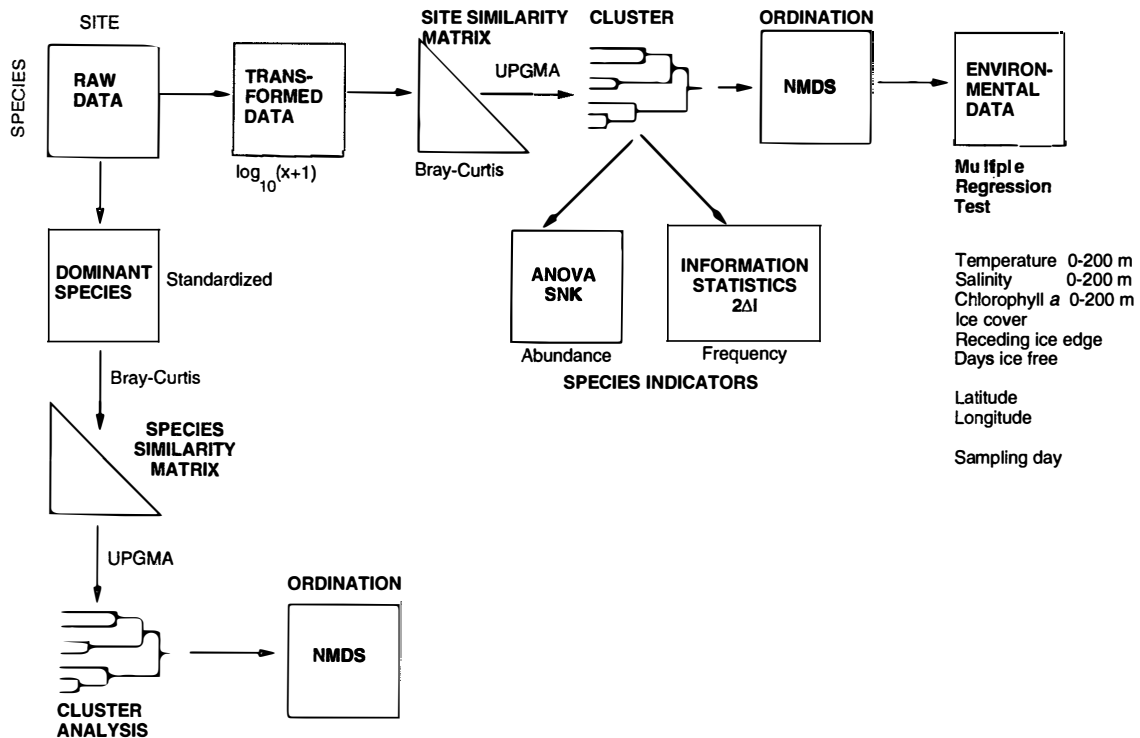
Fig. 2. Diagrammatic summary of the steps used in the multivariate analyses to define species relationships (comparison of species data), areas of common zooplankton composition (comparison of sampling sites), indicator species and possible environmental parameters affecting zooplankton distribution patterns. UPGMA=unweighted pair group average linkage, NMDS=non-metric multidimensional scaling, ANOVA/SNK=analysis of variance-student Newman-Keuls multiple range test, 2ΔI=Field's information statistic (after FIELD et al., 1982).

Species	Ratio RMT 1 to RMT 8 densities
Rhincalanus gigas	7.142
Calanus propinquus	22.038
Calanoides acutus	84.030
Metridia gerlachei	160.328

larger mouth area more accurately sampled adult krill. The densities of the four copepods species in the RMT 8 data matrix were thus corrected using BEAUMONT'S (1995) values and the data set reanalysed by cluster and NMDS to determine any difference in the definition of community structure and distribution patterns obtained using a more accurate data set. Biomass data is probably a more useful estimate of the relative contribution of a species to the zooplankton community rather than the number of individuals, especially in terms of studying carbon flux. Similarly, with more accurate density estimates for copepods there was now the opportunity to analyse the community structure using more accurate biomass data, expressed as grams 1000 m^{-3}, and to compare the results against those using density data.

The correction to the copepod densities for the re-analyses naturally resulted in a much greater contribution by the four main copepod species to the total zooplankton density. Hence only nine species were defined as dominant using the >4% numerical dominance definition Table 1. These species were mainly the three abundant

euphausiid and the four copepods. For the re-analysis of species association using adjusted data, the numerical dominance cut off value was reduced to >1% to include the same type of species used previously (Table 1), especially some of the carnivorous zooplankters such as chaetognaths that prey on copepods and are of course associated with them (HOSIE, 1994a,b; HOSIE and COCHRAN, 1994). The hydromedusae *Solmundella bitentaculata* has not been previously defined as a dominant species and was only >4% numerically dominant at one site, Station 8, where zooplankton abundances were low. This species also satisfied the >1% limit in some of the other 5 sites where it was caught.

The mean wind strength for each of the various sampling cruises in Prydz Bay were calculated using 3 or 4 hourly meteorological observations by ships' officers taken during the sampling period. The RSV AURORA AUSTRALIS is equipped with a sophisticated automatic meteorological data logging system, but the research vessel of the 1980's surveys NELLA DAN had no such system. Hence, the meteorological observation by officers was used as the only method common to all surveys although there is inherent error because of different observers. Further, the permanent weather sites in the region, Davis and Mawson, could not be used because of localised katabatic events.

3. Results

3.1. Hydrography and chlorophyll a

Figure 3a shows the geostrophic water flow (0–200 m) in the Prydz Bay region derived from CTD data by NUNES VAZ and LENNON (1996). Figure 3b shows a synthesis of other currents, known from sea-ice buoys and iceberg trajectories, current meters, as well as geostrophic flow (Fig. 3a), which are believed to influence the distribution of euphausiid larvae (HOSIE, 1991), but may also affect zooplankton distributions (HOSIE, 1994a,b; HOSIE and COCHRAN, 1994). Figures 4 and 5 show the horizontal geographic patterns of isotherms and isohalines, respectively. Both the surface and integrated isotherms show a distinct latitudinal zonation similar to previous surveys. The isohaline pattern is different from that seen in 1991 with no obvious explainable pattern, although Fig. 5 does show a distinct pattern of higher salinity water, >34.00‰, in the northwestern stations which is commensurate with a pattern of warm water (Fig. 4a). Similarly, low salinities coincided with very low temperatures in the south of Prydz Bay. Very cold water was found throughout the shelf region. A distinct thermocline occurred at approximately 10–15 m, a result of summer warming of the surface layer-summer surface water. This layer was considerably shallower than in 1991 (HOSIE and COCHRAN, 1994) or in earlier years (NUNES VAZ and LENNON, 1996). Melting ice produced a very strong halocline coincident with the thermocline. Below the thermo/haloclines, temperature and salinity traces were relatively uniform. In Prydz Bay at stations 20, 36, 59, 61, 62, and at 76 NNW of Cape Darnley temperatures were <−1.8°C. At shelf stations west of Cape Darnley and at 63 temperatures varied between −1.2 and −1.6°C below the thermocline although the traces themselves were uniform. Salinity traces below the halocline were also of two types. At stations 59, 62, 76, 77, 78, 91, 93, 94 salinity
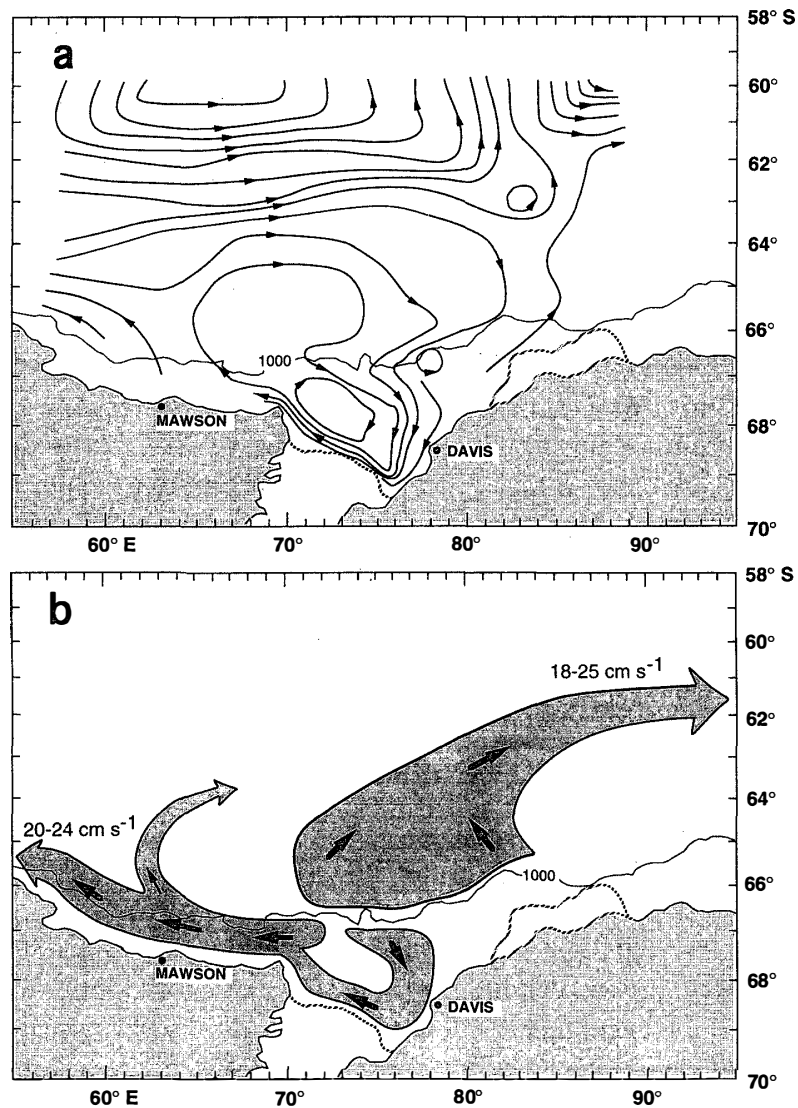
Fig. 3. *Horizontal water circulation patterns in the Prydz Bay region.*
(a) The geostrophic water flow redrawn from the geopotential
anomaly contours of NUNES VAZ and LENNON (1996), (b)
Apparent dispersal routes of euphausiid larvae, likely to affect
zooplankton distributions, determined from sea-ice buoy and
iceberg trajectories, current meters and geostrophic flow. Current
speeds shown were determined from iceberg trajectories. (From
HOSIE, 1991).

ranged from 34.00 to 34.2‰. This is much lower than previously recorded, indicative of the problems with the CTD unit, possibly reading 0.3 to 0.4‰ below the true value. At other shelf stations, 20, 36, 61, 63, 107, 108, and 120, salinities ranged generally from 33.4 to 33.9‰. No adequate explanation can be given for the lower salinities recorded at these stations other than the latter five stations were close to or in pack ice. Stations 20 and 36 were relatively ice free, as were most of the shelf stations with higher salinities. The same CTD unit was used at all sites. The coldest surface waters were found throughout the shelf waters west of Cape Darnley and in Prydz Bay
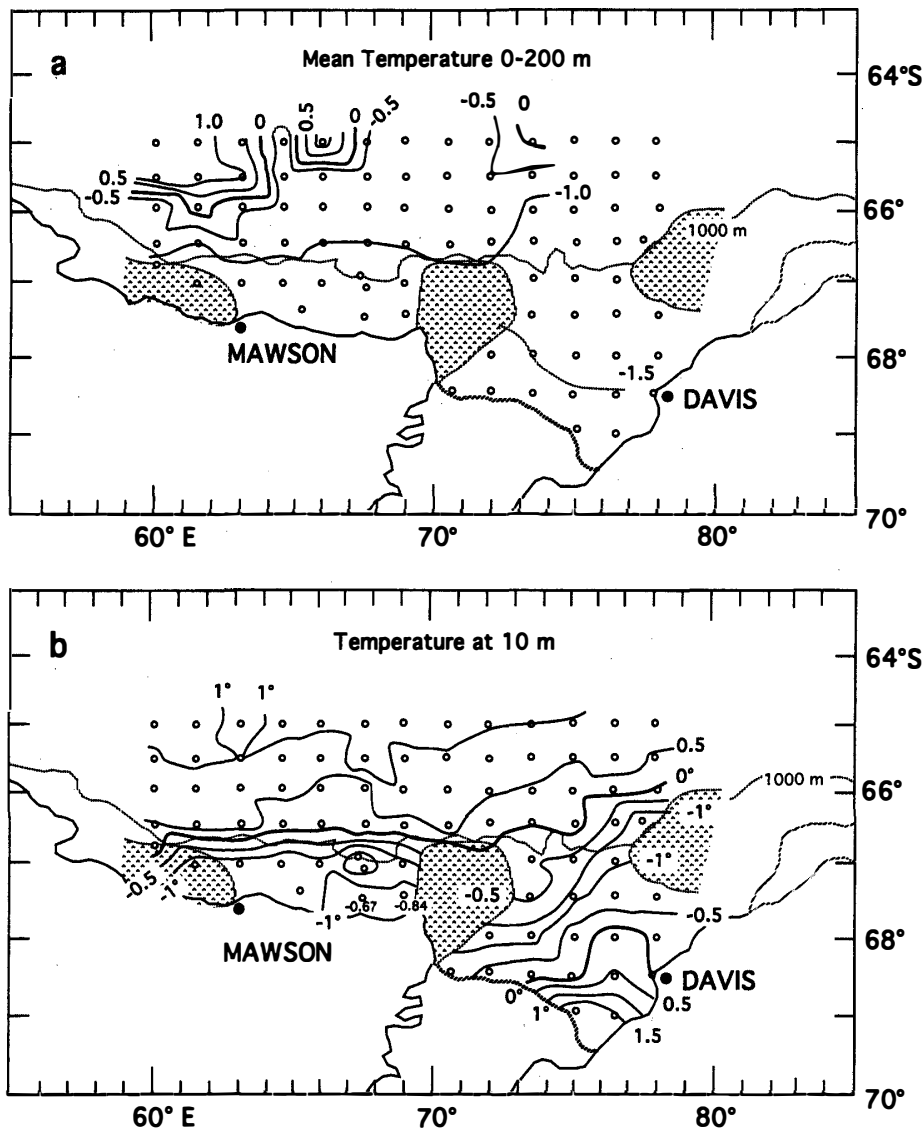
Fig. 4.   Geographic pattern of isotherms. (a) mean 0–200 m isotherms determined by
integrating 2 m recorded intervals, (b) isotherms at 10 m depth. Contour lines
were calculated and drawn by hand.

proper as a band extending diagonally from Station 5 southwesterly to Stn 62.
Although there was some association of cold surface waters with the persistent pack
ice shown in Fig. 4b, the association was less pronounced than in 1991. Instead, in
1993 there was a large area of quite warm surface water (0 to 1.5°+ and 10–15 m
deep) in the southern part of Prydz Bay indicative of a polynya that developed there
around the second week of December 1992 (Northern Ice Limit map). Such a polynya
usually develops in this area in early December each year (SMITH et al., 1984; STRETEN
and PIKE, 1984).

There were three distinct water masses north of the continental shelf-summer
surface water, the Antarctic winter water (WW) and the circumpolar deep water
(CDW). As with the shelf region, the summer surface water occupied the upper 20 to
55 m producing a well-defined seasonal thermocline. Between the summer water and
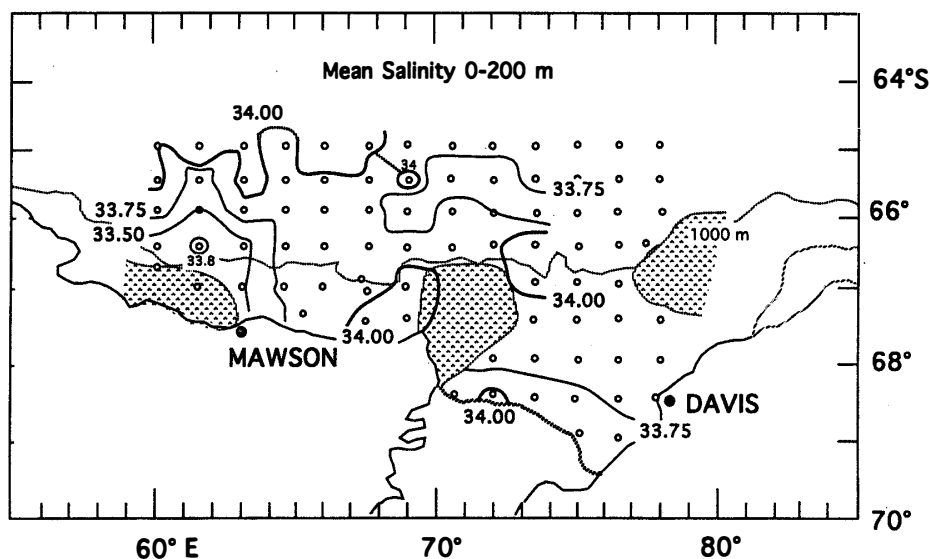
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Fig. 5.   Geographic pattern of mean 0–200 m isohalines determined by integrating 2
m recorded intervals. Contour lines were calculated and drawn by hand.
Note: isotherms at 10 m depth varied considerably and inconsistently to
permit contouring, hence, the geographic pattern is not shown.

the CDW was the winter water. The WW is characterized by temperatures $<-1.5°C$
and salinity in the range of 34.2 to 34.56‰ (Smith *et al.*, 1984). The CDW is typically
much warmer (0 to 2°C) producing a second thermocline between 100 and 150 m
depth.

The range of mean temperature and salinity values used in the regression analysis
were $-1.87°C$ at Station 61 to $+1.28°C$ at Stn 87, and 33.21‰ at Stn 108 to 34.33‰ at
Stn 47. Individual temperature values ranged from less than $-2.02°C$ between 82 and
142 m at Stn 59 to $+1.75°C$ at 80 m at Stn 87, and for salinity the range was 31.03‰ at
6 m at Stn 47 to 34.51‰ at 158 m Stn 47.

Figure 6 shows the distribution of mean chlorophyll *a* integrated for the upper
200 m and distribution of maximum chlorophyll *a* levels. Chlorophyll *a* values were
generally lowest in the northeastern sampling sites and in the centre of Prydz Bay
proper (longitude 75°E). Highest values occurred around the periphery of the bay,
west of Cape Darnley in shelf waters and offshore west of Mawson along transects 60°
E and 61° 30′ E. This is particularly noticeable in the maximum chlorophyll plots (Fig.
6b). Mean chlorophyll values ranged from 0.004 μg Chl *a* l^{-1} at Stn 32 to 1.94 μg Chl *a*
l^{-1} at Stn 78—many of the sites in the two western transects had values exceeding 1 μg
Chl *a* l^{-1}. Maximum chlorophyll values were generally near or just above the
thermocline, at >90% of the 62 sites where phytoplankton data was collected. Very
high maximum values at each site on the shelf were usually measured in the surface,
10 m or 25 m samples, with lesser peaks at 50 m and one maximum at 100 at Stn 35.
Maxima ranged from 0.005 at Stn 33 (50 m) to 4.53 μg Chl *a* l^{-1} at Stn 94 (10 m)
(mean maxima was 1.90 Chl *a* l^{-1}, SD=1.48, n=21). Chlorophyll values north of the
shelf varied considerably from east to west. Chlorophyll *a* maxima in this area ranged
from 0.006 at Stn 32 (50 m) to 3.33 μg Chl *a* l^{-1} at Stn 115 (25 m) (mean maxima 1.02
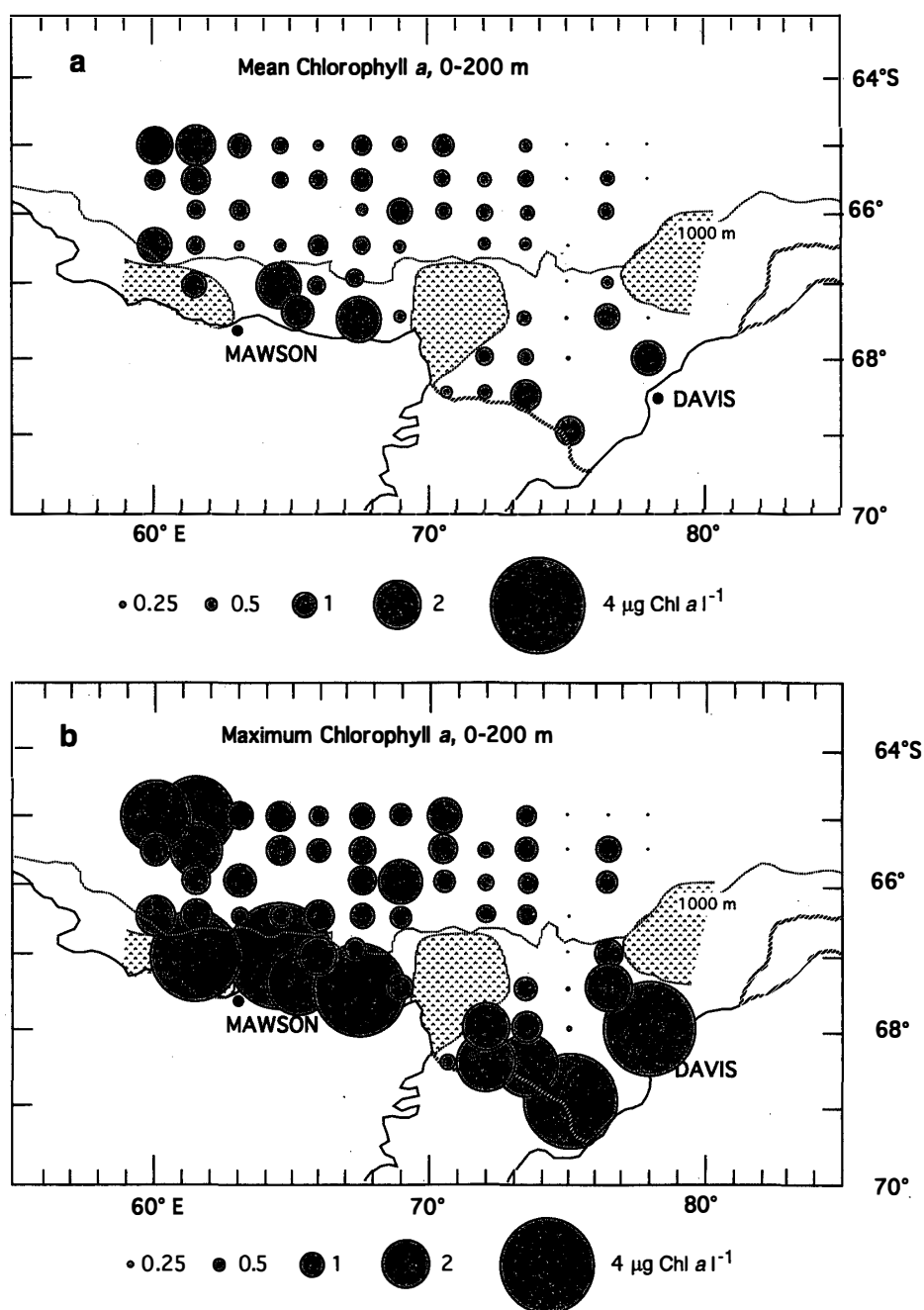μg Chl *a* l^{-1}, SD=0.69, n=41), with the majority of maxima occurring in the 50 m

Fig. 6.   Distribution of chlorophyll a concentrations as µg l⁻¹, (a) integrated for the
upper 200 m water layer, and (b) maximum chlorophyll values. The diameter
of the circles is proportional to the chlorophyll level.

samples ($n=28$), and occasionally, in the 0, and 25 m bottle samples, once only at 10
and 100 m.

3.2.   Comparison of sampling sites

Throughout the following descriptions, principal station cluster groups have been
annotated with a number, and where necessary subgroups have a letter suffix, e.g.
station Group 1, Group 2a. Capital letters have been used for species cluster groups,
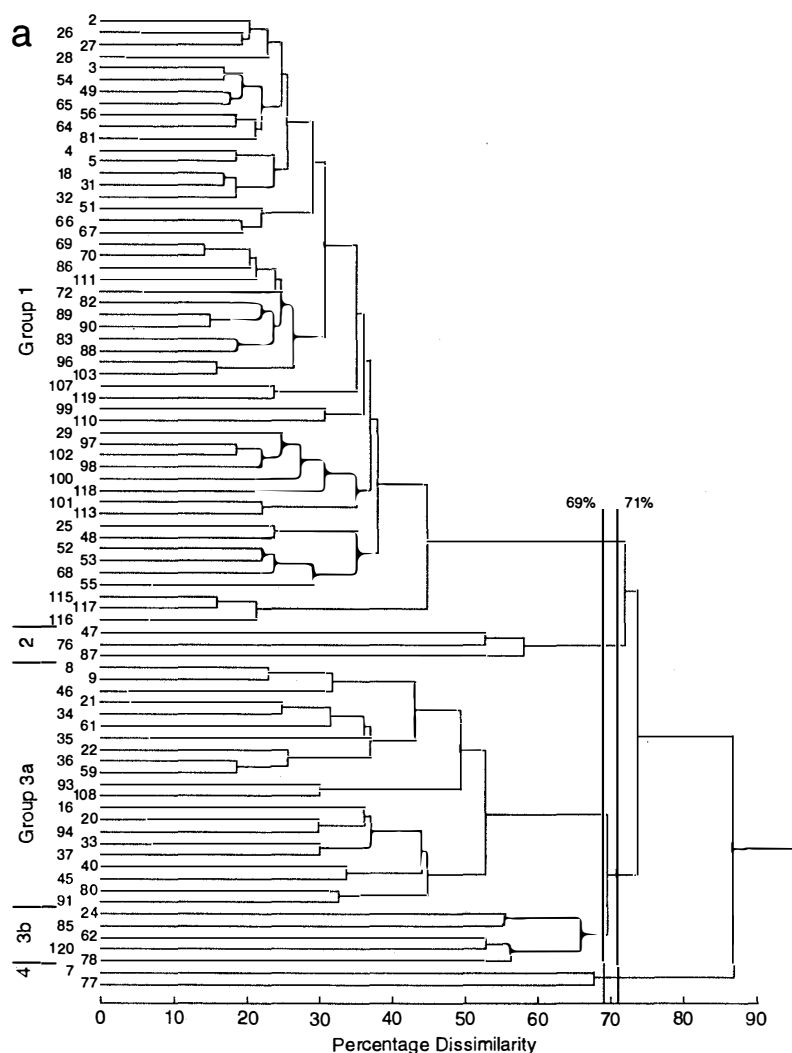
Fig. 7. Distribution patterns based on normal RMT 8 data set. (a) dendrogram of cluster analysis comparing zooplankton species composition at each sampling site, using Bray-Curtis dissimilarity index with UPGMA linkage, after $\log_{10}(X\pm1)$ transformation of species abundance data. (b) Ordination plots of the comparison of sampling sites using non-metric multidimensional scaling and Bray-Curtis index. Respective cluster groups identified in Fig. 7a are superimposed. Significant multiple regressions between ordination scores and environmental parameters are shown, as well as the fraction (%) of variance in the zooplankton data explained by the parameter (see Table 6) (see Hosie, 1994a,b; Hosie and Cochran, 1994). Axis scales are relative in NMDS, based on non-metric ranking of dissimilarity, and therefore are not shown. Stress value=0.13. (c) Geographical distribution of station groups defined by cluster analysis shown in Fig. 7a. Each station group is coded with the same shading or pattern corresponding to the zooplankton community, shown in Fig 17, which dominated that area. ●= 'outlier' sampling sites not grouped in the cluster analysis.

e.g. Group A.

Normal RMT 8 data set: Four groups can be defined at 71% dissimilarity which basically separates the stations into quite distinct oceanic and neritic groups (Fig. 7a). The largest group of 52 sites generally comprised stations north of the continental shelf edge (Fig. 7c). The oceanic Group 1 was characterized by a large number of
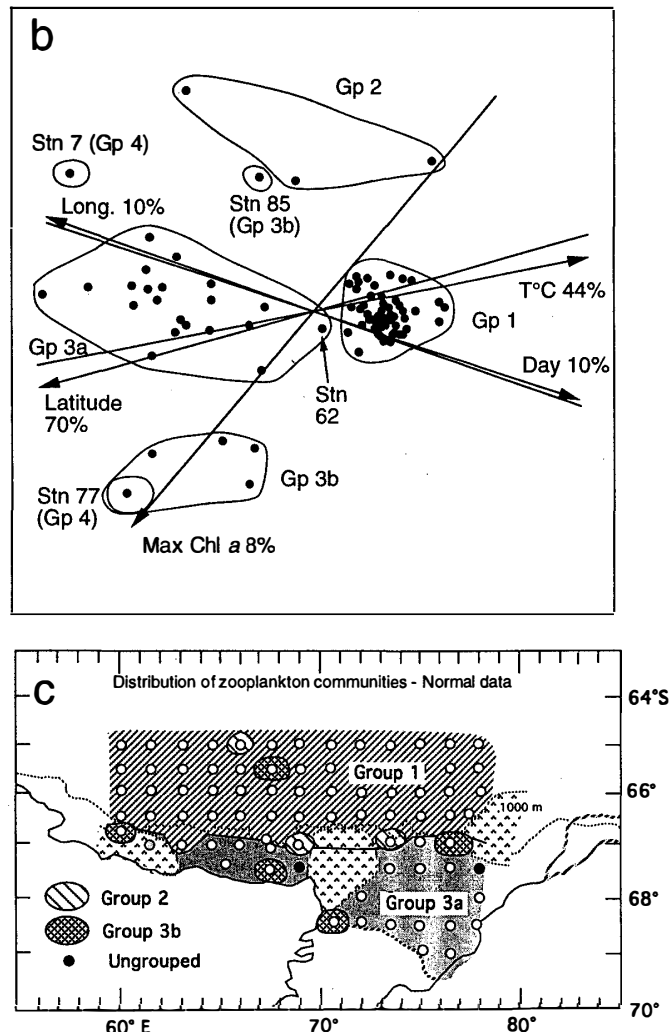
Fig. 7 (Continued).

both frequency and abundance indicators species, many of which have been previously defined as species typical of the Main Oceanic Community (Tables 2 and 3). The three sites (Stns 47, 76 and 87) comprising Group 2 had very high abundances of *E. superba*, and low abundances of other species in particular copepods (Table 3). This group fits the definition of the Krill Dominated Community (high krill-low zooplankton abundance) and would seem to be the only indication of the existence of this community. Table 3 also shows *T. macrura* as an abundance species indicator of these three site. This species had its highest density of 119 ind. 1000 m^{-3} at Stn 87, but was absent from Stns 47 and 76. The classification of *T. macrura* as an indicator species for these sites would not seem valid. Group 3 comprised most of the neritic stations and was typically characterised by *E. crystallorophias* as by both its higher abundance and frequency of occurrence (Tables 2 and 3). The pteropod *Limacina helicina* and the hydromedusae *Solmundella bitentaculata* were also frequency species indicators of the neritic group, the latter also an abundance indicator. Gammarids have often been indicator species of the neritic zone but notably not in the present study. The neritic group could be split further into two sub groups at 69%. Group 3a

Table 2. Normal data set. Frequencies of occurrence of indicator species distinguishing cluster groups defined in Fig. 7. Species in each sub-table are ranked according to information statistic. Species above the dotted line in each sub-table have a 2 ΔI>6.63 (p=0.01), and those below the line have 2 ΔI>3.84, (p=0.05). Maximum possible occurrences are; Group 1=52, Group 2=3, Group 3a=21 and Group 3b=5. *were not considered as dominant species and not used in SNK or inverse species analyses.

a. Group 1 (oceanic) indicators species from Group 3 (neritic).

Taxa	Group 1 (52)	Group 3 (26)
Sagitta marri	48	2
*Ostracoda	44	1
Rhincalanus gigas	52	8
Cyllopus lucasii	40	0
Clio pyramidata	51	8
*Calycopsis borchgrevinki	42	2
Tomopteris carpenteri	33	0
*Haloptilus oxycephalus	37	1
*Haloptilus ocellatus	35	1
*Heterorhabdus austrinus	33	1
*Cephalopoda	25	0
*Spongiobranchea australis	30	1
Thysanoessa macrura	52	16
Eukrohnia hamata	51	14
*Nematocarcinus longirostris	32	2
*Vanadis longissima	28	1
*Pegantha martagon	29	2
Salpa thompsoni	17	0
Clione antarctica	47	13
*Euchirella rostromagna	22	1
*Hyperiella dilatata	30	4
*Primno macropa	24	2
*Tomopteris cavalii	19	1
Calanus propinquus	52	21
Sagitta gazellae	52	21
Euphausia superba	46	14
*Protopelagonemertes hubrechti	11	0

b. Group 3 (neritic) indicator species from Group 1.

Taxa	Group 1	Group 3
Euphausia crystallorophias	2	22
Solmundella bitentaculata	0	6
Limacina helicina	38	26

c. Group 1 indicator species from Group 2 (KDC).

Taxa	Group 1	Group 2
Eukrohnia hamata	51	0
Euchaeta antarctica	51	0
Sagitta marri	48	0
Metridia gerlachei	48	0
Thysanoessa macrura	52	1
Calanoides acutus	52	1
Siphonophore (nectophore)	52	1
Clione antarctica	47	0
*Ostracoda	44	0
Clio pyramidata	51	1
Calycopsis borchgrevinki	42	0

d. Group 3 (neritic) indicator species from Group 2.

Taxa	Group 2	Group 3
None		
Limacina helicina	1	26
Siphonophore	1	26
Euchaeta antarctica	0	22

e. Group 3a indicator species from Group 3b.

Taxa	Group 3a	Group 3b
Euphausia crystallorphias	21	1
None		

comprises 21 sites and Group 3b of 5 stations, four of these neritic (24, 62, 78, 120) and Stn 85 an oceanic station. Group 3b sites had low abundance for all species with total abundance ranging from 2.93 to 8.9 individuals 1000 m^{-3}. Compared with Group 3a which ranged from 7.65 to 117.89 individuals 1000 m^{-3}. *E. crystallorophias* occurred at only one Group 3b site whereas it was an indicator species for Group 3a (Table 2). These groups exhibit a clear separation in the NMDS analysis (Fig. 7b) but Stn 85 is not in this group, being in fact ungrouped although closer to Group 2 (KDC). This site had low densities like other 3b sites, but it did have a reasonable proportion of krill (5 total) in relation to the overall low abundance, and this is perhaps why this site has more affinity with Group 2 than the neritic sites. We subsequently classed Stn 85 as an ungrouped station because of the differences in the cluster and NMDS analyses and was not used in any further analyses comparing station data.

Table 3. Normal data set. Mean abundances, analysis of variance (F) and SNK multiple range tests of dominant species in cluster groups defined in Fig. 7. Analyses were carried out on $\log_{10}(x+1)$ transformed abundances (ZAR, 1984)—values shown are number of individuals 1000 m^{-3}. Species with significant differences in mean abundance are shown in bold text, while those with significantly higher abundances in a cluster group according to SNK analysis are underlined. For ANOVA p, values; $*<0.05$, $**<0.005$, $***<0.0005$, $-$not significant. DF=2,78.

Species	Group 1 Mean	Group 2 Mean	Group 3 Mean	F	p
Calanoides acutus	17.51	3.81	1.49	15.68	***
Calanus propinquus	12.35	1.05	0.68	107.57	***
Clio pyramidata	2.72	1.42	0.13	42.39	***
Clione antarctica	0.46	0.00	0.18	9.21	***
Callianira cristata	0.01	0.00	0.00	0.81	—
Cyllopus lucasii	0.60	0.28	0.00	8.34	**
Euchaeta antarctica	2.29	0.00	0.69	13.2	***
Eukrohnia hamata	6.04	0.00	0.48	32.67	***
Euphausia crystallorophias	0.01	1.92	17.487	50.97	***
Euphausia superba	3.09	182.90	0.91	46.06	***
Hyperia macrocephala	0.03	0.00	0.07	0.405	—
Ihlea racovitzai	0.75	0.00	0.06	4.48	*
Limacina helicina	0.61	0.12	0.66	1.209	—
Metridia gerlachei	2.44	0.00	0.68	9.18	***
Pleurabrachia pileus	0.02	0.00	0.03	0.70	—
Rhincalanus sigas	23.64	0.98	0.14	73.25	***
Sagitta gazellae	6.47	1.73	0.52	87.44	***
Sagitta marri	1.15	0.00	0.01	45.80	***
Salpa thompsoni	1.65	0.28	0.00	2.76	—
Siphonophore (nectophore)	6.56	1.32	2.25	25.58	***
Solmundella bitentaculata	0.00	0.00	0.15	5.39	*
Thysanoessa macrura	6.94	39.71	0.18	16.62	***

The last group of Stns 7 and 77 were only connected to the other groups at 86.6% dissimilarity. There was a general paucity of species at Stn. 7 with a total of only 9 individuals including one *E. superba*, some pteropods and siphonophores. Notably, there were no copepods. Similarly, Stn 77 also had very low abundance of zooplankton, *e.g.* one *E. crystallorophias*, a few copepods and pteropods. Although the cluster analysis links the two stations together, albeit at 67.2%, the NMDS plot show the stations widely separated and with Stn 77 now clearly grouped with Group 3b stations (Fig. 7b). Examination of the raw data file shows that there is much similarity in the species composition, abundances and geography between Group 3b and Stn 77. Hence, we accepted the NMDS analysis and grouped Stn 77 with Group 3b for subsequent analyses. Stn 7 remains ungrouped.

Adjusted RMT 8 data set: The dendrogram derived from the data set with adjusted copepods was split initially at 65% dissimilarity, producing Stn 7 as an ungrouped station, a group of two of the high abundance krill sites (Stns 76 and 87), and a group of eight neritic and one oceanic site (Fig. 8). The remaining sites could be separated at 51% to produce Group 1 of 54 predominantly oceanic sites and Group 2

of 17 neritic sites (Fig. 8c). Stn 91 was previously neritic but is now classed as oceanic, although this station did exhibit a close affinity to the oceanic stations in the analysis above (Fig. 7b). Classification of the various groups is confirmed by NMDS which shows no overlap of groups, nor change in the classification of sites between the cluster and NMDS analyses (Fig. 8b). The grouping of stations produced a distribution map very similar to that derived from a normal RMT 8 data set using underestimated copepod abundances (Figs. 7c and 8c). Stn 47 was previously classified as a krill station, but is now grouped as oceanic and confirmed by NMDS. This station originally did have higher proportion of copepods than Stns 76 and 87. The new linking of Stn 47 to other oceanic sites would be a result of more weight given to copepods in the analysis after correction of copepod densities. The other two krill sites with their higher krill densities and still relatively low abundances of other
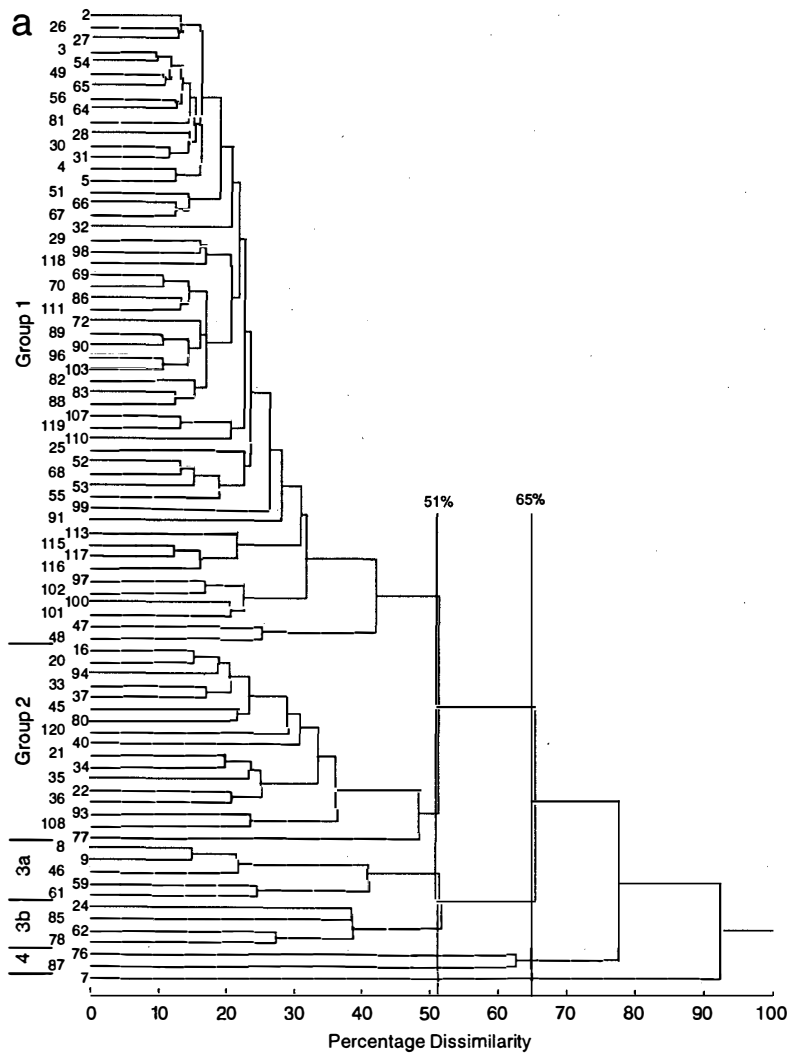

Fig. 8. Distribution patterns based on adjusted copepod data set. See Fig. 7 for full caption details. (a) dendrogram of cluster analysis comparing sampling sites. (b) NMDS ordination plot. Respective cluster groups identified in Fig. 8a are superimposed. See Table 7 for details of multiple regression. Stress value=0.11. (c) Geographical distribution of station groups defined by cluster analysis shown in Fig. 8a.
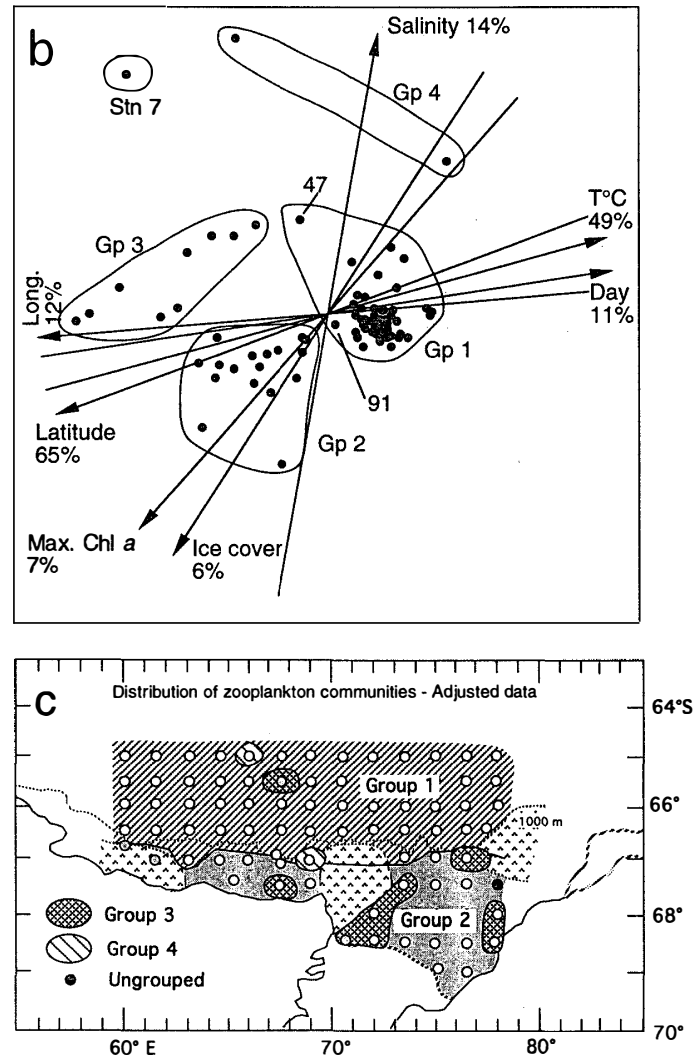
Fig. 8 (Continued).

zooplankton, even after correction, are still separate. Frequency and abundance species indicators of Group 1 oceanic sites are much the same as those in the analysis using normal RMT 8 (Tables 4 and 5). The notable exception is that *E. superba* is now an abundance species indicator for the oceanic group, albeit with relatively low abundance of 4.34 ind. 1000 m^{-3}. This is most likely a function of the Group 4 krill sites not being included in the ANOVA/SNK analysis because there was only two stations in this group, 76 and 87. Krill densities at these sites were much higher at 302.7 and 172.7 ind. 1000 m^{-3}, respectively.

The predominantly neritic Group 3 is distinguishable from the main neritic Group 2 sites by the low zooplankton abundance in general (Table 5) and specifically by the complete absence of *M. gerlachei* which is now a species indicator of both Group 1 oceanic and Group 2 (Tables 4 and 5). The low abundances and absence of this copepod at Stn 85 may explain the grouping of this site with the other Group 2 sites. *E. crystallorophias* and *S. bitentaculata* were again abundance species indicators of neritic sites (Table 5), whereas *L. helicina* was not. Group 3 could be split into

Table 4. Adjusted data set. Frequencies of occurrence of indicator species distinguishing cluster groups defined in Fig. 8. Species in each sub-table are ranked according to information statistic. Species above the dotted line in each sub-table have a $2\Delta I > 6.63$ (p=0.01), and those below the line have $2\Delta I > 3.84$ (p=0.05). Maximum possible occurrences are; Group 1=54, Group 2=17, Group 3a=5 and Group 3b=4. *were not considered as dominant species and not used in SNK or inverse species analyses.

a. Group 1 (oceanic) indicators species from Group 2 & 3 (neritic).

Taxa	Group 1	Group 2 & 3
Rhincalanus gigas	54	8
*Ostracoda	44	1
Cyllopus lucasii	40	0
*Sagitta marri	48	3
*Haloptilus ocellatus	36	0
Clio pyramidata	52	8
Tomopteris carpenteri	33	0
*Haloptilus oxycephalus	37	1
*Calycopsis borchgrevinki	42	3
*Heterorhabdus austrinus	33	1
*Cephalopoda	25	0
*Spongiobranchea australis	30	1
Eukrohnia hamata	52	13
*Nematocarcinus longirostris	32	2
*Vanadis longissima	28	1
Thysanoessa macrura	53	16
*Pegantha martagon	29	2
*Hyperiella dilatata	31	3
Salpa thompsoni	17	0
*Euchirella rostromagna	22	1
*Primno macropa	24	2
Calanus propinquus	54	21
Sagitta gazellae	54	21
*Tomopteris cavalii	19	1
Clione antarctica	47	14
*Ihlea racovitzai	32	6
*Protopelagonemertes hubrechti	11	0

b. Group 2 & 3 (neritic) indicator species from Group 1.

Taxa	Group 1	Group 3
Euphausia crystallorophias	3	21
Solmundella bitentaculata	0	6

Table 4 (Continued).
c. Group 2 (neritic) indicator species from Group 3 (neritic).

Taxa	Group 2	Group 3
Metridia gerlachei	17	0
Euchaeta antarctica	17	5

d. Group 3a (neritic) indicator species from Group 3b (neritic).

Taxa	Group 3a	Group 3b
None		
Euphausia crystallorophias	5	0

Table 5. Adjusted data set. Same as Table 3 but for in Fig. 8 and DF=2,77.

Species	Group 1 Mean	Group 2 Mean	Group 3 Mean	F	p
Calanoides acutus	1453.91	102.14	58.00	24.17	***
Calanus propinquus	264.44	15.26	4.61	129.15	***
Clio pyramidata	2.64	0.13	0.17	38.419	***
Clione antarctica	0.44	0.23	0.13	5.33	*
Cyllopus lucasii	0.58	0.00	0.00	7.74	**
Euchaeta antarctica	2.22	0.95	0.08	12.61	***
Eukrohnia hamata	5.85	0.62	0.04	27.87	***
Euphausia crystallorophias	0.03	20.83	11.05	55.45	***
Euphausia superba	4.34	1.31	0.21	4.62	*
Limacina helicina	0.63	0.63	0.52	0.42	—
Metridia gerlachei	377.87	165.67	0.00	31.84	***
Rhincalanus gigas	162.91	0.65	1.47	125.69	***
Sagitta gazellae	6.29	0.53	0.20	84.99	***
Salpa thompsoni	1.59	0.00	0.00	2.55	—
Siphonophore (nectophore)	6.59	2.04	1.62	27.904	***
Solmundella bitentaculata	0.00	0.16	0.14	5.31	*
Thysanoessa macrura	6.69	0.19	0.09	18.87	***

subgroups at the 51% dissimilarity cut. Group 3b comprised Stns 24, 62, 78 and the oceanic 85 and were notable for the absence of *E. crystallarophias* (Table 4). This euphausiid was also the only abundance indicator (Gp 3a) distinguishing the two sub groups ($F=27.730$, DF=1, 7, $P=0.0012$).

Adjusted biomass data set: The biomass data set derived from the adjusted RMT 8 data set produced much the same result, hence distribution patterns as seen with the density data sets (Figs. 7c, 8c and 9). There were only a few relatively minor differences. Three major groups were defined at 83% dissimilarity (Fig. 9a). The first

major group comprised oceanic stations and the three krill sites which can be separated at 78%, and for convenience are respectively labelled Groups 1 and 2. Note that Stn 47 is now grouped again with the other two krill sites 76 and 87 and Stns 24 and 37 which were previously neritic have now been classed as oceanic. This is perhaps a result of the greater influence of copepods in the adjusted data, notably *C. acutus* at the two sites, coupled with the paucity of *E. crystallorophias*. The NMDS plot does show these stations as having perhaps more affinity with the neritic sites as expected (Fig. 9b). Group 3 represents the majority of neritic sites but also Stn 85 again. Group 4 comprises the neritic sites of 62, 77, 78 and 120, plus also Stn 7 which previously was not grouped. These sites had generally low biomass, range 0.17 to 0.73 g 1000 m^{-3} (mean 0.41 g) compared to Group 3, range 0.62 to 18.07 g 1000 m^{-3} (mean 3.85 g, $n=20$). By comparison Group 1 biomass ranged from 1.06 to 45.00 g 1000 m^{-3} (mean 12.85 g, $n=55$) and the krill dominated Group 2 sites were 49.86,
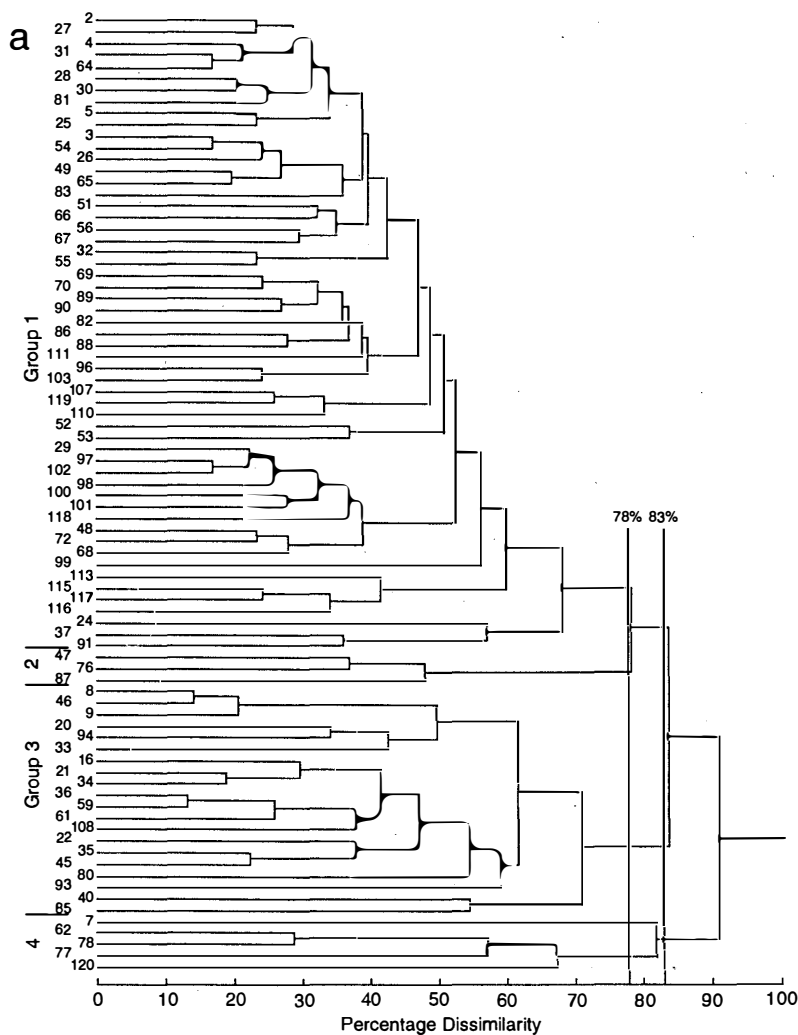

Fig. 9. Distribution patterns based on adjusted biomass data set. See Fig. 7 for full caption details. (a) dendrogram of cluster analysis comparing sampling sites. (b) NMDS ordination plot. Respective cluster groups identified in Fig. 8a are superimposed. Stress value=0.15. (c) Geographical distribution of station groups defined by cluster analysis shown in Fig. 9a.
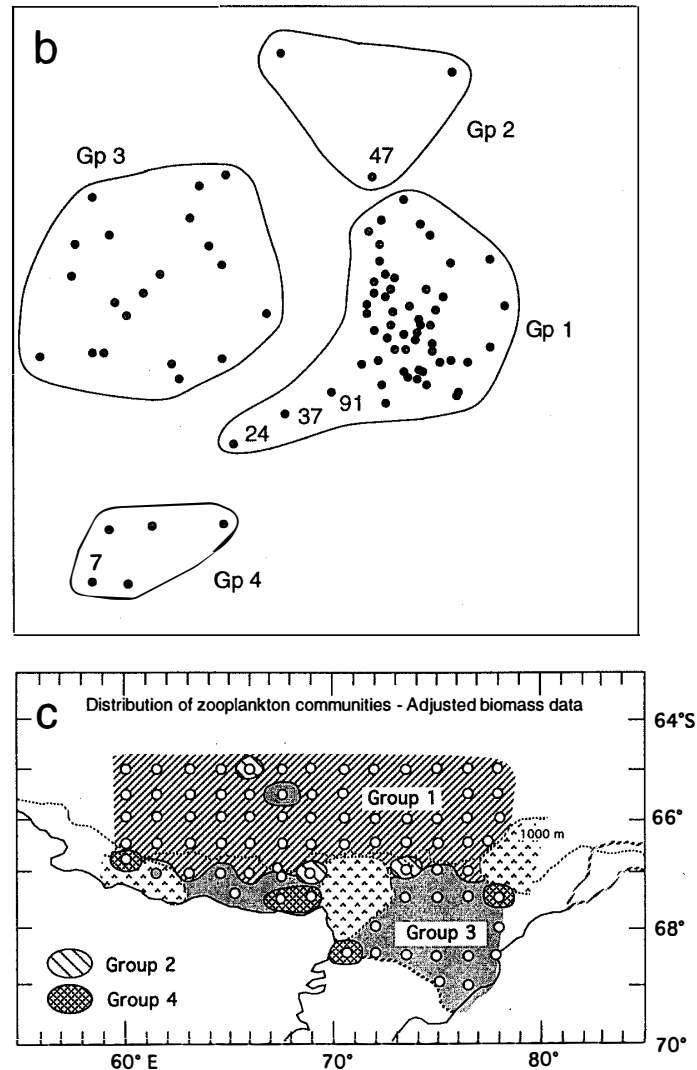
Fig. 9 (Continued).

260.93 and 250.54 g 1000 m^{-3} for Stns 47, 76 and 87, respectively. Given the similarity of results and distribution patterns between the biomass and density data sets, no further analyses were undertaken on the biomass data set.

3.3. Multiple regression

A clear north-south separation of sampling sites is evident in all of the distribution maps. Latitude, not surprisingly, explained most of the variation of the data in the NMDS ordination, 70% for the normal RMT 8 data and 65% for the adjusted data set (Tables 6 and 7, Figs. 7b and 8b). Simple correlation analysis between dominant species from the adjusted data and parameters with a significant score from Table 6b, shows that most of the dominant species were correlated with latitude (Table 7). Two of these, the neritic species *E. crystallorophias* and *S. bitentaculata*, had positive correlations. The rest were negative indicating decreasing abundance going south. This applies also to total zooplankton density as well as the total number of species at each site. There is no obvious east-west (longitudinal)

*Table 6.   Multiple regression analyses between environmental parameters and NMDS scores for two-axis ordination of comparison of sampling sites. See HOSIE, (1994a,b) or HOSIE and COCHRAN (1994) for details on multiple regression analyis and calculation of regression weights. Adj. R^2=Adjusted coefficient of determination which gives the fraction of the variance accounted for by the explanatory variable (JONGMAN et al., 1987). For ANOVA p values; *<0.05, **<0.005, ***<0.0005, ns=not significant.*

a. Normal data set

Variable	Direction cosines (Regression weights) X	Y	Adj. R^2	F	d.f.	p
Latitude	−0.964	−0.266	0.696	94.64	2,80	***
Temperature	0.982	0.190	0.436	21.85	2,52	***
Longitude	−0.943	0.333	0.098	5.45	2,80	*
Sampling day	0.950	−0.313	0.095	5.32	2,80	*
Max Chl *a*	−0.650	−0.760	0.077	3.53	2,59	*
Salinity	—	—	0.050	2.41	2,52	ns
Ice cover	—	—	0.037	2.56	2,80	ns
Ice recession	—	—	0.026	2.11	2,80	ns
Ice free	—	—	0.018	1.74	2,80	ns
Mean Chl *a*	—	—	–	0.91	2,59	ns

b. Adjusted data set

Variable	Direction cosines (Regression weights) X	Y	Adj. R^2	F	d.f.	p
Latitude	−0.936	−0.353	0.654	78.60	2,80	***
Temperature	0.964	0.264	0.492	27.10	2,52	***
Salinity	0.174	0.985	0.137	5.29	2,52	*
Longitude	−0.997	−0.084	0.120	6.58	2,80	*
Sampling day	0.989	0.150	0.115	6.31	2,80	*
Max Chl *a*	0.653	−0.758	0.069	3.25	2,59	*
Ice cover	−0.536	−0.844	0.062	3.72	2,80	*
Ice free	—	—	0.003	1.11	2,80	ns
Ice recession	—	—	–	0.93	2,80	ns
Mean Chl *a*	—	—	–	0.55	2,59	ns

pattern in the community maps, but longitude accounted for 10 and 12% of the variation in the NMDS analysis of the two density data sets. Some species had correlations with longitude, *e.g. C. acutus* (positive) and *R. gigas* (negative) and the same five species, plus siphonophores, also had correlations with the day of sampling (Table 7). Sampling day and longitude variables are closely aligned in the NMDS plots, which is understandable given that sampling progressed from east to west. Higher abundances of *C. acutus* were recorded at the oceanic stations of the two eastern transects, range 2405 to 9346 ind. 1000 m^{-3} (adjusted data). However, it is

Table 7. Correlation coefficients (r) for simple correlation analysis between dominant species from the adjusted data and parameters with a significant score from Table 6b. Only significant correlations are shown. n=number of sampling sites compared, DF=degrees of freedom.

Taxa	Day	Latitude	Longitude	Max. Chl *a*	Mean T°C	Mean salinity	Ice cover
Calanoides acutus	−0.433	−0.256	0.421	−0.325	—	—	—
Calanus propinquus	—	−0.498	—	−0.362	—	—	—
Clio pyramidata	—	−0.658	—	—	0.573	—	—
Clione antarctica	—	−0.247	—	—	—	—	—
Cyllopus lucasii	—	−0.343	—	—	0.342	—	—
Euchaeta antarctica	—	—	—	—	—	—	—
Eukhronia hamata	0.397	−0.372	−0.431	—	0.528	—	—
Euphausia crystallorophias	—	0.414	—	—	−0.325	—	0.289
Euphausia superba	—	—	—	—	—	—	—
Limacina helicina	0.285	—	−0.295	—	—	−0.296	—
Metridia gerlachei	—	−0.242	—	—	—	−0.472	—
Rhincalanus gigas	0.318	−0.327	−0.367	—	0.657	—	—
Sagitta gazellae	0.232	−0.491	−0.262	—	0.656	—	—
Salpa thompsoni	0.304	−0.218	−0.341	—	0.437	—	—
Siphonophore (nectophore)	0.229	−0.325	—	—	0.298	—	—
Solmundella bitentaculata	−0.295	0.369	0.256	0.371	—	—	—
Thysanoessa macrura	—	−0.315	—	—	0.445	—	—
Total abundance	−0.311	−0.357	0.292	−0.289	—	—	—
Total No. spp	—	−0.701	—	—	0.47	—	—
n=	83	83	83	62	55	55	83
DF	1,81	1,81	1,81	1,60	1,53	1,53	1,81

not possible to determine if the west to east differences in abundance is a genuine longitudinal relationship, *i.e.* the abundances were always higher in the east, or it is a function of abundances decreasing with time over the course of the sampling period and thus appearing longitudinal.

Only two environmental variables explained any variation in the normal RMT 8 NMDS analysis, temperature (44%) and maximum Chl *a* (8%) (Table 6a). Temperature also explained most of the variation in the NMDS community patterns from the adjusted data set with 49%, followed by salinity (14%), maximum Chl *a* (7%) and ice cover (6%) (Table 6b). This is reflected also in the simple correlations: of the 9 species correlated with temperature, *E. crystallorophias* was the only one to show a negative relationship. Two species were correlated with salinity and three with chlorophyll, notably *C. acutus* and *C. propinquus* (both negative); and only one species with ice cover, *i.e. E. crystallorophias*. The correlation between *S. bitentaculata* and chlorophyll, is spurious since the hydromedusan is presumably a carnivore. This species was not correlated with mean Chl *a*, whereas the two copepods were the only species that were correlated with mean Chl *a*: *C. acutus r* =−0.326, *n*=62, *P*=0.010; *C. propinquus r*=−0.257, *n*=62, *P*=0.044.

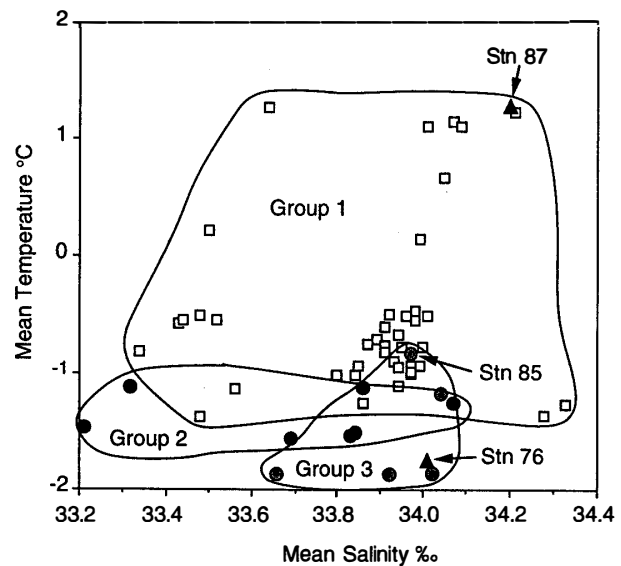A temperature-salinity plot for the adjusted data station groups shows that

Fig. 10. Temperature-salinity plot for each sampling site using mean values for 0–200 m. Station cluster groups identified in Fig. 8a are superimposed.

groups 2 and 3 (Stn 85 excluded) comprised sites of very cold water of less than −1°C, uniformly <−1.6°C below the 10–15 m thermocline (Fig. 10). Salinity was quite variable for Group 2, but narrower and of higher salinity for Group 3. There was a reasonable amount overlap between these groups and the oceanic Group 1 which occupied areas of higher water temperature but also wide salinity range. The oceanic group in 1991 had a narrow salinity range (HOSIE and COCHRAN, 1994).

3.4. Interannual abundance in relation to wind speed

Figure 11 shows the mean wind strength during the various sampling cruises in Prydz Bay as well as the corresponding abundances of *E. superba*, *E. crystallorophias*, and herbivorous copepods. Mean krill abundances were calculated for the entire sampling area for each cruise to permit comparison with the 1991 and 1993 surveys when the KDC was not prominent (HOSIE *et al.*, 1988; HOSIE, 1994a,b; HOSIE and COCHRAN, 1994). Mean abundances for herbivorous copepods and *E. crystallorophias* are for the main oceanic and neritic communities respectively. The patterns of variation in krill abundance closely followed that of the wind. The exception was the Nov.–Dec. 1982 abundance estimate which was biased due to predominantly horizontal trawls, rather than oblique, at depths and in leads between pack-ice where krill and zooplankton may have aggregated (HOSIE *et al.*, 1988). The similarity between abundance and wind patterns was perhaps more distinct with total herbivorous copepod abundances and *E. crystallorophias* abundance. All taxa shown in Fig. 11 declined in abundance with decline in mean ship recorded wind speed during the 1990's.

While the pattern of wind direction varied somewhat between years, four of the years exhibited a general easterly, south-easterly pattern, 1981, 1985, 1991 and 1993 (Fig. 12). South-east winds were particularly frequent in 1993 and northeasterly winds were more frequent in 1985. March 1987 was notable for the persistent and strong westerly and north-westerly winds. The wind patterns in 1982 were also quite distinct. That year and 1991, 1993 recorded the more frequent periods of calm or light variable
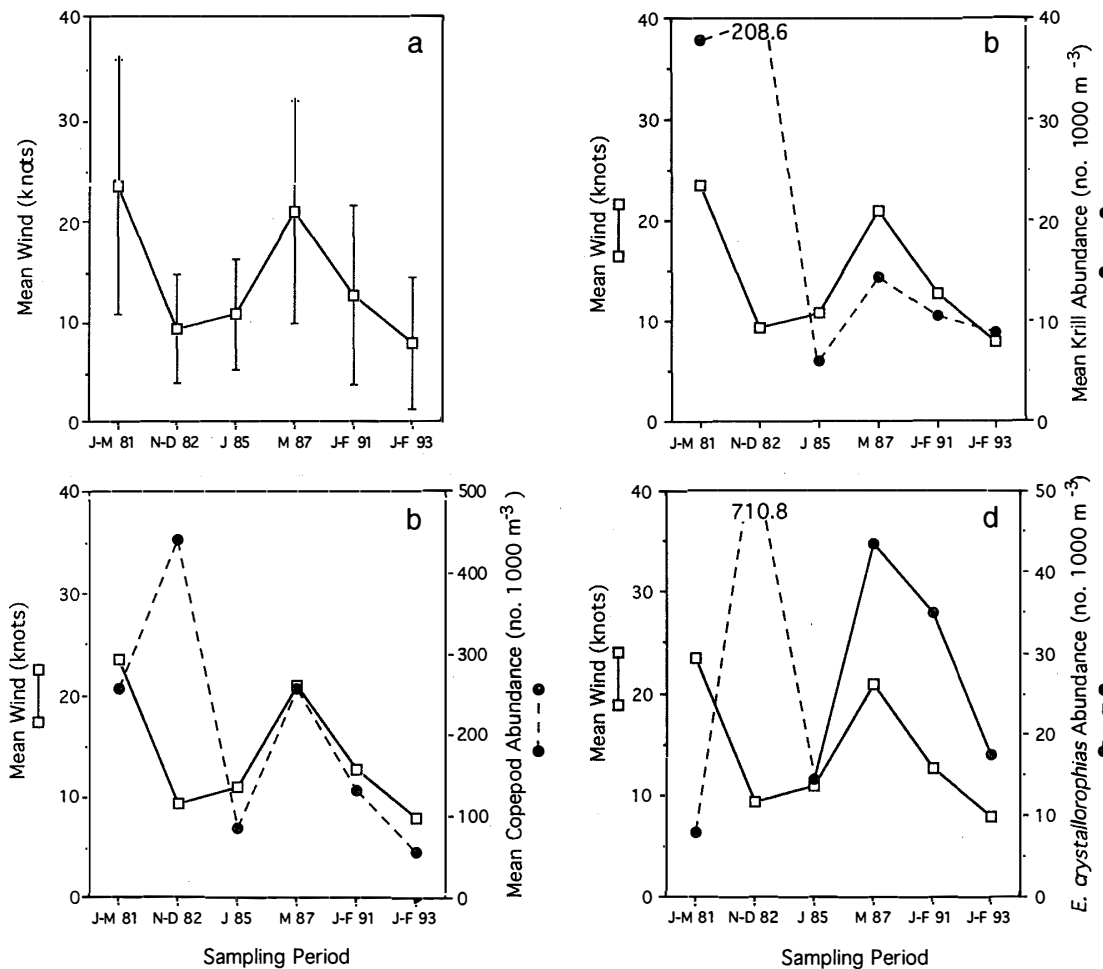
Fig. 11. Mean wind strength and associated mean abundance of krill, herbivorous copepods (C. acutus, C. propinquus, R. gigas, M. gerlachei) and E. crystallorophias for sampling surveys in the Prydz Bay region. Mean wind strength calculated using 3 or 4 hourly meteorological observations by ships' officers taken during the sampling period. Standard deviations are shown for the estimate of mean strength, but none are given for mean abundance estimates as they greatly exceed the mean values.

conditions of 10.7, 13.9 and 18.7%, respectively.

3.5. Species associations

Twenty-two species were included in the first inverse cluster analysis of species using the normal RMT 8 data. One major group, and a number of single or double species groups were defined at the 77% dissimilarity level (Fig. 13a). Group A comprised *E. superba* and the smaller euphausiid *T. macrura* linked at 64.4%. The associated NMDS plot shows the species widely spaced with *T. macrura* closer to Group B. Group B comprised 15 species, of which 13 were indicator species of the oceanic Station Group 1 (Tables 2 and 3). The salp *Ihlea racovitzai* was one taxon that was not an indicator, either abundance or frequency, whereas *L. helicina*, although grouped with the oceanic species, was a frequency indicator species for the neritic Station Group 3. The neritic *E. crystallorophias* was only loosely grouped with the

Jan.-March 1981 (2.34)
n=171

Nov.-Dec.1982 (10.7)
n=177

Jan. 1985 (1.4) n=139

March 1987 (1.1)
n=93

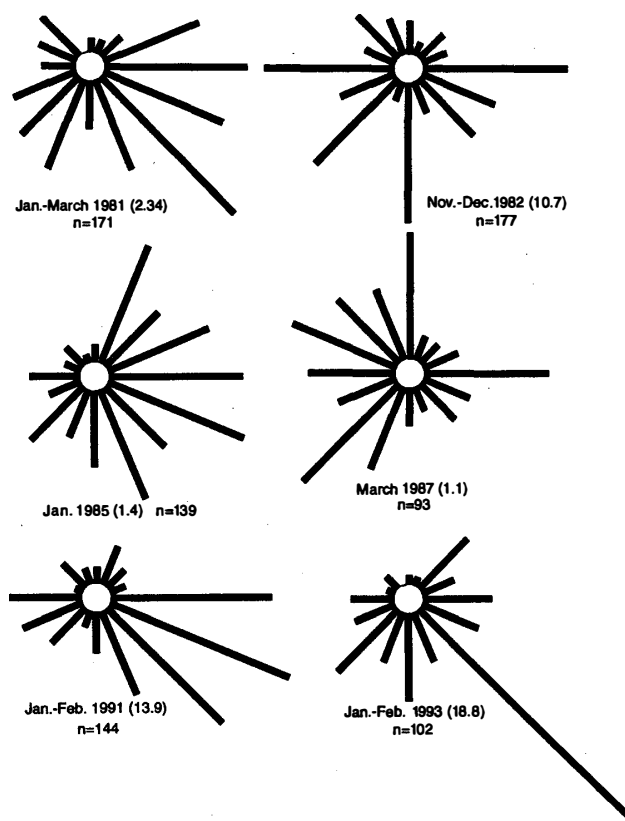Jan.-Feb. 1991 (13.9)
n=144

Jan.-Feb. 1993 (18.8)
n=102

Fig. 12. Wind direction patterns associated with each sampling cruise shown in Fig. 11. The length of each radial is proportional to the frequency of observations, not wind strength. n=the number of observations and the percentage frequencies of calm or light-variable wind observations are shown in parentheses.

other neritic indicator *S. bitentaculata* at 82%, and the NMDS plot shows a wide separation between these species. The remaining three species, the two ctenophores *Callianira cristata* and *Pleurabrachia pileus*, and the hyperiid *Hyperia macrocephala* were quite separate in both the cluster and NMDS analysis, and none were indicator species of any station group. *C. cristata* was not particularly abundant, 6 occurrences for the whole survey area, and was only classed as dominant at Stn 7 because of one specimen out of a total of 9 zooplankters caught at that site. Not surprising then, that it was so distantly separated from other species in the NMDS plot (Fig. 13b). Both *P. pileus*, and *H. macrocephala* were evenly distributed through neritic and oceanic sites in terms of frequency of occurrence.

In the second inverse analysis using the adjusted data, Stn 7 was classed as an outlier (GAUCH, 1982) and eliminated thus removing *C. cristata* as a dominant species. Seventeen species were subsequently defined as dominant using the 1% limit, all being dominant species in the previous analysis (Table 1). Both the cluster and NMDS analyses produced much the same results as the analysis of normal RMT 8 data (Fig. 14). The elimination of Stn 7 with its few specimens would have had minimal effect. Group A comprised *E. superba* and *T. macrura* and the main group B comprised the same oceanic species as classed above. In both the cluster and NMDS plots it is possible to see some subgrouping (at 69%), giving subgroup B3 of *R. gigas* and *Salpa thompsoni*, subgroup B2 of *L. helicina* and the rest in B1. These subgroups could be defined in normal RMT 8 cluster analysis at 69% but are more closely spaced in the NMDS plot (Fig. 13b), probably an influence of the widely dispersed single group species, especially *C. cristata, P. pileus*, and *H. macrocephala*, causing
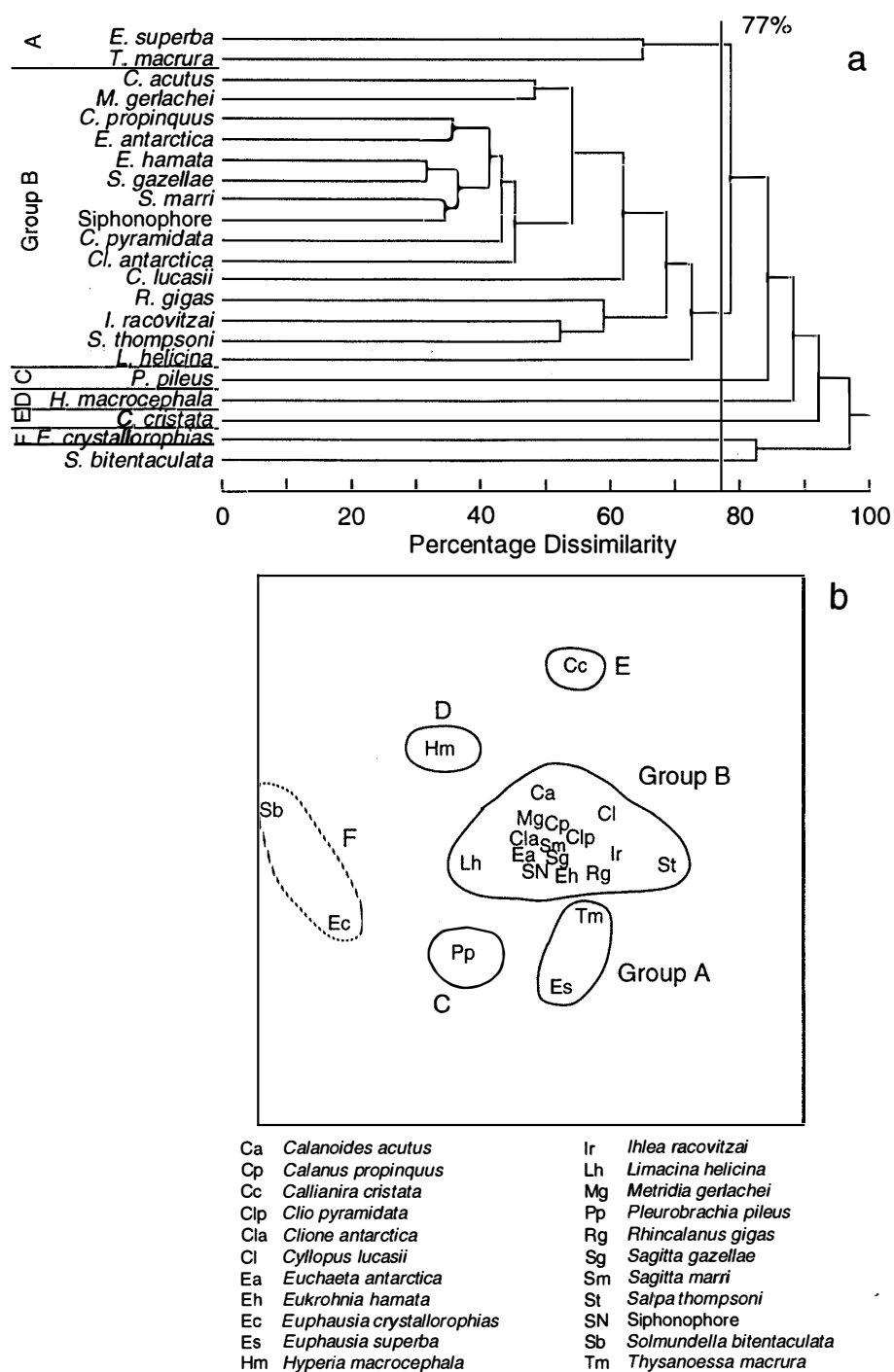
Fig. 13. Species associations based on normal RMT 8 data set. (a) Dendrogram of the inverse cluster analysis comparing dominant species, using Bray-Curtis dissimilarity index with UPGMA linkage, after standardizing species abundance (HOSIE, 1994a,b; HOSIE and COCHRAN, 1994). (b) NMDS inverse ordination plot comparing dominant species. Respective cluster groups identified in Fig. 13a are superimposed. Axis scales are relative in NMDS and therefore are not shown. Stress value=0.14.
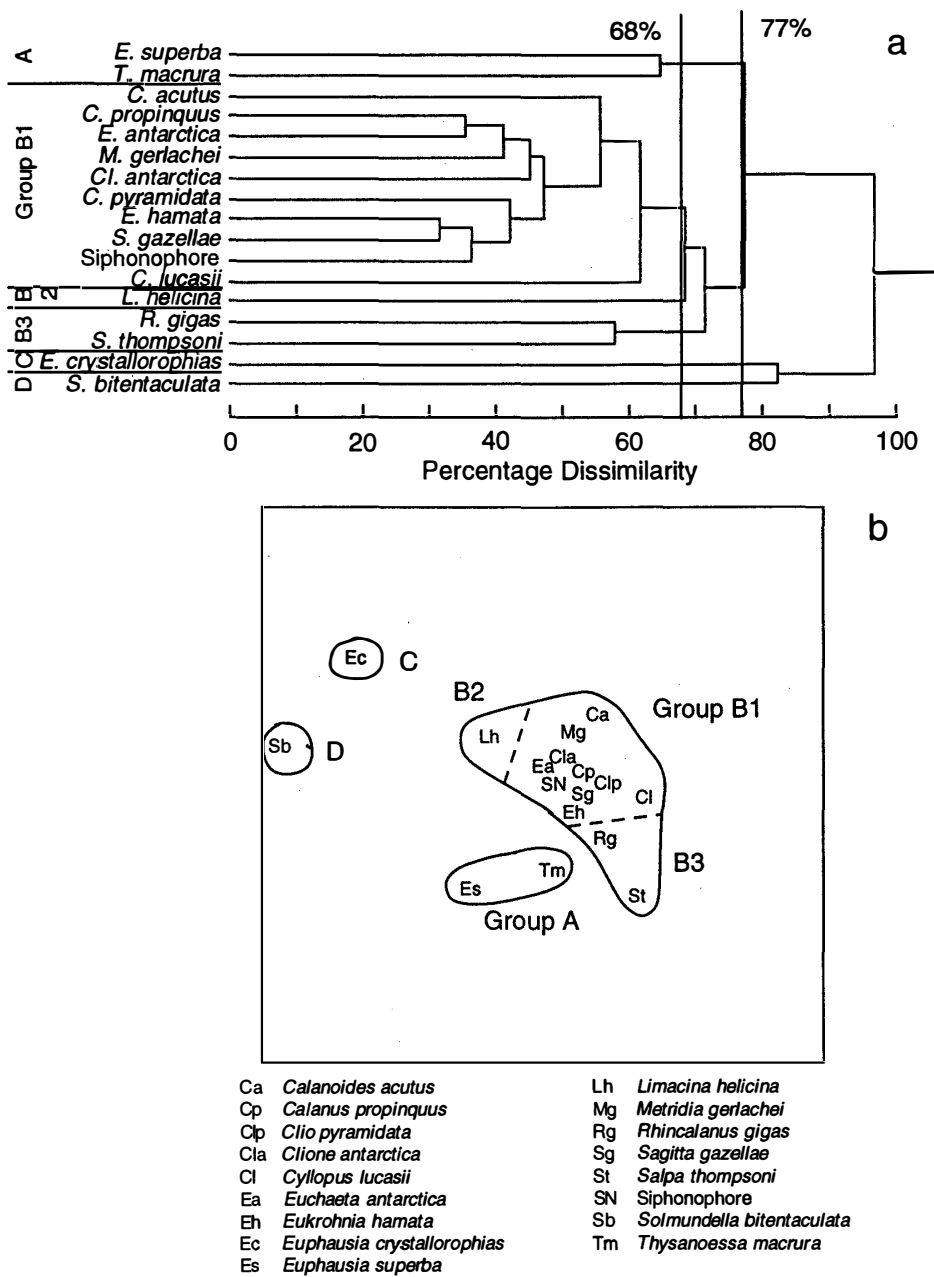
Fig. 14. Species associations based on adjusted copepod data set. See Fig. 13 for full caption details. (a) dendrogram of the inverse cluster analysis comparing dominant species. (b) NMDS inverse ordination plot comparing dominant species. Respective cluster groups identified in Fig. 14a are superimposed. Stress value=0.09.

compression of the oceanic group (GAUCH, 1982). The absence of these species in the analysis of adjusted data has resulted in the oceanic group expanding in size under the NMDS ranking system. Note that *E. crystallorophias* and *S. bitentaculata* are again widely separate from each other and other species still causing the other species to be grouped well to one side.

Both sets of cluster and NMDS analyses show that *E. superba* was primarily
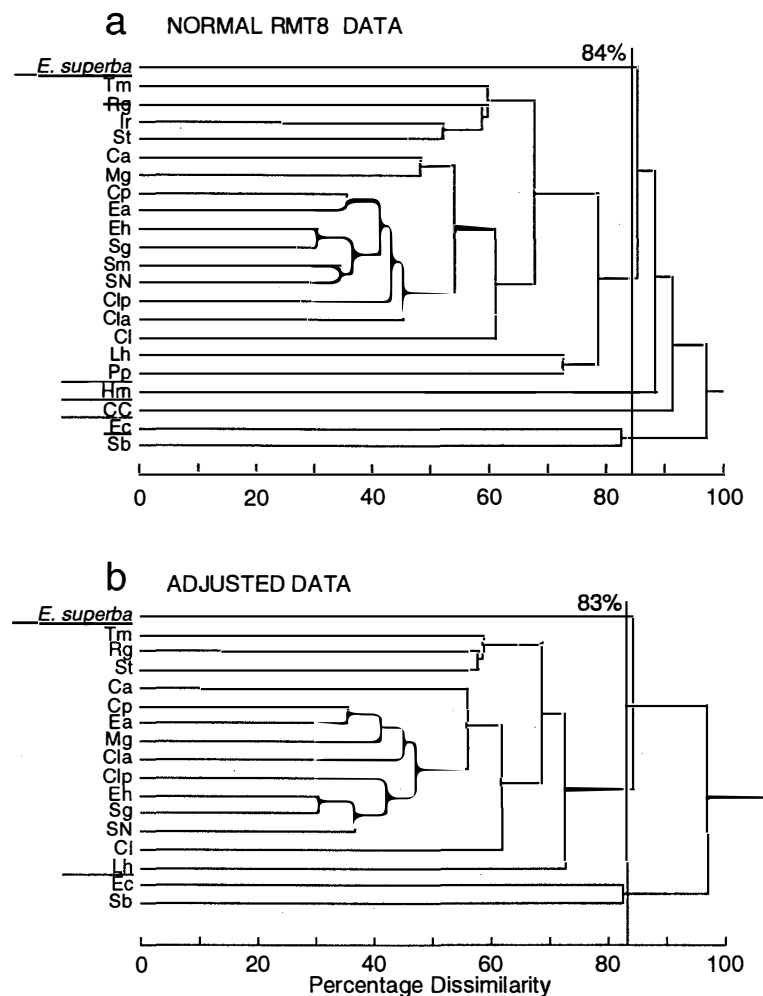
Fig. 15.   *Re-analysis of species associations for normal RMT 8 and adjusted copepod data set, after Station 87 was removed.* Euphausia superba *is now clearly shown as dissociated from other species.*

dissociated from all other species, but grouped with *T. macrura*, although it was an abundance indicator species of oceanic sites in the adjusted data analysis and a weak frequency indicator (5% group) of oceanic stations in the normal RMT 8 analysis. This association is an anomalous result caused by both species occurring in very high abundance at the one krill site (Stn 87) biasing the link, especially when coupled with the general low abundance of krill in the region. Reanalysis of the species associations with Stn 87 removed showed krill dissociated from the other species only linking with the oceanic group at 85.3% dissimilarity (Fig. 15). This is the pattern seen in the previous surveys. *T. macrura* was regrouped as oceanic, a more realistic association since this species is both an abundance and frequency indicator of the oceanic zone.

4.   Discussion

4.1.   *Coherence of neritic and oceanic communities*

Our previous definitions of the Prydz Bay zooplankton communities, their

composition and distribution patterns, were based on RMT 8 net data which have underestimated copepod densities. HUBOLD *et al.* (1988) found that copepods of >500 μm size were not adequately represented in their net samples which used 500 μm mesh. SIEGEL (1986) reported that the RMT 8 with 4.5 mm mesh may also undersample *E. superba* less than 20 mm in total body length. In some studies, for example PIATKOWSKI (1989b) and SIEGEL and PIATKOWSKI (1990) in the Atlantic sector and PAKHOMOV (1989, 1993) in Prydz Bay, copepods were excluded from analyses because the copepods would have been undersampled. However, given SIEGEL's (1986) observations for krill less than 20 mm, why remove copepods from data sets for being undersampled when other species of zooplankton, especially those <20 mm and narrow bodied (*e.g.* chaetognaths) are probably also not adequately sampled? Despite using data with underestimated copepod abundance, we have shown previously that a copepod dominating community (Main Oceanic Community) extends over a large area of the Prydz Bay region. There is doubt though, when using data sets with underestimated numbers or with copepods eliminated, that the communities defined may not reflect the true natural groups, *i.e.* the communities so defined are artificial.

Some studies have combined both RMT 1 and RMT 8 data in their analyses to more accurately define community structure and distributions (BOYSEN-ENNEN and PIATKOWSKI, 1988; BOYSEN-ENNEN *et al.*, 1991). We have not always had the ability to include RMT 1 data in a full analyses, either because the net was not used or because time and resources have constrained our ability to fully process RMT 1 samples other than for euphausiid larvae (*e.g.* HOSIE, 1991). BEAUMONT (1995) has defined the level of undersampling for the four most abundant copepod species, *C. acutus, C. propinquus, M. gerlachei* and *R. gigas*, and that degree of undersampling was different for each species. By applying her correction to the normal RMT 8 copepod data in 1993 and also 1991 (HOSIE and COCHRAN, 1994), we produced more accurate data sets, assuming that krill and other zooplankton of >20 mm body length are represented truly, for comparison with the normal RMT 8 data sets. Comparison of the distribution maps derived from the normal RMT 8 data, adjusted and biomass data show clearly that analyses of the three data sets have produced fundamentally the same results. One or two bordering sites near the shelf edge changed classification between oceanic and neritic, and the classification of neritic sub-groups varied, all being a function of the greater copepod numbers in the adjusted and biomass data and this is to be expected. The neritic subgroups in the normal RMT 8 data were distinguished primarily by differences in the distribution of *E. crystallorophias*, whereas *M. gerlachei* was additionally responsible for separating the neritic groups in the adjusted data. Ultimately, the same two basic groups were defined, oceanic and a neritic groups, with few sites being defined as krill sites, and the same indicator species were defined in both the normal and adjusted analysis. Further, re-analysis of the 1991 data after adjusting the copepod densities produced almost the same distribution map as before; the only significant difference being two neritic sites reclassified as a separate neritic group (Fig. 16).

On the basis of these results, it is reasonable to assume that the previous descriptions of Prydz Bay communities based on normal RMT 8 data 1981–1991
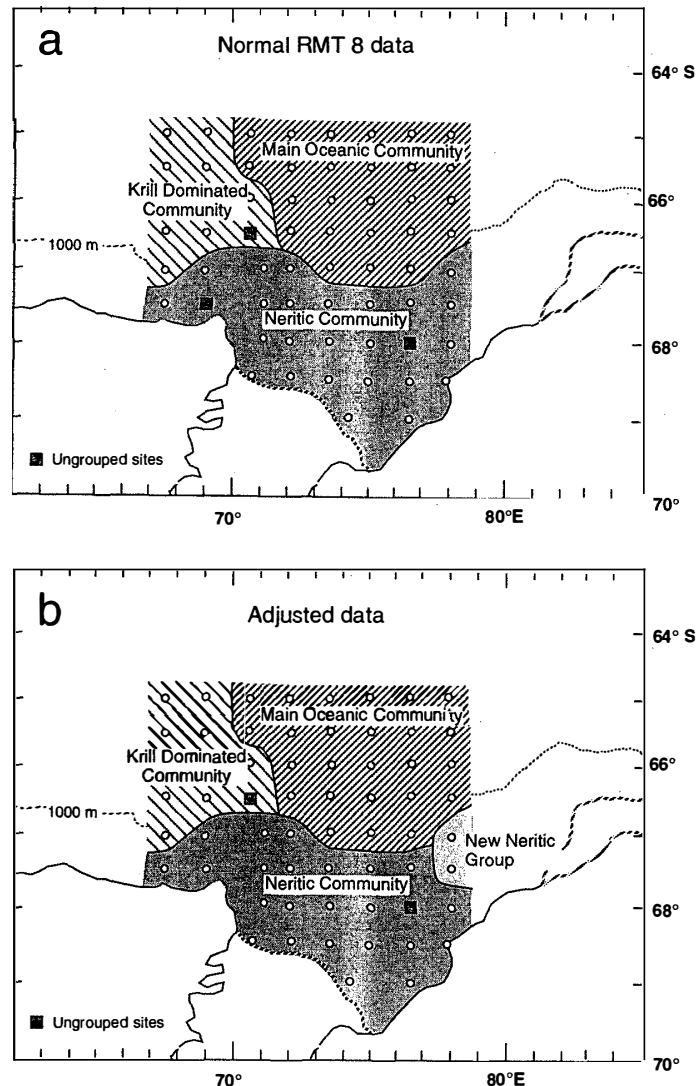
Fig. 16. January–February 1991 community distribution patterns. (a) original patterns based on normal RMT 8 data from Hosie and Cochran (1994), (b) community patterns based on re-analysis of same data set after adjusting copepod densities acording to Beaumont (1995).

(Hosie, 1994a; Hosie and Cochran, 1994) are valid and probably do portray the true zooplankton groups. Consequently, it is possible to conduct krill surveys as the primary study using the RMT 8 net, while studying and defining zooplankton communities, composition and distribution patterns as a secondary program. This is particularly useful if time and resources limit the ability to conduct a full zooplankton study with finer meshed nets. These results do not obviate the need for further studies to determine the level of undersampling in other zooplankton.

All the previous studies of zooplankton community structure in Antarctica have used abundance data. It could be argued that biomass, as an indicator of tissue or carbon, is a better estimate of the importance of a species or larger taxon in a community. Measuring the wet weight of small zooplankton, singularly or altogether as one species or taxon is the least accurate, albeit quickest, method for determining biomass mainly because of problems with variation in water content between and

within species (OMORI and IKEDA, 1984). Considering that the biomass data set produced almost identical results to those of the abundance data sets, and that numbers are easier to obtain, we recommend the continued use of abundance data for multivariate analysis.

The inverse analyses of the normal and adjusted data sets for species associations produced much the same result. This is expected as the data is standardised within each species (HOSIE, 1994a,b; HOSIE and COCHRAN, 1994), and therefore the standardised scores will be the same for both original and adjusted copepod densities. Adjustment of the copepod densities will only affect the definition of dominant species because the larger copepod densities will alter total zooplankton abundance and reduce the percentage composition of other species. FIELD et al., (1982) recommended a 4% limit for defining dominant species in a marine benthic community and this value was used previously for Prydz Bay zooplankton (HOSIE, 1994a,b; HOSIE and COCHRAN, 1994). Application of this value only produced 9 species in the adjusted data, and this did not include important taxa such as chaetognaths (ØRESLAND, 1990; HOSIE, 1994a). A 1% limit was thus used to define 17 species for the inverse analysis. The choice of value 1 or 4% is purely arbitrary but is dependent on the number of relatively abundant species required for a reasonable analysis of species association and definition of community structure.

There was good correspondence between the species associations shown in Figs. 13 and 14, and indicator species of the station groups. For example, nearly all of the Group B species in both inverse analyses were species indicators of the two Group 1 oceanic collection of stations. There were two exceptions in the normal data set; *L. helicina* which was classed as a frequency indicator of the neritic zone and *I. racovitzai* which did have a higher abundance in the oceanic group but was not considered significant in the SNK test. In turn, these associations and the composition of zooplankton communities in this study differ little from those described in the previous macroscale and mesoscale surveys (HOSIE, 1994a,b; HOSIE and COCHRAN, 1994). Species Group B, again for example, contains all of the species that comprise the assemblage defined as the main oceanic community, and there is no doubt that the two Station Group 1's represent that community.

The species associations have remained remarkably consistent in all the Prydz Bay surveys, perhaps one of the few constants in the study of the community ecology of this region. However, there are a number of small but notable differences in the analyses of the present and former studies. Gammarids were not included in the present analysis, although used previously, because they did not meet either the 4% or 1% limit. We presume that they are still indicative of the neritic zone along will larvae of *P. antarcticum* and of ice fish (HOSIE, 1994a). The hydromedusan *S. bitentaculata* was included in the neritic zone for the first time. It has occurred rarely in previous years, and had a low frequency of occurrence in this study, so should not be considered as a reliable indicator of the neritic area. Similarly, the gymnosome pteropod *Clione antarctica* was identified as a component of the oceanic community, whereas all gymnosome species collectively have never been dominant.

Construction and interpretation of the community structure in Fig. 17 is dependent on which data set is used and on the previous analyses by HOSIE (1994a).

NORTHERN OCEANIC
COMMUNITY

Salpa thompsoni

MAIN OCEANIC COMMUNITY

Calanoides acutus   Sagitta gazellae
Calanus propinquus   Clione antarctica
Euchaeta antarctica   Clio pyramidata
Rhincalanus gigas   Siphonophora
Eukrohnia hamata   Cyllopus lucasii
        Thysanoessa macrura

KRILL DOMINATED
COMMUNITY
Euphausia superba

Metridia gerlachei

NERITIC COMMUNITY   Euphausia crystallorophias
                     Solmundella bitentaculata

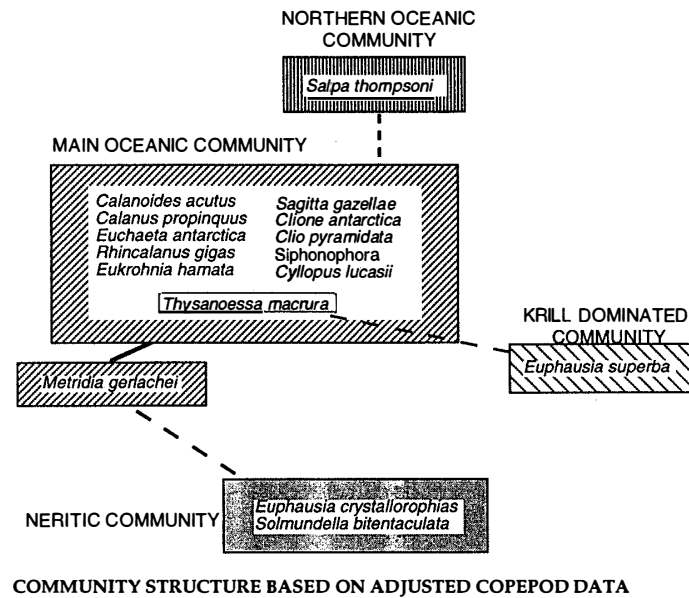COMMUNITY STRUCTURE BASED ON ADJUSTED COPEPOD DATA

Fig. 17.   Zooplankton communities based on analyses of the adjusted copepod data set. Shading within
each box (i.e. each assemblage) corresponds to the shaded areas in Figs. 7, 8 and 9 where that
assemblage predominated. Note: the northern oceanic community was not sampled during the
present survey.

L. helicina was depicted previously as an indicator of either the MOC or neritic zones.
In this study it was associated more with the MOC. ANOVA/SNK analysis showed an
even distribution of abundance for this species in the oceanic and neritic groups. It
was a weak frequency indicator of the neritic group—not so in the adjusted data
analysis. This species has displayed various associations, including neritic and
oceanic, in both Prydz Bay and the Antarctic Peninsula areas and is not considered a
reliable indicator species of any area (SIEGEL and PIATKOWSKI, 1990; HOSIE, 1994a;
HOSIE and COCHRAN, 1994). Consequently, it is not shown in Fig. 17.

Salpa thompsoni has been described previously as confined to, or more abundant
in, the West Wind Drift (FOXTON, 1966; SMITH and SCHNACK-SCHIEL, 1990). This was
certainly the case in January 1985 when S. thompsoni dominated the Northern
Oceanic Community in the waters north of the divergence in densities two orders of
magnitude higher than in the present study (HOSIE, 1994a). Salpa thompsoni formed
associations with other MOC species in the present study, although quite distantly in
the NMDS plot from adjusted data (Fig. 14b). This is probably due to the survey not
sampling the waters of the Antarctic Circumpolar current and hence the Northern
Oceanic Community. We assume on the basis of the previous Prydz Bay surveys and
other studies mentioned above that S. thompsoni is principally still the dominant
species of the NOC and is thus shown separate from the other species in community
structure (Fig. 17). The close association between S. thompsoni and R. gigas is not
surprising as the copepod often has higher abundances north of the divergence
(MARIN, 1987), and BUDNICHENKO and KHROMOV (1988) and BEAUMONT (1995) also
reported a northward increase in abundance of R. gigas in Prydz Bay. A more recent
study has described a possible feeding association between the copepod and salp

during a phytoplankton bloom (PERISSINOTTO and PAKHOMOV, 1996).

4.2. Environmental factors affecting neritic and oceanic patterns

A number of environmental parameters have been identified previously that may have controlling effects on the summer zooplankton community distribution patterns. Temperature was one parameter that was consistently correlated with community distribution (HOSIE, 1994a; HOSIE and COCHRAN, 1994). Temperature was again strongly correlated with the distribution patterns in the present study, both the normal and adjusted RMT 8 data and also with abundance of nine species (Table 7). Numerous species have known temperature ranges (FOXTON, 1971; LOMAKINA, 1966; KITTEL and STEPNIK, 1983). Many, including copepods, have wide circumpolar distributions but still exhibit preferences for warmer or colder waters (EVERSON, 1984). A very strong positive correlation was found for R. gigas. with temperature (Table 7). Euphausia crystallorophias has been described as a cold water stenothermic species (LOMAKINA, 1966). Adults of this species have not been collected in the warmer waters north of the continental shelf in the Prydz Bay region. Although ZMIJEWSKA (1983) suggested that M. gerlachei also has a preference for cold water regions of Prydz Bay, there was no evidence for such a preference in this study. The continental shelf edge approximates the boundary between two distinct temperature regimes, the uniformly very cold neritic water and the more complex, but generally warmer, water north of the shelf edge. The temperature boundary also approximates the separation of the neritic and oceanic communities. Whereas adult E. crystallorophias are never caught in the oceanic area, a number of oceanic species were identified, in the indicator species analyses (Tables 2, 3, 4 and 5), as not occurring in the neritic zone at all or having very low abundances, e.g. R. gigas, C. lucasi, E. hamata, S. gazellae, S. marri, H. ocellatus, S. thompsoni, T. carpenteri and cephalopods. It would seem that the main effect of temperature is the distinct separation of the neritic and oceanic communities. In geographically larger communities such as the oceanic, horizontal distributions of some species may change more gradually in response to temperature gradients.

Chlorophyll a was the only other parameter measured that has in the past been consistently correlated with the community distribution patterns. This is to be expected given that herbivorous copepods and euphausiids comprise the significant components of the zooplankton and are naturally dependent on phytoplankton. In the present study, mean Chl a did not explain any variation in the NMDS distributions for either normal and adjusted data. Maximum Chl a values at each site did explain 8 and 7% of the variation in the normal and adjusted data sets, with the two herbivorous copepods C. acutus and C. propinquus abundances negatively correlated to it. This may be a function of the higher maximum values occurring in neritic waters and the two western most transects correlating with the zooplankton communities strong latitudinal separation. A temporal development of a bloom in the oceanic area from East to West, during the course of sampling, cannot be discounted and confuses attempts to correlate phytoplankton and zooplankton patterns. It is also difficult to draw any conclusions about the relationship between zooplankton distributions and maximum Chl a values as the zooplankton abundances were

integrated for the upper 200 m by the oblique trawls whereas the chlorophyll peaks occurred at discrete depths. However, maximum chlorophyll values were generally near or just above the thermocline, and this often coincided with scattering layers detected hydroacoustically at the same depths.

Ice (recession and cover) and salinity have at times also been correlated with the community patterns. Ice may affect zooplankton communities directly or possible indirectly through the effect of ice on phytoplankton production during the annual retreat of the ice (HART, 1942; SMETACEK et al., 1990; SMITH and SCHNACK-SCHIEL, 1990). The effect of ice on the 1993 summer distributions can only be considered minimal if any, as ice cover, as the only correlating ice variable measured, explained just 6% of the variation in the distribution pattern of the adjusted data set. Similarly, salinity only explained a small amount of the variation (14%) in the adjusted data set, and any attempt to interpret the effect of salinity on the communities is extremely difficult given the problems of the CTD units.

4.3.   Factors implicated in interannual krill variability

The species associations between the present and past surveys in Prydz Bay have remained remarkably consistent, including the dissociation of krill from other species, but the same cannot be said of the geographic distributions of the communities. The obvious difference being the almost total absence of the Krill Dominated Community. This community was originally described, on the basis of large scale surveys, as being usually located along the continental shelf edge, between the oceanic and neritic communities, extending into shelf waters as far south as 67°30'S (HOSIE, 1994a). This distribution was also seen by BUDNICHENKO and KHROMOV (1988), PAKHOMOV (1989) and ICHII (1990). The 1991 survey was thus conducted to define more accurately the distribution patterns (HOSIE and COCHRAN, 1994). Instead, we observed quite different distributions, with the KDC difficult to define and apparently displaced west. There was also an associated general lower abundance of krill. There was some evidence of calmer than usual weather conditions during that survey and together with the unexpected distribution patterns we concluded that 1991 was perhaps an anomalous season. Hence, the reason for resurveying in 1993. However, this survey found even fewer krill and virtually no KDC other than three sites. Three hypotheses can be offered to explain the apparent absence of krill: first, there has been a genuine decline in total krill abundance in the general region; second, the KDC community pattern has changed, i.e. a large scale move to another area outside of the area sampled; third, the krill have changed behaviourally—instead of aggregating near the shelf they are more dispersed.

Decline in krill abundance: The patchy distribution of krill makes comparison of abundance estimates based on net sampling extremely difficult, especially interannual variation in mean abundance, because high statistical variances usually exceed the mean. This is particularly the case for research scale nets such as the RMT 8 (NAST, 1982; SIEGEL, 1985; HOSIE et al., 1988). Nonetheless, there is some evidence of a decreasing trend in krill densities in the net surveys of Prydz Bay, with the 1993 estimate approximately a quarter of that of 1981 (HOSIE, 1994a; HOSIE and COCHRAN, 1994, and present study). More substantial evidence of a decline has been observed in

Fig. 18. Mean total biomass estimates of krill in
    Prydz Bay (67° to 78°E, 65° to 67°30'S) for
    1985, 1991, 1992, 1993, with 95% confidence
    limits on the mean values based on the sampling
    variance (from PAULY and HIGGINBOTTOM,
    1994).
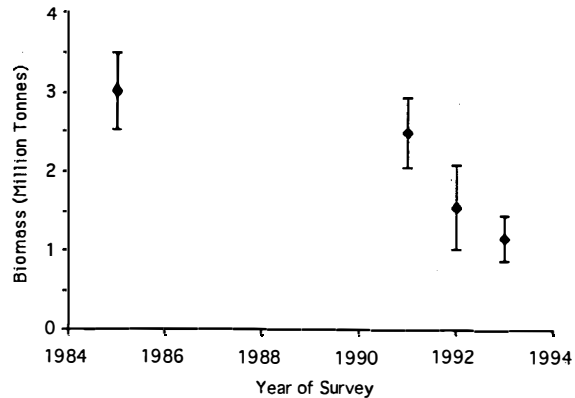
hydroacoustic estimates of total biomass for the same surveys between 1985 and 1993 (Fig. 18). The largest decrease occurred in the last few years with the 1993 biomass less than half that of 1991 (Fig. 18). Although hydroacoustics estimates are based on a much larger sample size than can be obtained by nets, and thus presumably more accurate, caution is still required when interpreting the hydroacoustic estimates because of the unknown contribution or bias of other zooplankton species in the hydroacoustic biomass estimate (HIGGINBOTTOM et al., 1988). No attempt has been made to quantify calibration uncertainty or more importantly the error associated with assuming all targets in the surveyed area are krill (PAULY and HIGGINBOTTOM, 1994). Despite the various sources of error, the decline in krill numbers from both net and hydroacoustic estimates cannot be dismissed entirely and warrants further investigation. Interestingly, the breeding success of Adelie penguins around Mawson was normal in the 1992/93 season, but exceptionally high chick mortalities have occurred since and is possibly a function of a paucity of krill in the foraging area near Mawson (KERRY et al., 1995 a,b)

Changed Distribution: A large scale change in the distribution seems the least likely scenario but cannot be discounted. The survey area was approximately 450 n miles from east-west by 240 n miles north-south on transects 2 and 3 (833 × 444 km), so quite a large area was surveyed. A complete change of distribution of krill to the north away from the shelf edge involves a translocation of approximately 200 km and considerably further if the krill were relocated west or east of the survey area. We have no information, at present, to support this hypothesis.

Change in behaviour: Instead of being concentrated near the shelf edge in aggregations or swarms, as as found in previous surveys, the krill may have dispersed and extended their distribution northward into the area dominated by copepods. There were few krill in the shelf waters. While the overall biomass of krill in the region would remain the same, the density of krill would be substantially reduced with copepods appearing more dominant because of their superior numbers, even in the normal RMT data set. The hydroacoustic survey during this study showed that the krill distribution was reasonably homogenous through the survey area with few aggregations of krill near the shelf edge (PAULY and HIGGINBOTTOM, 1994). This behaviour of dispersing over a wider area would explain the decrease in the krill densities measured by net sampling but it is not consistent with the drop in total

biomass of the region recorded by hydroacoustics (Fig. 18).

The prime purpose of comparing the environmental parameters with NMDS scores through multiple regression was to determine which environmental events may affect zooplankton community distribution patterns within each season. The analyses did not prove any cause-and-effect. Further, the analysis unfortunately does not provide a direct indication as to what has caused the significant changes in the community patterns, specifically the apparent absence of the Krill Dominated Community as discussed above. Changes in the pattern of ice retreat may have directly or indirectly affected the zooplankton and/or phytoplankton distributions in 1991 resulting in the unusual zooplankton community patterns (Hosie and Cochran, 1994). A large polynya usually appears by early December in the southern part of Prydz Bay near the Amery Ice Shelf (Smith et al., 1984; Streten and Pike, 1984), and then dissipates north towards the shelf edge to meet the southward receding ice edge. No polynya formed in the south in 1991 and there was no northward dissipation of ice. The polynya formed as usual in the 1992/93 season one month prior to the current survey, but an unusual krill community pattern still occurred. The influence of pack ice in the change in community patterns cannot be discounted but it would seem unlikely.

Small scale variations in the pattern of chlorophyll distribution occurs between years, but the general pattern of higher concentrations south of the shelf edge seen in previous years (Wright, 1987; Hosie, 1991; Hosie and Cochran, 1994) is evident in the present study. This is more clearly seen with the maximum Chl a (Fig. 6). The 1993 mean Chl a concentrations north of the shelf, where the krill community was expected, were higher than the same time in 1991 by approximately a factor of four (Fig. 6 and Hosie and Cochran, 1994, Fig. 6), whereas the 1993 concentrations were similar to those seen in the same area in the 1980's surveys when the Krill Dominated Community were prominent. The abundance of phytoplankton, measured as Chl a, would not seem to be a factor causing the changes in abundance. However, the concentration of the phytoplankton into a much shallower mixed layer may have had an effect.

Although the isotherm and isohaline patterns varied much between the 1991 and 1993 surveys, the general pattern of uniformly very cold water south of the shelf edge and the summer surface/Antarctic winter water/circumpolar deepwater complexity north of the shelf edge is the same in both years, as it was in previous surveys (Hosie, 1994b; Nunes Vaz and Lennon, 1996). Both the 1991 and 1993 surveys had much shallower mixed layers than observed previously in Prydz Bay. In 1991 the shallow mixed layer was at approximately 30 m (Hosie and Cochran, 1994). In the present study (1993), it was shallower at 10–15 m in the neritic zone and usually 20–30 m down to 50 m in the oceanic. In earlier surveys the mixed layer throughout usually extended to 50–60 m, sometimes as deep as 100 m (Smith et al., 1984; Nunes Vaz and Lennon, 1996). These quite shallow mixed layers are indicative of the calm weather experienced during the 1991 survey and the present study.

It has been suggested previously, that increases in krill abundances in the Prydz Bay region may be a function of increases in "atmospheric circulation activity" (Bibik, 1989; Bibik and Yakolev, 1991; Pakhomov, 1995), but those studies have produced

little if any hard evidence showing any relationship between krill abundance and atmospheric activity. On the other hand, PRIDDLE *et al.*, (1988) did provide some evidence linking substantial changes in krill distribution patterns to persistent southward air flow that occurs about every three years in the Atlantic sector. MURPHY *et al.* (1995) have examined evidence of possible ice-ocean-atmospheric interactions which can produce periodic anomalous patterns in maxima sea-ice extent that have a clockwise circumpolar precession. The authors further noted that such patterns are likely to have a serious impact on ice edge blooms and the Southern Ocean ecosystem in general. In our study, the patterns of variation in krill abundance between years closely followed that of the wind (Fig. 11). The similarity between abundance and wind patterns was not just confined to krill but was perhaps more distinct with total herbivorous copepod abundances and *E. crystallorophias* abundance. Further, the copepods and euphausiids showed a decline in abundance with decline in mean wind speed during the 1990's (Fig. 11). This is similar to the decline in total krill biomass for the region as determined by hydroacoustics (Fig. 18). We do not claim proof of any cause-and-effect relationship between abundances and wind strength. Nor can it be expected that the similarity in patterns seen in Prydz Bay will be observed elsewhere. Nonetheless, the fact that the two euphausiids and combined copepods showed very similar fluctuations with wind strength suggests that there is a genuine relationship. This is likely to initiate as a function of wind strength affecting the depth of the mix layer, consequently affecting the vertical distribution of phytoplankton. In the present study, the phytoplankton was generally associated with the thermocline and concentrated in a shallower mix layer than seen previously. How changes in the vertical distribution or concentration of phytoplankton affected the zooplankton communities, either in relation to abundance or major changes in distribution patterns, could not be determined from the present study. This is mainly because there was no opportunity for stratified trawling to map vertical distribution of zooplankton. Time was limited and the main purpose of the survey was to map horizontal distribution patterns. Large and mesoscale surveys such as those conducted in the Prydz Bay region and the Atlantic sector have proved invaluable in defining zooplankton community structures and associated distribution patterns. The relationship between atmospheric-hydrographic events and krill/zooplankton distributions, such as wind strength-mixed layer-plankton, will perhaps only be determined through fine scale surveys (1–10s of km) incorporating intensive stratified sampling.

preparation of this paper, domo arigato gozai mashita.   .

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