MULTIVARIATE ANALYSES OF THE MACROZOOPLANKTON COMMUNITY AND EUPHAUSIID LARVAL ECOLOGY IN THE PRYDZ BAY REGION, ANTARCTICA.

by

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STATEMENT

Except as stated herein this thesis contains no material which has been accepted for the award of any other higher degree or graduate diploma in any tertiary institution. To the best of my knowledge and belief this thesis contains no copy or paraphrase of material previously published and written by another person, except where due reference is made in the text.

Graham William Hosie 9 November 1992

ABSTRACT

Macrozooplankton data from the Prydz Bay region, collected between 1981 and 1991, and representing the months of September to March, were analysed using cluster analysis and non-metric multidimensional scaling to define the communities within the region, their distribution patterns, indicator species and species affinities. Four communities were identified. Three of these communities were dominated respectively by *Euphausia crystallorophias* (neritic), copepods-chaetognaths (main oceanic), and salps-hyperiids-small euphausiids (northern oceanic community). The fourth 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 outer shelf edge, usually between the main oceanic and neritic communities. Chlorophyll *a* abundance and temperature explained much of the variation in community distribution patterns. The annual recession of ice, pack-ice cover, and salinity also explained some of the variation. Water circulation seemed to have only a clear effect on community distributions at the end of summer in March, when distributional patterns exhibited a distinct longitudinal zonation compared to the strong latitudinal pattern seen through most of the summer.

In January 1984, 1985 and March 1987, net sampling surveys were carried out on the distribution and abundance of euphausiid larvae, primarily *E. superba*, in the Prydz Bay region. *E. superba* occurred in low abundance in January, probably due to sampling preceding the main spawning period, but occurred in very high abundance in the east of the region in March 1987. *Thysanoessa macrura* occurred throughout the study area in consistently high abundance. *E. crystallorophias* was marginally more abundant within its restricted range. Distinct north-south variations in larval age and developmental stages of *T. macrura* were observed indicating regional differences in spawning. *Euphausia frigida* was mainly confined to

the upper 200 m of the Antarctic Circumpolar Current. *E. superba* larvae produced north of the shelf break, between 70 to 83° E, moved north-east into the Antarctic Circumpolar Current. Larvae originating on the shelf moved rapidly west in the East Wind Drift. *E. crystallorophias* had the same westward dispersion, but some larvae appeared to return eastward via the Prydz Bay Gyre and remain in the region. However, the data indicate that most *E. superba* larvae, providing they survive injurious cold temperature and food deprivation, will leave the area, i.e. Prydz Bay krill may not be a self maintaining stock.

ACKNOWLEDGEMENTS

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Messrs Dick Williams, John Kirkwood and David O'Sullivan collected and processed specimens on FIBEX (1981) and ADBEX I (1982). Although

the species composition data were already published in ANARE Research Notes 7 and 31, I am still very grateful to Dick Williams for permitting complete access to the data sets for further detailed multivariate analyses. I thank Dick Williams for identifying ichthyoplankton in subsequent years. I am also grateful to Dick and Dr Harvey Marchant for their support, comments and many hours of discussion about the ecology of Prydz Bay.

Finally a special thanks goes to my wife Karen and daughters Katherine and Fiona. This study, and my employment with the Division, has meant that my family have had to cope with my frequent absences from home - including seven trips to Antarctica in eight years. They have been most supportive during that time - thanks girls.

CONTENTS

CHAPTER 1

INTRODUCTION

There have been a number of studies on Antarctic zooplankton prior to the commencement of the international BIOMASS program (Biological Investigations Of Marine Antarctic Systems and Stocks). Generally, these early studies were concerned mainly with the taxonomic description, life histories and large scale distribution of species or major taxonomic groups. They are too numerous to review in detail, but notable examples are: Ommaney (1936), Vervoort (1957) and Andrews (1966) for copepods; David (1955, 1958) for chaetognaths; the hyperiid *Themisto gaudichaudii* (Kane 1966); salps (Foxton 1966, 1971); the Antarctic krill *Euphausia superba* (Marr 1962; Mackintosh 1972, 1973); euphausiids in general (John 1936; Baker 1966); and studies of the distribution of zooplankton in general by Baker (1954), Foxton (1956), Voronina (1968) and Hopkins (1971). Early attempts to describe zooplankton communities include Mackintosh (1934), Hardy & Gunther (1936), and Voronina (1972). Everson (1984) and Smith & Schnack-Schiel (1990) have provided useful general reviews of the various early zooplankton studies.

The inception of the BIOMASS program in the late 1970's was the start of a new period of intensive cooperative research into the structure and dynamic functioning of the Antarctic marine ecosystem (Hempel 1983; El-Sayed in press). The main focus and emphasis of the program was the assessment of the stocks of the Antarctic krill *E. superba*. Krill were perceived as the central key component of the Antarctic marine ecosystem, but also as a major source of protein for human consumption. The possible impact of the krill fishery on the Antarctic marine ecosystem was therefore a major concern (Hempel 1983). During the course of BIOMASS, krill fishing developed rapidly into a major fishery with a sustained yield of approximately 400,000 tonnes per annum in recent years (Nicol 1989, 1991;

FAO 1991). Most of the research during and after BIOMASS has concentrated on the Atlantic sector of the Southern Ocean, an area noted for its particularly high abundances of krill (Marr 1962; Mackintosh 1973) and also where most krill fishing now occurs. During BIOMASS, 8 of the 11 participating nations conducted research in this region (Fig. 1.1). The other main BIOMASS area was the Indian Ocean Sector, also suspected of high krill biomass (Marr 1962; Mackintosh 1973). This area has in the past been the subject of long term commercial krill fishing by Japan and the former Soviet Union (Lubimova *et al.* 1985; Shimadzu 1985; Ichii 1990).

In addition to studying the biology of krill, the BIOMASS program also provided the opportunity to improve our knowledge of the ecology of the other zooplankton, necessary for understanding all aspects of the Antarctic marine ecosystem. The degree of interaction between krill and other zooplankton species, e.g. herbivorous copepods and salps, is of particular interest. For example, Kawamura (1986, 1987) tentatively suggested there had been a 10 to 100 fold decrease in the abundances of herbivorous copepods in the areas west and east of Prydz Bay. This decrease was considered a likely consequence of competition for food between copepods and a surplus 150 million tonnes of unconsumed krill - a product of declined whale stocks. The salp, *Salpa thompsoni,* is another species capable of competing with krill for food but may also consume large numbers of krill larvae (Huntley *et al.* 1989). The degree of interaction between krill and other herbivores has not been fully examined. Dietary studies of vertebrate predators have shown that zooplankton form important alternative pathways in the Prydz Bay food web (Williams 1985, 1989) and also in the Weddell Sea (Boysen-Ennen *et al.* 1991), further highlighting the need for research into zooplankton ecology in addition to krill studies.

There were few studies carried out on krill larvae in the early years. Fraser (1936) made the first description of the larval developmental stages of *E. superba.* Marr (1962) described the geographical distribution of each developmental stage, predominantly in the Atlantic sector. He also

described in detail the vertical distribution of krill larvae and proposed the model of deep water developmental ascent. Apart from those studies, knowledge of the ecology of krill larvae, as well as that of other Antarctic euphausiids, was virtually nonexistent. Serious studies into the ecology of krill larvae commenced in the late 1970's, prior to the first BIOMASS cruises, when Fevolden and the Hempels examined the geographical and vertical distributions of larvae in the Atlantic Sector (Fevolden 1979, 1980; Hempel 1979, 1981; Hempel & Hempel 1978, 1982; Hempel *et al.* 1979). Interest in the distribution and abundance of euphausiid larvae grew during BIOMASS, although most of the research emphasis was still directed at studying adult krill. Detailed knowledge of the fate of larvae and hence recruitment remains poor (Brinton *et al.* 1986, Miller & Hampton 1989). Further, most of the information to date is based on studies in the Atlantic sector, as is the case for the krill adults and macrozooplankton data.

The Australian Antarctic Division has so far conducted eight major marine science cruises to study the marine ecosystem in the Prydz Bay region of the Indian Ocean Sector (Table 1.1). The first five cruises were part of Australia's contribution to the BIOMASS program. Much of the research on the later cruises was conducted in support of CCAMLR (Convention for the Conservation of Antarctic Marine Living Resources). The main focus of the research has been consistently directed at understanding the ecology and general biology of krill, mainly adults, e.g. distribution, abundance and population structure (Higginbottom *et al.* 1988; Hosie *et al.* 1988; Higginbottom & Hosie 1989), metabolic activity (Ikeda & Bruce 1986), feeding (Ikeda & Dixon 1984; Marchant & Nash 1986), reproduction (Harrington & Ikeda 1986), behaviour (O'Brien 1987), and growth, moulting and development (see review by Ikeda 1985).

The purpose of this thesis is to describe both the zooplankton community and euphausiid larval ecology of the Prydz Bay region, particularly in defining the origin, dispersal and fate of larvae of *Euphausia*

Fig. 1.1 Map of the two main study areas during the First International BIOMASS Experiment (FIBEX) - one in the Scotia Sea and the other in the Indian Ocean sector of the Southern Ocean (reproduced from O'Sullivan 1981).

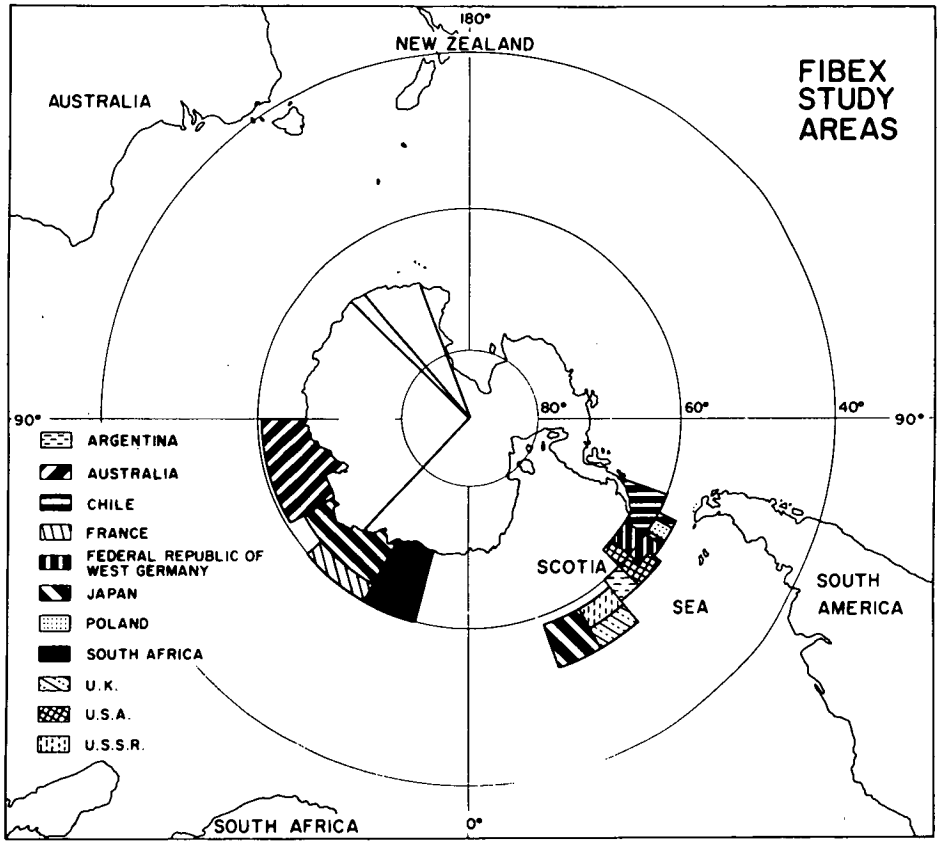


Table 1.1 Summary of Australian Antarctic Division marine science sampling surveys in the Prydz Bay region. FIBEX = First Internatioanl Biomass Experiment, ADBEX = Antarctic Division BIOMASS Experiment, SIBEX 1 & 2 = Second International BIOMASS Experiment (Phases 1 & 2), AAMBER = Australian Antarctic Marine Biological Ecosystem Research, FISHOG = Fish and Oceanography survey, NA = not available.

Cruise Name	Period in Prydz Bay Study Area	Principal Objectives	Primary Source of Sampling Details
FIBEX	20 January - 10 March 1981	Acoustic & net survey of krill	Williams *et al.* 1983
GEOSCIENCE	20 January - 3 March 1982	Seismic survey	Woehler *et al.* 1987b
ADBEX 1	19 November - 19 December 1982	Krill biology, oceanography	Williams *et al.* 1986
ADBEX 2 (SIBEX 1)	14 January - 6 February 1984	Krill biology	Ikeda *et al.* 1984
SIBEX 2	4-26 January 1985	Krill & zooplankton distribution, phytoplankton	Ikeda *et al.* 1986
ADBEX 3	21 September -13 December 1985	Crabeater Seal survey, krill biology	Hosie *et al.* 1987
AAMBER 1	15 February - 23 March 1987	Krill, fish and zooplankton distribution and biology	Hosie *et al.* 1991
AAMBER 2	15 January - 11 March 1991	Krill & zooplankton communities and fish distribution	Appendix I
FISHOG	18 February - 6 March 1992	Physical oceanography and fish (Heard Island)	NA

superba. Zooplankton and euphausiid larvae were collected on the cruises between 1984 and 1991, covering the periods of end of September to end of November and early January to end of March (Table 1.1) The data sets describing distribution, abundance and composition were analysed using a combination of multivariate and univariate techniques to define the zooplankton community structure and distribution patterns of larvae and zooplankton in relation to environmental parameters.

The cruises in 1981 and 1982 were carried out prior to the tenure of the present study. Zooplankton data were also collected on those cruises by Mr R. Williams (Australian Antarctic Division), during the course of determining the distribution of adult krill via net sampling. Zooplankton were identified, counted and collated for each sampling site (Williams *et al.* 1983, 1986), but no further analyses were performed. Mr Williams very kindly permitted complete access to the data sets for further detailed multivariate analyses. Although different sampling strategies were employed, to those preferred in this study, useful comparative and complementary results were obtained, covering mid-November to early March, and therefore have been included in this study.

Much of the work described in this thesis has been published in Hosie (1991a, & in press), or in part in Hosie & Kirkwood (1986), Hosie *et al.* (1988) and Hosie & Stolp (1989). Although the latter three papers were co-authored, all the work described in this dissertation is my own. In many aspects the data has been re-analysed since original publication, using the techniques developed during the course of the study. Co-authorship was given in recognition of the considerable assistance given in the collection and processing of catch samples. Much of the raw data has been included in the ANARE Research Series of data reports (Ikeda, Hosie & Kirkwood 1984; Ikeda, Hosie & Stolp 1986; Hosie *et al.* 1987, 1991).

CHAPTER 2

HYDROGRAPHY OF THE PRYDZ BAY REGION

Introduction

Hydrographic studies have been an integral part of all of the Australian Antarctic marine science cruises, primarily in support of the various studies into the Prydz Bay pelagic ecosystem. At nearly all biological sampling sites, plus a few specific oceanographic sites, continuous vertical profiles of conductivity/salinity and temperature were obtained using a Neil Brown Mark 3 CTD (conductivity-temperature-depth) probe (Kerry *et al.* 1987a, 1987b; Kerry & Woehler 1987; Woehler *et al.* 1987a 1987b; Woehler & Williams 1988). In addition to measuring the immediate physical parameters of individual sites, the data were used to define geopotential anomaly contours and hence geostrophic water flow in the region (Smith *et al.* 1984; Middleton & Humphries 1989). In support of the water circulation studies, 12 moorings with arrays of two, three or four Aanderaa current meters were deployed for approximately 12 months at a time at various localities on the continental shelf of Prydz Bay in 1985, 1986 and 1987 (Hodgkinson *et al.* 1988, 1991a, 1991b). Other independent studies have produced results useful in understanding the hydrography of the region and hence the possible effects on zooplankton distributions. These studies include the annual formation and retreat of pack-ice (Jacka 1983; Streten & Pike 1984), the movement of pack-ice (Allison 1989) and the movement of icebergs (Tchernia & Jeannin 1983). The purpose of this chapter is to review salient hydrographic data pertinent to the interpretation of zooplankton and euphausiid larvae distribution patterns. Consequently, salinity has been dealt with in less detail than temperature. It will be shown in subsequent chapters that salinity has little if any effect on zooplankton distributions.

Temperature and salinity

Longitudinal profiles of temperature isotherms, based on transects of CTD casts, are shown in Figs 2.1, 2.2 and 2.3. Examples of individual CTD salinity-temperature profiles are shown in Fig. 2.4 for sites on the continental shelf, Fig. 2.5 for sites just north of the shelf edge (circa 66°S) and Fig. 2.6 for sites further north (circa 63°S). The locations of the transects and individual sites are shown in Fig. 2.7. A noticeable degree of consistency is evident in the longitudinal profiles in the centre of the region (Figs 2.1 & 2.2), and is more evident in the site profiles within each of the three area examples (Figs 2.4, 2.5, 2.6).

Very cold water -1° to <-1.5°C was found throughout the shelf region. A distinct thermocline occurs at approximately 50 m, a result of summer warming of the surface layer - summer surface water (Fig. 2.4). Melting ice produces a very strong halocline coincident with the thermoclines (Figs 2.4b,c). Below the thermo/haloclines temperature and salinity traces were uniform. The coldest temperatures <-1.8°C were consistently observed close to the Amery Ice Shelf (Fig. 2.4) and also the West Ice Shelf (Fig. 2.3b).

Both the longitudinal profiles and the individual casts show the existence of three distinct water masses north of the continental shelf - the summer surface water, the Antarctic winter water (WW) and the circumpolar deep water (CDW). As with the shelf region, the summer surface water occupies the upper 40 to 50 m producing a pronounced seasonal thermocline. Between the summer surface water and the CDW is the winter water. The WW is characterised by temperature <-1.5°C and salinity in the range of 34.2 to 34.56 S‰ (Smith *et al.* 1984). The CDW is much warmer (0 to 2°C) producing a second thermocline. The WW layer is quite broad (>100 m) near the shelf at circa 66°S (Fig. 2.5), but narrows to about 50 m thick further north (Fig. 2.6). North of 63°S the WW layer again

Fig. 2.1 Longitudinal temperature profiles for transects **a)** 75°E for November-December 1982, **b)** 73°E for January 1984, **c)** 68°E for January 1985, and **d)** 78°E for January 1985 (from Middleton & Humphries 1989). Location of transects shown in Fig. 2.7.

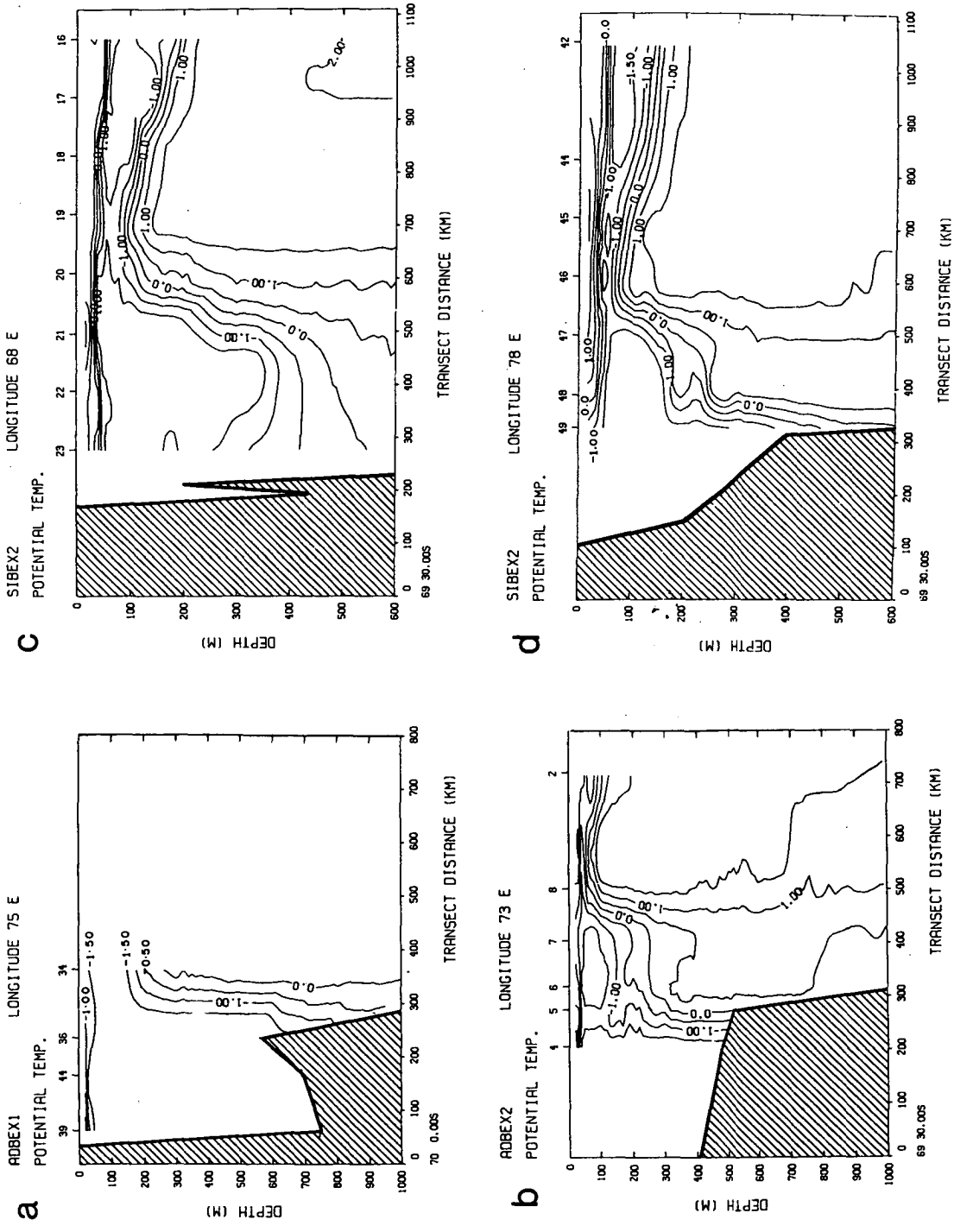


Fig. 2.2 Longitudinal temperature profiles for transects **a)** 72°E and **b)** 75°E for January-February 1991. Location of transects shown in Fig. 2.7.

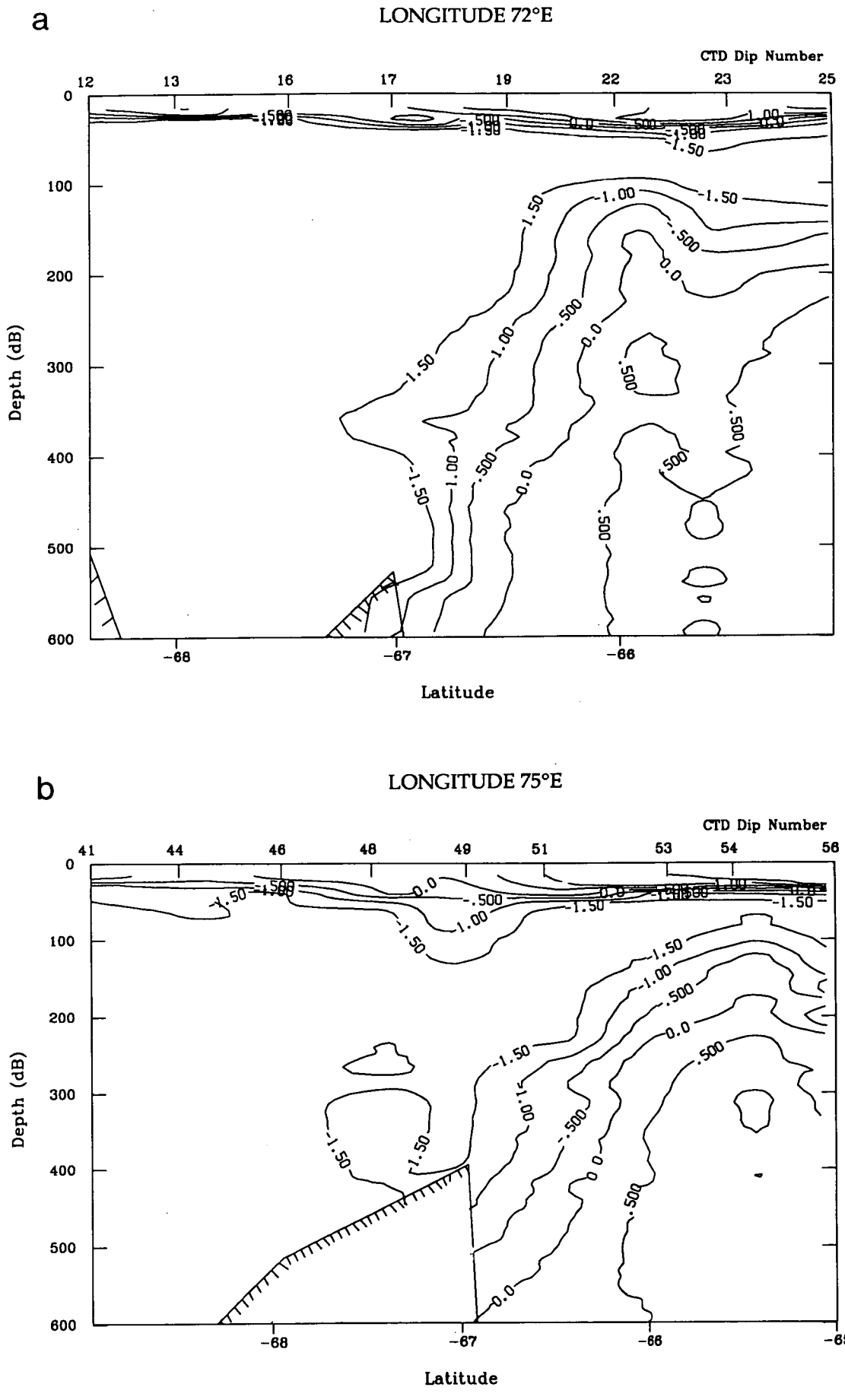
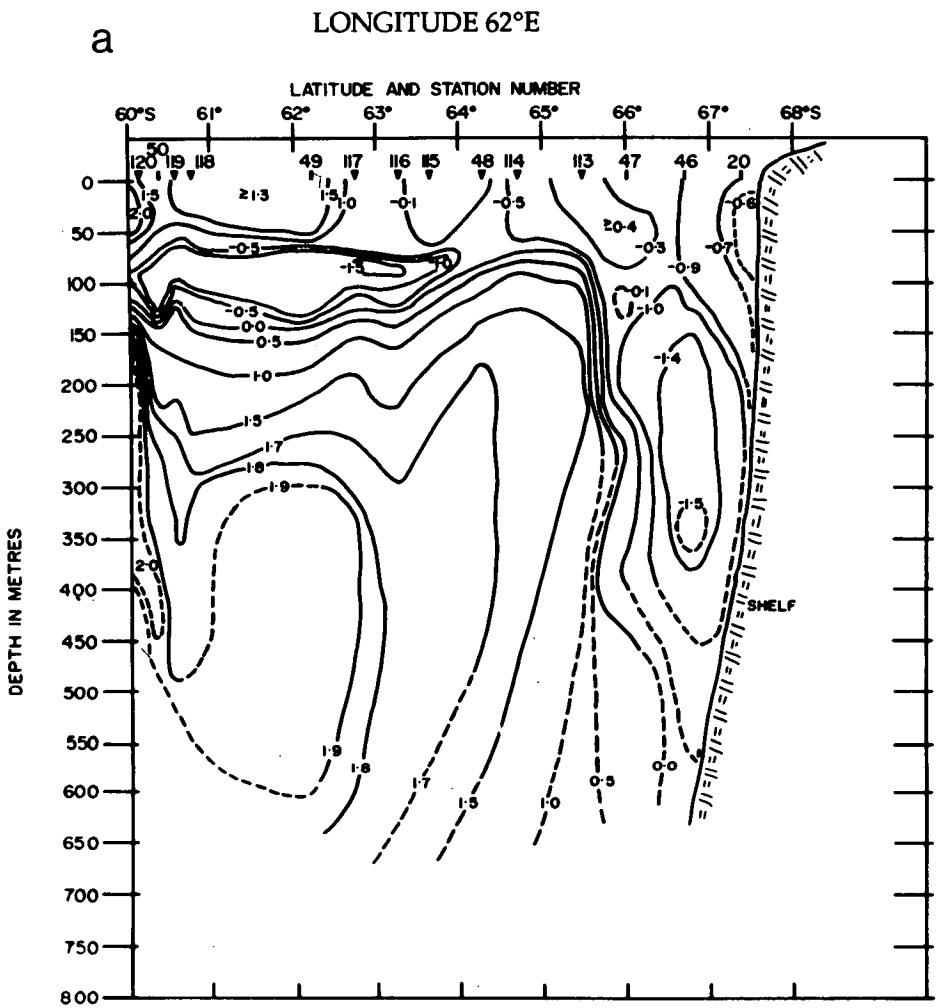


Fig. 2.3 Longitudinal temperature profiles for transects **a)** 62°E and **b)** 88°E for January-March 1981 (from Smith *et al.* 1984). Location of transects shown in Fig. 2.7. Note: profiles are shown in reverse direction to those in Figs 2.1 & 2.2.

2.3

a


LONGITUDE 62°E
LATITUDE AND STATION NUMBER
60°S 61° 62° 63° 64° 65° 66° 67° 68°S
120 119 118 49 117 116 115 48 114 113 47 46 20
DEPTH IN METRES
0 50 100 150 200 250 300 350 400 450 500 550 600 650 700 750 800
SHELF

b

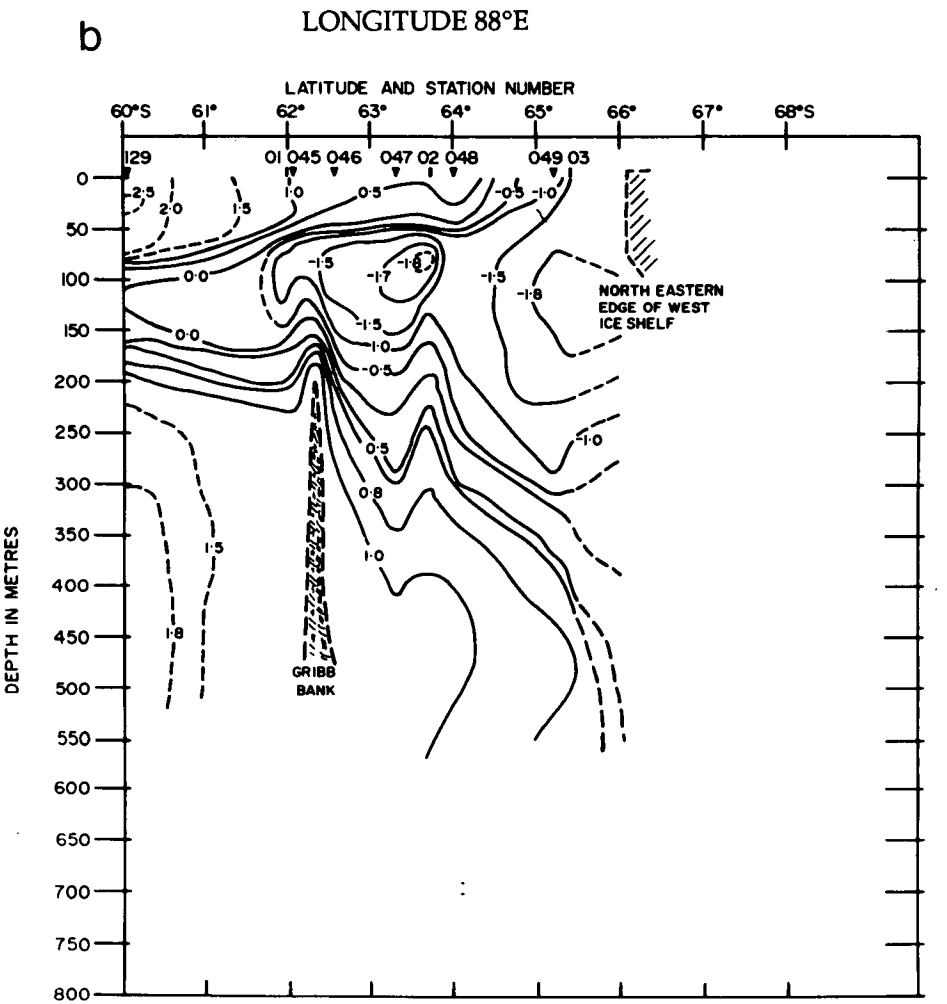

LONGITUDE 88°E
LATITUDE AND STATION NUMBER
60°S 61° 62° 63° 64° 65° 66° 67° 68°S
129 01 045 046 047 02 048 049 03
DEPTH IN METRES
0 50 100 150 200 250 300 350 400 450 500 550 600 650 700 750 800
NORTH EASTERN EDGE OF WEST ICE SHELF
GRIBB BANK

Fig. 2.4 CTD salinity-temperature vertical profiles for selected sites on the continental shelf for **a)** January 1981 (Kerry *et al.* 1987b), **b)** January 1985 (Kerry *et al.* 1987a), and **c)** January 1991 (next page). Location of sites shown in Fig. 2.7.

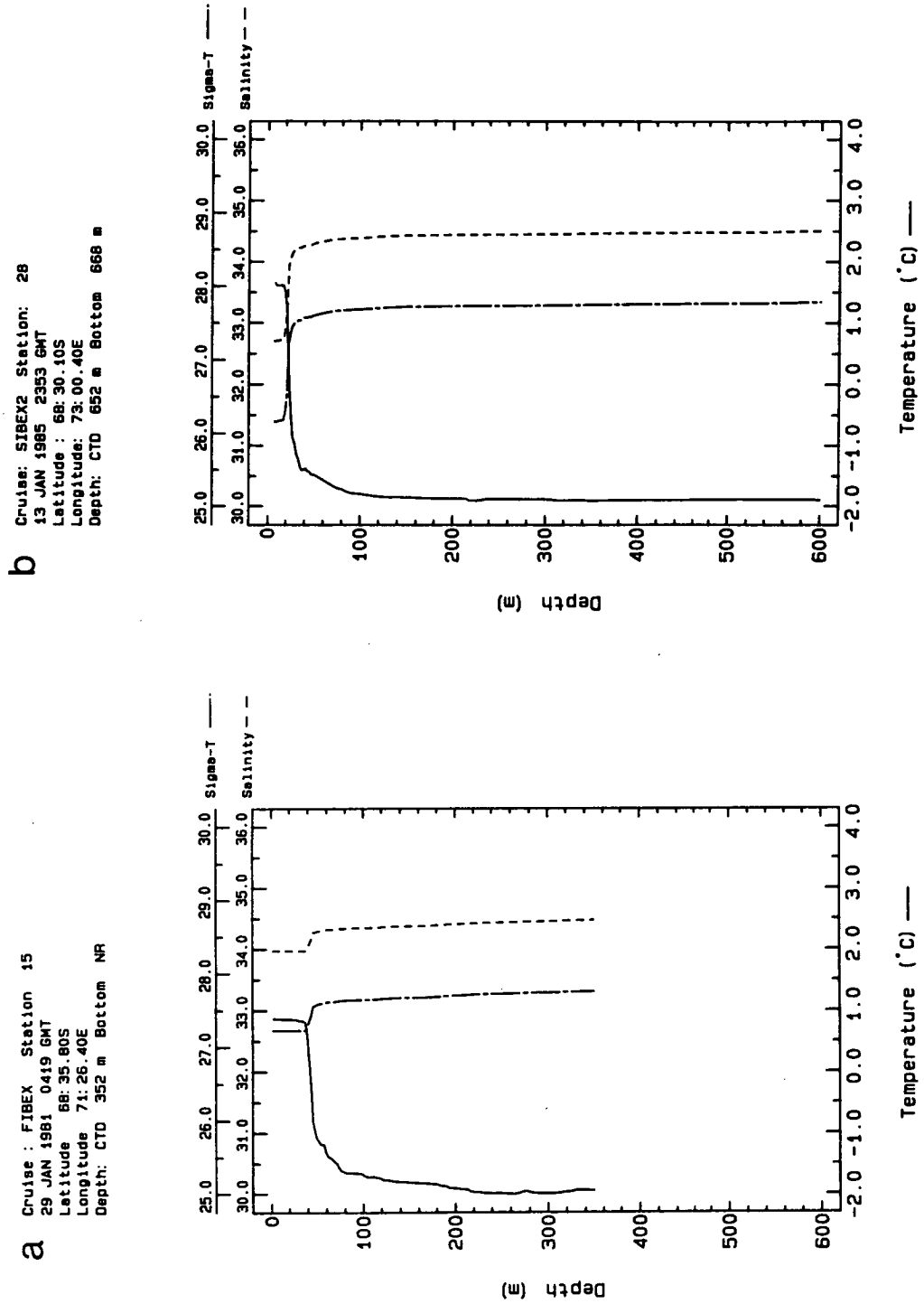


Fig. 2.4 Continued c) January 1991.

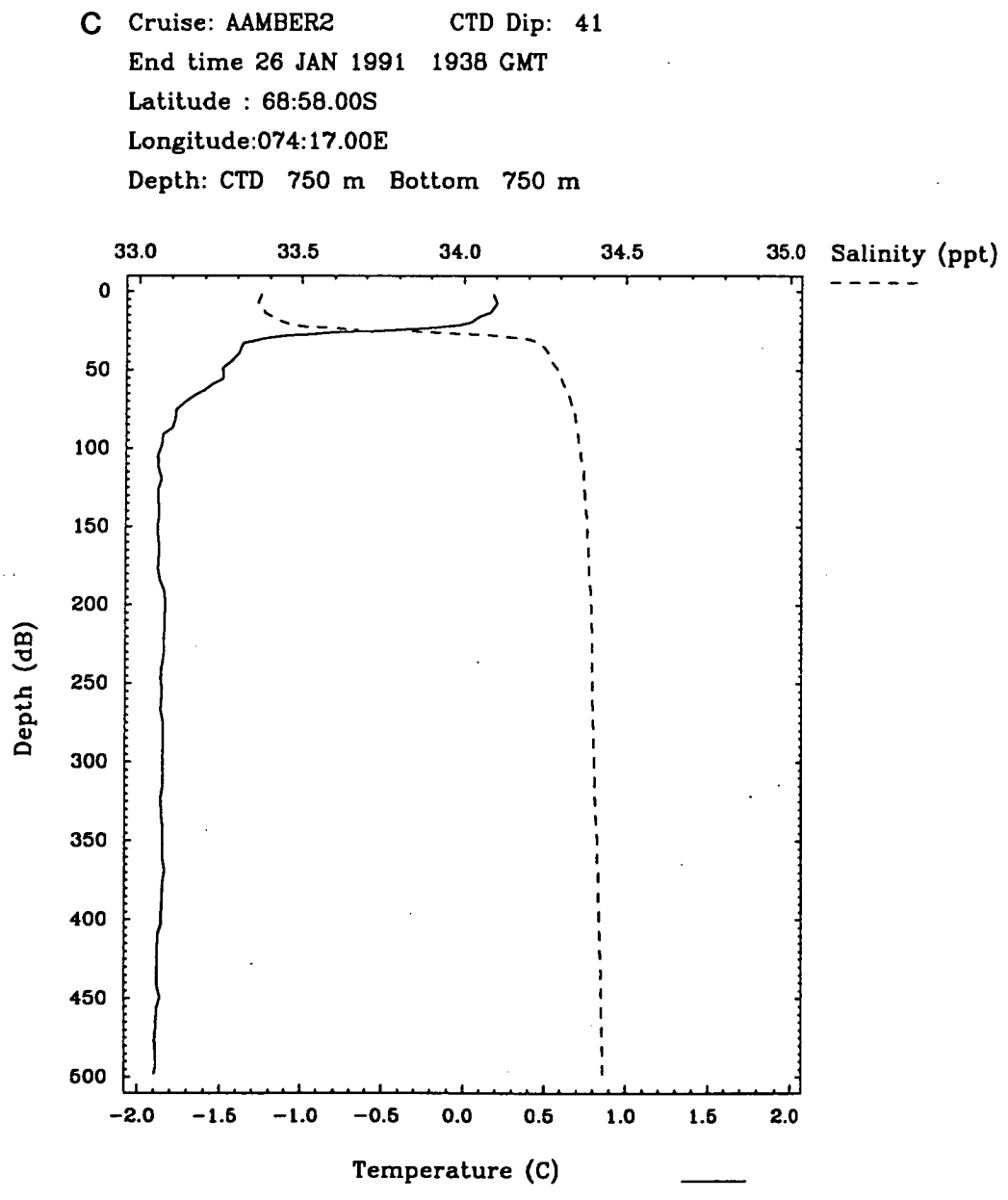


Fig. 2.5 CTD salinity-temperature vertical profiles for selected sites just north of the continental shelf edge (circa 66°S) for **a)** February 1981 (Kerry *et al.* 1987b), **b)** February 1982 (Woehler *et al.* 1987b), and next page **c)** December 1982 (Kerry & Woehler 1987) and **d)** January 1985 (Kerry *et al.* 1987a). Location of sites shown in Fig. 2.7.

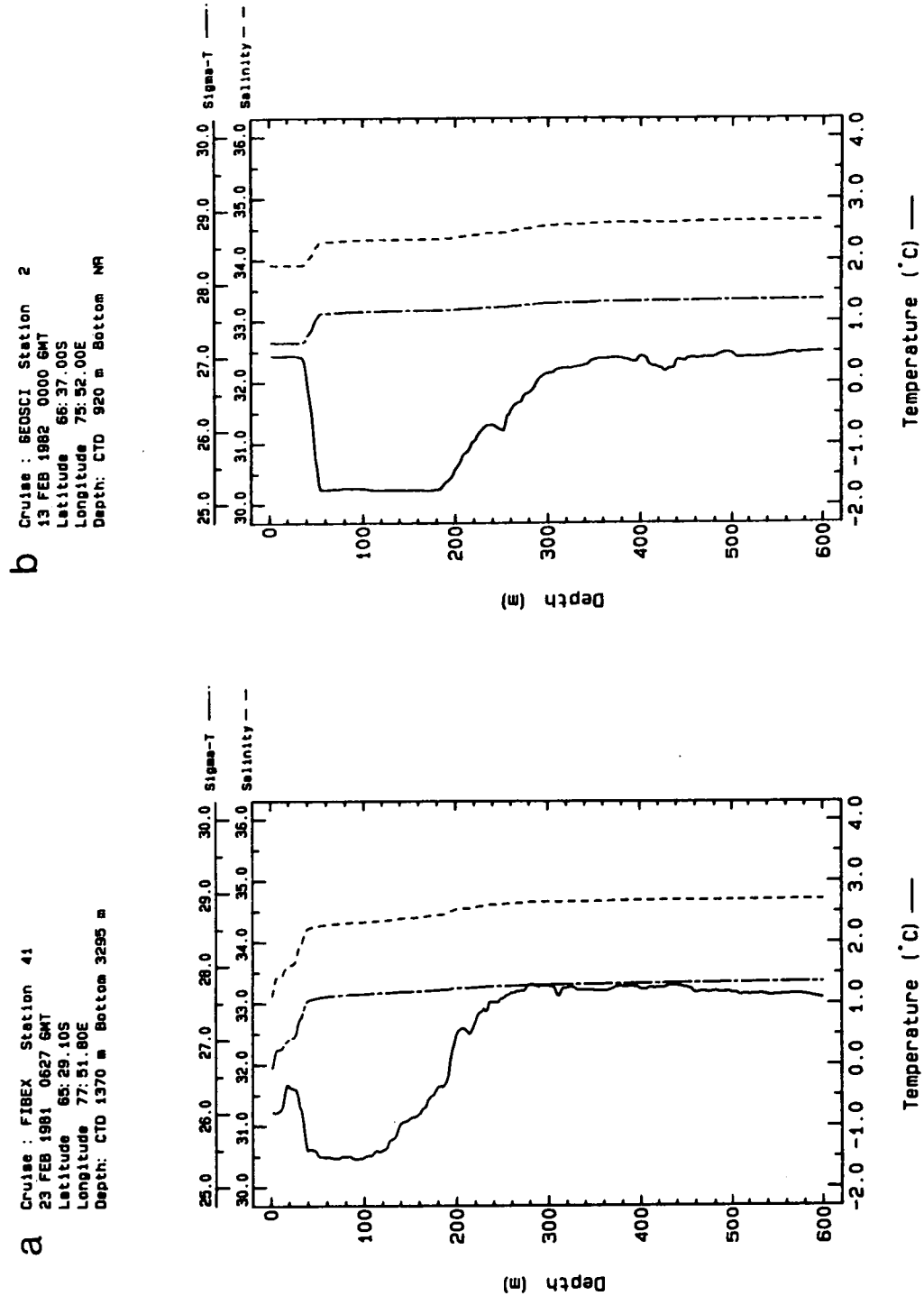


Fig. 2.5 Continued **c)** December 1982 and **d)** January 1985.

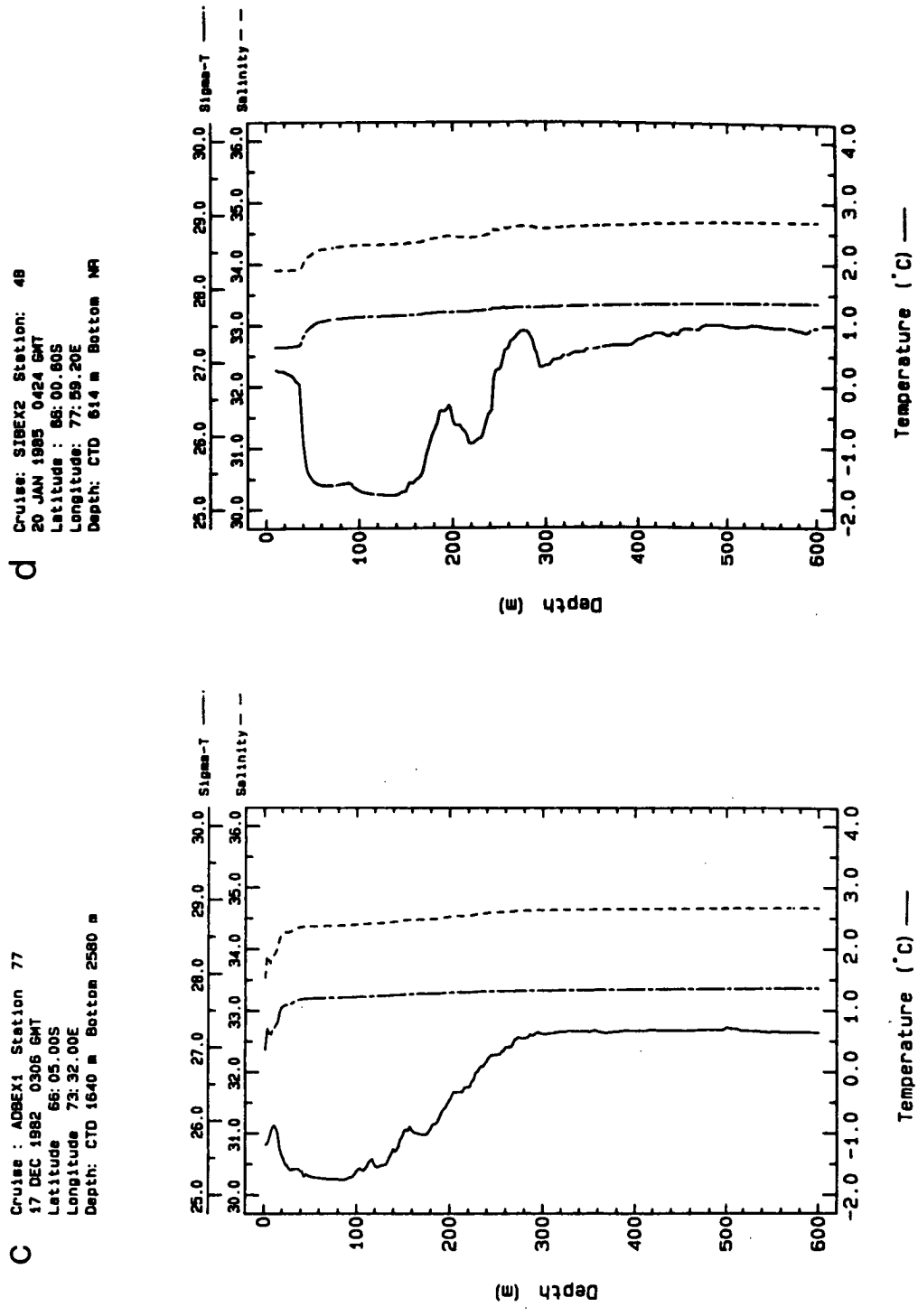


Fig. 2.6 CTD salinity-temperature vertical profiles for selected sites in the central north of the Prydz Bay region (circa 63°S) for **a)** & **b)** February 1981 (Kerry *et al.* 1987b), and next page **c)** March 1982 (Woehler *et al.* 1987b) and **d)** January 1985 (Kerry *et al.* 1987a). Location of sites shown in Fig. 2.7.

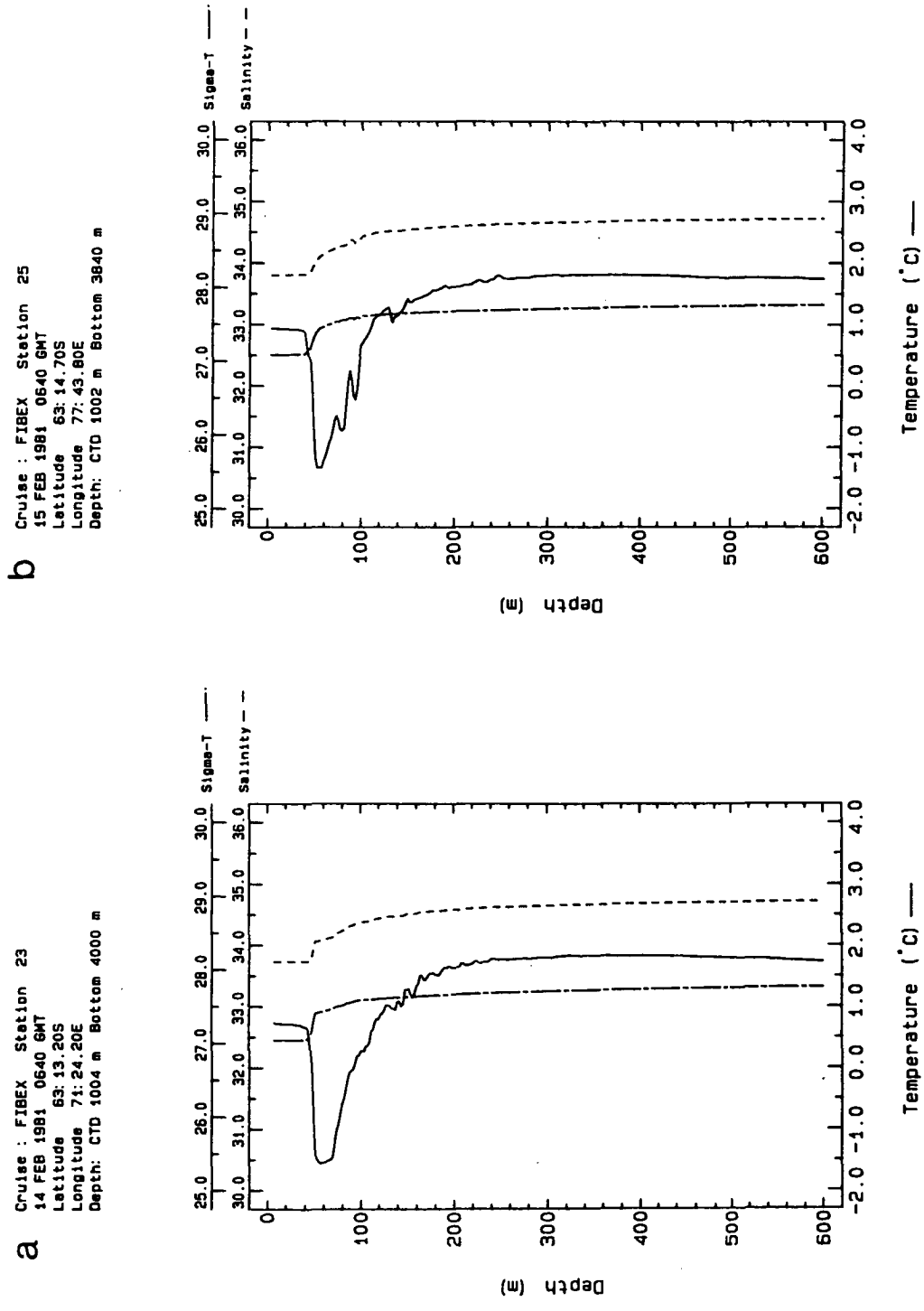


Fig. 2.6 Continued **c)** March 1982 and **d)** January 1985.

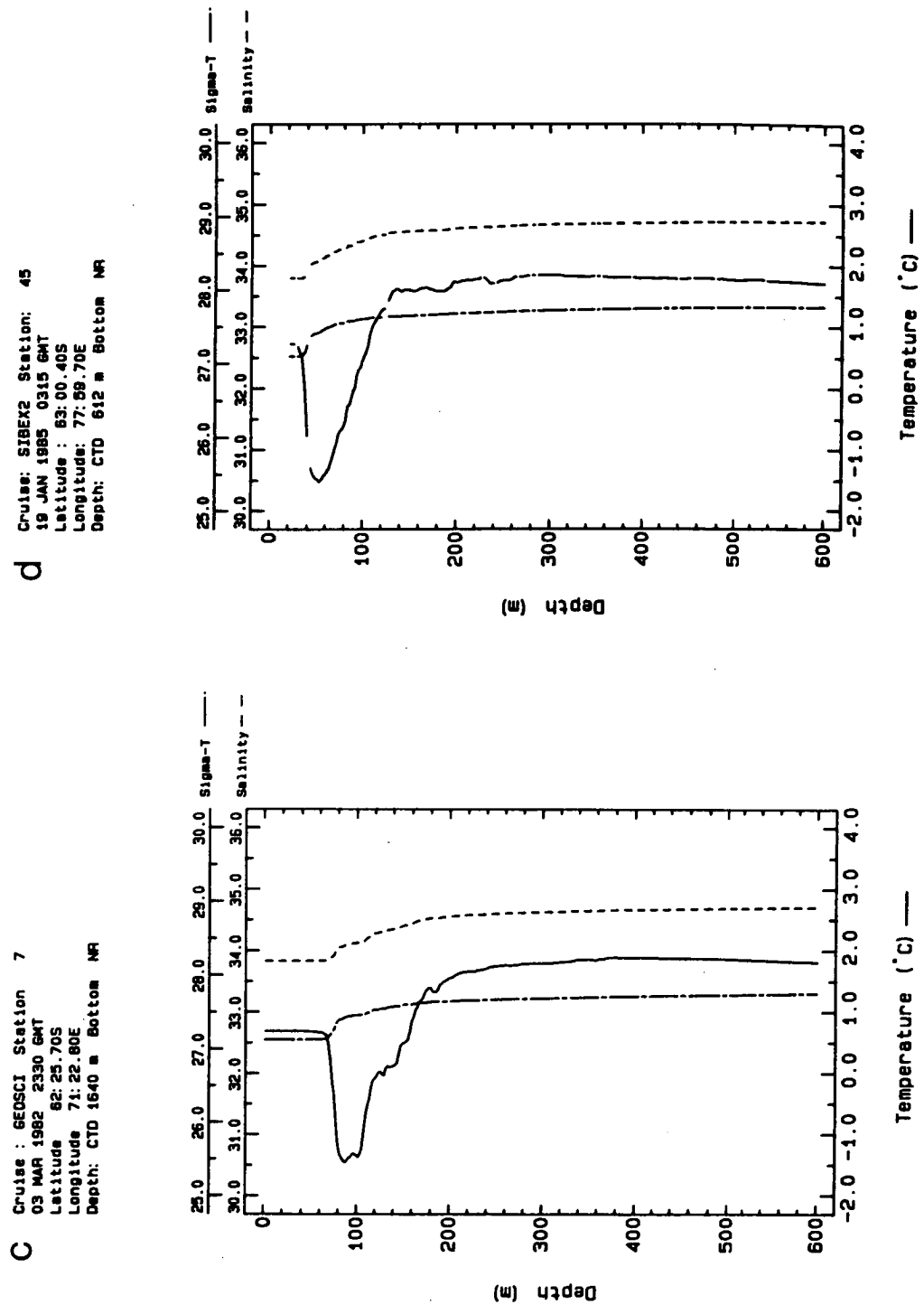


Fig. 2.7 Positions of transects and CTD cast profiles shown in Figs 2.1 to 2.6. The specific figure number is displayed against each transect and group of casts.

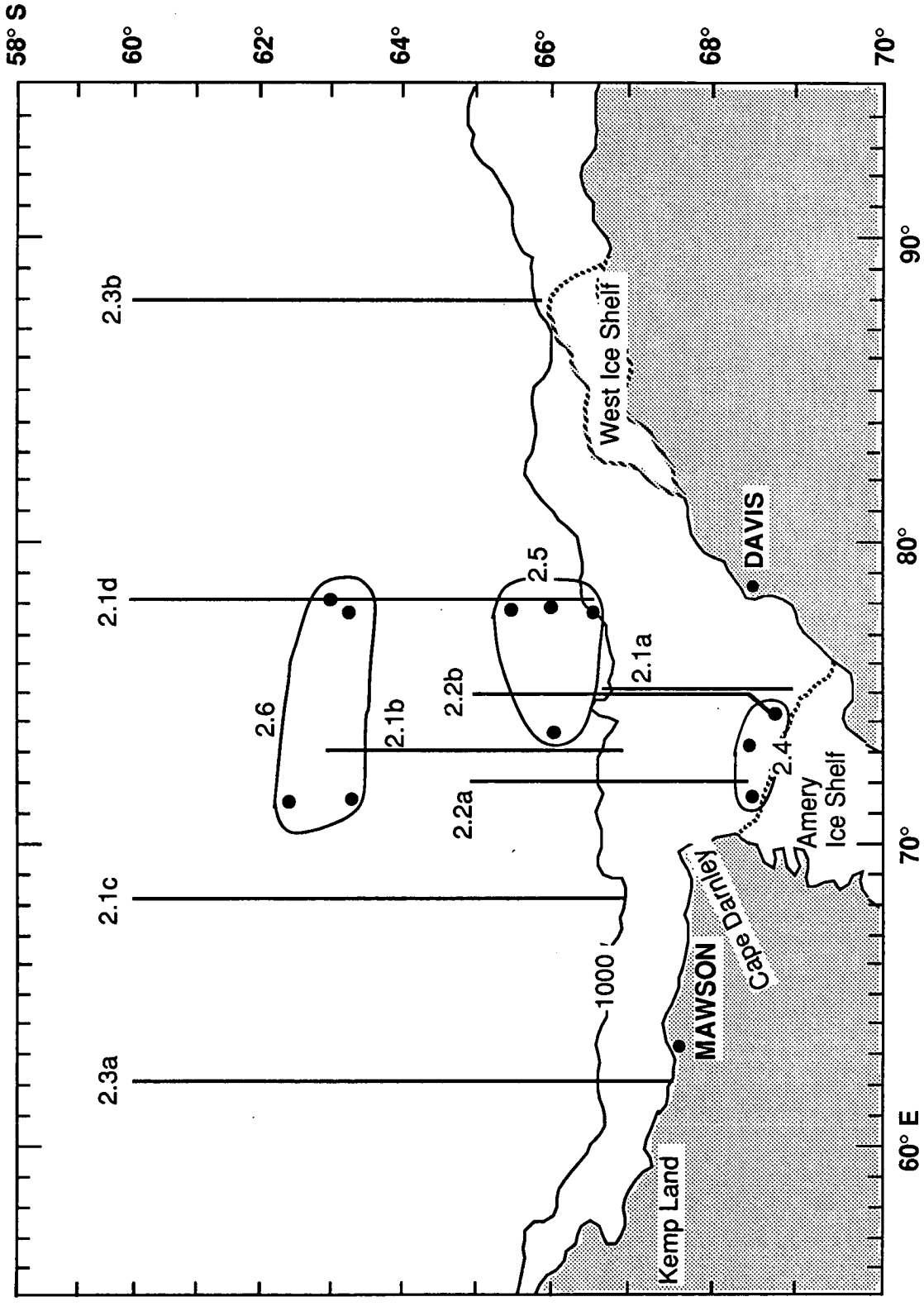


Fig. 2.8 Integrated 0-200 m isotherms for the period January to March for three surveys in 1985, 1981, 1987. Mean temperature was determined by integrating 2 m recorded intervals.

2.8

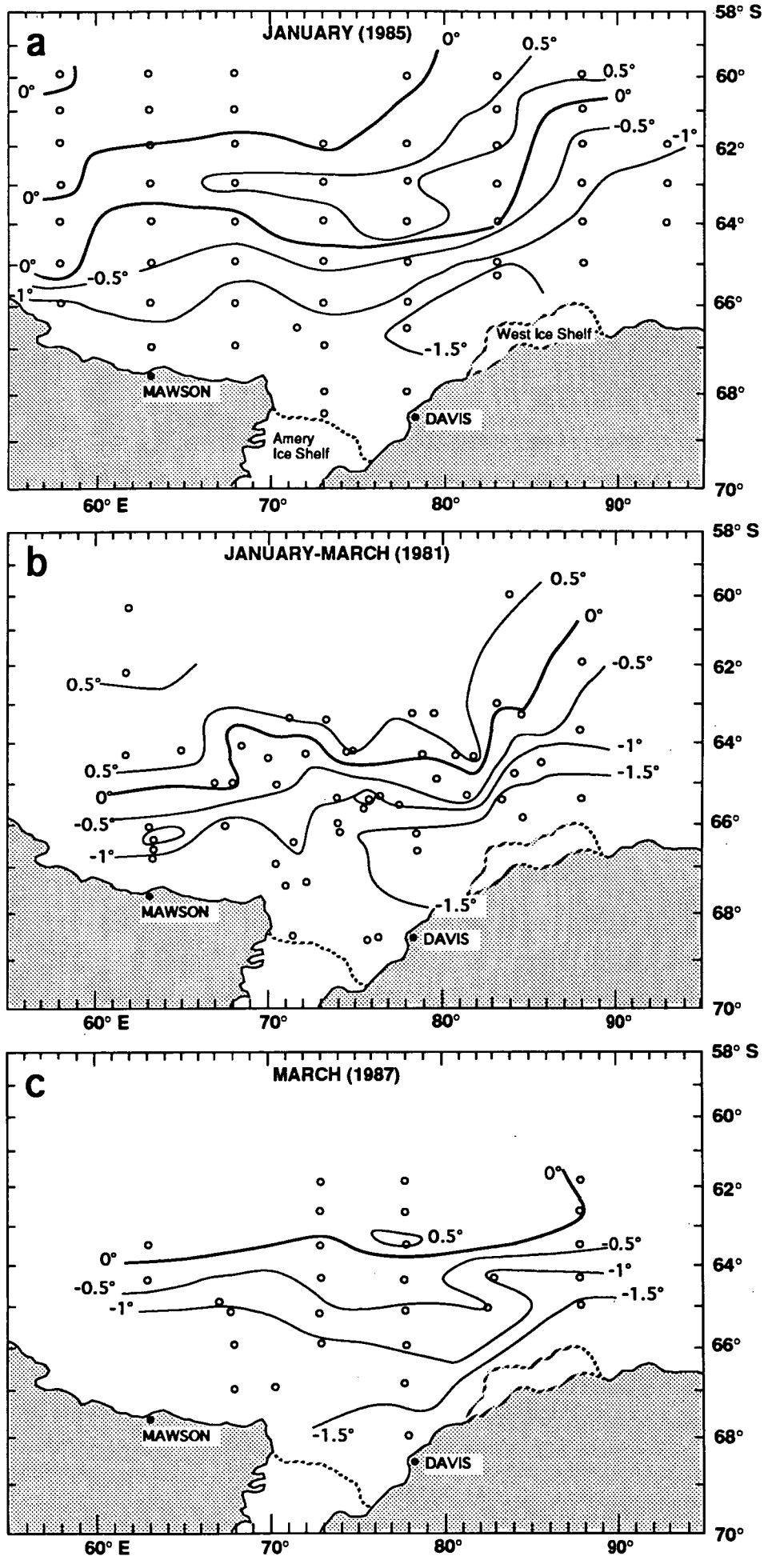
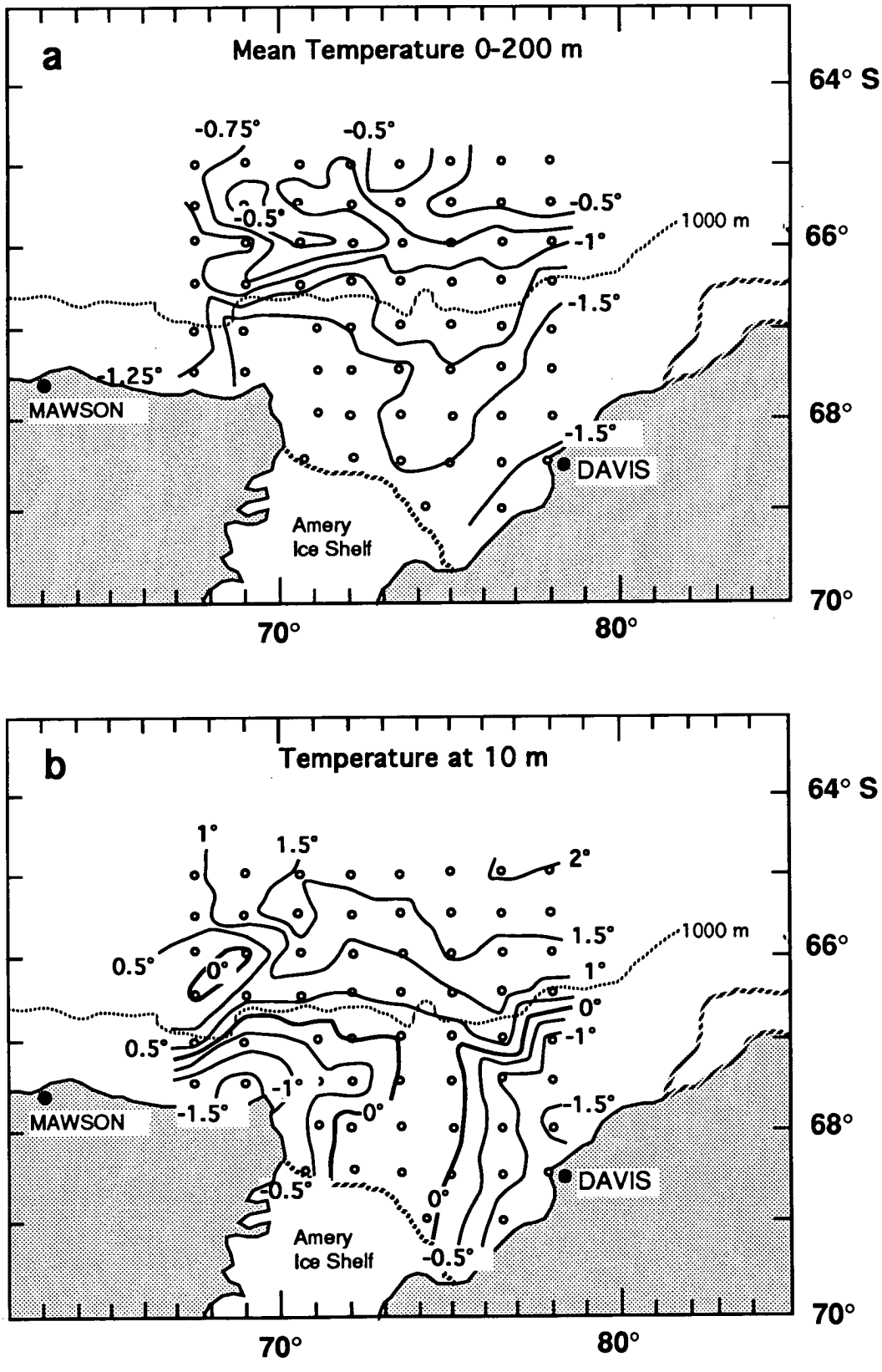

a
JANUARY (1985)
0°
0.5°
0.5°
0°
-0.5°
-1°
-1.5°
West Ice Shelf
MAWSON
DAVIS
Amery
Ice Shelf
b
JANUARY-MARCH (1981)
0.5°
0°
-0.5°
-1°
-1.5°
MAWSON
DAVIS
c
MARCH (1987)
0°
0.5°
-0.5°
-1°
-1.5°
MAWSON
DAVIS
58° S
60°
62°
64°
66°
68°
70°
60° E
70°
80°
90°

Fig. 2.9 Geographic pattern of isotherms for January-February 1991. **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.



thickens and deepens (Figs 2.1c,d; Smith *et al.* 1984). Immediately north of the shelf edge, and below about 100 m ,there is a distinct vertical stratification of isotherms between the waters of the shelf and the CDW (Figs 2.1, 2.2, 2.3).

Figure 2.8 shows the horizontal geographic pattern of integrated 0-200 m isotherms. At each sampling site the mean temperature was determined by integrating 2 m recorded intervals, consistent with the integration of zooplankton by the main sampling method of 0-200 m oblique hauls. A mainly latitudinal zonation is shown in Fig. 2.8, with water progressively warmer towards the north. There is, however, a distinct northerly displacement of isotherms east of 83°E where cool sub-zero water extends as far north as 61°S. The pattern of isotherms was relatively consistent amongst the years shown in Fig. 2.8, in particular the position of the 0°C isotherm in Figs 2.8a & b. Fig. 2.8a also shows an apparent intrusion of +0.5°C water extending from the north-east well into the centre of the region. Fig. 2.9a shows the integrated 0-200 m isotherms for the January-February 1991 for a higher sampling resolution for the continental shelf and shelf edge area. Latitudinal zonation is still evident and the position of the -1°C isotherm approximates the position of the same isotherm in Fig. 2.8. Isotherms at the 10 m layer for 1991 are shown in Fig. 2.9b. The notable feature is that coldest surface waters were found in the east of Prydz Bay, i.e. north and south of Davis, and in the west around Cape Darnley in association with pack-ice which persisted in those areas throughout that summer.

Water circulation

The same type of water circulation patterns have been described for the Prydz Bay region over a number of years by Grigor'yev (1968), Khimitsa (1976), Smith *et al.* (1984) and Middleton & Humphries (1989). The

horizontal circulation as determined for the region during January 1985 is shown in Fig 2.10 (R.A. Nunes Vaz & G.W. Lennon, personal communication 1990). The Prydz Bay gyre is located in the vicinity of 63° to 80°E and south of 63°S. The geostrophic water flow of the gyre is shown to move south onto the continental shelf between 72° and 76°E, before moving cyclonically past the Amery Ice Shelf then exiting west past Cape Darnley and Mawson Station. The westward transport of water along the shelf has been confirmed by satellite tracking of icebergs (Tchernia & Jeannin 1983) and sea ice (ICEX) buoys (Allison 1989), as well as by current meter moorings (Hodgkinson *et al.* 1988, 1991a,b). The easterly moving waters of the Antarctic Circumpolar Current (ACC) are clearly evident north of 63°S (Fig. 2.11).

The current meter moorings west of Davis, e.g. 85/3 recorded a generally southerly current with mean speeds in February 1985 of 4.3 to 6.3 cm s^{-1} between 150 to 640 m depth (Fig. 2.11). Another mooring (85/1) deployed on the edge of the continental shelf north-east of Cape Darnley, recorded a generally south-west to westerly current with mean speeds in February 1985 of 16.8 to 17.3 cm s^{-1} between 117 to 472 m depth. Later in 1985 the meters at this site recorded a distinct southerly component, especially the meter at 117 m, commensurate with the southward geostrophic flow. Mooring 85/4 was also deployed on the shelf edge near Mawson (Fig. 2.11). This site was characterised by a consistent very strong north-westerly water flow with mean speeds in March 1985 for the four meters of 39.4 to 75.1 cm s^{-1} (range 1.5 to 174.2 cm s^{-1}) between 178 and 620 m depth. In January 1986 the same mooring recorded mean speeds of 42.4 to 130.2 cm s^{-1} with the same north-westerly direction. The much higher speeds off Mawson were attributed to the East Wind Drift (EWD) converging onto the continental shelf somewhere between the 85/1 and 85/4 mooring sites and reinforcing the water flow along the shelf (Hodgkinson *et al.* 1988).

Fig. 2.10 The geostrophic water flow in the Prydz Bay region, redrawn from the geopotential anomaly contours of R.A. Nunes Vaz and G.W. Lennon (personal communication 1990).

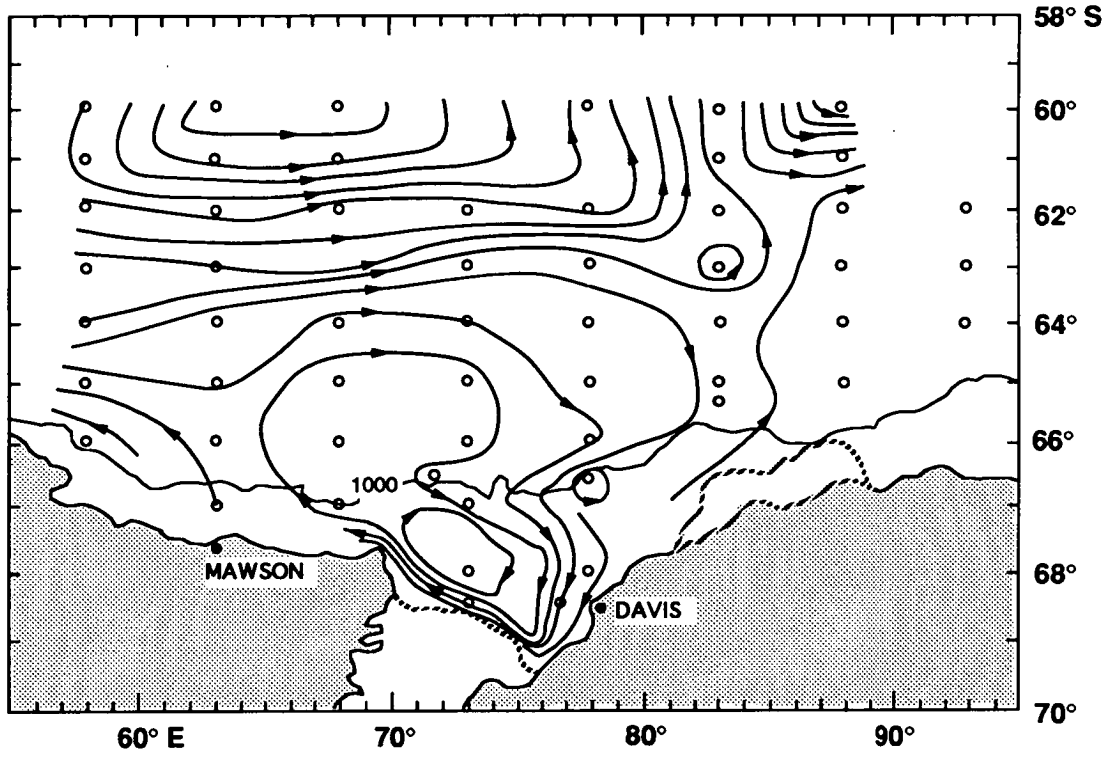


Fig. 2.11 Location of succesfully deployed and recovered current meter moorings. Arrows indicate mean direction of current for February-March of the year of deployment. Thickness and length of arrow is indicative of speed - see text for actual speed. Data from Hodgkinson *et al.* (1988, 1991a,b)

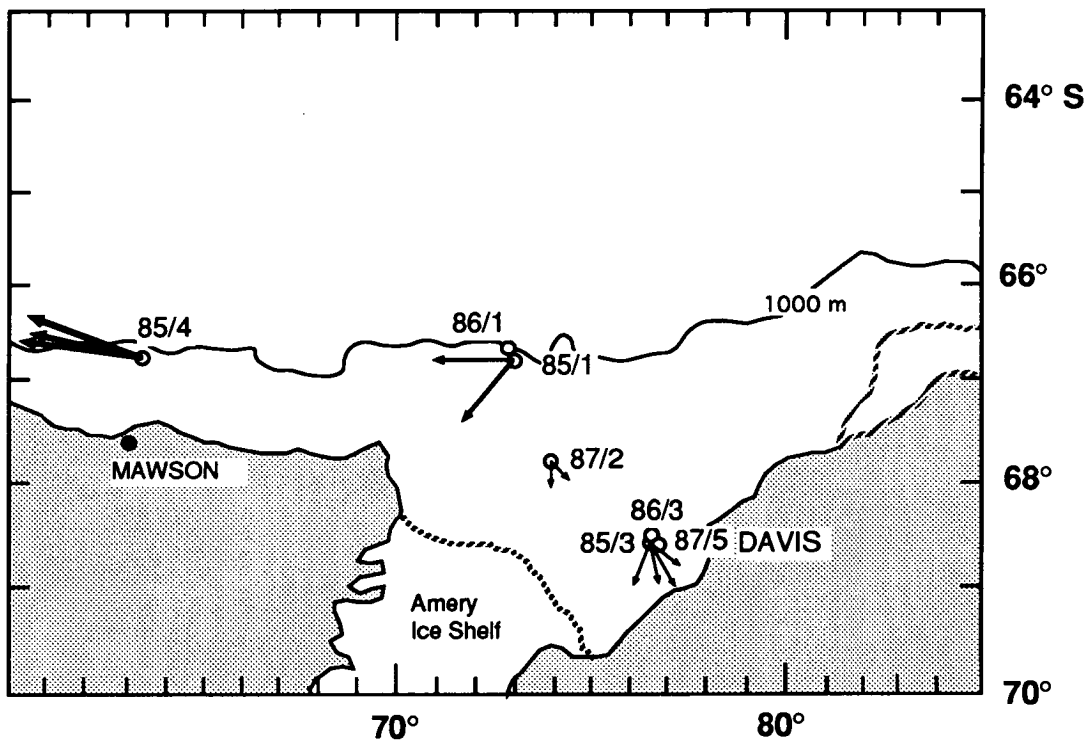


Fig. 2.12 Drift tracks of sea-ice (ICEX) buoys in the Prydz Bay region in February-March 1985. Numbers on the tracks are the last digit of the buoy (e.g. 1 = ICEX41). Stippled tracks indicate those periods when the buoys were within the sea-ice edge. The longitudinal positions of the buoys along the tracks are shown by the inset table. ★ = meteorological stations. Figure reproduced from Allison (1989).

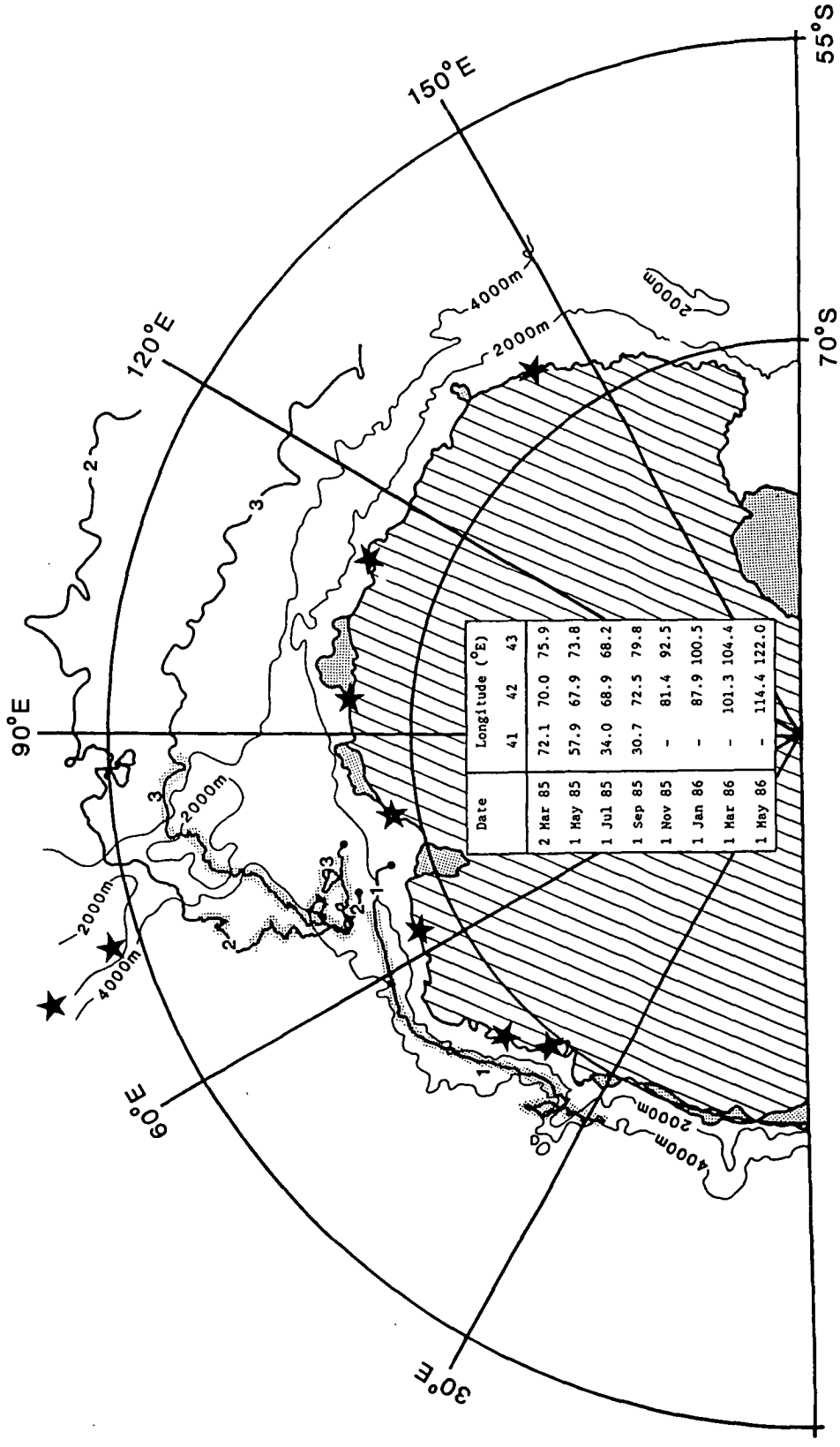


Fig. 2.13 Trajectories of icebergs entrained in the East Wind Drift, as tracked by satellite (redrawn from Tchernia & Jeannin 1983). Date notation is day/month/year. Iceberg numbers are those of Tchernia & Jeannin. ✪ = start position, ★ = end of tracking.

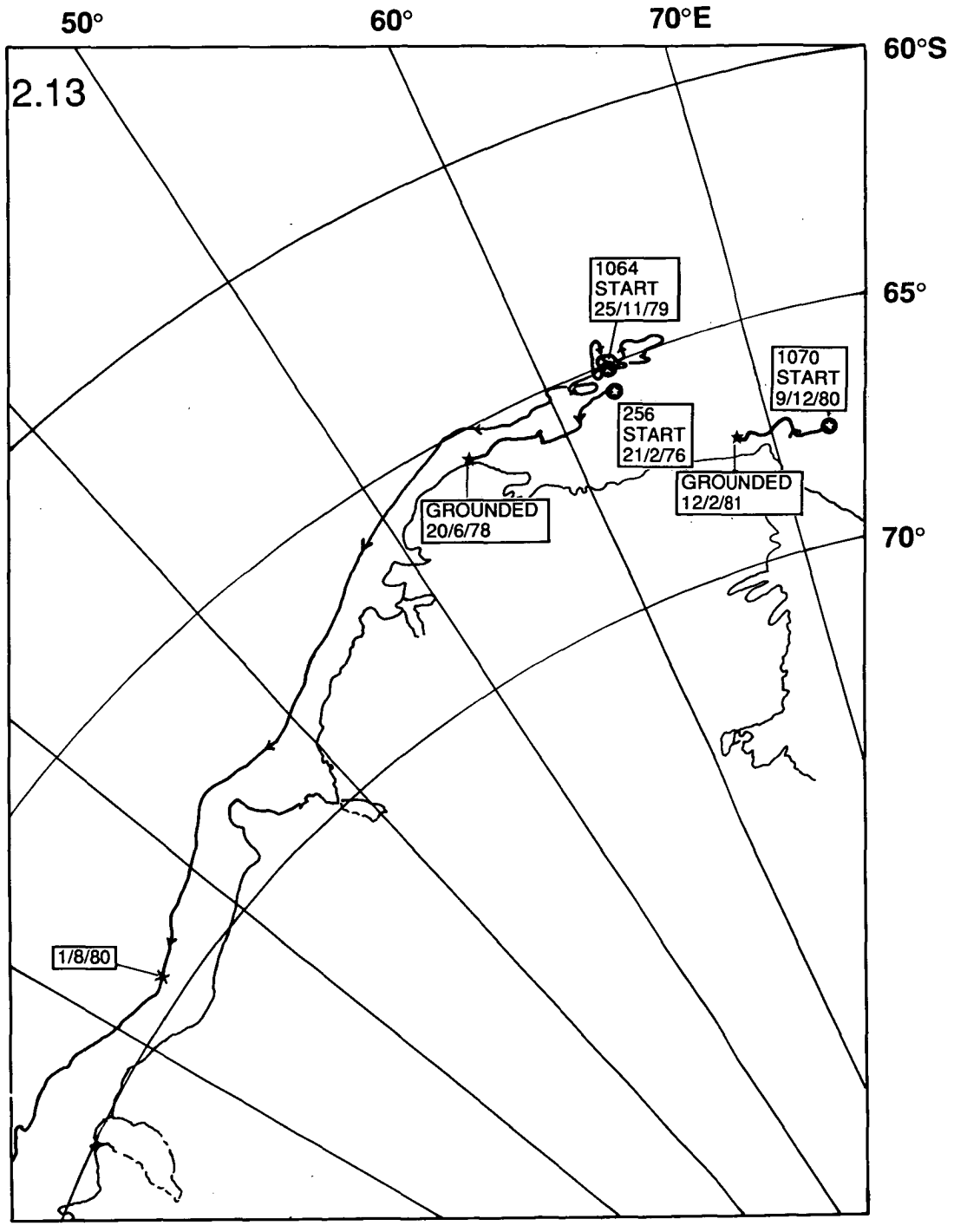
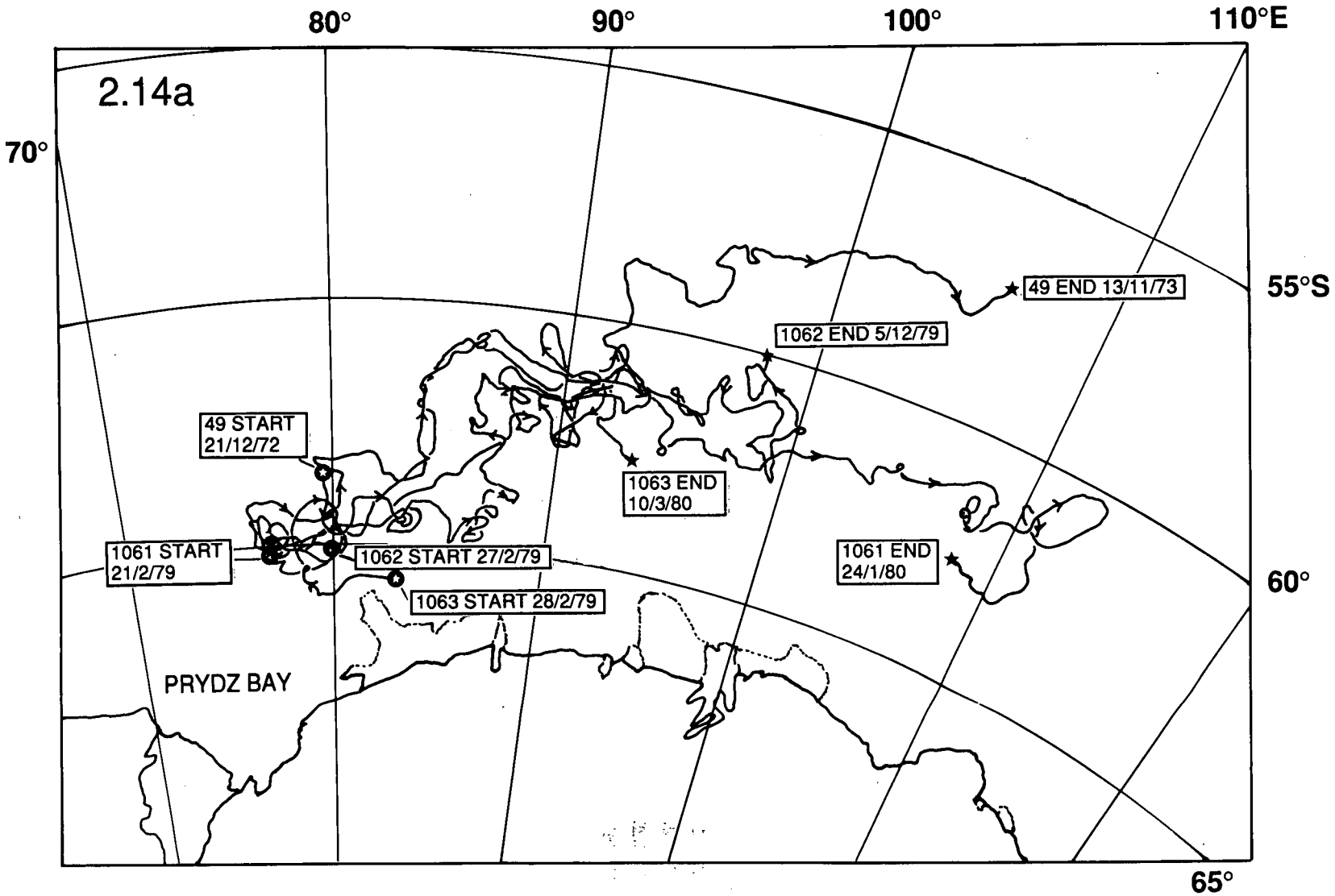
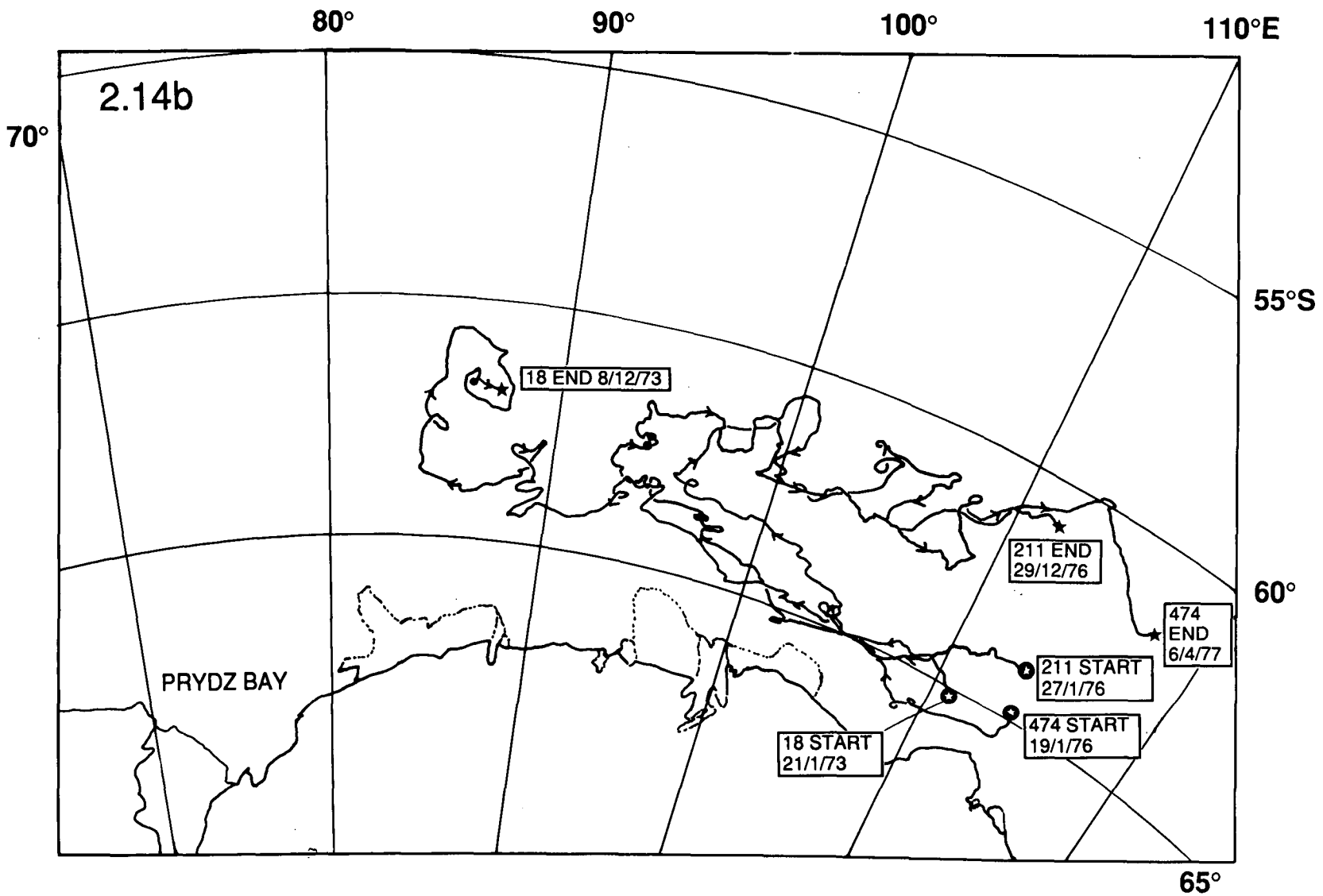

50°
60°
70°E
60°S
65°
70°
2.13
1064
START
25/11/79
1070
START
9/12/80
256
START
21/2/76
GROUNDED
12/2/81
GROUNDED
20/6/78
1/8/80

Fig. 2.14 Trajectories of icebergs in the eastern part of the Prydz Bay region, as tracked by satellite (redrawn from Tchernia & Jeannin 1983). **a)** ice bergs starting near the centre of the region and moving northeast then east, **b)** next page, icebergs entering the region from the east via the East Wind Drift, deflecting north then moving east similar to icebergs in **a)**. Date notation is day/month/year. Iceberg numbers are those of Tchernia & Jeannin. ✪ = start position, ★ = end of tracking.


2.14a
80°
90°
100°
110°E
70°
55°S
60°
65°
49 END 13/11/73
1062 END 5/12/79
49 START 21/12/72
1063 END 10/3/80
1061 START 21/2/79
1062 START 27/2/79
1061 END 24/1/80
1063 START 28/2/79
PRYDZ BAY


2.14b
80°
90°
100°
110°E
70°
55°S
60°
65°
18 END 8/12/73
211 END
29/12/76
474
END
6/4/77
211 START
27/1/76
474 START
19/1/76
18 START
21/1/73
PRYDZ BAY

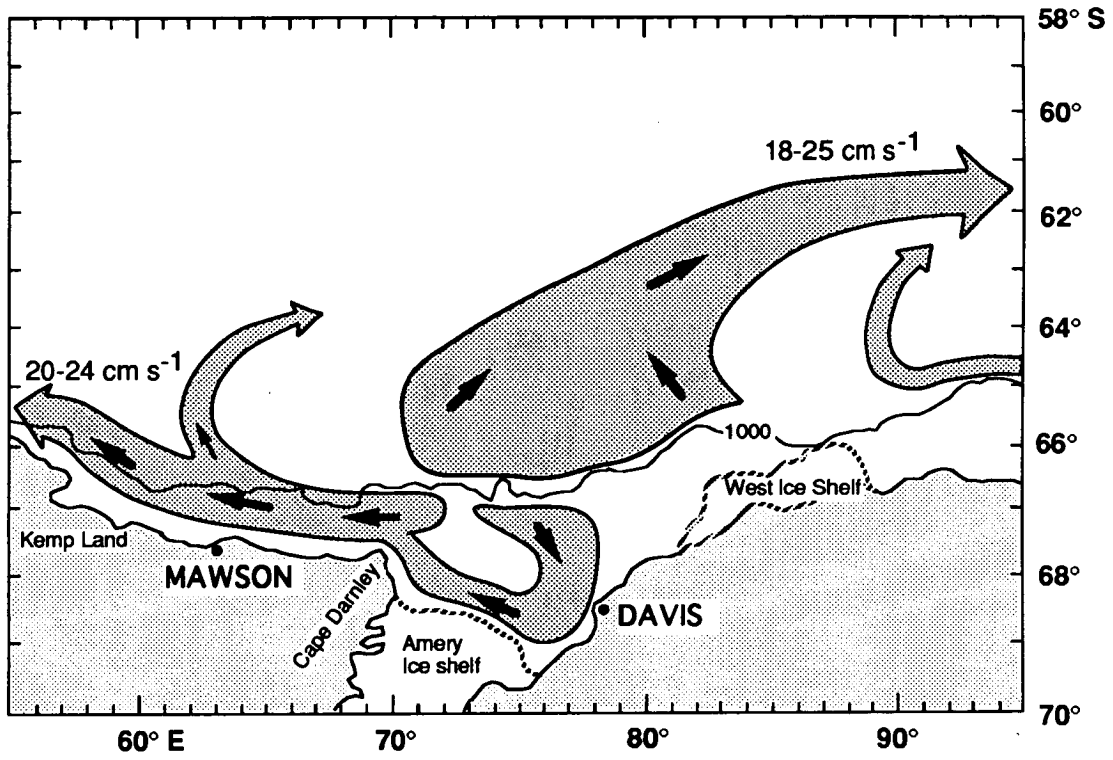


Fig. 2.15 Summary of currents likely to influence zooplankton distributions and dispersal of euphausiid larvae from the centre of the region, determined from sea-ice buoy and ice-berg trajectories, current meters and geostrophic flow. Current speeds shown are determined from ice-berg trajectories.

Sea ice (ICEX) buoys released on the shelf in Prydz Bay also moved west and out of the region past Enderby Land proceeding past 30°E while remaining in the EWD (Fig. 2.12). Icebergs in this region continued further, generally following the continental shelf edge (Fig. 2.13), until eventually turning north around 20 to 30°W. Icebergs entrained by the EWD averaged speeds along the shelf of 15.4 cm s^{-1}. Kumagori & Yanagawa (1958) found that icebergs did not respond to wind but only to currents at speeds that were 65 to 75% of the velocity of the current. Therefore the actual speed of the EWD, over the distance the icebergs were followed, was more likely 20.5 to 23.7 cm s^{-1}, which is consistent with the current meter estimates. Between 1973 and 1980 Tchernia & Jeannin (1983) also tracked four icebergs from an area north of the Prydz bay shelf, circa 63° 30' to 65° 30'S by 76° 30' to 83°E (Fig. 2.14a). These icebergs drifted north-east until reaching approximately 61°S before moving east in the Antarctic Circumpolar Current (ACC). The average speeds of the individual icebergs ranged between 13.9 to 16.2 cm s^{-1}. Application of Kumagori & Yanagawa's (1958) correction gives an actual water flow of 18.5 to 24.9 cm s^{-1}. Notably this flow closely follows the 0 to 0.5° C isotherms (Fig. 2.8) but is also contrary to the perceived southward course of the gyre (Fig. 2.10). Three ICEX buoys released in an area just off the Prydz Bay shelf, i.e. 65° 30' to 66°S by 70° to 77° 30'E, also had a similar north-easterly trajectory although slightly more variable (Fig. 2.12).

Summary of Data on Ocean Currents

Fig. 2.15 shows a synthesis of the various currents described, in addition to geostrophic flow, particularly those currents moving west along the shelf and north-east which are likely to influence the distribution of zooplankton and euphausiid larvae in the centre of the region. Further

examination of the Tchernia & Jeannin (1983) iceberg trajectories indicates the possible existence of another but reversing current between 85° and 95°E that would seem to originate as a northward deflection from the EWD, which then joins the north-easterly current (Fig. 2.15). Three icebergs studied by Tchernia & Jeannin (1983) were carried into the region along the shelf edge from the east by the EWD, turned between 85° and 95°E, and returned to the east along 61°S via ACC similar to other icebergs described above (Fig. 2.14b).

Sea ice

In the Prydz Bay region, sea ice begins to reform in March and reaches its maximum northern extent of approximately 58-60°S in September-October (Jacka 1983). The ice then dissipates more rapidly than it formed, with the ice edge retreating south in a distinct latitudinal pattern (Fig. 2.16). An examination of US Navy-NOAA Joint Ice Center satellite ice maps from numerous years showed that open water (a polynya) usually appears by early December in the southern part of Prydz Bay near the Amery Ice Shelf. This is at a time when the area to the north is still extensively covered by ice and the northern ice edge is still moving south. The occurrence of a large polynya in this area, or at least light pack-ice, has also been consistently observed from oceanographic and supply vessels operating in Prydz Bay (Smith *et al.* 1984; Streten & Pike 1984). Ice then dissipates north towards the shelf edge to meet the southward receding ice edge (Fig. 2.17). Most of the ice is gone by the end of January, and Prydz Bay remains generally ice-free through February (Zwally *et al.* 1983; Streten & Pike 1984).

Fig. 2.16 Pattern of ice edge retreat from September through to February based on mean monthly ice concentration contours averaged for the four years 1973-76 (reproduced from Zwally *et al.* 1983).

2.16

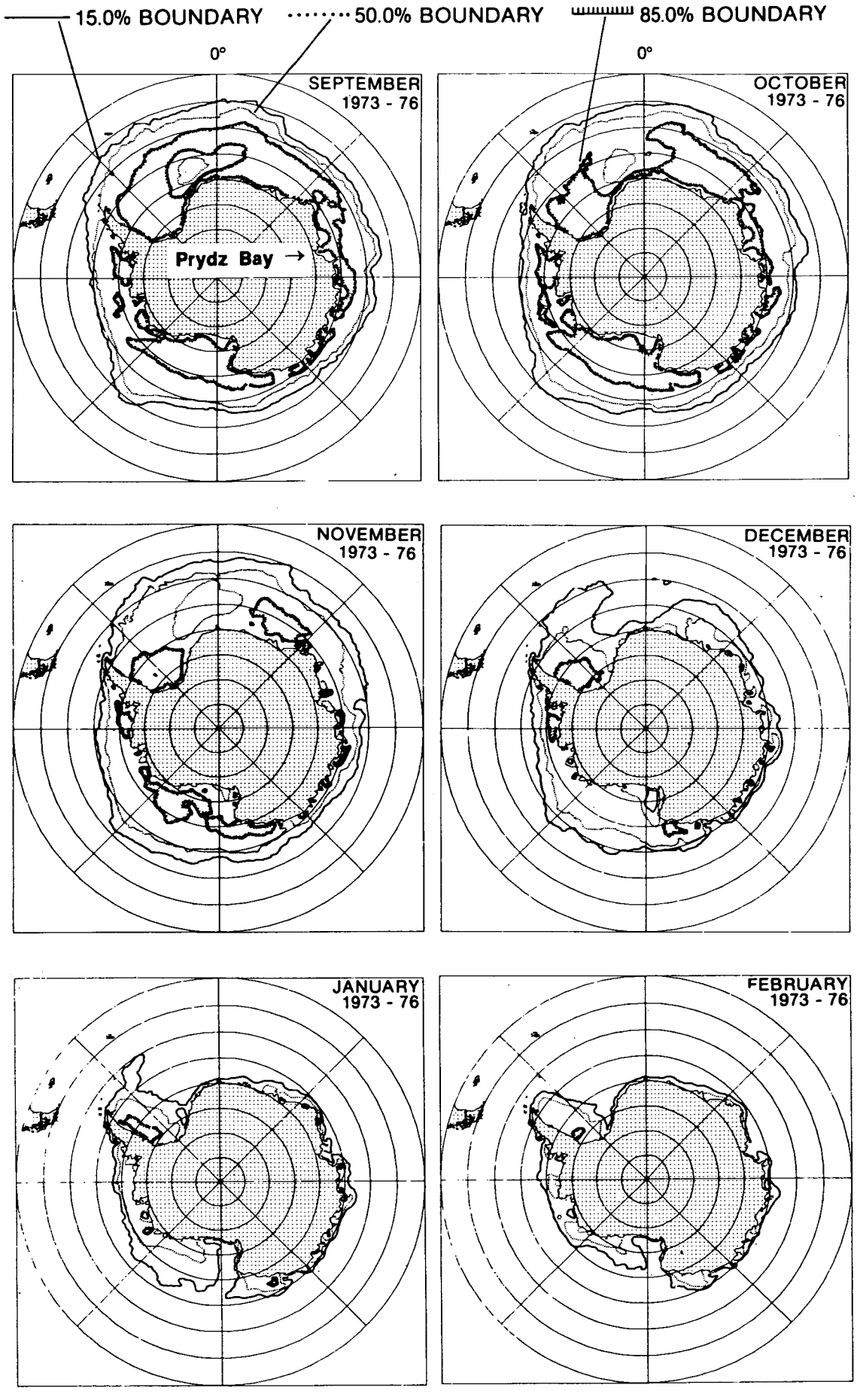
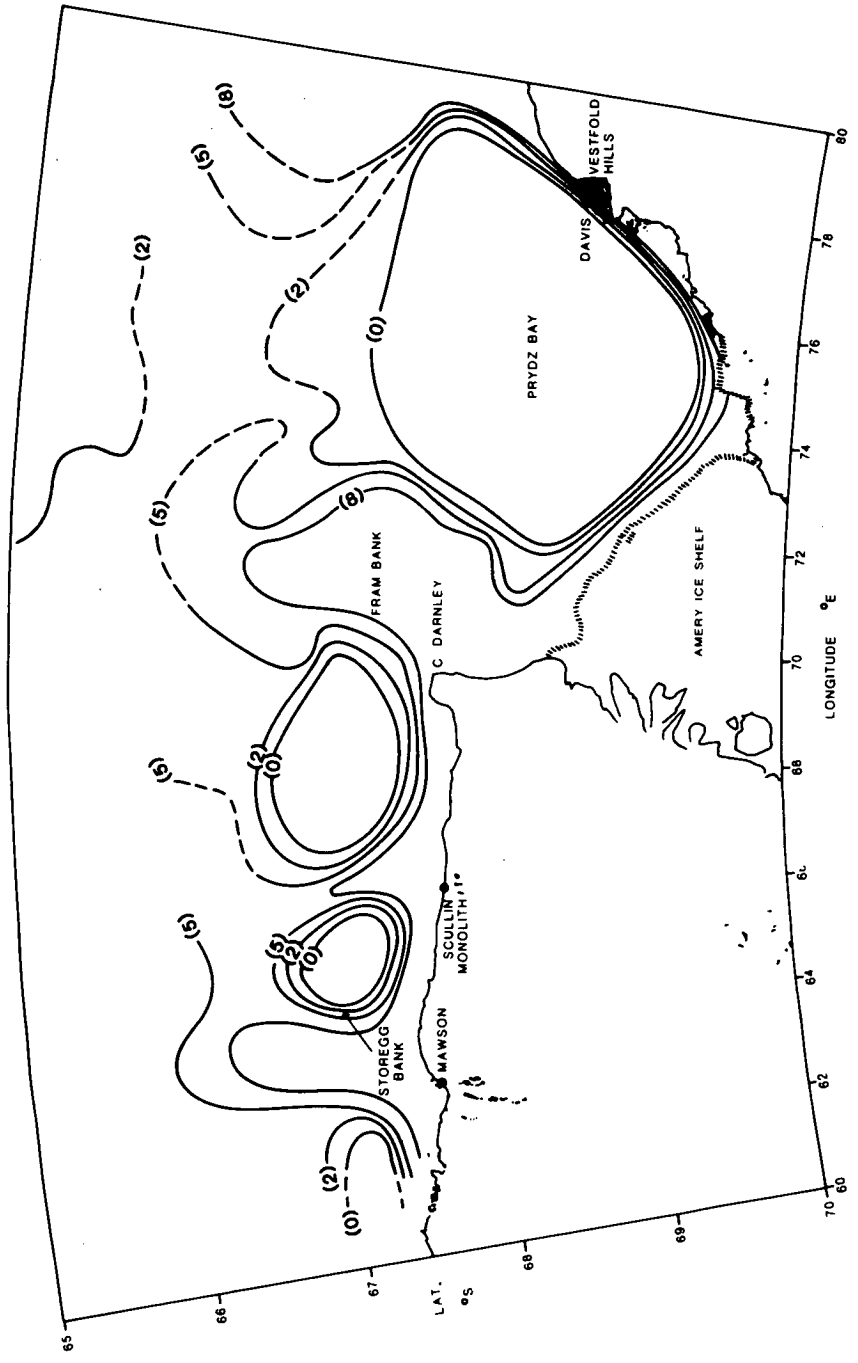

15.0% BOUNDARY
50.0% BOUNDARY
85.0% BOUNDARY
0°
SEPTEMBER
1973 - 76
Prydz Bay →
0°
OCTOBER
1973 - 76
NOVEMBER
1973 - 76
DECEMBER
1973 - 76
JANUARY
1973 - 76
FEBRUARY
1973 - 76

Fig. 2.17 Concentrations of sea-ice (in tenths) in the coastal zone of the Prydz Bay region during November to December 1982, showing the large Prydz Bay polynya plus other smaller inshore polynyas further west (reproduced from Streten & Pike 1984).



CHAPTER 3

MACROZOOPLANKTON COMMUNITIES 1981-1987

Introduction

The Antarctic krill, *Euphausia superba,* is perceived as the most important organism in the Antarctic marine ecosystem, in terms of its high abundance and position in the food web. It is, however, not the only important or dominant taxon in that ecosystem. Copepods collectively can form a significant component of the zooplankton biomass, at times exceeding that of krill (Everson 1984; Smith & Schnack-Schiel 1990; Conover & Huntley 1991). In the Indian and Pacific Ocean sectors, herbivorous copepods represented 66 to 73% of the zooplankton biomass (Voronina 1967; Hopkins 1971; Yamada & Kawamura 1987). In areas of low phytoplankton abundance and high copepod biomass, copepods consumed 55% of daily primary production (Schnack *et al.* 1985). Conover & Huntley (1991) suggested, on the basis of conservative abundance estimates, that Antarctic copepods must consume at least three times, perhaps as much as eight times, the primary production eaten by krill. Experimental studies have confirmed that copepods eat the same phytoplankton species as krill (Schnack 1985). Moreover, herbivorous copepods form an important alternative pathway in the food web. The fish *Pleuragramma antarcticum* feeds extensively on copepods (Kellermen 1987; Hubold & Ekau 1990; Boysen-Ennen *et al.* 1991). In turn this fish is a conspicuous component in the diet of vertebrate predators (Green & Williams 1986; Williams 1985, 1989). *Euphausia crystallorophias* is another zooplankter important in the diet of fish and birds (Williams 1985, 1989; Foster *et al.* 1987; Puddicombe & Johnstone 1988). Numerous other zooplankton taxa are important dietary components of the nototheniid fish *Pagothenia borchgrevinki,* e.g. the

pteropod *Limacina helicina*, the hyperiid *Hyperiella dilatata*, gammarids, chaetognaths, and copepods (Foster *et al.* 1987). In order to fully understand the various pathways in the food web, and the possible interactions between krill and other zooplankton species, detailed knowledge of the community ecology is required. This involves defining the number of communities in an area, their composition, the dominant species or species indicators, species affinities, distribution patterns and where possible the factors that control these patterns. There have been few such studies carried out in Antarctica waters and mostly in the Atlantic sector. Boysen-Ennen & Piatkowski (1988), Hubold *et al.* (1988) and Piatkowski (1989a) primarily focussed on the coastal regions of the southern and eastern Weddell Sea. Siegel *et al.* (1992) studied the zooplankton community structure under the sea ice of the northern Weddell Sea. Piatkowski (1989b) attempted to relate the complex zooplankton distribution patterns off the Antarctic Peninsula, to the hydrography of the region which he described as more complex than that of other parts of Antarctica. Siegel & Piatkowski (1990) studied the seasonal variability in the community patterns in this area and is one of few such studies in the Atlantic sector. The study by Atkinson *et al.* (1990) on seasonal variability of zooplankton patterns and oceanographic processes was the culmination of a number of studies by the British Antarctic Survey on the zooplankton in the waters around South Georgia. South Georgia is located close to the Polar Front and not surprisingly sub-antarctic species predominated (Atkinson *et al.* 1990).

All of the above mentioned studies described a number of communities or species assemblages within their particular study areas by applying multivariate analytical techniques (clustering and infrequently ordination) to some degree. Multivariate techniques have also been used to define the Antarctic midwater food webs in the Atlantic sector (Hopkins 1985a, Hopkins & Torres 1989) and McMurdo Sound (Hopkins

1987). In those three studies, the diets of zooplankton and micronekton were compared to define groups of organisms with similar diets, i.e. species of common trophic status, rather than defining species affinities amongst herbivores-omnivores-carnivores within a community. Those studies appeared to have assumed that only one community was involved each time. This assumption was not tested but was probably valid given the locality and relatively small size of each study area, particularly the Croker Passage (Hopkins 1985a,b) and McMurdo Sound sites (Hopkins 1987).

A few zooplankton studies have been carried out in the Prydz Bay region. Many were limited in terms of the taxa examined, the level of identification, the number of study sites or the level of community description, i.e. distribution and abundance only (Zmijewska 1983; Boden 1985; Yamada & Kawamura 1986; Budnichenko & Khromov 1988; Pakhomov 1989). Yamada & Kawamura (1986) looked at within seasonal variability of the abundance of some copepod species from six sites in the Prydz Bay region between 62 and 64°S. During the international BIOMASS program, Japan also conducted studies on the distribution and/or abundance of copepods, chaetognaths and euphausiids to the east of the Prydz Bay region south of Australia (Kawamura 1986; Terazaki & Wada 1986; Terazaki 1989). Zooplankton studies were also carried out west of the region in the inshore margins around Syowa station (e.g. Fukuchi *et al.* 1985; Tanimura *et al.* 1986).

This chapter describes the results of four geographically extensive surveys of the Prydz Bay region which were carried out between 1981 and 1987, and covered the months of November to March (late spring to early autumn). The zooplankton data sets derived from those surveys were analysed by a combination of multi- and univariate analytical techniques to define the zooplankton communities in the region, species composition and affinities, indicator species characteristic of each

community, and variability in community patterns. These patterns were compared with various environmental parameters to generate hypotheses as to which factors govern zooplankton distributions. A smaller survey was also undertaken in January 1984. This survey mainly involved trawls aimed at krill detected by hydroacoustics (Hosie *et al.* 1988), and therefore the zooplankton data obtained was dependent on the sampling methodology. The survey was also limited in the number of samples, and was therefore not included in the present analyses.

Methods

The Prydz Bay region study area was defined for the present purpose as being from 58° to 93° E and south from 60° S to the Antarctic coast. Figure 3.1 shows the station positions for the four sampling surveys in January to March 1981, November to December 1982, January 1985, and March 1987. Sampling methods on each cruise, together with sampling dates and number of sites sampled have been summarized in Table 3.1. Zooplankton were collected 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). During the 1981 and 1982 surveys, the volume filtered by the net was determined by multiplying the effective mouth area of the net by the distanced travelled, calculated as a function of ship's speed over the period the net was open. On subsequent voyages the net was equipped with a flowmeter. In calculating the volume filtered, the effects of towing speed and trajectory were taken into account (Roe *et al.* 1980; Pommeranz *et al.* 1982). Towing speed varied between 0.75 to 2 ms^{-1} (1.5 and 4 knots). The routine sampling method employed on the first two surveys was a horizontal tow. In 1981 this was primarily to nominal depths of 62 to 75 m, and in 1982 sampling depth varied between 0 and 180 m. During the

Fig. 3.1 Zooplankton sampling sites for the four surveys between 1981 and 1987. The 1000 m contour is shown.

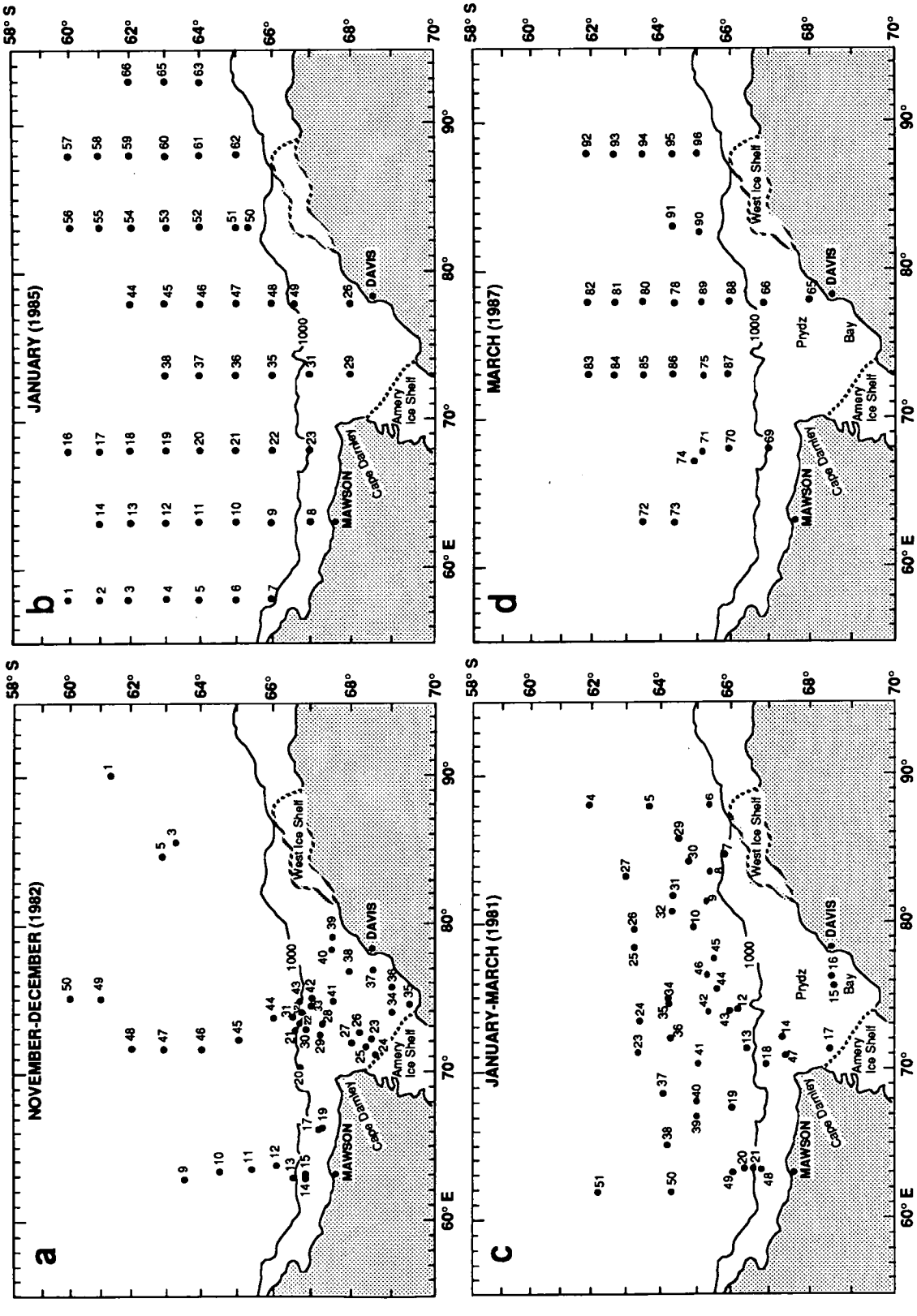


Table 3.1 Summary of sampling surveys. ADBEX = Antarctic Division BIOMASS Experiment, AAMBER = Australian Antarctic Marine Biological Ecosystem Research, FIBEX = First International BIOMASS Experiment, SIBEX 2 = Second International BIOMASS Experiment (phase 2), [a] principal sampling depth, [b] five hauls only.

Sampling period	Cruise name	No. Sites	Haul	Sample depth (m)	Full sampling details
20 January to 10 March 1981	FIBEX	44	Horizontal	62+75[a]	Williams *et al.* 1983
19 November to 19 December 1982	ADBEX 1	43	Horizontal Oblique[b]	0-180 various 0-120 various	Williams *et al.* 1986
4-26 January 1985	SIBEX 2	51	Oblique	0-200	Ikeda *et al.* 1986
7-23 March 1987	AAMBER 1	27	Oblique	0-200	Hosie *et al.* 1991

latter survey there were also five oblique hauls between 0 and 120 m. On the remaining surveys the net was towed obliquely between 0 and 200 m. A combined electro-mechanical net release and real time depth sensor was usually mounted above the net. Complete details of the sampling programs, e.g. sampling position, time, depth, conditions, etc, are provided by Williams *et al.* (1983, 1986); Ikeda *et al.* (1986) and Hosie *et al.* (1991).

Basic sorting of taxa was carried out on board ship. In particular specimens of *E. superba* were removed, as were 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 the species level where possible and counted. For the purposes of this study, zooplankton were defined as all species collected by the RMT 8. This included *E. superba* and ichthyoplankton, but not euphausiid larvae which were collected by other more efficient means, i.e. RMT 1 and bongo nets (see Chapter 6).

At each sampling site water samples were collected for phytoplankton pigment analysis, at depths of 0, 10, 25, 35, 50, 75, 100 and 200 m, using a General Oceanics rosette sampler with twelve 5 L Niskin bottles (Wright & 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 (Kerry *et al.* 1987a, 1987b; Kerry & Woehler 1987; Woehler & Williams 1988 - see Chapter 2 for review of oceanography).

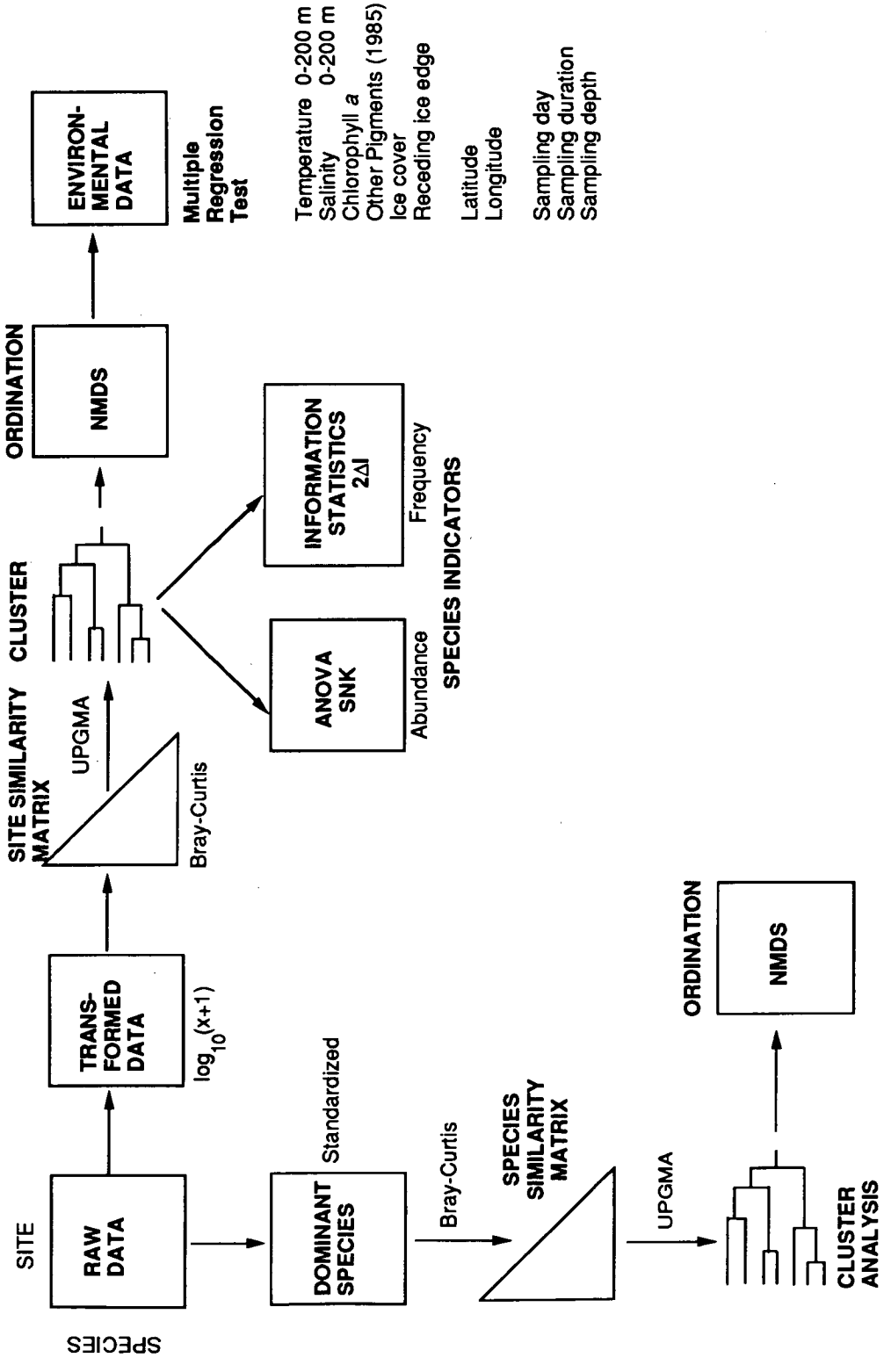
Data Analyses

Species by sampling site matrices for each cruise, expressed as density values of number of individuals 1000 m^{-3}, were analysed using both cluster analysis and non-metric multidimensional (NMDS) ordination. Sampling sites were first compared to define areas with similar species composition (q-type analysis). Multivariate and univariate statistical tests were subsequently applied to test the validity of observed patterns and to relate these patterns to environmental parameters. The inverse comparison analysis of species data (r-type analysis) was also undertaken to define species associations or affinities. A flow chart summarizing the numerical analyses is shown in Fig. 3.2 and is primarily a modification of the methodology recommended by Field *et al.* (1982) and Kruskal & Wish (1978). Multivariate analyses were carried out using BIOΣTAT II (Pimental, R.A. & Smith, J.D., 1985 Sigma Soft, Placentia, California).

Prior to the comparison of sampling sites, data were transformed using the $\log_{10}(X+1)$ function to reduce the bias of very high abundance species and to give more weighting to species likely to have been undersampled, e.g. copepods. Cluster analysis was carried out first using the Bray-Curtis dissimilarity index (Bray & Curtis 1957) coupled with unweighted pair group average linkage (UPGMA). The Bray-Curtis index was chosen because of its ability to deal with matrices with a high component of zero data entries, i.e. it will not be influenced by joint absences (Field *et al.* 1982). In the case of the January 1985 data set, nearly 70 % the matrix comprised zero values.

Sampling site cluster groups identified by the cluster analysis were further analysed to define indicator species which characterised each site group. Two types of indicator species were defined. The first type consisted of species which distinguished cluster groups by their frequency of occurrence, i.e. they were more frequent in one cluster group than

Fig. 3.2 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).



another. These "frequency" type indicators were defined using Field's information statistic ($2\Delta I_i$) (Field *et al.* 1982). Every taxon (species), i, was compared between two cluster groups by the following formula:

$$2\Delta I_i = 2(I_{ti} - I_{1i} - I_{2i}) \qquad (3.1)$$

where I_{ti} = total information content of both cluster groups combined, $I_{ti} = N_t \log N_t - A_{ti}\log A_{ti} - (N_t - A_{ti})\log(N_t - A_{ti})$; N_t = number of samples in both cluster groups together ("potential presences"): A_{ti} = number of samples in which Species i is actually present; $(N_t - A_{ti})$ = number of samples from which Species i is absent. Similarly, the information content I_{1i} and I_{2i} are obtained for Clusters 1 and 2 respectively. Field's information statistic basically provides an index of the degree of difference in the frequency of occurrence of a species between two cluster groups, in relation to the number of sites. The resulting $2\Delta I_i$ values were compared with chi-square values at 5% and 1% probability levels for 1 degree of freedom, on the premise that $2\Delta I_i$ approximates a chi-square distribution (Field *et al.* 1982).

Quite often a species was common to two or more site cluster groups, but had a significantly higher abundance in one particular group. Therefore, the second type of species indicator comprised species that distinguish a group by their higher abundance. These "abundance" indicator species were defined by analysis of variance and further tested for significance using the student Newman-Keuls (SNK) multiple range test (Zar 1984). To avoid spurious low abundance rare indicator species, and also to reduce computing time, only numerically dominant species were used in the ANOVA. These dominant species were the same as those defined and used in the comparison of species (see below). Reliable indicator species should ideally be abundant.

Following the cluster analyses the data sets were further subjected to non-metric multidimensional scaling (NMDS) ordination. This analysis provided a view or "map" of the sampling site similarities in two, three or four dimensional space, in addition to the cluster analysis dendrogram which is fundamentally one dimensional. NMDS is considered to be one of the most robust ordination techniques available, especially in coping with a large number of zero counts (Field *et al.* 1982; Gray *et al.* 1988). The power of NMDS lies in its use of rank order information rather than quantitative values in between sample comparisons of the form "sample site 1 is more similar to site 2 than it is to site 3," and constructs a "map" of the sites that attempts to satisfy all such conditions (Clarke & Green 1988; Gray *et al.* 1988). Another advantage of NMDS is that a "stress" value is produced for each ordination (4, 3, 2 axes), indicating the goodness-of-fit between the original data and the derived "map." The lower the value, often expressed between 0 and 1, the better the fit. The stress value is allied to the sum of squares in a regression analysis (Domanski 1984). Kruskal & Carmore (1971, in Domanski 1984) produced the following more easily interpretable guidelines:

Stress	Goodness-of-fit
0.40	Poor
0.20	Fair
0.10	Good
0.05	Excellent
0.00	Perfect

The stress value was then used, via the graphical method of Kruskal & Wish (1978), to select the least number of axes which adequately summarised the data set. This method involves plotting the stress value against the respective number of ordination axes and selecting the

ordination at the point of maximum change in direction or "elbow" of the curve. An example is shown in Fig. 3.3. In this study a 2 axes ordination was found to suffice in all cases.

Prior to ordination, "outlier" sample sites identified by cluster analysis were removed from the data set to obviate problems associated with such outliers, e.g. biasing or dominating the ordination, often compressing the distribution of the remaining sites (Gauch 1982). Outliers are sites with a peculiar species composition and thus have a very low similarity with other sites.

New ordination scores derived from the NMDS were compared by multiple regression analysis with various environmental parameters to determine which of these parameters may best explain the zooplankton distributions. The environmental parameters compared were: integrated temperature and salinity between 0 and 200 m using 2 m intervals; chlorophyll *a* integrated for 0 - 100 m in 1982 and 1985, and surface values in 1981 and 1987; pack-ice cover in tenths and finally receding ice edge. In January 1985, other known phytoplankton marker pigments of distinct phytoplankton groups were also included in the analysis (Table 3.2). There are distinct thermoclines throughout the region and haloclines in the waters of the continental shelf (Figs. 2.4 to 2.6). However, there was no knowledge of where zooplankton were distributed in the water column in relation to these structures. Zooplankton abundances were integrated for the upper 200 m in the oblique trawls, whereas the horizontal trawls sampled only one depth layer at each site. Instead, integrated salinity and temperature values were used as indicative scores of general oceanographic patterns, e.g. horizontal thermal gradients and fronts (Brandt & Wadley 1981), for the purpose of comparison with zooplankton NMDS scores. The receding ice parameter was defined as the time in days from when the pack-ice was at its most northerly extent, taken as mid-October, to when the ice had receded or dissipated exposing

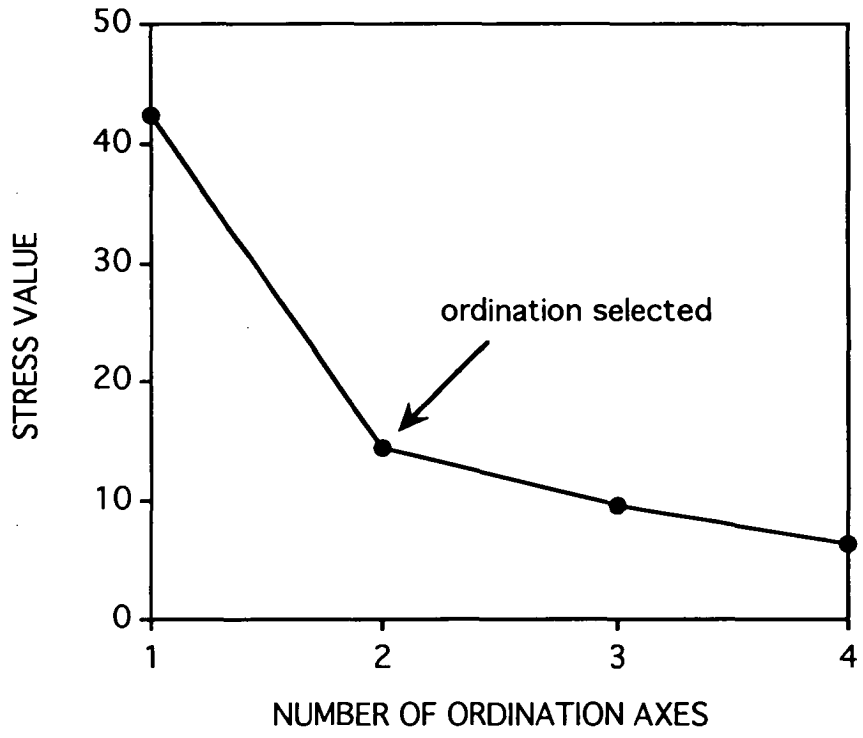


Fig. 3.3 The graphical method of Kruskal and Wish (1978) for selecting the appropriate level of NMDS ordination, i.e. the least number of axes, that adequately summarises the ecological data set. The example shown is the January 1985 comparison of species associations. A two axes ordination was selected in this case.

Table 3.2 Known phytoplankton marker pigments, with their sources, used in the January 1985 multiple regression analysis. Data from (Wright 1987).

Pigment	Source
Chlorophyll *a*	all photosynthetic algae
Fucoxanthin	diatoms, chrysophytes
Hexfucox (19' - hexanoyloxyfucoxanthin)	some prymnesiophytes e.g. *Phaeocystis*
Fucox-x	chrysophytes, prymnesiophytes
Peridinin	dinoflagellates
Alloxanthin	cryptophytes
Zeaxanthin	cyanobacteria
Chlorophyll *b*	prasinophytes, chlorophytes
Prasinoxanthin	prasinophytes

the sampling site. Pack-ice cover was estimated at the time of net sampling, and ice recession was measured for each season from the Northern Ice Limit maps produced weekly by the U.S. Navy-NOAA Joint Ice Center (Navy Polar Oceanography Center, Suitland), as well as by consulting the Antarctic Division Antarctic Sea Ice Extent database (Jacka 1983). Sampling methodology may cause variation in the zooplankton data. Hence, sampling day, the time since the start of a survey, duration of the haul and sampling depth were included in the regression analyses. Time of day was not included in the analysis because of the limitations of tests to resolve satisfactorily angular-linear correlations (Zar 1984). Latitude and longitude of sampling sites were also compared with the ordination scores to ascertain the type and degree of zonation in the distributions. The actual multiple regression analysis involved treating each parameter as the dependent variable and the ordination scores for each axis, which are a collective summary of the ecological data, as the independent variables. The direction of maximum correlation of the regression line is at an angle θ_r with the r^{th} axis. The direction cosine, or regression weight, c_r of that angle is derived from Kruskal & Wish's (1978) formula:

$$c_r = b_r / \sqrt{b_1^2 + b_2^2 + \ldots b_r^2} \qquad (3.2)$$

where b_1, b_2, etc. are the regression coefficients from the multiple regression $a + b_1x_1 + b_2x_2 + \ldots b_rx_r$, and x_r are the ordination scores of the axes.

Water circulation is one parameter expected to have a substantial effect on the distribution of zooplankton, but cannot be included in the regression analysis. Instead, the geographical distribution patterns of station groups, defined by multivariate analysis, were compared visually with known water currents shown in Figs 2.10 & 2.15. Fig. 2.10 shows the geostrophic water flow in the Prydz Bay region derived from CTD data by

Table 3.3 Dominant species used in inverse cluster analyses 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, for any sampling cruise. Species abreviations used in the NMDS plots (Fig. 3.9) are shown.

Taxa	Abbreviation
Appendicularia	Ap
Calanoides acutus	Ca
Calanus propinquus	Cp
Clio pyramidata	Clp
Cyllopus lucasii	Cl
Electrona antarctica	Ela
Euchaeta antarctica	Ea
Eukrohnia hamata	Eh
Euphausia crystallorophias	Ec
Euphausia frigida	Ef
Euphausia superba	Es
Euphausia triacantha	Et
Gammaridae	Ga
Haloptilus ocellatus	Ho
Hyperiella dilatata	Hd
Ihlea racovitzai	Ir
Limacina helicina	Lh
Metridia gerlachei	Mg
Pagetopsis macropterus	Pm
Pleuragramma antarcticum	Pa
Rhincalanus gigas	Rg
Sagitta gazellae	Sg
Sagitta marri	Sm
Salpa thompsoni	St
Siphonophora (Nectophores)	SN
Themisto gaudichaudii	Tg
Thysanoessa macrura	Tm
Tomopteris carpenteri	Tc

R.A Nunes Vaz & G.W. Lennon (personal communication 1990). Figure 2.15 shows a synthesis of other currents, known from sea ice buoy and iceberg trajectories, current meters, as well as geostrophic flow (Fig. 2.10), which are believed to influence the distribution of euphausiid larvae (Chapter 6), but may also affect other zooplankton distributions.

The inverse analysis of the data sets to define species affinities, also involved cluster analysis as the first step, with Bray-Curtis index and UPGMA linkage, followed by NMDS to map species associations in two-dimensional space. However, prior to analysis a data set was reduced to a subset of common dominant species to avoid spurious associations amongst very low abundance rare species, caused by their chance occurrence at one site. Following the example of Field *et al.* (1982), dominant species were defined as those with a >4% numerical dominance for any given sampling site, for any sampling cruise, providing that a species was regularly observed in all surveys. Table 3.3 lists these species along with their abbreviations used in the NMDS plots. There were 26 main species/taxa so defined, plus two additional species *Ihlea racovitzai* and larvae of *Pagetopsis macropterus*. These additional species were only found in 1981 and 1982, but both were defined as indicator species of the inshore area and were therefore included in the analyses. There was also a higher frequency of sampling on the shelf during those cruises.

The species data were standardized according to Field *et al.* (1982), i.e.:

$$Y_{ij} = 100\, X_{ij} / \sum_{j=1}^{n} X_{ij} \qquad (3.3)$$

where X_{ij} = abundance of the *i* th species in the *j* th sample; $\sum_{j=1}^{n} X_{ij}$ = summed abundance of the *i* th species over all samples; Y_{ij} = corresponding standardized score.

Results

Analyses for each sampling period are presented in the order of the months sampled, rather than in historical order. Throughout these 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, e.g. Group A, with numeric suffixes for sub-groups.

November-December 1982

Three distinct cluster groups were defined at 70 % dissimilarity, showing a clear zonation between in shore and off shore station groups (Figs. 3.4a, 3.5a). The in shore, continental group of sites was further divided at 65 % dissimilarity into stations south of 68° S (Group 3a), which were characterized by *Euphausia crystallorophias, Pleuragramma antarcticum* and the larvae of channichthyid fish. Between this group and the continental shelf edge were stations (Group 3b) also characterized by high abundances of *E. crystallorophias* but also by the adult krill *E. superba,* both in terms of frequency and great abundance (Tables 3.4 and 3.5).

Cluster Group 1 was primarily an oceanic group of stations, with a few sites just on the continental shelf. Although there are 25 sites in this

Fig. 3.4 Dendrograms of cluster analyses comparing sampling sites for each survey. The Bray-Curtis dissimilarity index was used for the comparison with UPGMA linkage, after $\log_{10}(X+1)$ transformation of species abundance data. Selection of station groups was arbitrary for each survey.

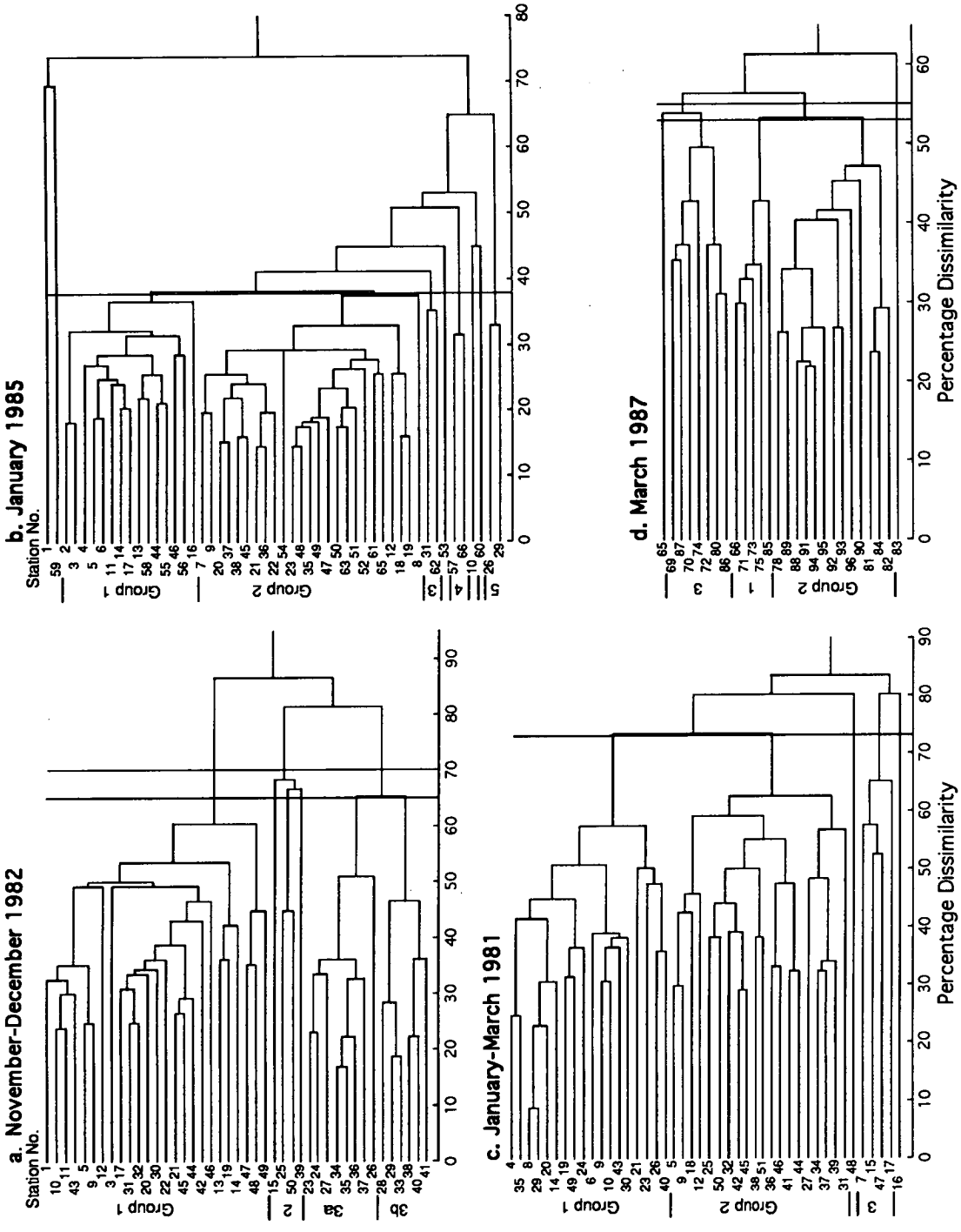
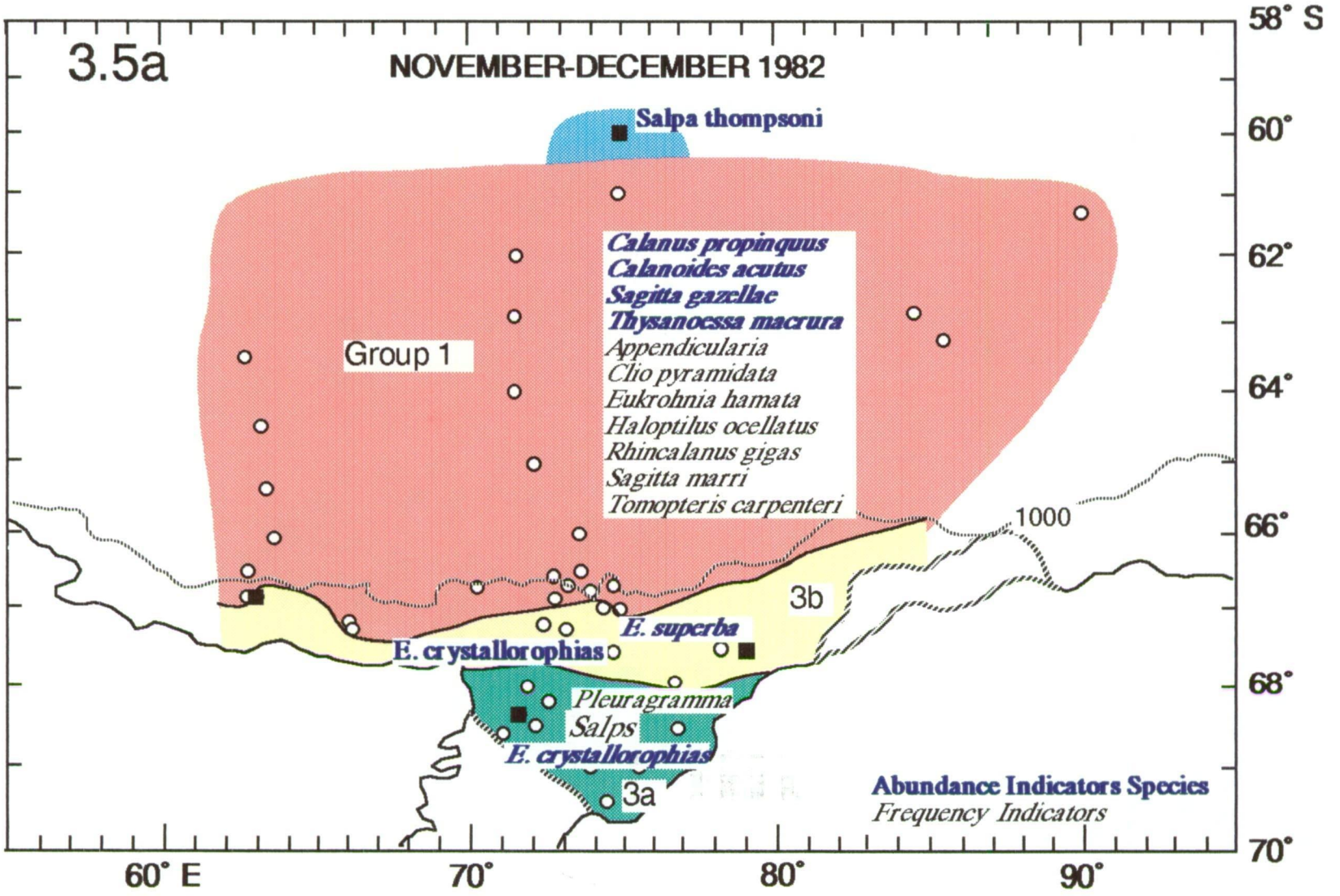
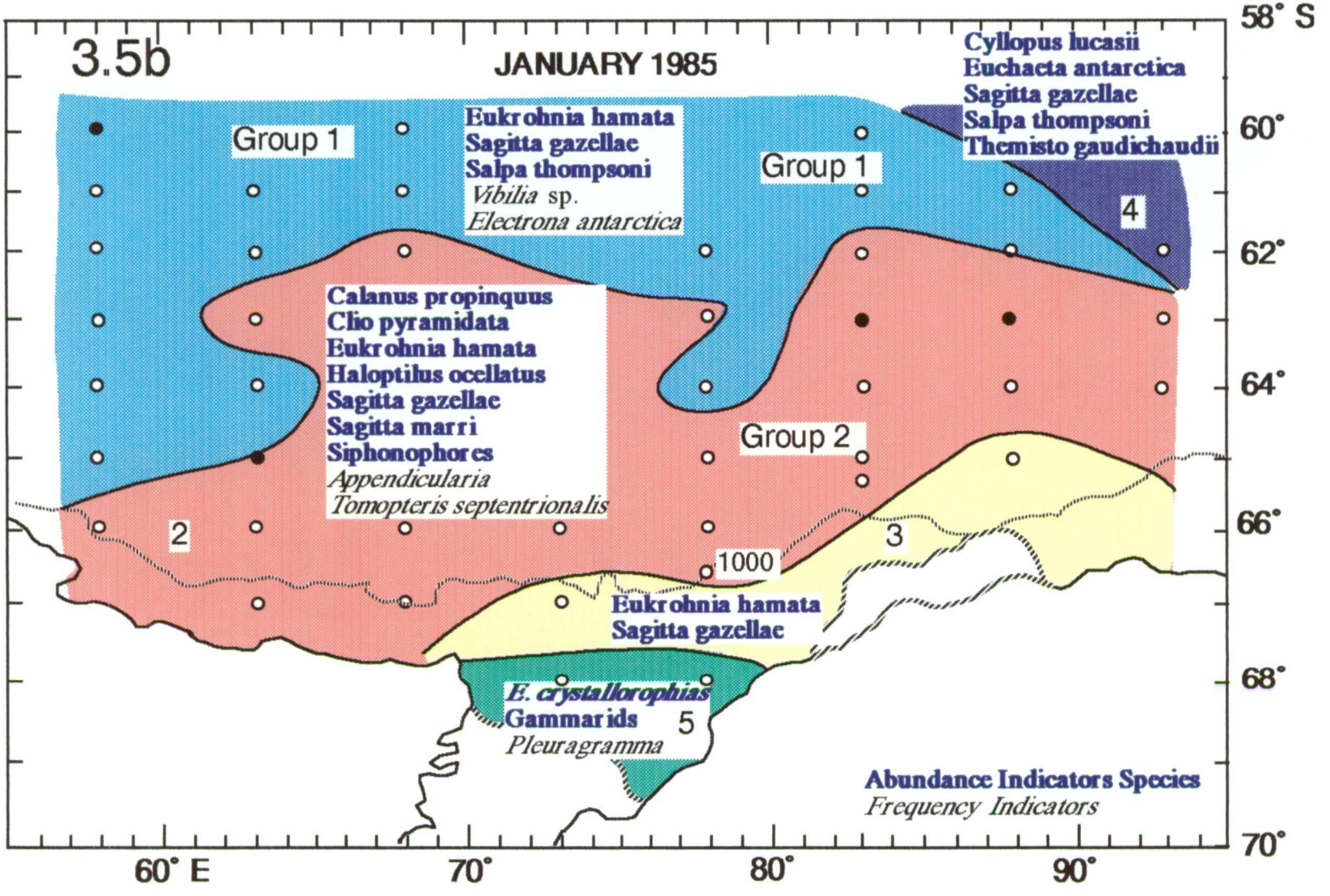
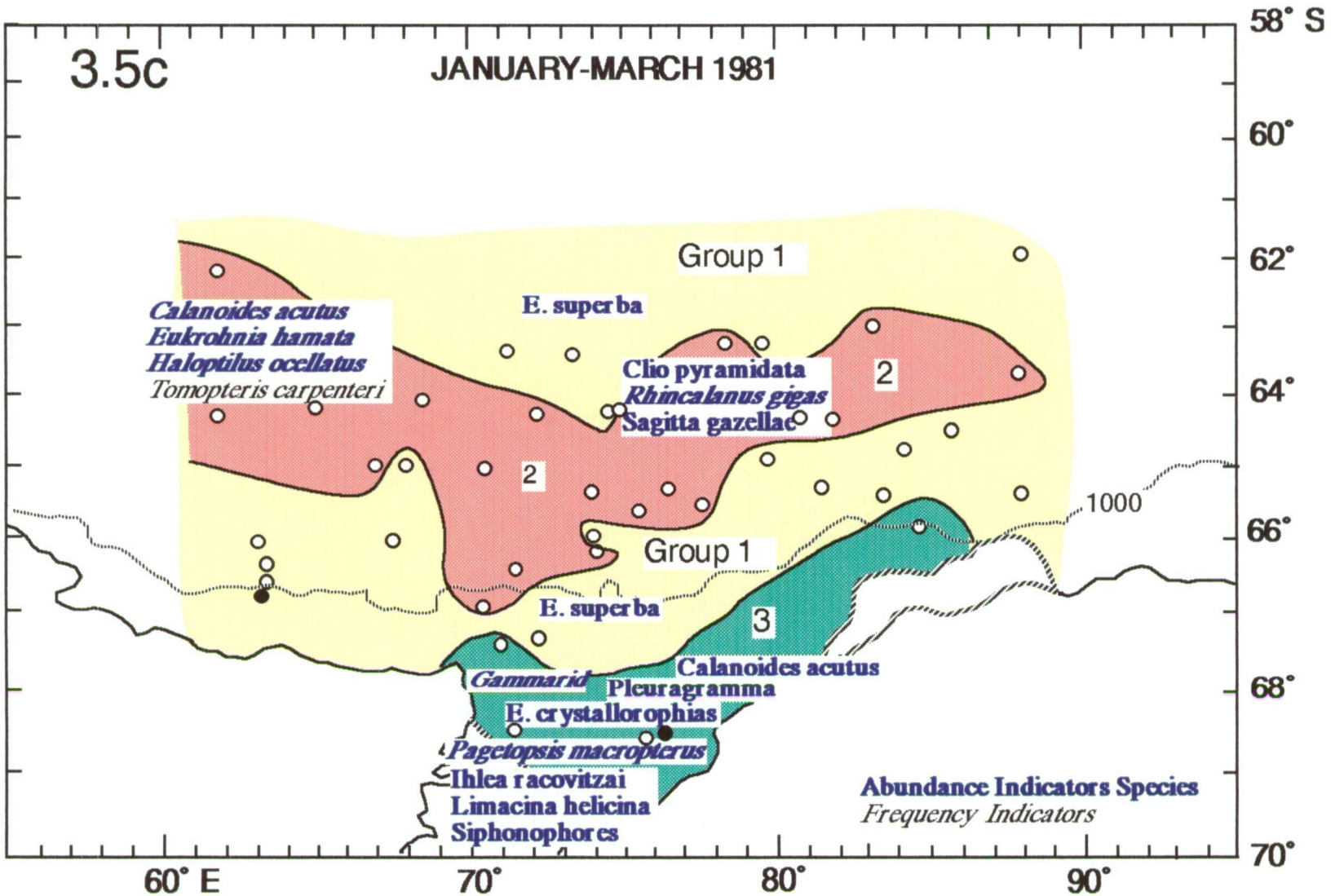


Fig. 3.5 Geographical distribution of station groups defined by cluster analyses shown in Fig. 3.4. Indicator species listed in blue bold type are those characterizing an area (station group) by their unique higher abundance identified by SNK analysis (Tables 3.5, 3.7, 3.11, 3.12). Indicator species in black italic type are those with a higher frequency of occurrence in that station group as identified by Field's information statistic (Tables 3.4, 3.8, 3.10). Note: in many cases species were both abundance and frequency indicator species . Station groups with common species composition between years have the same colour (see Discussion - Fig. 3.10).

O = sampling sites, ● = "outlier" sampling sites not grouped in the cluster analyses, ■ = Station Group 2 in November-December 1982 in **a**.


3.5a
NOVEMBER-DECEMBER 1982
Salpa thompsoni
Calanus propinquus
Calanoides acutus
Sagitta gazellae
Thysanoessa macrura
Appendicularia
Clio pyramidata
Eukrohnia hamata
Haloptilus ocellatus
Rhincalanus gigas
Sagitta marri
Tomopteris carpenteri
Group 1
1000
3b
E. superba
E. crystallorophias
Pleuragramma
Salps
E. crystallorophias
3a
Abundance Indicators Species
Frequency Indicators
58° S
60°
62°
64°
66°
68°
70°
60° E
70°
80°
90°


3.5b
JANUARY 1985
Group 1
Eukrohnia hamata
Sagitta gazellae
Salpa thompsoni
Vibilia sp.
Electrona antarctica
Group 1
Cyllopus lucasii
Euchacta antarctica
Sagitta gazellae
Salpa thompsoni
Themisto gaudichaudii
4
Calanus propinquus
Clio pyramidata
Eukrohnia hamata
Haloptilus ocellatus
Sagitta gazellae
Sagitta marri
Siphonophores
Appendicularia
Tomopteris septentrionalis
Group 2
2
3
1000
Eukrohnia hamata
Sagitta gazellae
E. crystallorophias
Gammarids
Pleuragramma
5
Abundance Indicators Species
Frequency Indicators
58° S
60°
62°
64°
66°
68°
70°
60° E
70°
80°
90°


3.5c
JANUARY-MARCH 1981
58° S
60°
62°
64°
66°
68°
70°
60° E
70°
80°
90°
Group 1
E. superba
Calanoides acutus
Eukrohnia hamata
Haloptilus ocellatus
Tomopteris carpenteri
Clio pyramidata
Rhincalanus gigas
Sagitta gazellae
2
2
1000
Group 1
E. superba
3
Gammarid
Calanoides acutus
Pleuragramma
E. crystallorophias
Pagetopsis macropterus
Ihlea racovitzai
Limacina helicina
Siphonophores
Abundance Indicators Species
Frequency Indicators

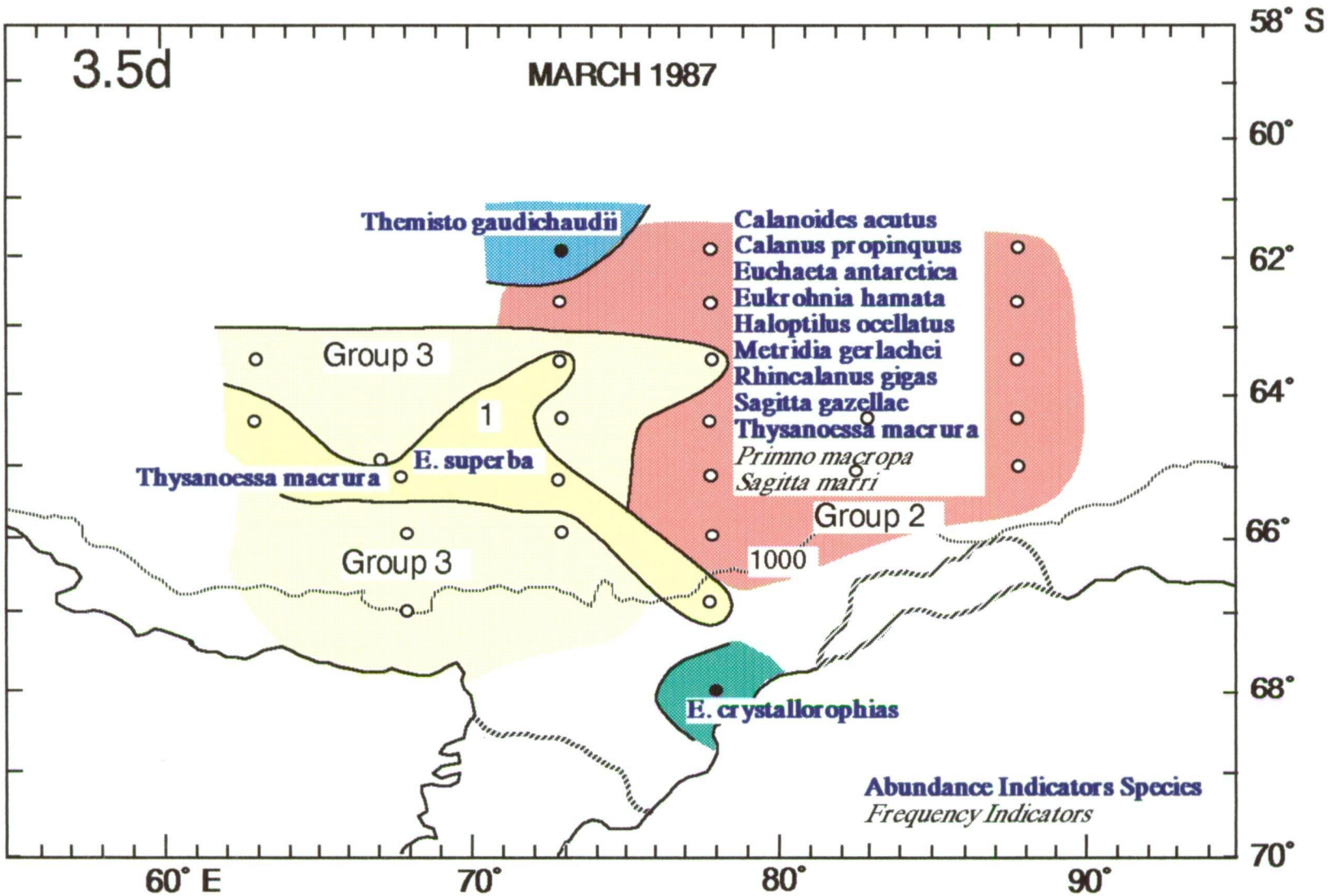

3.5d
MARCH 1987
58° S
60°
62°
64°
66°
68°
70°
60° E
70°
80°
90°
Themisto gaudichaudii
Calanoides acutus
Calanus propinquus
Euchaeta antarctica
Eukrohnia hamata
Haloptilus ocellatus
Metridia gerlachei
Rhincalanus gigas
Sagitta gazellae
Thysanoessa macrura
Primno macropa
Sagitta marri
Group 3
1
E. superba
Thysanoessa macrura
Group 2
Group 3
1000
E. crystallorophias
Abundance Indicators Species
Frequency Indicators

Table 3.4 November-December 1982. Frequencies of occurrence of indicator species distinguishing cluster groups defined in Fig. 3.4a. 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 = 25, Group 2+3 = 20, Group 3a = 8 and Group 3b = 6. * not dominant species and were not used in SNK or inverse species analyses.

a. Group 1 (oceanic) indicators species

Species	Group 1	(Group 2+3)
Calanus propinquus	25	5
Calanoides acutus	25	6
**Vanadis antarctica*	20	1
**Primno macropa*	21	2
**Clione limacina*	20	3
Tomopteris carpenteri	16	1
Rhincalanus gigas	18	2
**Tomopteris septentrionalis*	12	0
Sagitta gazellae	24	8
Eukrohnia hamata	18	3
**Spongiobranchaea australis*	18	3
**Calycopsis borchgrevinki*	9	0
Haloptilus ocellatus	9	0
Thysanoessa macrura	24	10
Sagitta marri	8	0
Clio pyramidata	21	7
Appendicularia	11	1

b. Group 2+3 (inshore) indicator species

Species	Group 2+3	Group 1
Euphausia crystallorophias	15	6
**Hyperiella macronyx*	13	4
**Cryodraco antarcticus* larvae.	7	0
*Channichthyidae larvae.	6	0
Pleuragramma antarcticum	12	5
**Chionodraco* sp. larvae	10	3

c. Group 3a indicator species from Group 3b

Species	Group 3a	Group 3b
None		
**Hyperiella macronyx*	8	2
Salpa thompsoni	8	2

d. Group 3b indicator species from Group 3a

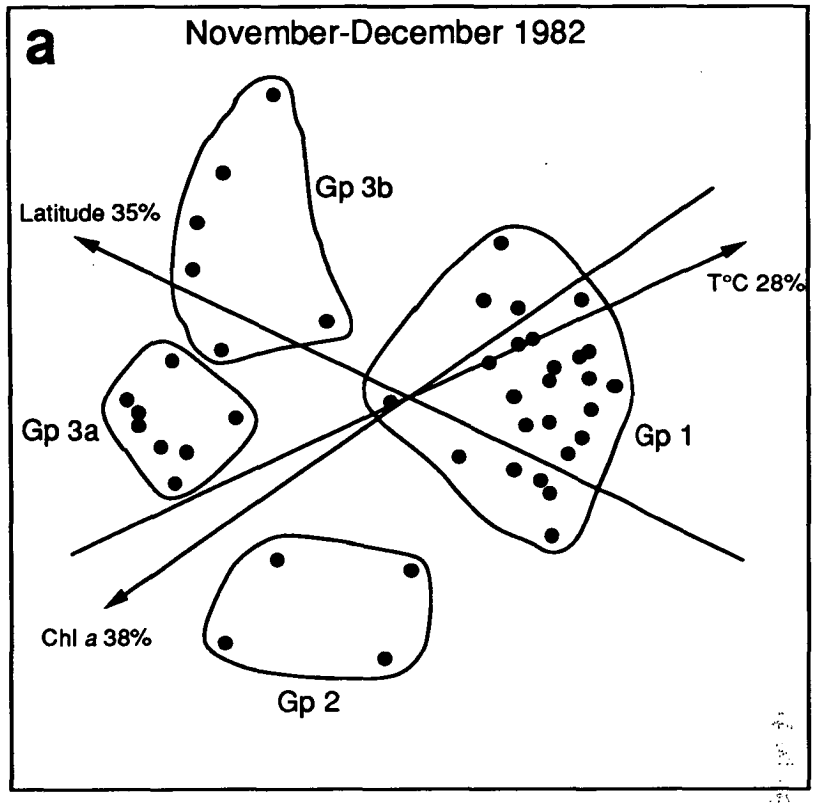
Species	Group 3b	Group 3a
None		
Euphausia superba	6	2

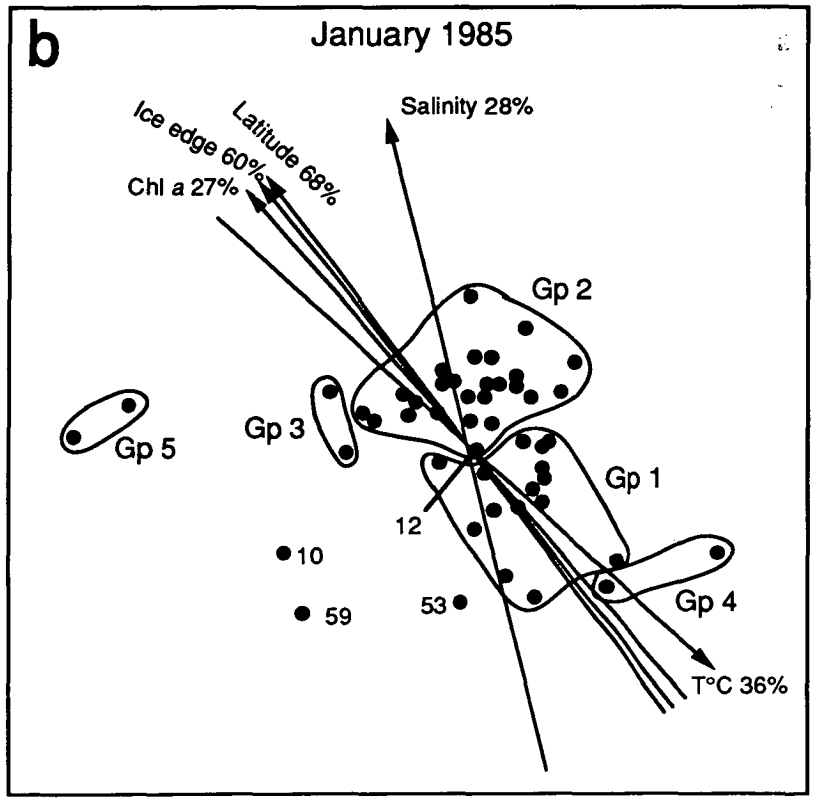
Table 3.5 November-December 1982. Mean abundances, analysis of variance (F) and SNK multiple range tests of dominant species in cluster groups defined in Fig. 3.4a. Analyses were carried out on $\log_{10}(x+1)$ transformed abundances (Zar 1984) - values shown are number of individuals 1000 m^{-3}. Species 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 =3,39.

Species	Group 1 Mean	Group 2 Mean	Group 3a Mean	Group 3b Mean	F	P
Appendicularia	0.07	0.00	0.00	0.001	1.41	–
Calanoides acutus	339.04	1.09	0.68	2.01	21.30	***
Calanus propinquus	43.47	0.70	0.02	0.07	25.03	***
Clio pyramidata	2.37	0.04	0.08	0.02	5.81	**
Cyllopus lucasii	0.49	0.08	0.03	0.04	2.88	*
Electrona antarctica	0.02	0.00	0.00	0.00	0.43	–
Euchaeta antarctica	1.44	0.04	0.00	0.001	1.60	–
Eukrohnia hamata	1.52	0.29	0.01	0.37	2.82	–
Euphausia crystallorophias	4.92	0.70	938.02	407.79	33.54	***
Euphausia frigida	0.001	0.00	0.00	0.00	0.23	–
Euphausia superba	82.23	0.07	1.07	859.44	24.97	***
Gammaridae	0.03	0.10	0.02	0.10	1.71	–
Haloptilus ocellatus	0.65	0.00	0.00	0.00	2.19	–
Hyperiella dilatata	0.19	0.15	0.30	0.07	1.43	–
Ihlea racovitzai	0.21	0.00	0.00	0.00	0.45	–
Limacina helicina	1.16	0.08	1.59	0.07	1.25	–
Metridia gerlachei	17.41	0.12	0.08	0.10	2.41	–
Pagetopsis macropterus	0.00	0.01	0.02	0.00	2.91	*
Pleuragramma antarcticum	0.16	0.01	1.63	1.11	4.74	*
Rhincalanus gigas	39.53	0.45	0.00	0.07	4.05	*
Sagita gazellae	4.74	0.33	0.06	0.12	10.17	***
Sagitta marri	0.07	0.00	0.00	0.00	1.12	–
Salpa thompsoni	3.30	103.92	3.86	1.68	8.03	***
Siphonophore nectophore	1.95	0.22	0.01	0.11	2.68	–
Themisto gaudichaudii	0.01	0.00	0.00	0.00	0.40	–
Thysanoessa macrura	65.49	0.25	0.11	1.56	10.07	***
Tomopteris carpenteri	0.44	0.00	0.01	0.00	2.42	–

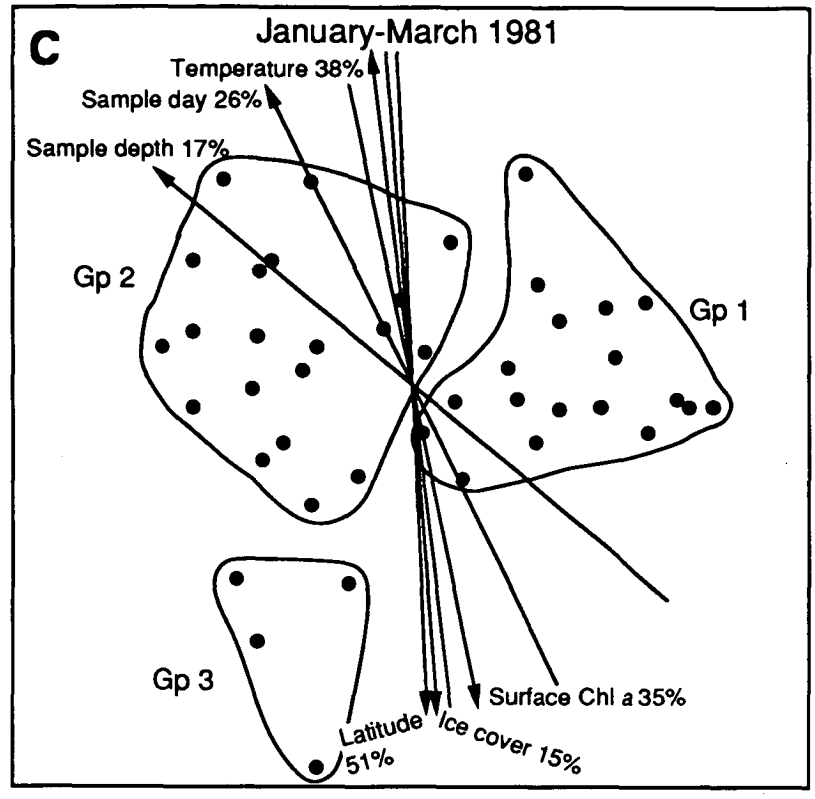
Fig. 3.6 Ordination plots of sampling sites for each survey using non-metric multidimensional scaling and Bray-Curtis dissimilarity index. Respective cluster groups indentified in Fig. 3.4 are superimposed. Significant multiple regressions between ordination scores and environmental parameters are shown, as well as the fraction (%) of variance in the zooplankton data explained by the parameter (see Table 3.6). Direction of regression line was determined from Equation 3.2. Axis scales are relative in NMDS, based on non-metric ranking of dissimilarity, and therefore are not shown. Stress values are **a** 0.15, **b** 0.14, **c** 0.18, **d** 0.18. **c) & d)** shown next page.

3.6


a
November-December 1982
Gp 3b
Latitude 35%
T°C 28%
Gp 3a
Gp 1
Chl a 38%
Gp 2


b
January 1985
Ice edge 60%
Latitude 68%
Salinity 28%
Chl a 27%
Gp 2
Gp 5
Gp 3
Gp 1
12
10
59
53
Gp 4
T°C 36%

3.6


c
January-March 1981
Temperature 38%
Sample day 26%
Sample depth 17%
Gp 2
Gp 1
Gp 3
Surface Chl a 35%
Latitude 51%
Ice cover 15%

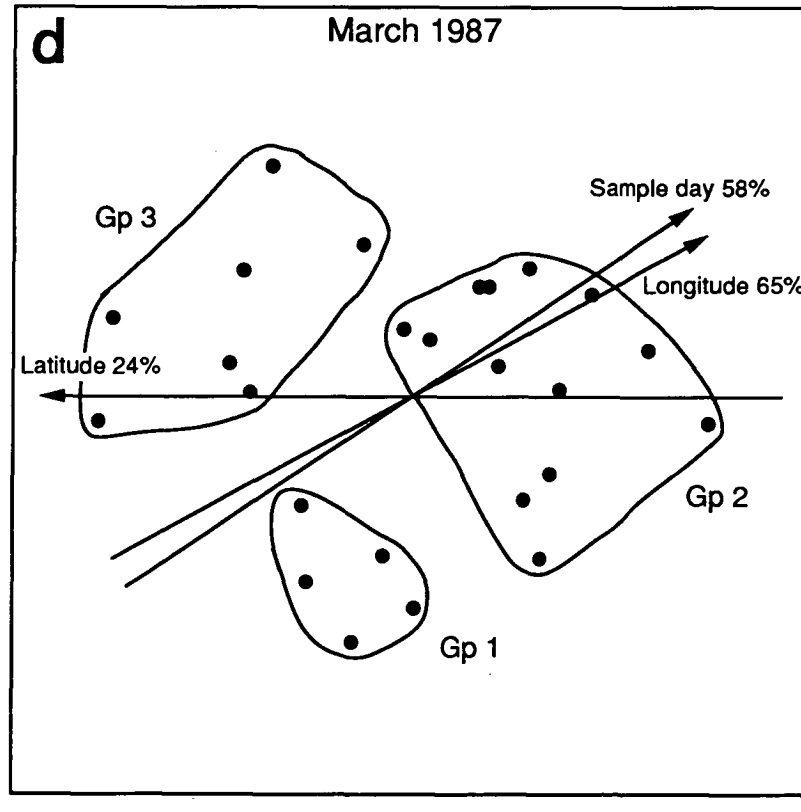
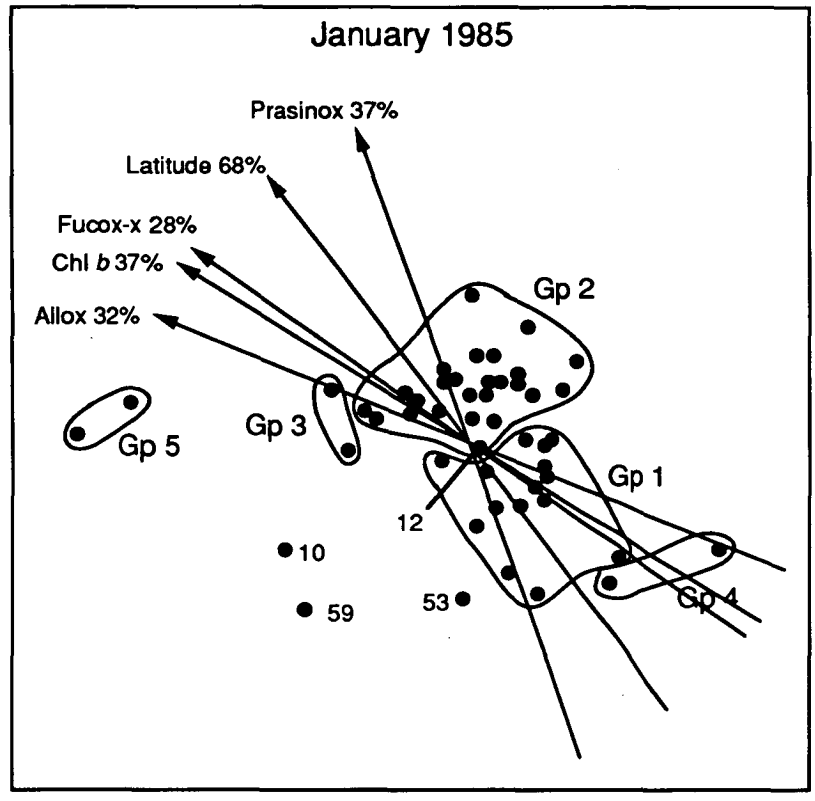

d
March 1987
Gp 3
Sample day 58%
Longitude 65%
Latitude 24%
Gp 2
Gp 1

Fig. 3.7 Additional NMDS ordination plots of sampling sites for Janury 1985 (Fig. 3.6b), with significant multiple regressions between ordination scores and phytoplankton pigments (Table 3.9). Cluster groups indentified in Fig. 3.4b are superimposed.



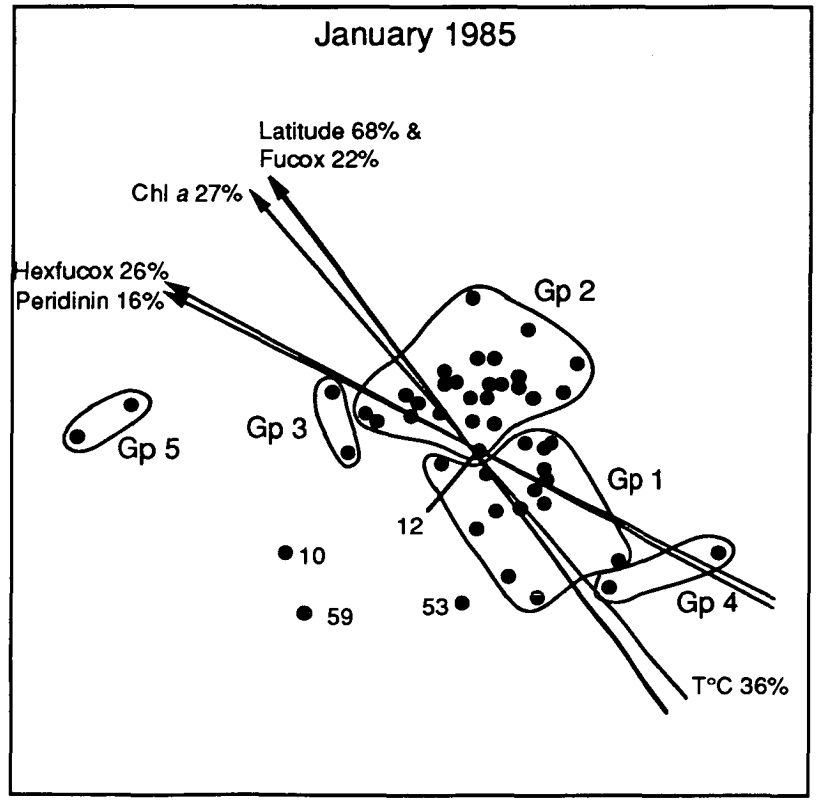


Table 3.6 Multiple regression analyses between environmental parameters and NMDS scores for two-axis ordination of comparison of sampling sites. Regression weights are derived from Equation 3.2. Adj.R^2 = Adjusted coefficient of determination which gives the fraction of the variance accounted for by the explanatory variable (Jongman *et al.* 1987). For ANOVA P values; * < 0.05, ** < 0.005, *** < 0.0005, ns = not significant. Tables **c.** & **d.** on next page.

a. November-December 1982

	Direction Cosines (Regression Weights)					
VARIABLE	X	Y	Adj. R^2	F	DF	P
Chlorophyll a	-0.819	-0.573	0.378	6.785	2,17	*
Latitude	-0.897	0.442	0.347	12.151	2,40	***
Temperature	0.906	0.424	0.284	7.136	2,29	**
Salinity	—	—	0.040	1.623	2,28	ns
Sampling Day	—	—	0.014	1.294	2,40	ns
Longitude	—	—	-0.007	0.848	2,40	ns
Sampling Depth	—	—	-0.010	0.798	2,40	ns
Duration Haul	—	—	-0.028	0.435	2,40	ns
Pack Ice Cover	—	—	-0.040	0.198	2,40	ns

b. January 1985

	Direction Cosines (Regression Weights)					
VARIABLE	X	Y	Adj. R^2	F	DF	P
Latitude	-0.595	0.804	0.684	52.924	2,46	***
Ice Recession	-0.617	0.787	0.604	37.653	2,46	***
Temperature	0.735	-0.678	0.355	11.725	2,37	***
Salinity	-0.234	0.972	0.279	8.559	2,37	**
Chlorophyll a	-0.652	0.759	0.271	8.805	2,40	**
Duration Haul	—	—	0.065	2.660	2,46	ns
Sampling Depth	—	—	0.062	2.590	2,46	ns
Longitude	—	—	0.002	1.044	2,46	ns
Sampling Day	—	—	-0.015	0.644	2,46	ns

Table 3.6 Continued.

c. January-March 1981

VARIABLE	Direction Cosines (Regression Weights) X	Y	Adj. R^2	F	DF	P
Latitude	0.047	-0.999	0.509	22.257	2,39	***
Temperature	-0.113	0.994	0.381	11.788	2,33	***
Chl a at surf.	-0.199	-0.980	0.349	9.582	2,30	**
Sampling Day	-0.431	0.902	0.263	8.334	2,39	**
Sampling Depth	-0.760	0.650	0.173	5.282	2,39	*
Ice cover	0.077	-0.997	0.146	4.514	2,39	*
Ice recession	—	—	0.034	1.719	2,39	ns
Longitude	—	—	-0.028	0.437	2,39	ns
Duration Haul	—	—	-0.031	0.382	2,39	ns
Salinity	—	—	-0.035	0.402	2,33	ns

d. March 1987

VARIABLE	Direction Cosines (Regression Weights) X	Y	Adj. R^2	F	DF	P
Longitude	0.877	0.480	0.649	23.161	2,22	***
Sampling Day	0.828	0.560	0.584	17.873	2,22	***
Latitude	-1.000	-0.016	0.237	4.737	2,22	*
Duration Haul	—	—	0.132	2.824	2,22	ns
Surface Chl a	—	—	0.070	1.756	2,18	ns
Sampling Depth	—	—	-0.021	0.750	2,22	ns
Temperature	—	—	-0.037	0.609	2,20	ns
Pack Ice Cover	—	—	-0.053	0.397	2,22	ns
Ice Recession	—	—	-0.085	0.062	2,22	ns

group, the spatial coverage is not sufficient to determine if there is further off shore zonation. There were a number of frequency ($2\Delta I$) indicator species for the oceanic group, many with significantly high abundances (Tables 3.4 and 3.5).

Group 2 represented a very loose grouping of 4 sites. One site, station 50, is located in the far north of the Prydz Bay region, while three of the sites are located on the continental shelf. The cluster was fragmented at 65% dissimilarity, but at 81.3% was grouped with the other continental shelf stations. The NMDS plots also show the four sites as a distinct group (Fig. 3.6a) more closely aligned with Group 3. There was no unique species distinguishing this group from the others in terms of frequency indicators. Group 2 did have a significantly higher abundance of *Salpa thompsoni* (Table 3.5), which would be the prime reason why the northern station is linked with the in shore sites. *Antarctomysis maxima* was also in high abundance in this group but only at the one site close to the Amery Ice Shelf.

Much of the region was covered by pack-ice, but the degree of pack-ice cover did not explain any of the geographic variation (Table 3.6a). Integrated chlorophyll *a* accounted for most of the variation in the data at 38%, while 28% of the variation could be explained by mean temperature (Table 3.6a, Fig. 3.6a). Fig. 3.5a shows quite a distinct north-south pattern, but latitude explained only 35 % of the data. In the three-axis ordination, latitude accounted for 65% of the variation ($F = 27.0$, $DF = 3,39$, $P < 0.0005$). Latitude was mainly associated with the third axis, and consequently was less evident when the ordination was reduced to two axes. There was no correlation between sampling parameters and the ordination scores.

In the inverse analysis, comparison of species, 27 of the taxa listed in Table 3.3 were analysed. The euphausiid *E. triacantha* was not collected in this particular year, but was regularly observed in other years. Four

groups of species were defined at 90% dissimilarity (Fig. 3.8a). The major group (A) comprised 19 species, with most being indicator species of the oceanic station Group 1 (Tables 3.4a and 3.5). This assemblage contained all of the dominant copepods, chaetognaths, siphonophores, appendicularians and the euphausiid *Thysanoessa macrura*. Three sub-groups could be further defined at 80% dissimilarity but the NMDS analysis showed that these sub-groups overlapped considerably (Fig. 3.9a). The split at 90% would therefore appear justified. Group B mainly comprised species associated with the continental shelf. *E. crystallorophias, P. antarcticum* and *P. macropterus* were identified as indicator species of the southern part of Prydz Bay (Fig. 3.5a), while *E. superba* was an indicator of the northern part of the shelf. Gammarids, which were also part of Group B, were identified as indicator species of the shelf region in 1981 (see below), but not so for 1982. The cluster analyses and NMDS plot both show that *E. superba* formed a sub-group (86% dissimilarity) from the three inner shelf species which reflects the difference between the shelf sub-groups defined previously (Fig. 3.5a). The NMDS plot also indicates that the hyperiid *Hyperiella dilatata* has perhaps more affinity with the in shore species group (Fig. 3.9a). The salp *S. thompsoni* was clearly separate from other species. As mentioned above this species characterised the station Group 2, particularly Station 50 in the north where the catch consisted almost entirely of salps. The fourth group (D) comprised just two species, *Euphausia frigida* and *Themisto gaudichaudii*. The latter species was an indicator of northern waters in January 1985 and March 1987, while the larvae and adults of *E. frigida* are usually restricted to waters north of the divergence (John 1936; Chapter 6).

Fig. 3.8 Dendrograms of inverse cluster analyses comparing dominant species, defined as those with a >4% numerical dominance for any given sampling site, for any sampling cruise (Table 3.3). The Bray-Curtis dissimilarity index was used for the comparison with UPGMA linkage, after standardizing species abundance (Equation 3.3). Selection of species groups were arbitrary for each survey.

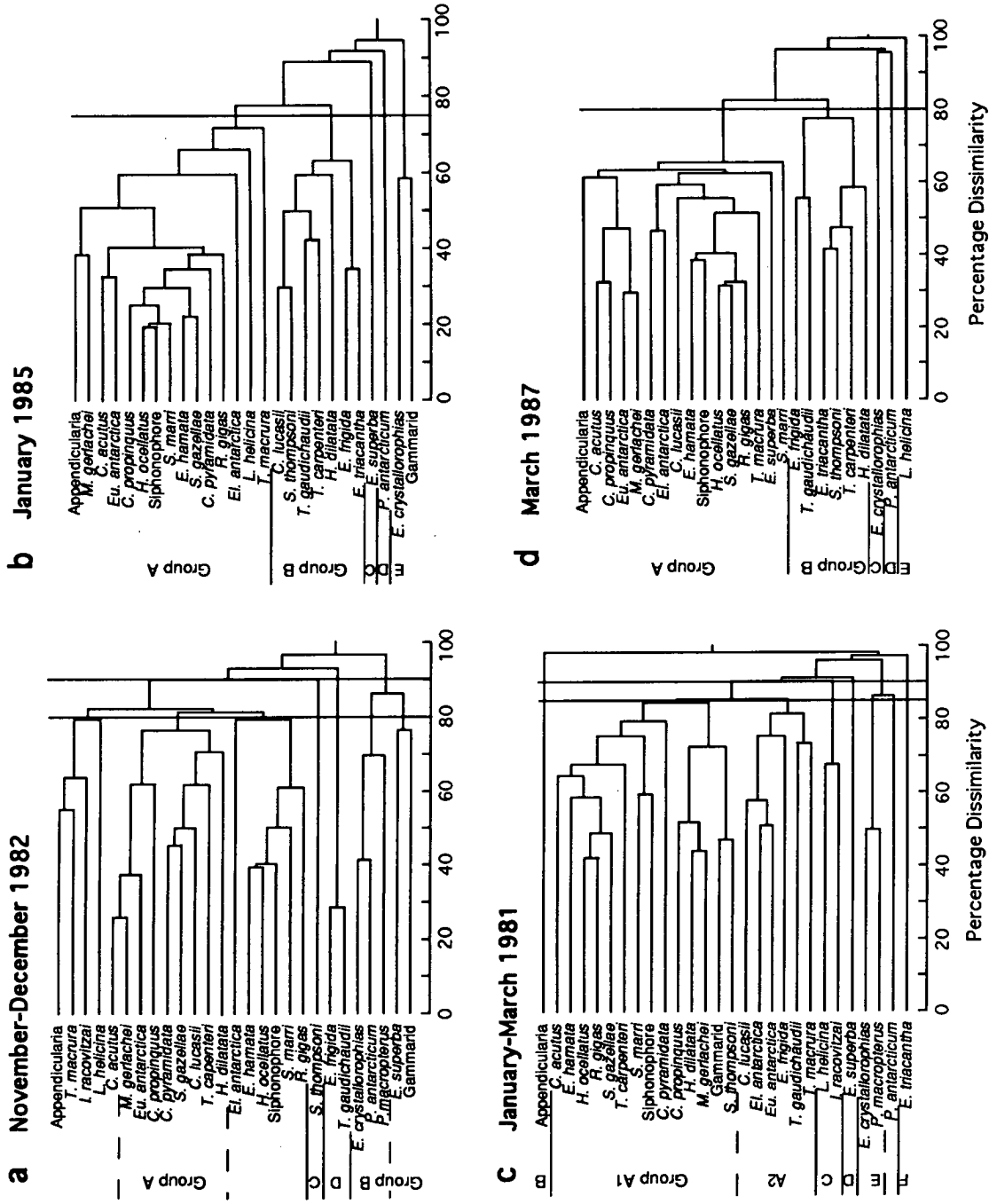
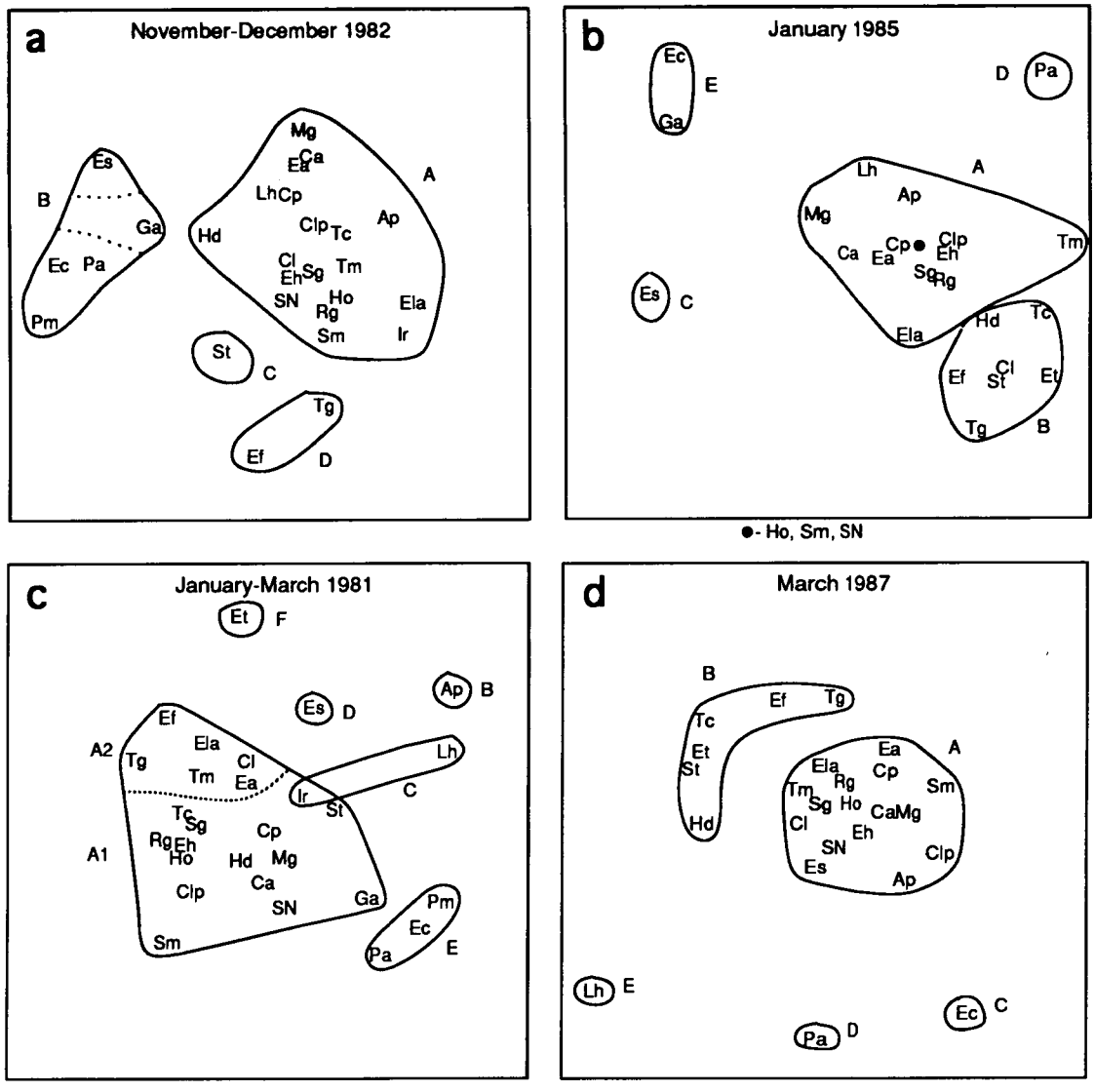


Fig. 3.9 NMDS inverse ordination plots comparing dominant species. Respective cluster groups indentified in Fig. 3.8 are superimposed. Species abbreviations used in the plots are shown in Table 3.3. Axis scales are relative in NMDS and therefore are not shown. Stress values are **a** 0.17, **b** 0.14, **c** 0.22, **d** 0.16.



Cluster analysis showed two distinct outlier stations, 1 and 59. Station 1 (Fig. 3.1b) was characterised by a very high abundance of *S. thompsoni,* which represented more than 98% of the biomass of the catch. Station 59 returned the lowest abundance for any sampling site with very few taxa caught compared to the other stations. Subsequent re-analysis, after removing these stations, produced exactly the same groupings as the first cluster analysis for the rest of the stations.

At 38% dissimilarity two main groups were defined with 15 and 25 stations each respectively, three smaller groups of two stations each, and three sites which were ungrouped (Figs. 3.4b, 3.5b). Group 5, comprising the continental shelf sites 26 and 29, was the only group distinct from the rest of the sites at 64% dissimilarity. This group was characterised by *E. crystallorophias* and *P. antarcticum,* but also by the complete absence of prominent species such as *Haloptilus ocellatus, Sagitta marri* and *S. thompsoni* (Tables 3.7 and 3.8). The lack of clear separation amongst the rest of the cluster groups, and the low dissimilarity, indicates some degree of homogeneity in the zooplankton composition in the off shore stations. Nonetheless, the geographic plot of stations shows a further partitioning, mainly latitudinally, amongst the off shore stations (Fig. 3.5b). The boundary between Group 1, the northern stations, and Group 2 occupying the middle of the Prydz Bay region does meander to some degree. Further, the NMDS plot (Fig. 3.6b) shows that Station 12 in Group 2 is perhaps more aligned with Group 1. These two groups, as well as Groups 3 and 4, share common abundance indicator species, e.g. *Eukrohnia hamata,* and *Sagitta gazellae,* which distinguish these groups from the in shore stations (Table 3.7). These two species were also the only indicator species of Group 3, which was closely aligned with Group 2 (Fig 3.6b). Group 2 was also characterised by the higher abundance of a

Table 3.7 January 1985. Mean abundances, analysis of variance (F) and SNK multiple range tests of dominant species in cluster groups defined in Fig. 3.4b. 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 =4,41.

Species	Group 1 Mean	Group 2 Mean	Group 3 Mean	Group 4 Mean	Group 5 Mean	F	P
Appendicularia	0.19	0.83	1.64	0.00	0.00	4.84	**
Calanoides acutus	5.51	15.97	9.93	2.28	3.57	9.01	***
Calanus propinquus	5.38	24.13	10.16	6.60	2.78	13.70	***
Clio pryamidata	5.49	18.90	2.15	7.09	1.91	6.23	**
Cyllopus lucasii	1.21	0.22	0.00	11.48	0.00	19.52	***
Electrona antarctica	0.69	0.45	0.00	1.10	0.00	2.22	–
Euchaeta antarctica	0.85	3.47	1.16	6.27	1.05	10.89	***
Eukrohnia hamata	26.75	41.11	15.41	1.07	2.04	11.41	***
Euphausia crystallorophias	0.00	0.88	0.31	0.00	14.48	13.32	***
Euphausia frigida	2.25	1.91	0.00	15.75	0.00	2.66	*
Euphausia superba	3.61	8.20	14.49	1.72	6.06	1.20	–
Euphausia triacantha	0.22	0.53	0.00	3.09	0.00	2.38	–
Gammaridae	0.00	0.01	0.05	0.00	0.62	8.17	***
Haloptilus ocellatus	0.97	3.53	0.71	0.60	0.00	11.77	***
Hyperiella dilatata	0.20	0.08	0.06	0.61	0.00	2.89	*
Limacina helicina	0.19	1.03	0.06	0.10	0.00	1.30	–
Metridia gerlachei	0.17	4.54	4.53	0.06	2.29	6.71	***
Pleurogramma antarcticum	0.01	0.17	0.00	0.00	0.12	0.19	–
Rhincalanus gigas	40.87	38.54	7.51	2.35	1.17	7.02	***
Sagitta gazellae	17.84	17.38	4.65	6.21	0.56	9.35	***
Sagitta marri	1.25	3.04	0.89	0.00	0.00	12.98	***
Salpa thompsoni	113.46	6.86	0.00	489.68	0.00	25.64	***
Siphonophore nectophore	9.42	19.27	5.68	2.41	1.60	17.04	***
Themisto gaudicaudii	0.42	0.07	0.00	9.99	0.00	25.22	***
Thysanoessa macrura	4.70	8.16	4.88	11.75	0.68	1.83	–
Tomopteris carpenteri	0.47	0.38	0.00	5.61	0.00	2.80	*

Table 3.8 January 1985. Frequencies of occurrence of indicator species distinguishing cluster groups defined in Fig. 3.4b. 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 = 15, Group 2 = 25, Group 5 = 2 and total number of sites = 49. * not dominant species and were not used in SNK or inverse species analyses.

a. Group 1 (northern oceanic) indicators species

Species	Group 1	Remaining Sites
**Vibilia* sp.	13	7
Electrona antarctica	15	17
None		

b. Group 2 (southern oceanic) indicator species

Species	Group 2	Remaining Sites
Appendicularia	21	7
**Tomopteris septentrionalis*	18	7

c. Group 5 (neritic) indicator species

Species	Group 5	Remaining Sites
None		
Euphausia crystallrophias	2	2
Pleuragramma antarcticum	2	3

number of other species compared to their abundance in Group 1, e.g. *Calanus propinquus* and siphonophores (Table 3.7).

The salp *S. thompsoni* also had a wide geographic range, although abundances decreased southwards, and was not found in Groups 3 and 5. However, this species dominated the northern stations with its exceptionally high abundances and is thus the most notable indicator species in Groups 1 and 4. North of 63° S this species comprised 73% of the total zooplankton biomass by wet weight, and 90% north of 62° S. The outlier Station 1 was also noted for a high proportion of salps in the catch and should thus belong to station Group 1. The high abundance of salps undoubtedly would have masked the contribution of other species as indicators for Group 1.

Apart from the abundance indicators, there were a few frequency indicator species that discriminated Groups 1 and 2, these being *Vibilia* sp. and *Electrona antarctica* larvae for Group 1, and appendicularians for Group 2 (Table 3.8). The latter taxon was also an abundance indicator. The myctophid *E. antarctica* occurred at all Group 1 stations, but also at 15 of the 25 sites in Group 2. Consequently this species had a $2\Delta I$ score that was only significant at the 5% level, while appendicularians and *Vibilia* sp. were both significant at 1%.

The northeastern Group 4 was characterised by the high abundance of the two hyperiids *Cyllopus lucasii* and *T. gaudichaudii,* the copepod *Euchaeta antarctica* and chaetognath *S. gazellae* but also by the absence of the chaetognath *S. marri* which occurred in all Group 1 and 2 stations.

The geographic plot of station groups displays a distinct latitudinal zonation. Not surprisingly then, latitude produced the highest correlation value with ordination scores explaining 68% of the variation in the 2 axes ordination (Table 3.6b). The receding ice edge was the best of the environmental variables explaining 60% of the variation. Integrated values of temperature, salinity and chlorophyll *a* explained 36%, 28%

and 27% of the variation, respectively. Zeaxanthin (cyanobacteria) was the only phytoplankton marker pigment that did not correlate with NMDS scores. Four pigments in particular explained a greater amount of the variation than chlorophyll *a*. These were chlorophyll *b* (38%), prasinox (37%), alloxanthin (32%) and fucox-x (28%) (Table 3.9a, Fig. 3.7). These pigments also formed significant regressions directly with latitude (Table 3.9b), although Fig. 3.7 shows that their respective regression lines against NMDS scores were not as closely aligned with the latitude regression as were the ice, temperature and chlorophyll *a* regressions (compare Fig. 3.6b with Fig. 3.7). Both chlorophyll *b* and prasinox are marker pigments for prasinophytes, e.g. in Prydz Bay waters species of *Mantoniella* (Marchant *et al.* 1989). Density and the number of taxa at sampling sites were two community variables weakly negatively correlated with chlorophyll *b* : for density F=4.645, Adj. R^2=0.076, R=-0.312, P=0.039, DF=1,43; and taxa F=4.297, Adj. R^2=0.070, R= -0.301, P=0.047, DF=1,43. There was no correlation between these community parameters and prasinox. None of the sampling parameters was correlated with the ordination scores.

In the inverse analysis of species, all 26 of the major dominant species were analysed. The two additional species *I. racovitzai* and *P. macropterus* were not observed in this year. Five groups were defined at 75% dissimilarity - two main groups, a minor group of two species and two singles species groups (Fig. 3.8b). In the larger group of 15 species (Group A), all three chaetognath species, two of the six copepod species, the siphonophores, and *Clio pyramidata* were indicator species of the main oceanic station Group 2 in the centre of the region (Fig. 3.4b). Group A also contained *Metridia gerlachei, Calanoides acutus, Rhincalanus gigas,* and appendicularians which occurred in higher abundances in the station Group 2, though this was not considered significant in the SNK multiple range test (Table 3.7). *S. gazellae* and

Table 3.9 a. Multiple regression analyses between phytoplankton pigments and NMDS scores for two-axis ordination of comparison of sampling sites in January 1985. Regression weights are derived from Equation 3.2. **b.** Linear regression of phytoplankton pigments and latitude. 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. January 1985 Multiple Regression - phytoplankton pigments and zooplankton

	Direction Cosines (Regression Weights)					
VARIABLE	X	Y	Adj. R^2	F	DF	P
Chlorophyll *b*	-0.848	0.529	0.375	13.586	2,40	***
Prasinox	-0.333	0.943	0.372	13.440	2,40	***
Alloxanthin	-0.925	0.381	0.321	10.944	2,40	***
Fucox-x	-0.814	0.581	0.275	8.956	2,40	**
Chlorophyll *a*	-0.652	0.759	0.271	8.805	2,40	**
Hexfucox	-0.880	0.476	0.260	8.382	2,40	**
Fucoxanthin	-0.599	0.801	0.219	6.891	2,40	**
Peridinin	-0.892	0.452	0.163	5.083	2,40	*
Zeaxanthin	—	—	-0.001	0.980	2,40	ns

b. January 1985 Linear Regression - phytoplankton pigments and latitude

VARIABLE	Adj. R^2	R	F	DF	P
Prasinox	0.422	0.660	31.651	1,41	***
Chlorophyll *a*	0.321	0.581	20.887	1,41	***
Fucox-x	0.312	0.573	20.056	1,41	***
Chlorophyll *b*	0.311	0.572	19.938	1,41	***
Fucox	0.310	0.571	19.861	1,41	***
Alloxanthin	0.243	0.511	14.484	1,41	***
Hexfucox	0.224	0.492	13.107	1,41	**
Peridinin	0.159	0.423	8.941	1,41	**
Zeaxanthin	0.139	0.399	7.78	1,41	*

E. hamata were also abundance indicator species of the northern station group (Group 1). The next species group (B) of 7 species contained three species, *C. lucasii, S. thompsoni* and *T. gaudichaudii* which were defined as indicator species for the northern station group. In addition, the two euphausiids have distributions known to be confined primarily to waters of the Antarctic Circumpolar Current (ACC) (John 1936; Baker 1966; Kittel *et al.* 1985; Smith & Schnack-Schiel 1990). The NMDS analysis showed a close association between the two species Groups A and B (Fig. 3.9b), but also suggests the larvae of *Electrona antarctica,* a frequency indicator species of the northern stations, have as much affinity with Group B as Group A. Group E comprised the in shore species assemblage, i.e. *E. crystallorophias* and gammarids. *P. antarcticum* was also a shelf indicator species, but was isolated from the other species (Figs 3.8b & 3.9b). *E. superba* was also classified as a single species group at the 75% dissimilarity level. The NMDS analysis more clearly shows the dissociation of *E. superba* from the other species (Fig. 3.9b).

January-March 1981

Three main cluster groups were defined at 73% dissimilarity (Figs 3.4c & 3.5c). Group 3 comprised 4 continental shelf stations. In addition to *E. crystallorophias,* gammarids and the larvae of *P. antarcticum,* a number of other species were defined as indicator species for shelf stations, including siphonophores and the copepod *C. acutus* (Tables 3.10 & 3.11). The latter two taxa were previously described as indicators of the oceanic stations. Station 16 (Fig. 3.1c) west of Davis was defined as an outlier, but distantly grouped with the in shore sites at 79.9% dissimilarity. This site comprised only 8 taxa and 71 specimens in total, with a density of 2.4 individuals 1000 m^{-3}, which is considerably less than

Table 3.10 January-March 1981. Frequencies of occurrence of indicator species distinguishing cluster groups defined in Fig. 3.4c. 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 = 18, Group 2 = 20, Group 3 = 4. * not dominant species and were not used in SNK or inverse species analyses.

a. Group 2 indicators species from Group 1

Species	Group 2	Group 1
Eukrohnia hamata	19	3
Haloptilus ocellatus	12	1
Calanoides acutus	19	8
**Vanadis antarctica*	16	5
Rhincalanus gigas	20	12
Tomopteris carpenteri	20	12

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

Species	Group 3	Group 1
Pagetopsis macropterus	4	1
Gammaridae	4	2
* Hippolytidae larvae	3	0

Table 3.11 January-March 1981. Mean abundances, analysis of variance (F) and SNK multiple range tests of dominant species in cluster groups defined in Fig. 3.4c. 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 =2,39.

Species	Group 1 Mean	Group 2 Mean	Group 3 Mean	F	P
Appendicularia	0.03	0.00	0.00	2.15	–
Calanoides acutus	2.08	9.24	21.35	7.88	**
Calanus propinquus	4.40	12.61	1.84	2.03	–
Clio pryamidata	0.97	6.36	0.05	6.49	**
Cyllopus lucasii	0.36	0.66	0.03	0.43	–
Electrona antarctica	0.33	0.29	0.00	0.43	–
Euchaeta antarctica	0.13	1.69	0.66	2.28	–
Eukrohnia hamata	0.02	1.12	0.16	4.54	*
Euphausia crystallorophias	0.002	0.004	7.92	14.62	***
Euphausia frigida	0.82	0.32	0.05	0.32	–
Euphausia superba	168.46	3.20	0.86	62.44	***
Euphausia triacantha	0.00	0.01	0.00	0.54	–
Gammaridae	0.01	0.03	0.10	3.48	*
Haloptilus ocellatus	0.002	0.13	0.01	5.99	*
Hyperiella dilatata	0.01	0.09	0.02	3.04	–
Ihlea racovitzai	0.01	0.37	1.00	4.03	*
Limacina helicina	0.05	0.02	0.69	4.05	*
Metridia gerlachei	0.06	0.84	0.74	2.53	–
Pagetopsis macropterus	0.002	0.001	0.91	23.19	***
Pleuragramma antarcticum	0.03	0.02	22.82	35.64	***
Rhincalanus gigas	0.20	13.86	0.31	20.29	***
Sagitta gazellae	0.21	2.68	0.07	10.22	***
Sagitta marri	0.001	0.03	0.00	0.97	–
Salpa thompsoni	0.62	0.55	0.53	0.01	–
Siphonophore nectophore	0.05	0.33	0.61	3.29	*
Themisto gaudichaudii	2.69	4.31	0.02	0.63	–
Thysanoessa macrura	28.30	15.84	0.84	1.31	–
Tomopteris carpenteri	0.23	0.58	0.01	2.54	–

the mean density of Group 3 zooplankton of 63.0±78.6 individuals 1000 m^{-3}. The most abundant species at Station 16 were *E. crystallorophias,* and the larvae of *P. antarcticum* and *P. macropterus*. This similarity in composition explains the link with Group 3 sites.

Group 2 represents the main group of stations lying east-west in the middle of the region (Fig. 3.5c). This group was distinguished by much the same species, copepod and chaetognaths (Tables 3.10 & 3.11), that characterised the oceanic groups described above, i.e. Group 1 in Fig. 3.5a and Group 2 in Fig. 3.5b. Group 1 separates Group 2 oceanic stations from the in shore stations but also borders Group 2 to the north. The single indicator species of this group was *E. superba,* which represented nearly 80% of Group 1 catches in terms of density (Table 3.11). Station 48 was an outlier, distantly linked with Groups 1 and 2 at 80.3% dissimilarity (Fig. 3.4c). This station just north of Mawson (Fig. 3.1c), had the highest abundance of *S. thompsoni* for any site, as well as a very high abundance of *C. pyramidata.* At other stations with a high proportion of *C. pyramidata* there were no salps. This coupled with the low abundance of other species would explain the lack of similarity with other sites.

In the NMDS ordination, latitude explained 51% of the variation in the data, while mean temperature and surface chlorophyll *a* values accounted for 38% and 35% of the variation respectively (Table 3.6c, Fig. 3.6c). The only other environmental parameter correlated with the ordination scores was pack-ice cover which explained <15% of the variation. The time in days since the start of the sampling period explained 26% of the observed pattern. In addition, the choice of sampling depth, this being a cruise when horizontal trawls were employed, also accounted for some 17% of the variation in the data.

Six groups were defined in the comparison of species cluster analysis at the 90% dissimilarity level, comprising a major group of 20 species and a number of single and double species groups (Fig. 3.8c). The main group

(Group A) could be split into two sub-groups at the 85% level. The NMDS analysis shows a split at this level is valid. Group A1 is similar in composition to the main species assemblages discussed above (Groups A in Figs 3.8a,b) and for 1987 (see below). This group also contained the indicator species for the main oceanic group of stations (Group 2 in Fig. 3.5c). Gammarids were also found in this group and yet were defined as frequency and abundance indicators of the shelf group of stations (Fig. 3.5c). The NMDS analysis (Fig. 3.9c) does shows the gammarids more closely aligned with the Group E shelf species of *E. crystallorophias, P. antarcticum* and *P. macropterus*. Group A2 contained species described as being associated with northern stations in 1985, but also contained three species, *Euchaeta antarctica, Electrona antarctica* and *T. macrura* described in the previous 1982 and 1985 surveys as belonging to the main species group of copepod/chaetognath/siphonophores (Group A in Figs 3.9a,b). In turn, *S. thompsoni* was included in Group A1, whereas in other years (Figs 3.8a,b) it was either isolated or associated with the *E. frigida, E. triacantha, C. lucasii* and *T. gaudichaudii* species group (Group B in Fig. 3.9b). Nor was *E. triacantha* associated with these species in this particular sampling season (Fig. 3.9c). This may well be an artefact of analysis caused by this species' low abundance in 1981. Appendicularians were also in very low abundance and were also a single species cluster group. However, the NMDS analyses does group appendicularians with *Limacina helicina*. This latter species was grouped with the salp *I. racovitzai* in the cluster analysis (Fig. 3.8c), but in the ordination *I. racovitzai* was separate from *L. helicina* and grouped with Group A1. *E. superba* was clearly dissociated from the other species at 91% dissimilarity. As noted above, this species occurred in high abundance in station Group 1 (Fig. 3.5c) and was the only indicator species for that group of stations.

Overall, there is some disagreement between the cluster and ordination results, some interchange of species between species groups, as well as different and additional indicator species for the shelf area. These differences may be attributable in part to some degree of geographical mixing of species groups detected due to the extended sampling - with sampling period accounting for 26% of the variation in the comparison of sampling sites. The interchange of species between Groups A1 and A2 could also be due to the lack of sampling north of 62° S resulting in the poor representation of northern species and therefore not being discerned as a distinct group as observed in 1985.

March 1987

The cluster analysis produced two main groups and one outlier Station 83 in the north (Fig. 3.1d) at the 55% dissimilarity level (Fig. 3.4d). Station 83 was dominated by the hyperiid *T. gaudichaudii,* which represented 55% of the catch in terms of wet weight. At 53 % dissimilarity, three main groups were defined, plus an additional outlier, Station 65 near Davis (Fig. 3.1d). This station was dominated by *E. crystallorophias,* representing 85% of the catch by wet weight and yet this site was linked to Group 3 which had no *E. crystallorophias* representation (Table 3.12). The NMDS plot (Fig. 3.6d) shows three distinct main station groups, and validates the selection at 53%.

The major group (Group 2) comprised most of the stations in the eastern part of the region and was distinguished from the western sites by very high abundance of the same copepod and chaetognath species that characterised the main oceanic groups in other years. Group 3 stations were characterised by low abundances - the mean total zooplankton density for the dominant species was nearly 10 times lower than that of

Table 3.12 March 1987. Mean abundances, analysis of variance (F) and SNK multiple range tests of dominant species in cluster groups defined in Fig. 3.4d. 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 =2,22.

Species	Group 1 Mean	Group 2 Mean	Group 3 Mean	F	P
Appendicularia	0.00	0.55	0.04	2.10	–
Calanoides acutus	4.75	141.45	12.30	19.22	***
Calanus propinquus	1.54	67.61	3.80	19.93	***
Clio pyramidata	2.35	30.44	0.89	1.74	–
Cyllopus lucasii	0.87	2.07	0.11	1.30	–
Electrona antarctica	0.03	0.40	0.00	2.49	–
Euchaeta antarctica	0.45	6.11	0.18	4.87	*
Eukrohnia hamata	1.79	13.28	4.39	4.50	*
Euphausia crystallorophias	0.15	0.05	0.00	0.90	–
Euphausia frigida	0.43	5.11	0.00	2.13	–
Euphausia superba	44.95	11.44	0.23	12.84	***
Euphausia triacantha	0.55	0.95	0.00	1.09	–
Haloptilus ocellatus	0.56	2.30	0.61	5.34	*
Hyperiella dilatata	0.09	0.09	0.10	0.00	–
Limacina helicina	0.00	0.00	0.01	1.32	–
Metridia gerlachei	1.12	7.40	0.06	5.05	*
Pleuragramma antarcticum	0.50	0.00	0.03	2.00	–
Rhincalanus gigas	3.34	40.05	8.84	8.73	**
Sagitta gazellae	1.88	5.14	1.61	5.35	*
Sagitta marri	0.04	1.81	0.08	4.96	*
Salpa thompsoni	2.23	27.09	0.13	1.47	–
Siphonophore nectophore	2.60	4.21	3.36	0.25	–
Themisto gaudichaudii	3.01	10.88	1.62	0.72	–
Thysanoessa macrura	5.40	7.17	0.78	11.41	***
Tomopteris carpenteri	0.02	0.05	0.01	0.61	–

Group 2 (Table 3.12). There were no indicator species for Group 3. The predominant species in Group 1 sites was *E. superba*, which comprised 76% to 92% of the catch wet weight. *T. macrura* was both a Group 1 and 2 indicator species, i.e. Group 3 was distinguished by the low abundance of this species (Table 3.12).

There were few frequency indicators. Group 2 was distinguished from the remaining sites by the chaetognath *Sagitta marri* which occurred in 11 of the 13 Group sites and three of the remaining 12. Group 2 was specifically separated from Group 1 by the hyperiid *Primno macropa* (not a dominant species) which was found in 9 of the Group 2 sites and not in any of Group 1. The 2ΔI information scores for *S. marri* and *P. macropa* were only significant at 5%.

Latitudinal zonation was a feature of the previously discussed data sets. The March 1987 data set, however, exhibited a distinct longitudinal zonation. In the NMDS ordination, longitude explained 65% of the variation, while latitude accounted for 24% (Table 3.6d, Fig. 3.6d). The time in days since the start of the sampling period also explained a significant amount of the observed pattern - 58%. In the 3-axes ordination, integrated temperature and ice recession explained 75% ($F = 22.9$, $DF = 3,19$, $P < 0.0005$) and 27% ($F = 4.0$, $DF\ 3,21$, $P = 0.02$) of the variation, respectively. However, these parameters were mainly correlated with the third axis (regression weight = -0.994) and were not significant variables when the ordination was reduced to two axes (Table 3.6d).

Gammarids, *I. racovitzai* and *P. macropterus* were not observed in this season and therefore only 25 species were used in the inverse species analysis. Two major groups were defined at 82% (Fig. 3.8d). Group A comprised the same main species group identified in the other three years, i.e. all the copepod and chaetognath species, siphonophores, appendicularians and *T. macrura*. Nine of the species were abundance

indicators of the main station Group 2 in the eastern half of the Prydz Bay region (Fig. 3.5d). Unlike previous years, *E. superba* was clearly linked with this group of species (Figs. 3.8d, 3.9d). Group B comprised *T. gaudichaudii* (dominant at Station 83), *S. thompsoni,* and the two euphausiids *E. frigida* and *E. triacantha*. *Tomopteris carpenteri* and *H. dilatata* were also associated with these species. This species grouping was also defined in the 1985 data set (compare Groups B in Figs. 3.8 b,d). *C. lucasii* previously associated with *E. frigida* and *T. gaudichaudii* in 1981 and 1985, was linked with the main species Group A. The remaining three species, *E. crystallorophias, P. antarcticum* and *L. helicina* formed single species groups. The continental shelf group of species was not a distinct group in the comparison of species. This is mainly due to sampling being restricted to just one site west of Davis where *E. crystallorophias* was the dominant species. Although *P. antarcticum* was also collected at this site, the two species did have different distributions. *P. antarcticum* was also found at stations 70 and 71, while *E. crystallorophias* was found at stations 66 and 96 (Fig. 3.1d).

Discussion

Species Assemblages

There was considerable consistency in the species associations defined for each year, despite different sampling methodology and sampling at different times of the year. Further, there was good correspondence between the species groups and the indicator species defined for the station groups. Consequently, the various species associations shown in Figs. 3.8 and 3.9, can be combined into four principal species assemblages or communities that can be related back to

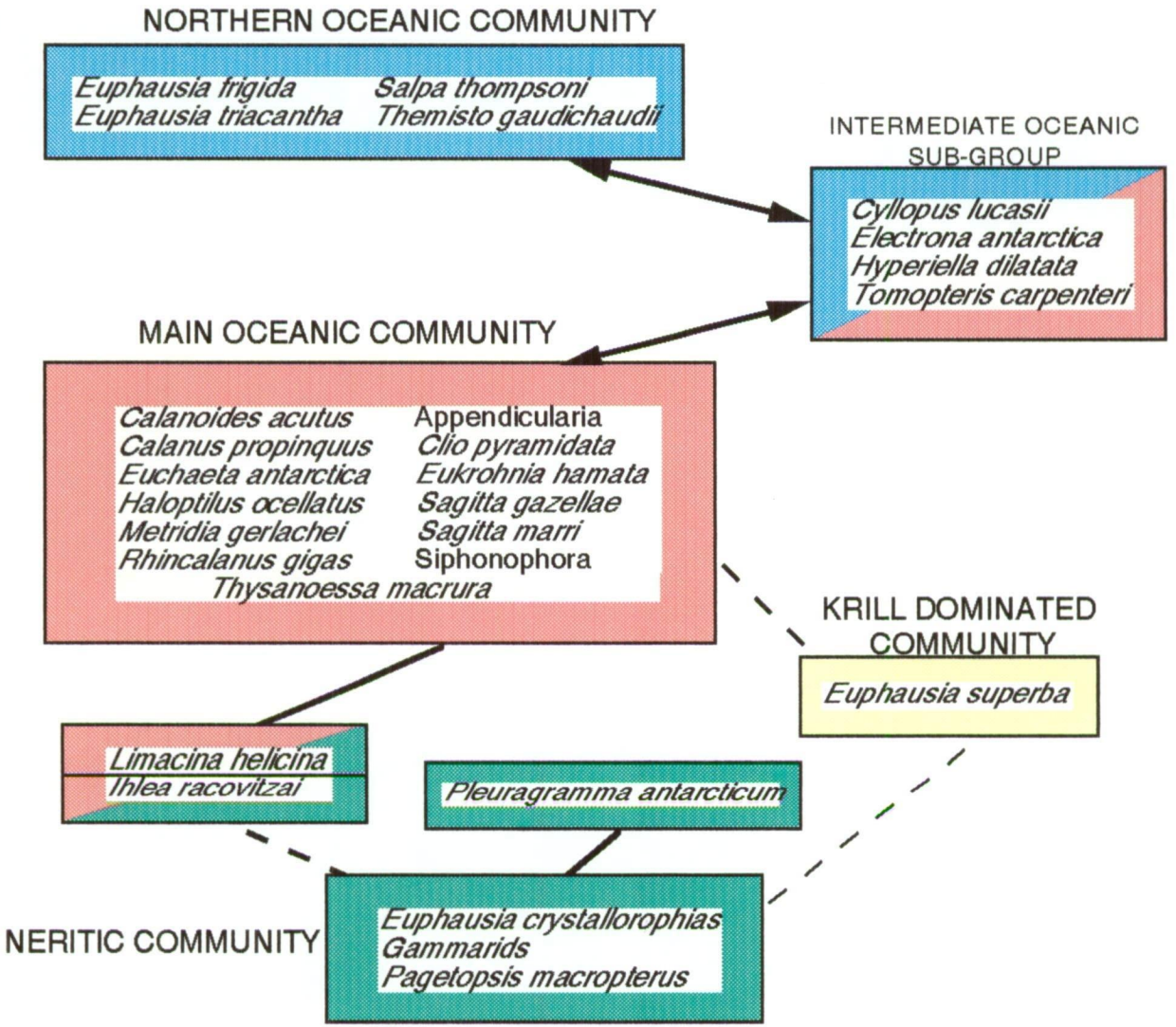
specific geographical areas where these assemblages are dominant. These communities are the neritic, the main oceanic community, a northern oceanic community and an *E. superba* dominated community (Fig. 3.10). Each assemblage is coded with a colour corresponding to the areas in Fig. 5 where that assemblage predominated.

Neritic Community. The neritic or shelf group was characterised by *E. crystallorophias.* When present, gammarids and the larvae of *P. macropterus* formed a close association with this euphausiid. This assemblage dominated the in shore region of Prydz Bay south of 67° 30'S, although these species were found elsewhere on the shelf. *Pleuragramma antarcticum* is also a neritic species but only formed a partial association with the other three species. Differences in the respective distributions of *P. antarcticum* and *E. crystallorophias* are probably the main reason why there is a slight dissociation. The larvae of *P. antarcticum,* especially those <25 mm in length, are readily carried off shore. Their distribution closely follows the western boundary of the Prydz Bay gyre (Fig. 2.10). Williams & Duhamel (in press) describe this in more detail. The larvae of *E. crystallorophias* are also carried off shore by the gyre, whereas the adult *E. crystallorophias* are confined to the shelf (Chapter 6). Both the larvae of *P. antarcticum* and *E. crystallorophias* are useful indicators of water of Prydz Bay/shelf origin moving off shore.

Main Oceanic Community. The main oceanic assemblage comprised the bulk of the numerically dominant species found in the region. This included all the abundant copepod species, particularly the herbivores *C. propinquus, C. acutus* and *R. gigas,* as well as the associated carnivores such as chaetognaths. Chaetognaths are one of the principal predators of copepods, with *E. hamata* alone responsible for reducing the copepod biomass by as much as 12% (Øresland 1990). Included in this assemblage are the euphausiid *T. macrura,* the pteropod *C. pyramidata,* appendicularians and siphonophores collectively. All

Fig. 3.10 Zooplankton communities derived from the comparison of species analyses (Figs 3.8 & 3.9) and indicator species defined for the station groups. Each assemblage is coded with a colour corresponding to the areas in Fig. 3.5 where that assemblage predominated.

3.10


NORTHERN OCEANIC COMMUNITY
Euphausia frigida
Euphausia triacantha
Salpa thompsoni
Themisto gaudichaudii
INTERMEDIATE OCEANIC SUB-GROUP
Cyllopus lucasii
Electrona antarctica
Hyperiella dilatata
Tomopteris carpenteri
MAIN OCEANIC COMMUNITY
Calanoides acutus
Calanus propinquus
Euchaeta antarctica
Haloptilus ocellatus
Metridia gerlachei
Rhincalanus gigas
Thysanoessa macrura
Appendicularia
Clio pyramidata
Eukrohnia hamata
Sagitta gazellae
Sagitta marri
Siphonophora
KRILL DOMINATED COMMUNITY
Euphausia superba
Limacina helicina
Ihlea racovitzai
Pleuragramma antarcticum
NERITIC COMMUNITY
Euphausia crystallorophias
Gammarids
Pagetopsis macropterus

species in this assemblage are notable for having wide circumpolar distributions. For example, the copepods (Vervoort 1951), the three chaetognaths (O'Sullivan 1982) and *T. macrura* (Mauchline & Fisher 1969) have distributions that extend south from the Antarctic Convergence onto or near the continental shelf. The copepod *H. ocellatus* is usually found south of 60°S (Vervoort 1951). During this study, members of this assemblage were at times collected at shelf stations, and hence overlapped the distribution of the neritic assemblage. In 1981 (Fig. 3.5c), siphonophores and *C. acutus* were also abundance indicator species of the shelf region. A Polish survey in 1969, where a much finer plankton mesh (50 μm) was used than that of the present study, found copepodites of *C. acutus, C. propinquus* and *M. gerlachei* widely distributed over the shelf region of Prydz Bay (Zmijewska 1983). While the species of the main oceanic community have extensive geographic distributions, the present study has shown they were generally more abundant in, and thus dominated, the region between the continental shelf edge and 62-63°S. The northern limit approximates the southern boundary of the Antarctic Circumpolar Current (ACC). Pakhomov (1989) also found pteropods and siphonophores to be major abundant groups in the area south of the Antarctic Divergence in the Prydz Bay region, but not north of the divergence, nor in shelf waters. The oceanic and neritic zones were distinguished both by the differences in species composition as revealed by the information statistic, and also by the differences in abundances of species common in both areas.

The salp *I. racovitzai* and the pteropod *L. helicina* were two species that were not distinctly associated with either the neritic or oceanic communities. Both species were associated primarily with the main oceanic community but were also abundance indicators of the neritic zone in 1981. *L. helicina* has been described as a typical inhabitant of the shelf regions in the Weddell and Ross Seas (Smith & Schnack-Schiel

1990), but also as being a member of both the neritic and oceanic communities around the Antarctic Peninsula (Piatkowski 1989b; Siegel & Piatkowski 1990). Little is known of the detailed distribution and ecology of *I. racovitzai* other than it has a wide circumpolar distribution south of the convergence but may prefer waters colder than 0°C (Foxton 1971). Neither *I. racovitzai* or *L. helicina* can be considered as reliable indicator species.

Northern Oceanic Community. Differences in species abundances was perhaps the main feature distinguishing the northern oceanic and main oceanic communities, rather than differences in species composition. The northern assemblage comprised four main species, the euphausiids *E. frigida, E. triacantha,* the hyperiid *T. gaudichaudii* and the salp *S. thompsoni.* These species have been described previously as being confined to or more abundant in the waters of the West Wind Drift (Baker 1966; Foxton 1966; Kane 1966; Smith & Schnack-Schiel 1990). Both *S. thompsoni* and *T. gaudichaudii* were collected at most stations north of the shelf, but had significantly higher abundances in the northern waters, generally north of 62°S, where they were abundance indicator species of that region. The exceptionally high abundance of salps in January 1985 would have concealed the importance of some of the species of the main oceanic assemblage which were also found in northern waters. Pakhomov (1989) also observed higher abundances of *S. thompsoni* and *T. gaudichaudii* in waters north of the Antarctic Divergence in Prydz Bay in both February/March 1985 and 1986. Pakhomov reported that *E. frigida* was also more abundant north of the divergence. In the present study, neither *E. frigida* or *E. triacantha* was found to be an indicator of northern waters. Both species were sparsely distributed through most of the oceanic area. *E. frigida* was more abundant in the two north-eastern stations in January 1985 (Group 4 in Table 3.7, Fig. 3.5b), but this was not significant in terms of SNK, nor did

the two species have significantly high abundances in any other station group. Nonetheless, these species did form associations with *S. thompsoni* and *T. gaudichaudii* (Fig. 3.9b,d), although this is less evident in January-March 1981 when northern waters were not sampled in detail. The larvae of *E. frigida* are confined to waters of the ACC (Chapter 6), and are perhaps better indicators than the adults.

Electrona antarctica, C. lucasii, H. dilatata and *T. carpenteri* formed an intermediate oceanic sub-group of species that were, at different times, associated either with the northern assemblage or the main oceanic assemblage. Species of *Cyllopus* and *Vibilia* are obligate symbionts of salps (Madin & Harrison 1977), and Ainley *et al.* (1988) reported the close association of these taxa with *S. thompsoni* in the Weddell Sea. Similarly in January 1985, *C. lucasii* and *Vibilia* sp. were commonly distributed in the northern waters where *S. thompsoni* was most abundant. All three species were indicators of the northern sites (Fig. 3.5b). Moreover, both the cluster (Fig. 3.8b) and NMDS analyses (Fig. 3.9b) show a very close affinity between *C. lucasii* and *S. thompsoni* in January 1985. The NMDS analyses also showed that in November 1982 the hyperiid *H. dilatata* had a closer affinity to the neritic species than with the main oceanic assemblage (Fig. 3.9a). In January (1985) *H. dilatata* had a near equidistant affinity with the main oceanic and northern species communities (Fig. 3.9b), while in March 1987 this species was clearly associated with the northern species group (Fig. 8d). Siegel & Piatkowski (1990) described the same situation in the Antarctic Peninsula region, with *H. dilatata* moving from the neritic community in spring (November) to the oceanic in summer (February). They concluded that this species was not a reliable indicator species. Although the polychaete *T. carpenteri* and the larvae of the myctophid *Electrona antarctica* are members of the intermediate sub-group, their oceanic distributions are not in dispute. The myctophid was never found on the shelf during this

study, while *T. carpenteri* was only found at two shelf sites, once each in 1981 and 1982.

Krill Dominated Community. Euphausia superba was, for most of the time, dissociated from all other species. Krill did form a distant association with the neritic species in 1982 and a more substantial association with the main oceanic assemblage in 1987. However, in those surveys plus 1981, krill were important abundance indicators of geographic areas distinct from the main oceanic and neritic distributions. In 1985, krill were not indicators of any station group, but were most abundant in station Group 3 near the shelf edge between the oceanic and neritic zones (Table 3.7). Hydroacoustic studies in that season also indicated a higher biomass of krill in the shelf edge area (Higginbottom *et al.* 1988). Studies by Pakhomov (1989), Bibik & Yakolev (1991) and Ichii (1990) have also shown that krill are more abundant near the continental shelf edge between 60° and 80°E in Prydz Bay. The shelf region was proposed as a major spawning region for krill (Chapter 6). The results from 1981, 1982 and 1985 of the present study have also shown that krill were primarily localized and are dominant near the continental shelf edge in a transition zone between the neritic and oceanic assemblages. In the krill dominated areas the non-krill zooplankton abundance is consistently lower (Fig. 3.11). In turn, the areas of high zooplankton abundance, generally dominated by the oceanic assemblages, are areas where krill were in very low abundance.

The low zooplankton abundances in the krill dominated areas may be a result of *E. superba* excluding other species from these areas via competition. Figure 3.12 shows that the combined mean abundances of the herbivorous copepods *C. acutus, C. propinquus* and *R. gigas* in the krill dominated areas decrease in relation to increases in krill abundance for the four surveys. Decreases in copepod numbers would also result in associated decreases in carnivores such as chaetognaths which depend on

Fig. 3.11 Comparison of mean krill, *E. superba*, density with remaining mean non-krill zooplankton density for each station group for the four surveys (Tables 3.5, 3.7, 3.11, 3.12). Station groups are ordered according to increasing krill abundances. Note: station group order for January 1985 (**b**) is near to north-south.

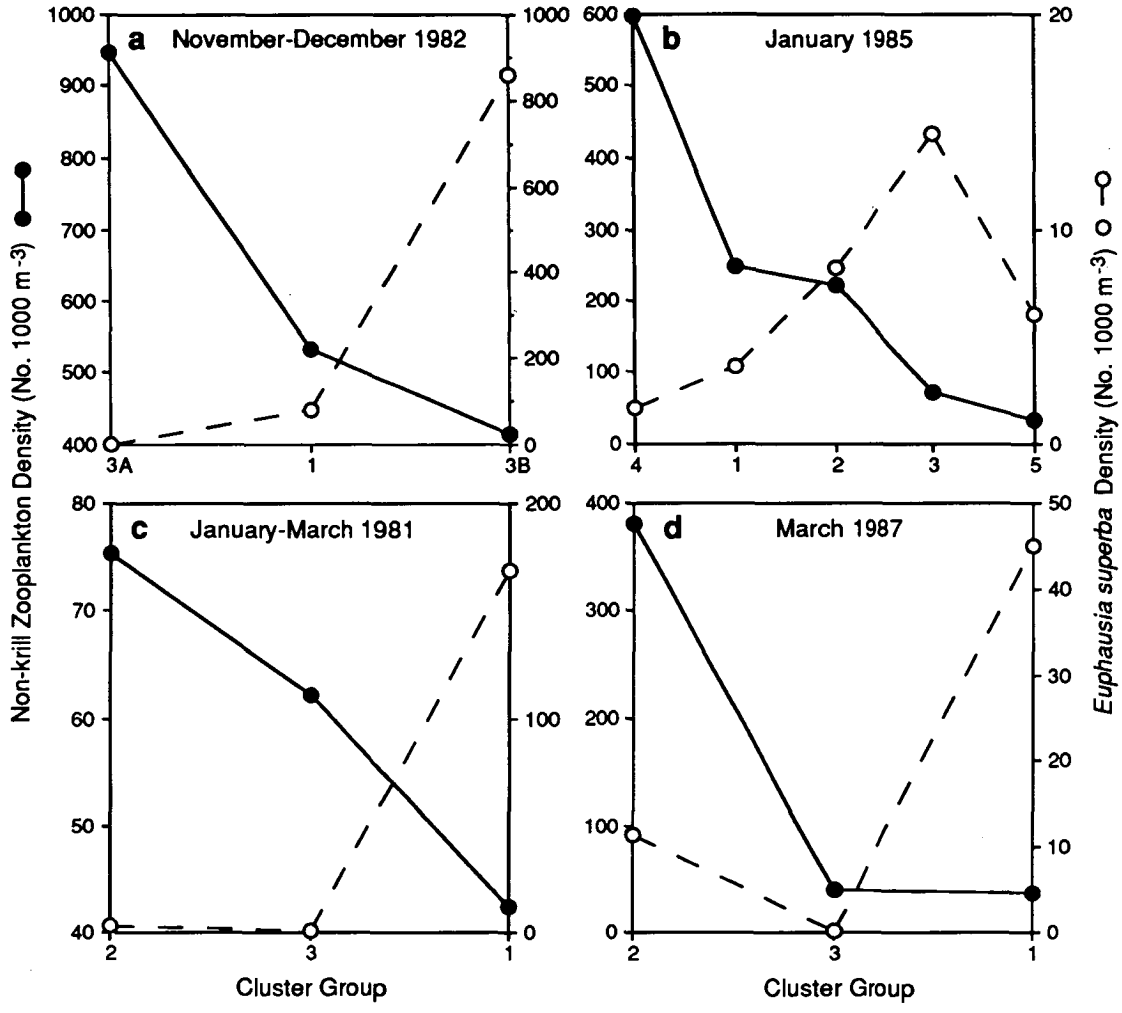
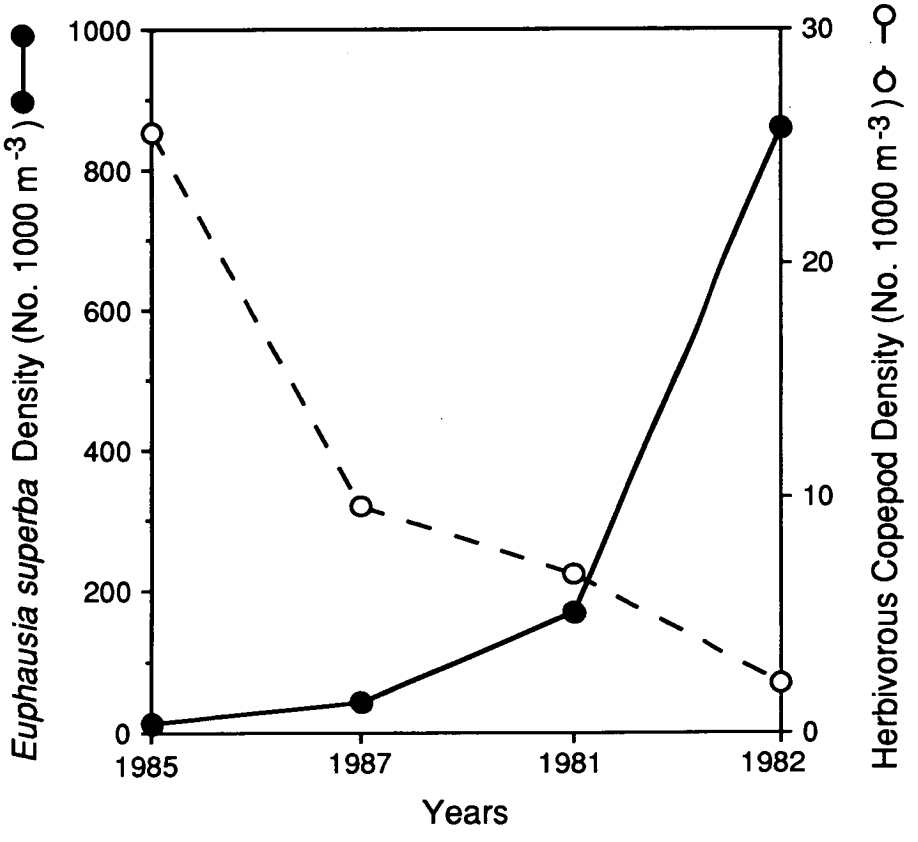


Fig. 3.12 Comparison of mean *E. superba* density with combined mean abundance of the herbivorous copepods *C. acutus, C. propinquus* and *R. gigas* in the krill dominated community areas for the four surveys. Survey years are ordered by increasing copepod abundance.



copepods. The reverse situation of herbivorous zooplankton excluding krill from the main oceanic community is possible, although at a localized level, krill would be expected to exclude other species from their living space as krill formed dense aggregations. A super swarm sampled in Prydz Bay was devoid of other species of zooplankton (Higginbottom & Hosie 1989).

An alternative to the "exclusion" theory, is that krill may simply dominate a region which is unsuitable for either the neritic or oceanic species. Neritic species would presumably avoid an oceanic existence, whereas the shelf edge is either the southern limit of oceanic species distributions or their abundance decreases towards and onto the shelf. In this study a number of species were consistently in very low abundance or more often absent from the shelf or near the shelf area, i.e. appendicularians, *Electrona antarctica, H. ocellatus, S. marri, C. lucasii* and *T. carpenteri,* as well as all members of the northern oceanic community. In addition, a number of widely distributed species had abundances that diminished toward the continent, i.e. *R. gigas, S. gazellae, E. hamata, C. pyramidata* and siphonophores (Table 3.7). Budnichenko & Khromov (1988) observed a similar north-south decrease in abundance of *R. gigas* in Prydz Bay in 1984. Figure 3.11 shows a clear trend of decreasing non-krill zooplankton abundance from the northern station groups towards and onto the shelf in January 1985. Figure 3.11 is also consistent with the theory of exclusion through competition. The exclusion theory could account for the distribution of the krill dominated community to the north of the main oceanic community in 1981, as well as the western distribution of the krill community away from the shelf edge in 1987, whereas the "unfavourable conditions" theory could not. On the other hand, the creation of large discrete areas of few zooplankton through exclusion alone is difficult to imagine and would perhaps be better explained by the "unfavourable conditions" alternative. Both

theories have merit and there is no reason why both situations could not be combined insofar as the exclusion of the zooplankton from an area is facilitated by their initial diminished numbers. Regardless of which theory prevails, it would appear that competition for resources is minimized through geographical separation of the main herbivorous groups - *E. crystallorophias* in the inner shelf area, copepods further off shore, and krill primarily in between with almost no overlap with salps in the far north.

There was much speculation and discussion during the Final BIOMASS Colloquium in Bremerhaven, September 1991, whether *E. superba* is really as important in Prydz Bay, and in other areas, as originally perceived. Certainly, a greater part of the oceanic region is dominated by copepods and salps, while the inner shelf is dominated by *E. crystallorophias,* an important dietary component of various vertebrates (Puddicombe & Johnstone 1988; Williams 1985, 1989). This study has shown, without doubt, that *E. superba* is the principal dominant species of large areas of the southern Prydz Bay region. These areas overlap the summer distribution of minke whales (Ichii 1990), and also various fish and birds that at times feed extensively on krill (Montague 1984; Williams 1985,1989; Green 1986; Green & Johnstone 1988; Ichii 1990; Armstrong & Siegfried 1991). Krill should still be viewed as the most important single species in the Prydz Bay area.

Geographical Variability and Controlling Factors

Sampling resolution of the shelf region was perhaps not ideal for an area of rapid transition between two communities. The amount of sampling that was carried out suggests little variability in the northern boundary of the neritic group, with this community consistently

dominating the region south of 67°S. It is more difficult to comment on the geographical variability in the northern oceanic community because this area was only covered in detail in 1985. There is no evidence to suggest much variability in the geography of the West Wind Drift, especially in relation to the southern boundary. Indeed there is evidence of consistency in the northern zooplankton, with Pakhomov (1989) describing near identical distributions and relative abundances of salps and hyperiids in the West Wind Drift in Prydz Bay for the January-February period of 1985 and 1986.

The greatest amount of variability was displayed by the main oceanic and krill dominated communities. For three of the years there was strong latitudinal zonation, although the north-south width varied somewhat, while there was a distinct longitudinal zonation between the two communities in March 1987. There are species that will favour or live in certain temperature and salinity regimes, e.g. *E. crystallorophias* lives in waters of predominantly <-1°C, while *S. thompsoni* is restricted to the warmer waters of the West Wind Drift. Temperature did account for much of the zooplankton data variation in three of the four years (Table 3.6). In January 1985 all four community zones were well represented and, along with temperature, salinity did explain some of the variation in the zooplankton distributions. The main oceanic and krill communities dominated the regression analyses in the other three years, and it would seem that horizontal salinity gradients have less or no effect on the collective zooplankton distributions between and within these communities. It also remains to be determined what effect vertical stratification of the water column has on community distributions.

The presence and duration of pack-ice cover is an important factor affecting the structure of the pelagic food web (Smith & Schnack-Schiel 1990). This influence comes firstly from the rotting early summer ice providing a favourable substrate facilitating high production of ice algae,

and thus an important and rich food source for krill and zooplankton (Smetacek *et al.* 1990). Secondly, as the ice recedes the melt water stabilizes the surface water layers where phytoplankton blooms rapidly develop (Hart 1942; Smetacek *et al.* 1990). The effects of ice recession could not be determined in November-December 1982, as much of the region was still covered by ice. Neither did the degree of pack-ice cover explain any of the data variation. Ice usually dissipates by the beginning of January in Prydz Bay (Jacka 1983). In January 1985, ice recession did account for a substantial amount of the variation, more so than chlorophyll *a*. Ice recession and phytoplankton were also proposed as a factor influencing the distribution pattern of *T. macrura* developmental stages during the same period (Chapter 6). The zooplankton and ice recession correlation may also be coincidental, since the two parameters both have a latitudinal pattern. Figure 3.6b shows the close alignment in ice and latitude regressions. There was no similar correlation between ice recession and zooplankton observed in the later months of 1981, 1987, but then this may not be expected 2 to 3 months after the ice has gone.

Smith *et al.* (1988) cautioned that the "snapshot" approach of comparing biological and environmental events from the same point in time, as described above, may not adequately reveal true relationships because different rates of environmental processes and community responses are involved. Despite such differences between the phyto- and zooplankton, chlorophyll *a* was another variable, along with temperature, that accounted for much of the variation in three of the four years. Presumably at the start of summer, the plankton interactions are driven by the receding ice. However, the exact relationship or nature by which chlorophyll affects zooplankton distributions, particularly in later months, is not clear and still needs to be established. For example, in this study, no significant relationship was found between chlorophyll *a* and any zooplankton community parameter, e.g. abundance or number

of taxa at a site. Nonetheless, by the end of summer, as shown by the March 1987 patterns, chlorophyll *a* no longer has an influence on the distribution patterns of the zooplankton and instead the north-easterly current became the single important controlling factor (Fig. 2.15).

Various studies have demonstrated consistency in the horizontal water circulation patterns in the Prydz Bay region between years, with little intra-annual variation (Khimitsa 1976; Tchernia & Jeannin 1983; Smith *et al.* 1984; Allison 1989; Hodgkinson *et al.* 1988, 1991a, 1991b; Middleton & Humphries 1989; see Figs. 2.10 to 2.15). Currents were expected to have a major influence on the distribution of the zooplankton throughout the summer sampling period. The currents near the shelf, as shown in Fig. 2.15, are believed to be responsible for the dispersion of euphausiid larvae (Chapter 6). Apart from the West Wind Drift, the north-easterly current out of Prydz Bay (Fig. 2.15) was the only other major current that would appear to have had an effect on zooplankton distributions at the community level. There was some indication in January 1985, that the main oceanic community was carried north-easterly, following the dispersal route of euphausiid larvae (Chapter 6). This pattern may also be an artefact of the analyses, as the boundary between the main and northern oceanic communities was based on a relatively low level of dissimilarity (38%). The likely effects of the north-easterly current were more pronounced in March 1987 when the main oceanic community was concentrated in the eastern part of the Prydz Bay region. No effect of this current was evident in 1981 or 1982. Neither would it seem that the Prydz Bay gyre or the East Wind Drift had any appreciable effect on community distributions, although both currents have been identified as transporting euphausiid larvae and larvae of neritic fish species off shore (Chapter 6; Williams & Duhamel in press).

Sampling Methods

The correlation between ordination scores and sampling day in the January-March 1981 data indicates that a significant time component was introduced into the data set by the protracted sampling period (Table 3.6c). More than likely, during the course of the 48 day sampling period, the very communities being sampled and defined had undergone a substantial change, possibly in distribution or composition. This complicated the analyses and interpretation of the data, especially in relation to defining possible causal effects. A sampling period of this duration is therefore not recommended. Instead, sampling surveys like the present study, should not extend beyond approximately 30 days, which was the length of the 1982 survey where no time component was detected.

The length of the sampling period was also correlated with ordination scores in March 1987 (Table 3.6d). This relationship, however, was probably not a valid result, but a statistical artefact caused by the sampling progressing from west to east coupled with a longitudinal zonation in the zooplankton. Sampling day was strongly correlated with longitude ($r=0.78$, $F=35.83$, $P<0.001$, $DF=24$) and Fig. 3.6d shows the close alignment of the sampling day and longitude regressions.

Analysis of the 1981 data was further complicated by the horizontal tows at fixed depths explaining some of the variation in the data. Different vertical migration patterns exhibited by zooplankton passing through a fixed sampling layer will most likely produce a bias in the data. Some species may not be adequately sampled at all. Oblique sampling over a greater depth range, e.g. 200 m, will mask the vertical migration bias, and is thus a better method in order to determine large scale community structures and patterns.

CHAPTER 4

MESOSCALE ZOOPLANKTON COMMUNITY DISTRIBUTION PATTERNS - JANUARY-FEBRUARY 1991.

Introduction

The four large scale surveys described in the previous chapter identified the existence of three zooplankton communities in the continental shelf edge area of Prydz Bay. A neritic community was located in the southern part of the Prydz Bay continental shelf, dominated by *Euphausia crystallorophias*, gammarids and larvae of *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 characterised 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 outer 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 hydroacoustic techniques (Higginbottom *et al.* 1988; Bibik & Yakolev 1991), research scale nets (Pakhomov 1989) and commercial trawls (Ichii 1990).

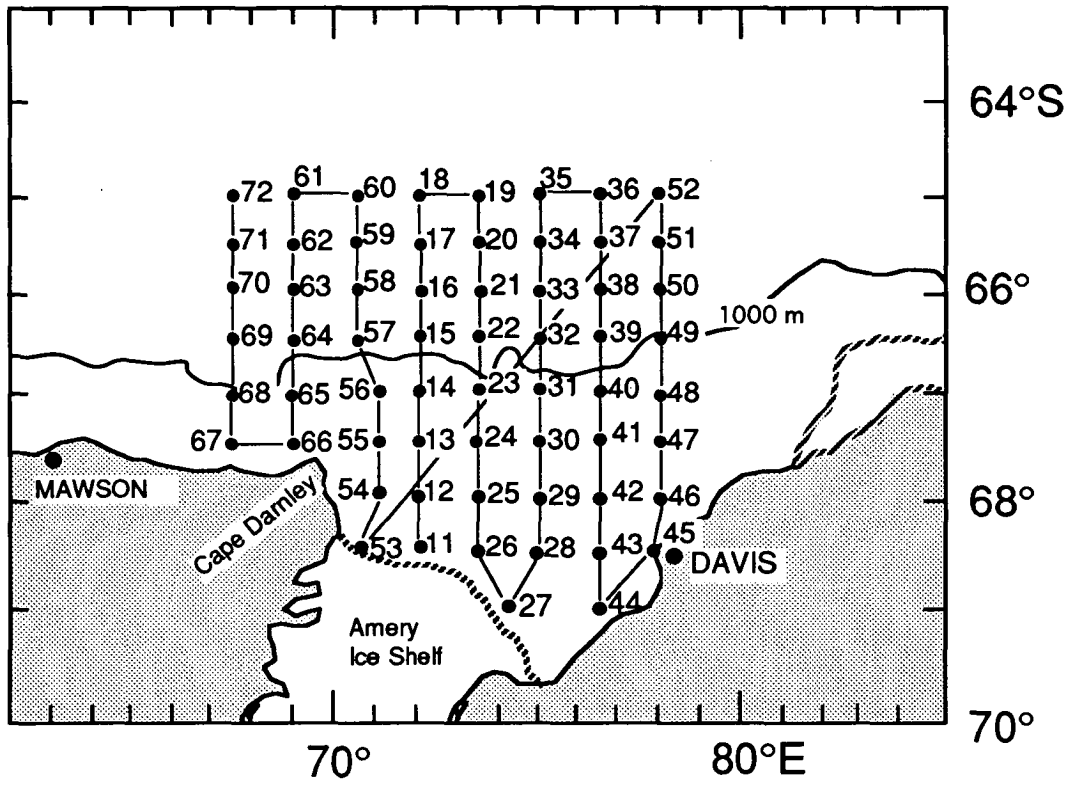
The continental shelf edge of Prydz Bay was thus identified as an area of particular interest because of the dominance of krill but also as an area of rapid transition between three major communities. It was also noted in the previous chapter that the sampling resolution of the shelf region in the earlier surveys was perhaps not ideal for accurately defining the distributions of these communities. In addition to describing the overall distribution and composition of zooplankton, the previous large scale surveys were designed for the purpose of studying the then

suspected larger scale distributions of adult krill (Marr 1962, Mackintosh 1973; Lubimova *et al.* 1985; Hosie *et al.* 1988), and later in 1985 and 1987 the distribution of the larvae of krill and other euphausiids (Chapter 6). 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), with the prime objective of more accurately defining the distributions and boundaries of the three main zooplankton communities 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 Chapter 3. The patterns defined in the present study were compared with various environmental parameters to determine which factors govern the zooplankton distributions at the mesoscale level, as compared to those parameters (Table 3.6) that explained macroscale distribution patterns. The distribution of the krill dominated community in relation to the shelf edge was of particular interest.

Methods

The Prydz Bay-continental shelf study area was defined for the present purpose as being from 67° 30' 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 eight longitudinal transects which were 1.5° of longitude apart (Fig. 4.1). Sampling commenced on 19 January in the south of Prydz Bay at station 11 - then progressed eastward to station 52 in the north-east. Sampling continued from station 53, again in the south of the bay, before progressing westward and finishing at station 72 on 14 February 1991. Sampling was originally planned to start along the western transect 67° 30'E, then continuing eastward. However, heavy

Fig. 4.1 Cruise track of the RSV *Aurora Australis*, 19 January to 14 February 1991, showing net sampling sites and the 1000 m contour are shown.



pack-ice (9-10/10 cover) extended from Mawson, through the western part of the study area, to at least 71°E. Sampling therefore started further East on the first relatively ice free transect 72°E. The pack-ice around Cape Darnley persisted throughout the sampling period and was the reason for the course deviation along transect 70° 30', between stations 53 and 57. Zooplankton were collected at each sampling site in a 0-200 m downward oblique haul using a Rectangular Midwater Trawl (RMT 8) - the same net system used in the macroscale studies and described in Chapter 3. 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 prior to retrieval. The net was equipped with a 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). Complete details of the sampling program, e.g. sampling position, time, depth, conditions, etc, are provided in Appendix I.

Shipboard and post-cruise processing of specimens was the same as described in Chapter 3. Unlike the macroscale surveys, ichthyoplankton were not included in the present analyses. Ichthyoplankton are the subject of another more detailed study on fish ecology in Prydz Bay (Williams 1992).

At each sampling site water samples were collected for phytoplankton pigment analysis, at depths of 0, 15, 30, 45, 60, 75, 90, 105, 120, 135 and 150 m, using a General Oceanics rosette sampler with twelve 5 L Niskin bottles (Wright 1987). The chlorophyll *a* level in each bottle was determined on board using a Turner Designs TD10 fluorometer. A Neil Brown Mark 3 CTD was mounted on the rosette which provided continuous profiles of conductivity/salinity and temperature.

Data Analyses

Cluster, non-metric multidimensional scaling (NMDS) and multiple regression analyses of the zooplankton data set, for both the comparison of sampling sites and species associations, were essentially the same as described in Chapter 3 and summarised in Fig. 3.2. The only difference from the previous macroscale surveys was that dominant species used in the ANOVA and species associations analysis were redefined. The reasoning was that the present study focussed more on the shelf area of Prydz Bay than in previous years and a different dominant species composition was anticipated. In addition, the mesoscale sampling survey did not cover the distribution of the northern oceanic community (NOC), which was generally found north of 63°S. Seventeen species were subsequently defined as >4% numerically dominant in the sampling area and these are shown in Table 4.1. The ctenophore *Pleurobrachia pileus* was the one new species that was not defined previously as a dominant species in the region (Chapter 3). Another five taxa were defined in the 1981 to 1987 surveys as numerically dominant in the southern part of the Prydz Bay region (Table 4.1) and were therefore included in the analysis to determine if species affinities had changed. Appendicularians were also described in the previous chapter as dominant in the southern part of the region. Few specimens were collected and from only two sites in the present study and hence this taxon was not included. Dominant species of the NOC were also not included, i.e. *Euphausia frigida, E. triacantha, Salpa thompsoni* and *Themisto gaudichaudii.*

Table 4.1 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 1991, or previously defined as dominant in the area in 1981 to 1987 surveys (Chapter 3).

Taxa with >4% numerical dominance in 1991
Calanoides acutus
Calanus propinquus
Clio pyramidata
Cyllopus lucasii
Decapod larvae
Euchaeta antarctica
Eukrohnia hamata
Euphausia crystallorophias
Euphausia superba
Ihlea racovitzai
Limacina helicina
Metridia gerlachei
Pleurobrachia pileus
Rhincalanus gigas
Sagitta gazellae
Siphonophora (Nectophores)
Thysanoessa macrura
Taxa defined as dominant 1981 to 1987
Gammaridae
Haloptilus ocellatus
Hyperiella dilatata
Sagitta marri
Tomopteris carpenteri

Results

Throughout these 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, e.g. Group A.

Comparison of Sampling Sites

An initial cluster analysis of sampling sites showed that there were three distinct outlier stations. Station 42 north-west of Davis (Fig. 4.1) had an exceptionally high abundance of *E. crystallorophias,* 1816 individuals 1000 m^{-3}, which represented approximately 98% of the catch both in numbers and wet weight biomass. Station 57 recorded the highest density of *E. superba,* 429 individuals 1000 m^{-3}, which represented 97% of the catch numbers and nearly 99% of the catch weight. Station 66 near Cape Darnley was the shallowest sampling site at 148 m. The RMT trawl only sampled down to 120 m. This site was characterised by low numbers of animals, 96 individuals for 2.34 grams, the lowest return for any sampling site.

Removal of the outlier sites from the data set and re-analysis produced two distinct cluster groups at the 50% dissimilarity level and two additional sub-groups at 48% (Fig. 4.2). The NMDS ordination showed that the three groups were quite distinct (Fig. 4.3). Group 1 comprised the majority of continental shelf stations, while Groups 2a and 2b were predominantly off-shelf sites separated east-west respectively (Fig. 4.4). The neritic sites were characterised by the euphausiid *E. crystallorophias* and by gammarids, both in terms of frequency of occurrence and high abundance (Tables 4.2a and 4.3). *Euchaeta antarctica,*

Fig. 4.2 Dendrogram of cluster analysis comparing zooplankton species composition at each sampling site. The Bray-Curtis dissimilarity index was used for the comparison with UPGMA linkage, after $\log_{10}(X+1)$ transformation of species abundance data.

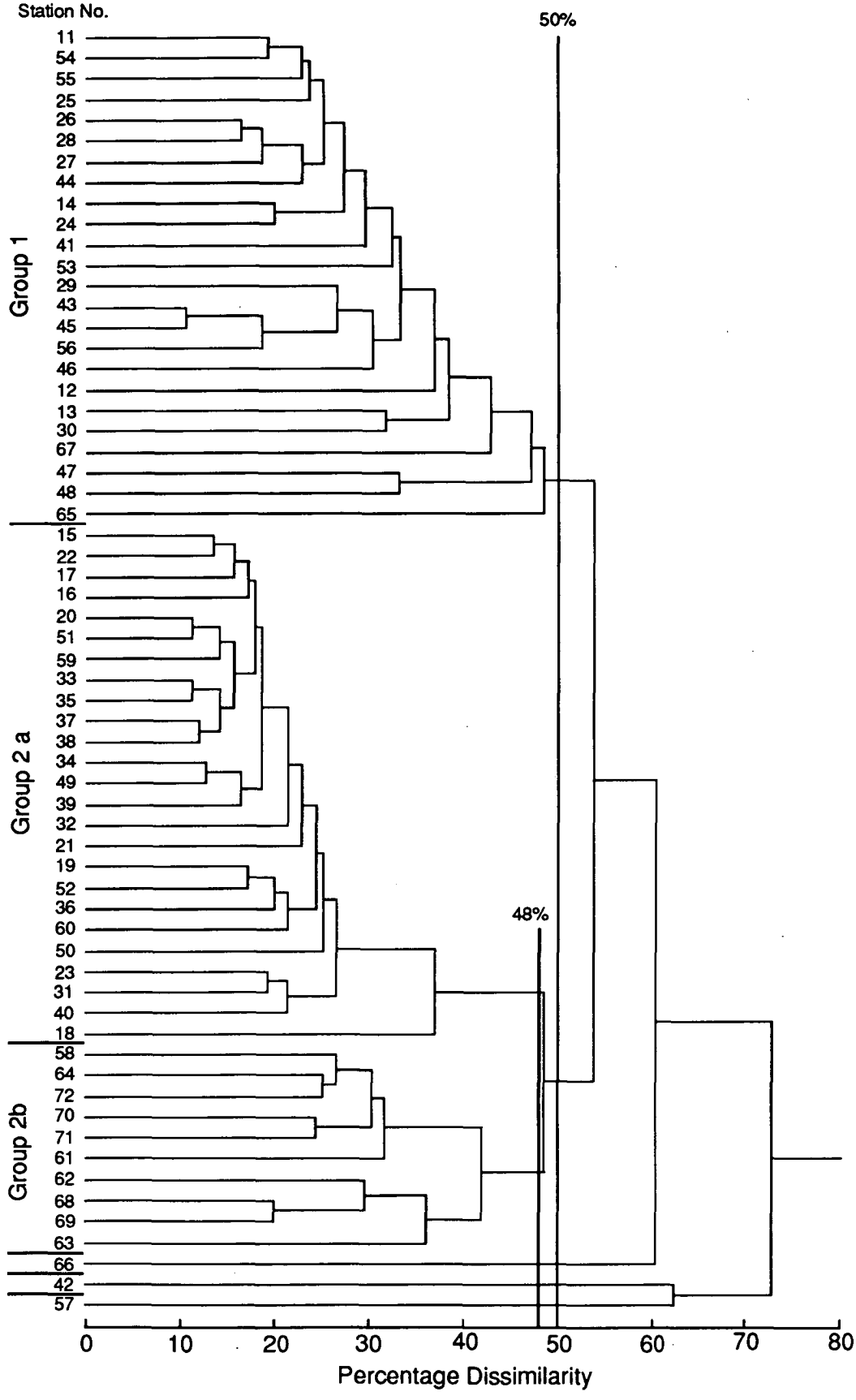
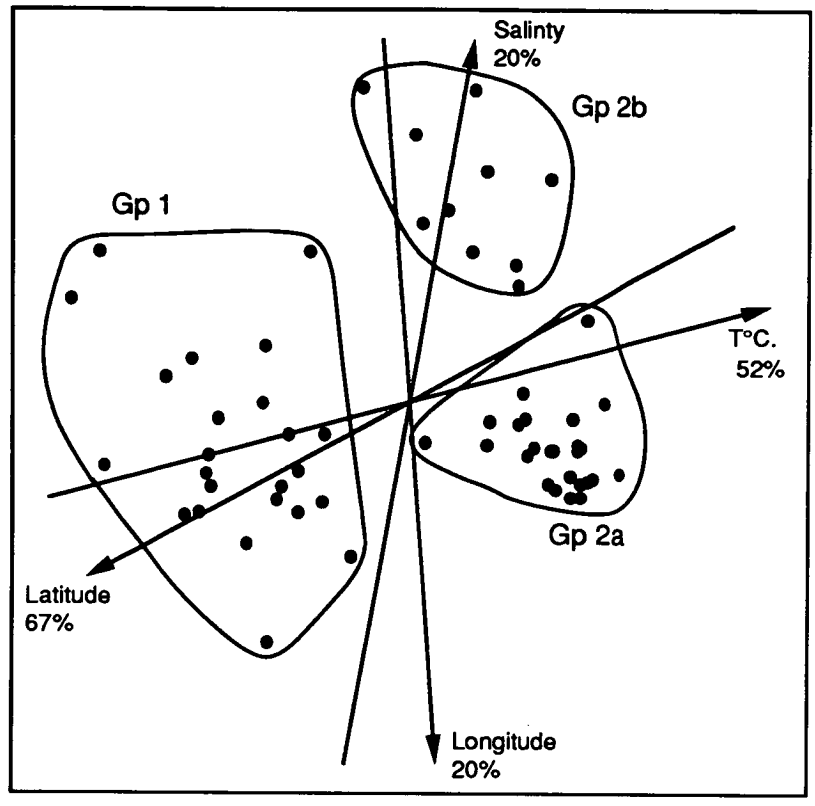


Fig. 4.3 Ordination plots of the comparison of sampling sites using non-metric multidimensional scaling and Bray-Curtis dissimilarity index. Respective cluster groups identified in Fig. 4.2 are superimposed. Significant multiple regressions between ordination scores and environmental parameters are shown, as well as the fraction (%) of variance in the zooplankton data explained by the parameter (see Table 4.4). Direction of the regression line was determined from Equation 3.2. Axis scales are relative in NMDS, based on non-metric ranking of dissimilarity, and therefore are not shown. Stress value = 0.14.

4.3 January-February 1991



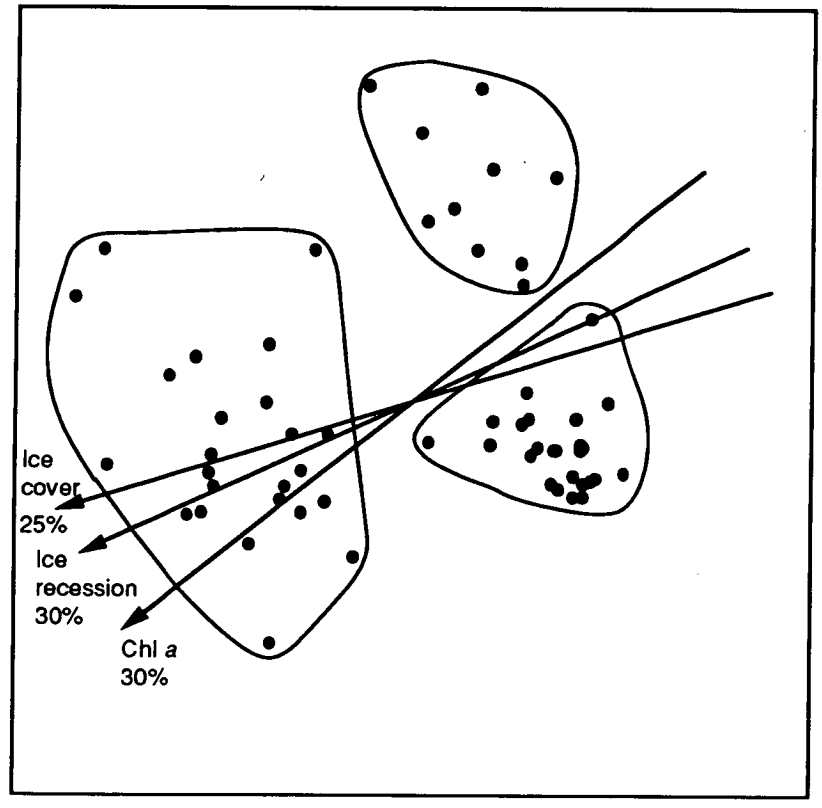


Fig. 4.4 Geographical distribution of station groups defined by cluster analysis shown in Fig. 4.2. Indicator species listed in blue bold type are those characterizing an area (station group) by their unique higher abundance identified by SNK analysis (Table 4.3). Indicator species in black italic type are those with a higher frequency of occurrence in that station group as identified by Field's information statistic (Table 4.2). Note: in many cases species were both abundance and frequency indicator species. Each station group is coded with the colour corresponding to the zooplankton community, shown in Fig 3.10, which dominated that area. ■ = "outlier" sampling sites not grouped in the cluster analysis.

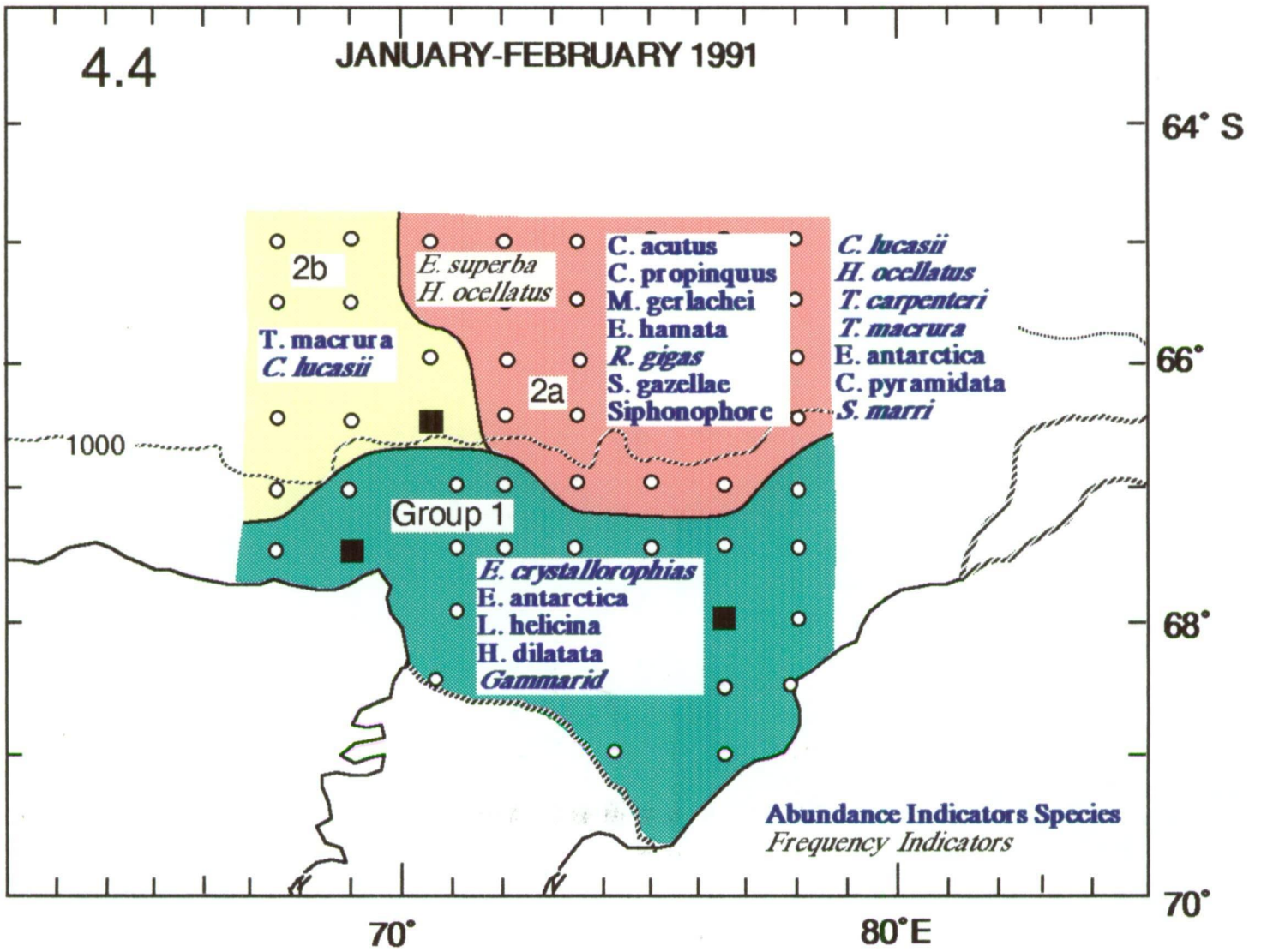

4.4
JANUARY-FEBRUARY 1991
64° S
66°
68°
70°
70°
80°E
1000
2b
T. macrura
C. lucasii
E. superba
H. ocellatus
2a
C. acutus
C. propinquus
M. gerlachei
E. hamata
R. gigas
S. gazellae
Siphonophore
C. lucasii
H. ocellatus
T. carpenteri
T. macrura
E. antarctica
C. pyramidata
S. marri
Group 1
E. crystallorophias
E. antarctica
L. helicina
H. dilatata
Gammarid
Abundance Indicators Species
Frequency Indicators

Table 4.2 Frequencies of occurrence of indicator species distinguishing cluster groups defined in Fig. 3. 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 = 24, Group 2a = 25 and Group 2b = 10. * were not considered as dominant species and not used in SNK or inverse species analyses.

a. Group 1 (neritic) indicators species

Species	Group 1	Group 2
Euphausia crystallorophias	23	2
Gammaridae	12	3

b. Group 2a (oceanic) indicator species from Group 1

Species	Group 2a	Group 1
Haloptilus ocellatus	20	0
Sagitta marri	22	1
Rhincalanus gigas	25	5
**Heterorhabdus austrinus*	19	0
**Calycopsis borchgrevinki*	19	1
**Haloptilus oxycephalus*	19	1
**Euchirella rostromagna*	18	1
Cyllopus lucasii	16	1
**Primno macropa*	16	1
*Cephalopoda	11	0
Tomopteris carpenteri	10	0
Thysanoessa macrura	25	16
*Ostracoda	24	14
**Vanadis antarctica*	7	0
**Travisiopsis levinseni*	6	0

c. Group 2b (oceanic) indicator species from Group 1

Species	Group 2b	Group 1
*Cephalopoda	9	0
**Calycopsis borchgrevinki*	9	1
Cyllopus lucasii	9	1
**Heterorhabdus austrinus*	7	0
Rhincalanus gigas	10	5
**Haloptilus oxycephalus*	6	1
**Euchirella rostromagna*	5	1

d. Group 2a indicator species from Group 2b

Species	Group 2a	Group 2b
None		
Euphausia superba	25	6
Haloptilus ocellatus	19	6

Table 4.3 Mean abundances, analysis of variance (F) and SNK multiple range tests of dominant species in cluster groups defined in Fig. 4.2. 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 =2,56.

Species	Group 1 Mean	Group 2a Mean	Group 2b Mean	F	P
Calanoides acutus	9.66	71.51	5.88	62.40	***
Calanus propinquus	4.17	36.60	2.00	72.26	***
Clio pyramidata	1.23	2.05	0.70	8.70	**
Cyllopus lucasii	0.004	0.33	0.31	9.30	***
Decapoda larvae	0.20	0.24	0.08	1.16	–
Euchaeta antarctica	2.78	3.64	0.38	14.78	***
Eukrohnia hamata	1.21	9.18	1.36	48.81	***
Euphausia crystallorophias	35.02	0.20	0.00	54.81	***
Euphausia superba	0.86	19.10	12.26	2.93	-
Gammaridae	0.17	0.01	0.03	6.78	**
Haloptilus ocellatus	0.00	0.20	0.01	27.76	***
Hyperiella dilatata	0.19	0.05	0.04	6.96	**
Ihlea racovitzai	0.78	0.30	0.12	1.11	–
Limacina helicina	0.44	0.20	0.13	4.97	*
Metridia gerlachei	8.02	16.30	0.56	28.52	***
Pleurabrachia pileus	0.14	0.01	0.00	2.74	-
Rhincalanus gigas	0.06	8.30	1.62	132.81	***
Sagita gazellae	1.12	7.30	2.98	76.44	***
Sagitta marri	0.01	0.87	0.07	32.32	***
Siphonophore nectophore	1.14	6.98	4.42	71.64	***
Thysanoessa macrura	0.39	4.69	2.29	15.89	***
Tomopteris carpenteri	0.00	0.06	0.01	7.74	**

Limacina helicina and *Hyperiella dilatata* were also abundance species indicators of the shelf area (Table 4.3). Group 2a was distinguished by the high abundance of several species of copepod and chaetognaths, as well as siphonophores, the euphausiid *Thysanoessa macrura* and by *Clio pyramidata* (Table 4.3). Many of these species were also frequency species indicators along with a further eight numerically minor species (Table 4.2b). Group 2b shared a number of species indicators with Group 2a which also discriminated 2b oceanic sites from Group 1 neritic (Table 4.3). Groups 2a and 2b did have similar species composition but there was notably lower abundances of these species in Group 2b (Table 4.3). However, these two sub groups were distinguished by the higher frequency of *E. superba* and *Haloptilus ocellatus* in Group 2a (Table 4.2d). The $2\Delta I$ scores for these species were only significant at the 5% level. Table 4.3 shows higher abundances of *E. superba* in Groups 2a and 2b but these were not considered significant, i.e. *E. superba* was not an abundances species indicator. However, if the two oceanic groups are treated together in the ANOVA and SNK analyses then *E. superba* was an abundance indicator discriminating the oceanic region from the neritic ($F = 5.96$, $P = 0.017$, $DF = 1,57$). There were no additional species indicators revealed in this treatment from those shown in Table 4.3.

Multiple Regression

Figure 4.4 shows a clear north-south separation of sampling sites. Latitude, not surprisingly, explained 67% of the variation of the data in the NMDS ordination (Table 4.4, Fig. 4.3). The oceanic groups displayed an east-west separation, and longitude explained 20% of the data variation (Fig. 4.3). The environmental variable that explained most of the variation was temperature (52%), and salinity the least (20%) (Table

Table 4.4 Multiple regression analyses between environmental parameters and NMDS scores for two-axis ordination of comparison of sampling sites. Regression weights are derived from Equation 2. 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.

	Direction Cosines (Regression Weights)					
VARIABLE	X	Y	Adj. R^2	F	DF	P
Latitude	-0.875	-0.484	0.669	59.655	2,56	***
Temperature	0.966	0.257	0.520	32.366	2,56	***
Ice Recession	-0.908	-0.418	0.299	13.348	2,56	***
Chlorophyll *a*	-0.781	-0.625	0.299	12.958	2,54	***
Pack Ice Cover	-0.955	-0.297	0.245	10.420	2,56	***
Salinity	0.174	0.985	0.200	8.250	2,56	**
Longitude	-0.079	0.997	0.200	8.249	2,56	**
Sampling Day	-0.064	0.998	0.194	7.977	2,56	**
Duration Haul	—	—	0.059	2.813	2,56	ns
Sample Depth	—	—	0.051	2.567	2,56	ns

4.4). Figure 4.3 shows temperature closely aligned with latitude and salinity with longitude. Chlorophyll *a* explained 30% of the variation in the data, and ice a similar amount. There would seem to be no affect of haul duration or sampling depth on the data, but the time since the start of the sampling (Sampling Day) did explain 20% of the data variation.

Species Associations

Twenty-two species were included in the inverse cluster analysis of species. Stations 42, 57, and 66, identified as outliers in the cluster analysis of sampling sites, were removed as the extremely high abundances or unusual catch composition as described above were expected to cause a bias (Gauch 1982). One major group, and a number of single or double species groups were defined at the 70% dissimilarity level (Fig. 4.5).

Group A comprised 15 species, of which 14 were species indicators of the oceanic Station Group 2a (Tables 4.2b and 4.3, Fig. 4.4). Decapod larvae was the one taxon that was not an indicator. In March 1981 decapod larvae of the family Hippolytidae were frequency indicators of the neritic area (Table 3.10b). Decapod larvae in the present study were only numerically abundant in the southern Station 44 where they comprised 6.7% of the catch. These larvae could not be identified. The larvae were difficult to identify at many sites, but those that could be identified showed that the larvae of the Nematocarcinidae were found mainly off the shelf, while those on the shelf were of the family Hippolytidae. Given the likely in shore/off shore differences, the grouping of decapod larvae in Group A was probably spurious. Group B consisted of 2 species, *L. helicina* and *H. dilatata*. The NMDS plot (Fig. 4.6) shows that this group has a close affinity with the oceanic Group A. In the cluster

Fig. 4.5 Dendrogram of inverse cluster analysis comparing dominant species for January-February 1991. The Bray-Curtis dissimilarity index was used for the comparison with UPGMA linkage, after standardizing species abundance (Equation 3.3). Six groups were defined at 70% dissimilarity.

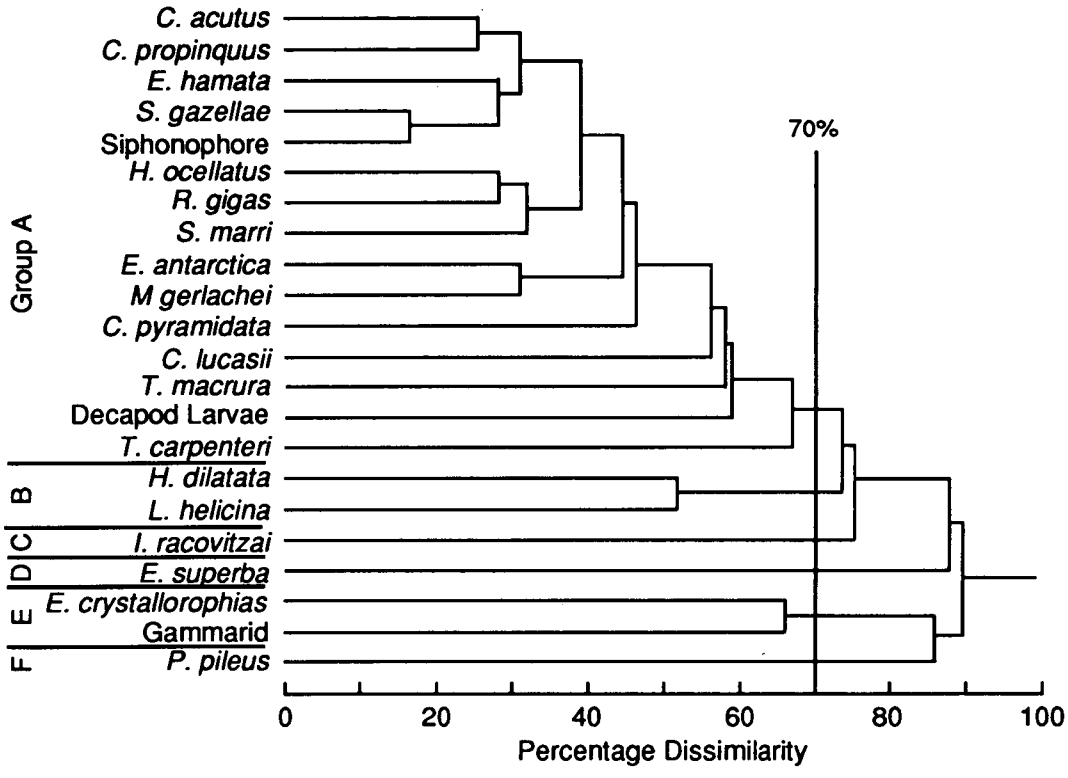
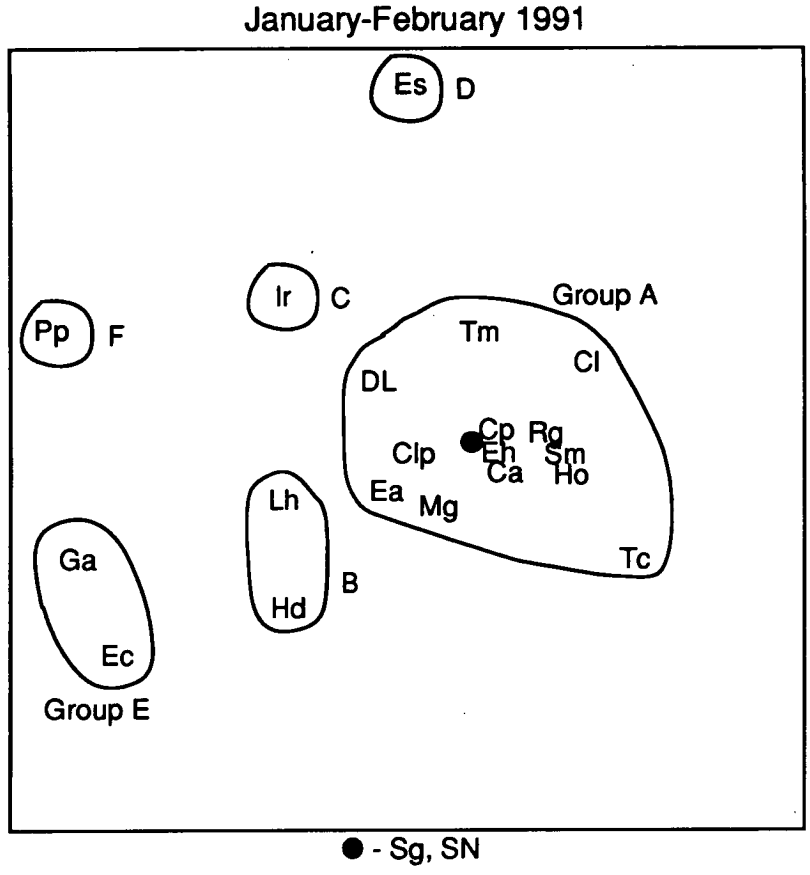


Fig. 4.6 NMDS inverse ordination plot comparing dominant species. Respective cluster groups identified in Fig. 4.5 are superimposed. Axis scales are relative in NMDS and therefore are not shown. Stress value = 0.16.



Ca	*Calanoides acutus*	Hd	*Hyperiella dialtata*
Cp	*Calanus propinquus*	Ir	*Ihlea racovitzai*
Clp	*Clio pyramidata*	Lh	*Limacina helicina*
Cl	*Cyllopus lucasii*	Mg	*Metridia gerlachei*
DL	Decapod Larvae	Pp	*Pleurobrachia pileus*
Ea	*Euchaeta antarctica*	Rg	*Rhincalanus gigas*
Eh	*Eukrohnia hamata*	Sg	*Sagitta gazellae*
Ec	*Euphausia crystallorophias*	Sm	*Sagitta marri*
Es	*Euphausia superba*	SN	Siphonophore
Ga	Gammarid	Tm	*Thysanoessa macrura*
Ho	*Haloptilus ocellatus*	Tc	*Tomopteris carpenteri*

analysis, these groups were linked at 74% dissimilarity. However, *L. helicina* and *H. dilatata* were abundance indicators of the neritic Station Group 1, and hence the division of groups at 70% dissimilarity would seem warranted. *Euphausia crystallorophias* and gammarids were also species indicators of the neritic group of stations (Table 4.2a and 4.3) and thus would be expected to have a closer affinity with Group B than is shown in Fig. 4.6.

The NMDS plot shows that the ctenophore *P. pileus* was dissociated from all other species (Fig. 4.6). It was loosely grouped with *E. crystallorophias* and gammarids at 86% in the cluster analysis (Fig. 4.5). This species was confined to the continental shelf waters where it occurred at 8 of the Group 1 stations and 2 of the oceanic Group 2b sites. Although this species' higher frequency of occurrence in shore was not considered significant in the 2ΔI analysis, it would still seem to be primarily associated with the neritic zone.

Ihlea racovitzai was not an indicator of any particular area, although it was identified previously as a neritic species in 1981. It would appear to be more abundant in the neritic zone in this study but was not considered significant (Table 4.3).

Both the cluster analysis and the NMDS show that *E. superba* was clearly dissociated from all other species, despite the fact it was an abundance indicator species of off shore sites in general and specifically a frequency indicator of Station Group 2b.

Discussion

Species Assemblages

There was good correspondence between the species associations shown in Figs 4.5 and 4.6, and indicator species of the station groups. In turn, there was little in the way of any difference in these associations and the composition of zooplankton communities previously described from the macroscale surveys (Fig. 3.10). For example, Species Group A in Fig. 4.5 contains all of the species that comprise the assemblage defined as the main oceanic community. Station Group 2a was dominated by these species in significantly high abundances, and clearly represents the main oceanic community. Species Group A also contains *C. lucasii* and *T. carpenteri* that were defined as a transition group between the main oceanic and the northern oceanic communities; the latter group was generally confined to waters north of 62°S.

Appendicularians were also defined as a member of the main oceanic community, but were of course excluded from the present analyses because of their extremely low abundances. The other minor differences in the composition of the main oceanic species affinities between this study and those of the previous macroscale surveys, involved decapod larvae and the hyperiid *H. dilatata*. *Hyperiella dilatata* was originally classified as a member of both main oceanic and northern oceanic communities. Some affinity was indicated with the neritic species in November-December 1982. In the present study, *H. dilatata* displayed a more substantial association with the neritic zone where it was a species indicator. Siegel & Piatkowski (1990) also noted that this species was indicative of either neritic or oceanic waters depending on the time of year. The result of the Prydz Bay surveys support Siegel & Piatkowski's observation that *H. dilatata* is not a reliable indicator species.

Decapod larvae, specifically those of the family Hippolytidae, were defined as indicators of neritic waters in the January-March 1981 survey of the Prydz Bay region. The inclusion of decapod larvae with the oceanic species in Group A may be a spurious association caused by the grouping of all decapod larvae as one taxon, despite possible differences in species distributions. For example, the larvae of the Nematocarcinidae, one group that could be identified with confidence, primarily had an oceanic distribution. The decapod larvae were generally low in abundance, and were thus grouped to produce one substantial taxon for analysis. This treatment may not have been valid.

By comparison with the main oceanic community, the neritic community had a much lower diversity of dominant species, with *E. crystallorophias* being the one species occurring persistently in high abundance in all surveys. Gammarids generally occurred in low abundance, but still regularly formed a close association with *E. crystallorophias* as seen in Fig. 4.5 and 4.6 and also in the previous surveys. While it may not be valid to treat all decapod larvae as one taxon, the same is not true for gammarids which always have a primarily neritic distribution. The other species previously shown to have close associations with *E. crystallorophias* and gammarids are the larvae of *Pleuragramma antarcticum* and *Pagetopsis macropterus*. Ichthyoplankton were not included in the present study as they will be the subject of a separate study (Williams 1992).

The pteropod *Limacina helicina* and the salp *Ihlea racovitzai* were identified previously as species associated with either the neritic or main oceanic communities. In this study, *L. helicina* was distributed widely throughout the study area, but was more abundant in the shelf waters where it was an abundance species indicator. Siegel & Piatkowski (1990) also reported neritic and oceanic distributions for this species. *I. racovitzai* was dissociated from all other species. It was also widely

distributed with no significantly higher abundances in any particular area. Neither species can be considered as a reliable indicator species.

Pleurobrachia pileus was the first species of ctenophore to be included in as analyses of Prydz Bay species associations. Past abundances of ctenophores have been very low, i.e. <4% numerical dominance for any site. This species primarily had a neritic distribution occurring at nine of the on-shelf sites and only at one oceanic site immediately off the shelf. *P. pileus* was dissociated from other species but did exhibit a closer affinity with the neritic groups than with oceanic species (Fig. 4.6). This species, however, has been described as having a cosmopolitan distribution (Moser 1909; O'Sullivan 1986).

Euphausia superba exhibited a distinct dissociation from all other species (Fig. 4.6). In 1981 and 1985, krill were also clearly dissociated from other zooplankton, whereas in 1982 krill formed a distant association with neritic species and a more substantial association with the main oceanic community species in 1987. However, in those latter two surveys, and also in 1981, *E. superba* was a significant abundance species indicator of geographic areas distinct from those dominated by neritic and oceanic zooplankton communities. The krill dominated community was subsequently defined on the basis of this species' demonstrated dissociation and geographic dominance.

Geographic Variability

While there is clear consistency in the species associations between the present and past surveys in Prydz Bay, the same cannot be said of the geographic distributions of the communities. Most notable was the apparent absence of the krill dominated community, despite the clear dissociation exhibited by this species in Fig. 4.6. This community is

usually located along the continental shelf edge, between the oceanic and neritic communities, extending into shelf waters as far south as 67°30'S as seen in 1982 (Fig. 3.5a). In this study adult krill were primarily confined to the waters north of the continental shelf edge. The few krill found on the shelf were predominantly juvenile (Appendix II). As mentioned above, a characteristic of the krill dominated community is the significant high abundance of krill, but an additional characteristic is the very low abundance of non-krill zooplankton compared with other areas. Krill thus form the majority component of catches. In 1981, 1982 and 1987, when the krill dominated community was evident, mean krill abundances represented 80, 68 and 57% of the mean total zooplankton abundance respectively. *E. superba* was in higher abundance in Station Group 2a, where it was also a frequency species indicator distinguishing Group 2a from 2b. However, the non-krill species composition and associated high abundances clearly identified Group 2a as the main oceanic community. Further, krill represented only 10% of the total zooplankton abundance and the ANOVA/SNK analyses showed that the higher abundance of krill in that area was not significant.

The station group with both the lowest zooplankton abundance compared with the other areas, and of course the highest proportion of krill, was Group 2b. Krill represented 35% of the mean total zooplankton abundance, which is much lower than other years when the krill dominated community was prominent. By definition then Group 2b should represent the krill dominated community, even though krill abundance was not significantly high. This being the case, the krill dominated community which normally separates the neritic and oceanic communities was apparently displaced to the west.

Priddle *et al.* (1988) provided evidence that long periods of low krill abundances often occurred two to three times a decade in the Scotia Sea - Bransfield Strait area. These decreases in abundance were considered to

be a result of changes in distribution rather than due to mortality. The January 1985 survey was similar to the present study with low krill abundances, albeit based on a much lower sampling resolution, and the krill dominated community was not obvious. Assuming that the krill community distribution observed in the present study and 1985 were anomalous, there are insufficient data to indicate whether this is a regular phenomenon as observed in the Atlantic sector.

Controlling Factors

A number of parameters were identified (Table 4.4) which may control the observed zooplankton community distributions. However, it needs to be borne in mind when interpreting these results, that a significant time component was introduced into the data set, indicated by Sampling Day explaining 19% of the data variation. During the course of sampling some characteristic of the communities had probably changed, e.g. distribution or composition. A time component was also evident in the distribution patterns of krill maturity stages in 1991 (Appendix II). This further highlights the need for brevity in the sampling period when studying zooplankton communities and causal effects (Chapter 3).

Strong latitudinal zonation was evident in the distribution patterns which is a consistent feature of all of the previous surveys in Prydz Bay. Some longitudinal zonation was also exhibited in the two off shore station groups. Longitudinal zonation was observed in only one previous survey in March 1987 (Fig. 3.5d) when the main oceanic community was concentrated in the eastern part of the Prydz Bay region, probably by the north-easterly current shown in Fig. 2.15. The result was an east-west separation of the main oceanic and krill dominated communities, similar to that seen in the present study. There is no clear

indication that a similar north-easterly current caused the 1991 zonation, i.e. concentrating the main oceanic community in the east, or that another current (in Fig. 2.15) could be responsible for displacing the apparent krill community (Group 2b) west. The observed distributions of Groups 2a and 2b do have some correspondence with the geostrophic water flow shown in Fig. 2.10. Station group 2b as shown in Fig. 4.4 was positioned in the centre of the Prydz Bay gyre, although there is no knowledge of how far west or north Group 2b extended. The distribution of the main oceanic community corresponds with the eastern part of the gyre (Fig. 2.10). The southward water flow would explain this communities' distribution extending into shelf waters between 73° and 77°E, although there appears to be little evidence of this in the temperature profiles (Fig. 2.2). This in turn may have contributed to the displacement of the krill community. It would also suggest that the north-easterly current was either not present or was not influential in the dispersion of plankton.

The north-easterly current was proposed as a major dispersal route for *E. superba* larvae (Chapter 6). After the completion of the present grid survey, a Hardy continuous plankton recorder (CPR) was deployed to collect *E. superba* larvae along that dispersal route. Two RMT 1 (1 m^2, 300 μm mesh) trawls were carried out to supplement the CPR survey. The trawl sites (64°10'S, 83°59'E; 64°01'S, 84°34'E) were centred in an area where very high abundances were observed in March 1987 (Fig. 6.16c). The two RMT 1 hauls produced very few larvae, and only seven calyptopis stage larvae were collected by the CPR (own unpublished data). The paucity of krill further suggests that there was no effective north-easterly current in 1991.

Temperature was a factor that explained some of the variation in other seasons, January-March 1981, November-December 1982 and January 1985. These were the larger geographic surveys encompassing

the distributions of all four zooplankton communities (Fig. 3.10) and large temperature gradients. In the 1991 study, temperature explained a much more substantial amount of the variation in the data (52%), suggesting temperature has a greater influence in controlling zooplankton at the mesoscale level. Numerous species have known temperature ranges (Foxton 1971; Everson 1984; Lomakina 1966; Kittel & Stepnik 1983). In the case of *E. crystallorophias* and *E. superba,* their reported temperature ranges are wider than the ranges of mean temperature observed in this study (Lomakina 1966; Kittel & Stepnik 1983). It could be argued that temperature was only correlated with the zooplankton NMDS scores, ie there was no causal relationship. Both the zooplankton community distributions and temperature had obvious latitudinal patterns. Figure 4.3 shows the close alignment between the temperature and latitudinal regressions.

Salinity was one parameter not particularly consistent in explaining zooplankton patterns - only once in the previous four macroscale surveys, in January 1985 (28%), and now in this study (20%). It remains to be determined if salinity has anything other than a minimal effect on community distributions.

Phytoplankton would naturally be expected to have some influence on the distribution of the zooplankton. In this study chlorophyll *a* explained a reasonable amount of the data variation (30%), which is commensurate with the previous macroscale surveys where chlorophyll *a* also explained much of the zooplankton patterns (27 to 38%) observed between November and March (Table 3.6). The exception was the end of summer, March 1987, when chlorophyll *a* appeared to have no influence on zooplankton distributions and instead water circulation was the single important controlling factor. Overall, chlorophyll *a* would seem to be the one environmental parameter that consistently explains zooplankton distributions for most of the summer period.

There is obvious consistency through all of the surveys in relation to the amount of variation in the zooplankton patterns explained by chlorophyll *a*. There is also consistency in the general geographic distribution of phytoplankton with the highest chlorophyll *a* values always found in the waters of the continental shelf. The 1991 season was different in that chlorophyll *a* levels south of the shelf edge were higher than previously recorded, and concentrated in a much shallower mixed layer of 30 to 50 m depth than the usually observed 60 to 100 m (Dr. S.W. Wright, personal communication). This immediately begs the question, were the anomalous zooplankton distributions, specifically the displacement of the krill dominated community, a result of the equally unusual phytoplankton abundances? The manner by which phytoplankton influences zooplankton distributions is yet to be established, especially the role that phytoplankton might play in the geographic separation of *E. superba* and *E. crystallorophias* and their respective communities.

Ice recession exhibits a distinct latitudinal pattern and, like temperature mentioned above, ice recession may only be correlated with zooplankton distributions, i.e. no direct causal effect. Notably, the pattern of ice recession observed in 1991 was quite different from that usually seen. A large polynya usually appears by early December in the southern part of Prydz Bay near the Amery Ice Shelf (Fig. 2.17). This pattern was observed in the 1984/85 summer when ice recession explained 60% of the zooplankton data. In 1991, ice dissipated only from north to south - no polynya formed in the south and there was no northward dissipation of ice. Much of the pack-ice then remained in the bay throughout the summer period. Light pack of 2 to 4/10 cover extended north and south-west of Davis. A more substantial cover of ice remained in the west of the bay, extending around Cape Darnley to the west and north of the cape to the shelf edge. Ice in this area was sufficiently dense, up to 9 to 10/10

cover, to necessitate a deviation in the 70°30'E transect (Fig. 4.1, stations 54, 55, 56).

The persistent pack-ice, the absence of ice break out from the south, and the shallow mixed layer are all indicative of the generally calm weather conditions experienced during the survey period. There is however, no proof that the ice or oceanographic/phytoplankton events produced the unexpected zooplankton community patterns, but they provide further evidence, albeit circumstantial, that 1991 was perhaps an anomalous season. The challenge for future research will be to actually establish the causal effects.

CHAPTER 5

ZOOPLANKTON AND EUPHAUSIID LARVAE IN LATE WINTER/SPRING 1985.

Introduction

The majority of ecological studies on Antarctic krill, adults and larvae, and zooplankton have primarily occurred during the austral summer-early autumn period, December to March occasionally April. This is a period of minimal ice cover, or at the least at the start of summer it is a period of rapid ice melt or retreat. There have been few studies carried out in the pack-ice zone during winter (June to August), e.g. Daly (1990) and Lancraft *et al.* (1991), or during the period of maximum ice cover in October (Jacka 1983; Zwally 1983). Daly (1990) studied the winter development, growth and feeding of krill larvae and juveniles in the marginal ice zone of the Weddell-Scotia Seas area. Lancraft *et al.* (1991) studied the distribution, abundance and community composition of zooplankton during the same study as Daly (1990). There has not been a similar study in the Prydz Bay region.

In September-November 1985 (austral late winter-spring), a marine science research cruise was undertaken in the western Prydz Bay region, with the prime purpose of studying the ecology of the Crabeater seal *Lobodon carcinophagus*. In addition, there was an opportunity to carry out a study of the composition, distribution and abundance of euphausiids and other zooplankton in the post-winter pack-ice zone, when the sea ice was near to its maximum northern extent (Jacka 1983). The distribution of krill in relation to the ice edge was of particular interest. The net sampling was supplemented with a diving program to observe and collect krill from under the pack-ice. The pack-ice conditions and the limitations of the vessel, M.S. *Nella Dan*, restricted the number

of sampling sites, the area surveyed and methods of sampling. Despite the limitations, this chapter provides useful background information that complements the more detailed summer-early autumn studies in the previous and subsequent chapters.

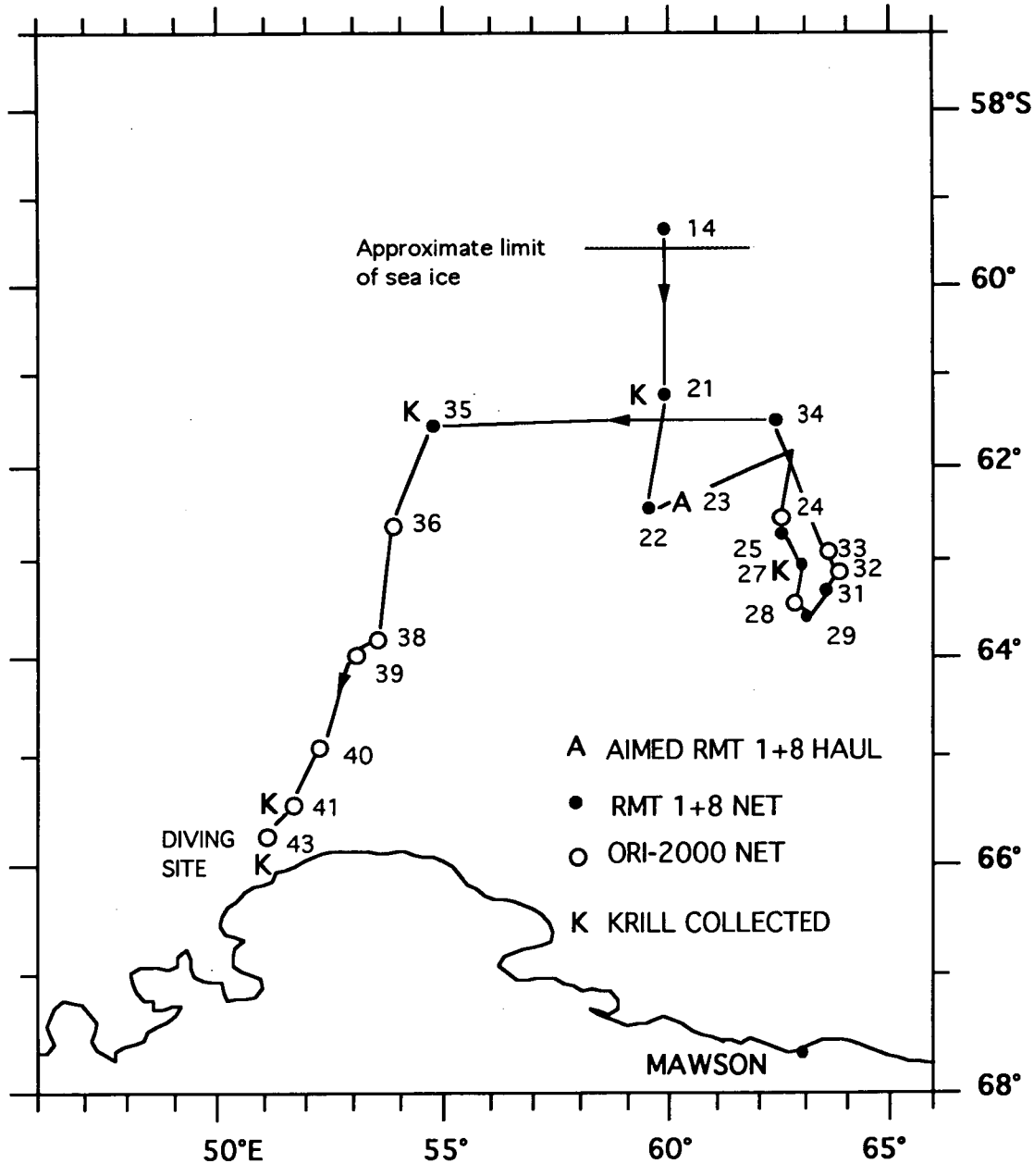
Methods

The survey area and sampling sites are shown in Fig. 5.1. Sampling commenced on 27 September and finished on 25 November 1985. A combined Rectangular Midwater Trawl RMT 1+8 net (Baker *et al.* 1973), and an Ocean Research Institute conical net (ORI-2000, Omori 1965) were the two main net systems used for sampling krill *Euphausia superba* and other zooplankton.

The RMT 8 had a mesh of 4.5 mm and a nominal mouth area 8 m^2; corresponding sizes were 300 μm mesh and 1 m^2 for the RMT 1. The RMT 1+8 net had an electro-mechanical opening-closing mechanism, a real-time depth recorder and both nets were equipped with flowmeters. The effects of towing speed and trajectory were considered in calculating the volume filtered (Roe *et al.* 1980; Pommeranz *et al.* 1982). At each station, a shallow oblique haul (0-200 m) was made. This was often in a lead or a polynya. When ice conditions permitted an additional deep oblique haul (200-1000 m) was also made. One aimed horizontal tow was also made in a polynya at a target located by a Simrad EK 120 echo sounder.

The ORI-2000 net had a mouth area of 2 m^2 and 2 mm mesh. This net was used when it was unsafe to tow the RMT 1+8 net due to ice, or when the ship had stopped for the night. Vertical hauls were made usually from 1000 m, although occasional hauls varied between 10 and 2000 m. The cod end was weighted to facilitate deployment to the

Fig. 5.1 Cruise track and net sampling stations. The cruise track shown is only for the duration of the net sampling program. The approximate northern limit of the sea ice as observed during the cruise is shown, together with stations where krill were collected.



required depth. Hauling speed varied between 0.7 and 1.3 m s^{-1}. The volume of water filtered was determined by multiplying the mouth area by the amount of wire out.

Under-ice diving was carried out either from the ship or through two ice-holes nearby. During this study the ship was beset off Enderby Land (Station 43, Fig. 5.1) and constantly drifting. Krill were collected by hand nets carried by the diver. These nets were difficult to move through the water with any speed but proved to be the most successful method at hand. Observations on the behaviour of krill were also achieved by means of underwater video and 16 mm cine-camera (O'Brien 1987).

Complete details of the sampling program, e.g. sampling position, time, depth, conditions, etc., as well as detailed catch compositions are provided in Hosie *et al.* (1987).

On board the ship, large and fragile zooplankton (jellyfish, salps, etc.) were sorted from the rest of the specimens. All specimens were preserved in Steedman's solution (Steedman 1976) for later examination at the Antarctic Division. Zooplankton in the RMT 8 samples were identified to species, weighed and counted. Euphausiid larvae were extracted from the RMT 1, identified, classified to developmental stages and counted under a dissecting microscope.

Although different nets and sampling methods were used in this study, an attempt was made to compare sampling sites by cluster analysis to define areas with similar zooplankton composition. Data from RMT 8 and ORI-200 nets were used. The Bray-Curtis dissimilarity index (Bray-Curtis 1957) was used for the comparison, coupled with unweighted-pairs group average linkage (UPGMA). Prior to analysis, data were transformed using the $\log_{10}(X+1)$ function to reduce the bias of high abundance species (Field *et al.* 1982). A full description of the analytical methodology is presented in Chapter 3.

Results

Most of the *E. superba* (156 specimens) were observed and collected by SCUBA divers at station 43, during the besetment of *Nella Dan* near the Enderby Land coast. Only 17 individuals were collected by the RMT 8 and ORI-2000 nets from the other sampling sites including one furcilia V and two furcilia VI at station 27 on 27 October (Fig. 5.1). In addition, 3 specimens (1 juvenile and 2 furcilia VI) were collected on 27 September 1985 by means of a small conical net, 1 m^2 mouth area and 500 µm mesh, drifted from the ship near the ice edge at 57° 29.4'S, 085° 07.0'E.

Fig. 5.2 shows the frequency distributions of the larval stages of the two euphausiids *Thysanoessa macrura* and *Euphausia frigida,* for the upper 200 m. Only calyptopis larvae of these two species were collected in either the shallow or deep hauls. For both species, more advanced calyptopis II and III stages were only found at sites north of 62°S, i.e. only calyptopis I larvae were found between 62°S and the southern limit of RMT 1 sampling at Station 31 (63° 18'S). Gravid and spent *T. macrura* females were only collected at sites north of 63°S. The frequency distributions of developmental stages were the same in the 200-1000 m layer as in the upper 200 m for both species, although the overall abundances were much lower in the deeper layer (Table 5.1). The larvae of the other euphausiids *E. superba, E. crystallorophias* and *E. triacantha* were not collected by the RMT 1 net.

Three main groups were identified in the cluster analysis at the 43% dissimilarity level (Fig. 5.3). These groups corresponded with net type and sampling method, i.e. RMT 8 shallow, RMT 8 deep and vertical ORI-2000 hauls. This result was anticipated to some degree and therefore no further analysis was carried out on the data such as a comparison of species associations. The remaining sampling sites, mainly vertical ORI-2000 hauls, were ungrouped at 43% dissimilarity. The numerically most

Fig. 5.2 Frequency distribution of euphausiid larval stages collected in the RMT 1 net for the 0-200 m oblique hauls. Note that the ordinate is a $\log_{10}$ scale. CI, CII, CIII = calyptopis stages I, II and III.

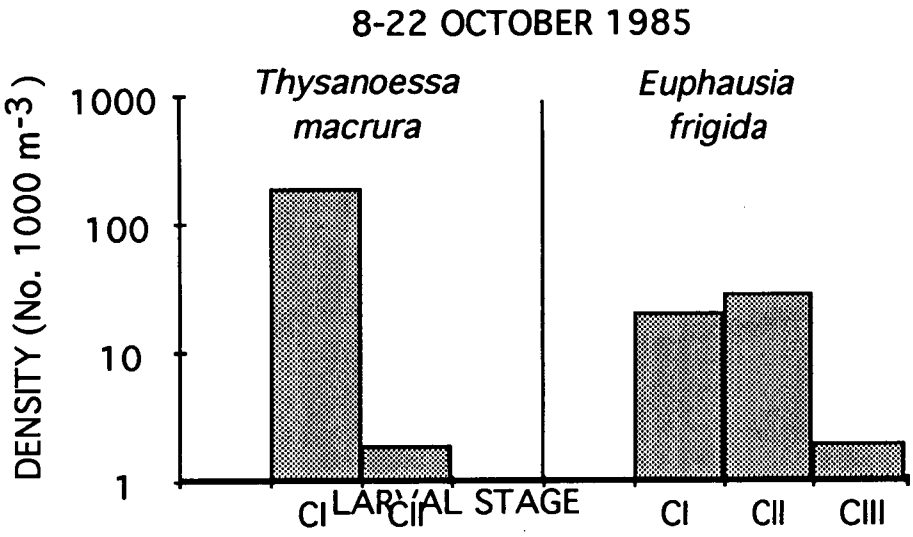
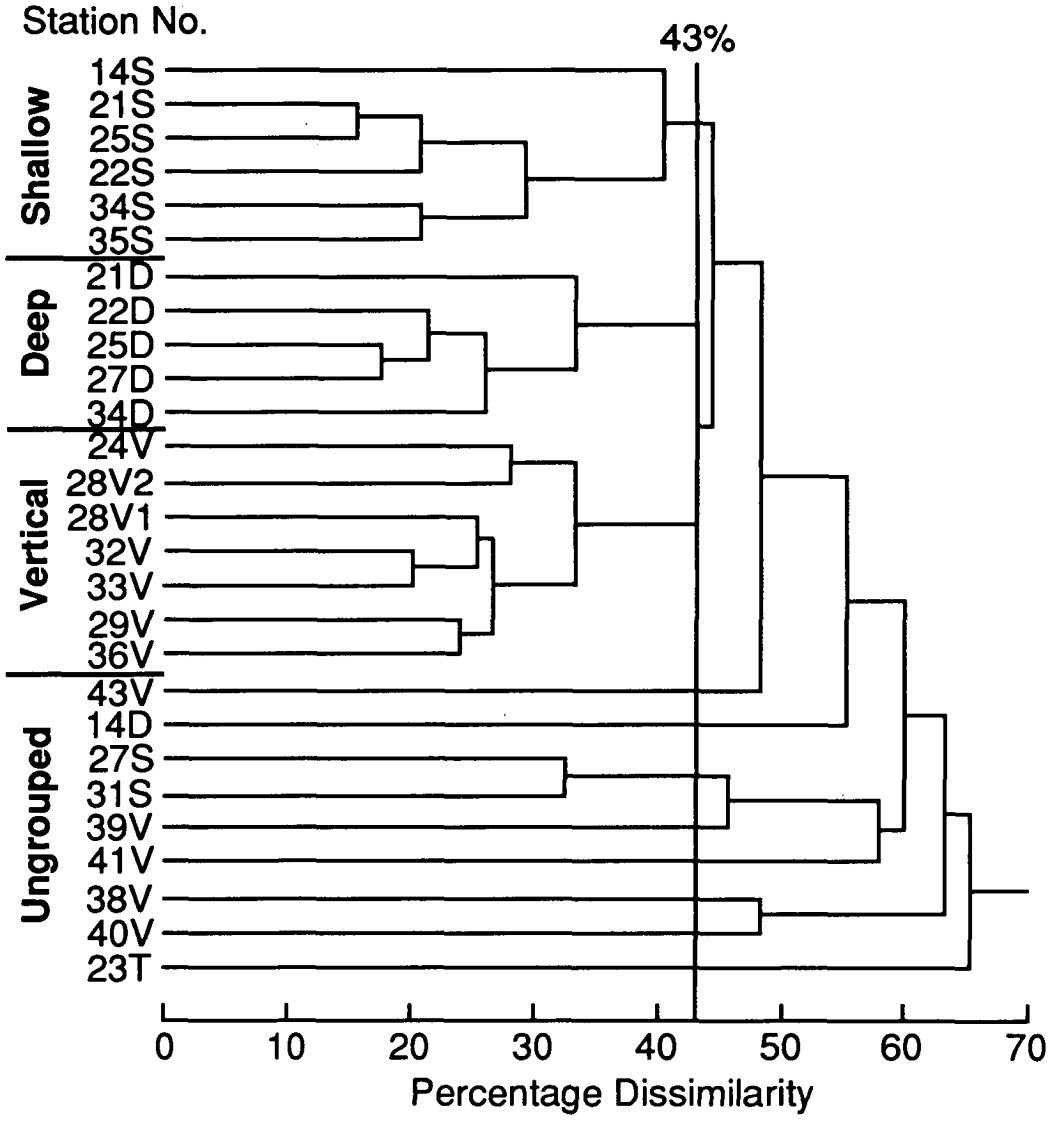


Table 5.1 Estimated mean densities (No. individuals 1000 m^{-3}) for euphausiid larvae collected in the RMT 1 net integrated for all sampling sites. n = number of RMT 1 sampling sites.

Depth (m)	n	*Thysanoessa macrura*			*Euphausia frigida*		
		Mean	SD	Range	Mean	SD	Range
0-200	8	183.20	274.81	6.77-799.28	49.87	110.86	0-322.13
200-1000	6	20.76	19.03	0.81-52.95	3.12	6.46	0-16.27

Fig. 5.3 Dendrogram of cluster analysis comparing zooplankton species composition at each sampling site. The Bray-Curtis dissimilarity index was used for the comparison with UPGMA linkage, after $\log_{10}(X+1)$ transformation of species abundance data. S = shallow 0-200 m RMT 8 hauls, D = deep 200-1000 m RMT 8 hauls, V = ORI-2000 vertical haul, T = RMT 8 horizontal target trawl.



abundant species are shown in Fig. 5.4 for shallow, deep RMT 8 hauls and ORI-2000 vertical hauls. These were species comprising >4% of the total zooplankton abundance for any sampling site for either RMT 8 or ORI-2000 hauls.

The copepod *Rhincalanus gigas* was the most abundant zooplankter at most sampling sites and for any sampling method. *Calanoides acutus* was the next most abundant copepod. *Thysanoessa macrura* was the most abundant euphausiid and next most abundant zooplankton species. The two chaetognaths *Sagitta gazellae* and *Eukrohnia hamata* were the predominant carnivores. Higher abundances tended to be recorded in the ORI-2000 net principally due to the finer mesh. However, the upper 200 m hauls had higher abundances of *R. gigas, C. acutus, S. gazellae,* siphonophores, *Salpa thompsoni* and *T. macrura,* while *Euchaeta antarctica, E. hamata, Sagitta maxima* and *S. marri* were more abundant in the deeper layers. The rest of the species occurred too infrequently or only in substantial numbers in the 0-1000 m verticals, to allow any comment on their vertical distribution.

Most of the species shown in Fig 5.4 are members of the main oceanic community. *S. thompsoni* is a dominant species of the northern oceanic community and the ctenophore *Callianira cristata,* collected closer to the coast at stations 41 and 43, was not described in the previous chapter as a dominant species. The total mean abundance of the abundant species shown in Fig. 5.4 for the RMT 8 upper 200 m hauls was 124.2 individuals 1000 m^{-3}. This estimate is within the range of mean abundance estimates for the main oceanic community observed in Prydz Bay during the months of November to March, but notably higher than the estimate from January-March 1981 (Table 5.2).

The copepod *Calanus propinquus* generally occurred in very low numbers. However, at station 23, in a polynya, an opening-closing RMT 8 haul aimed at a hydro-acoustic target located at 45-55 m depth produced

Fig. 5.4 Mean densities of numerically dominant adult zooplankton species for **a)** shallow RMT 8, **b)** deep RMT 8 oblique hauls and **c)** ORI-2000 vertical hauls. Dominant species were defined as those comprising >4% of the total zooplankton abundance at any sampling site for either RMT 8 or ORI-2000 hauls. Densities are number of individuals 1000 m^{-3}.

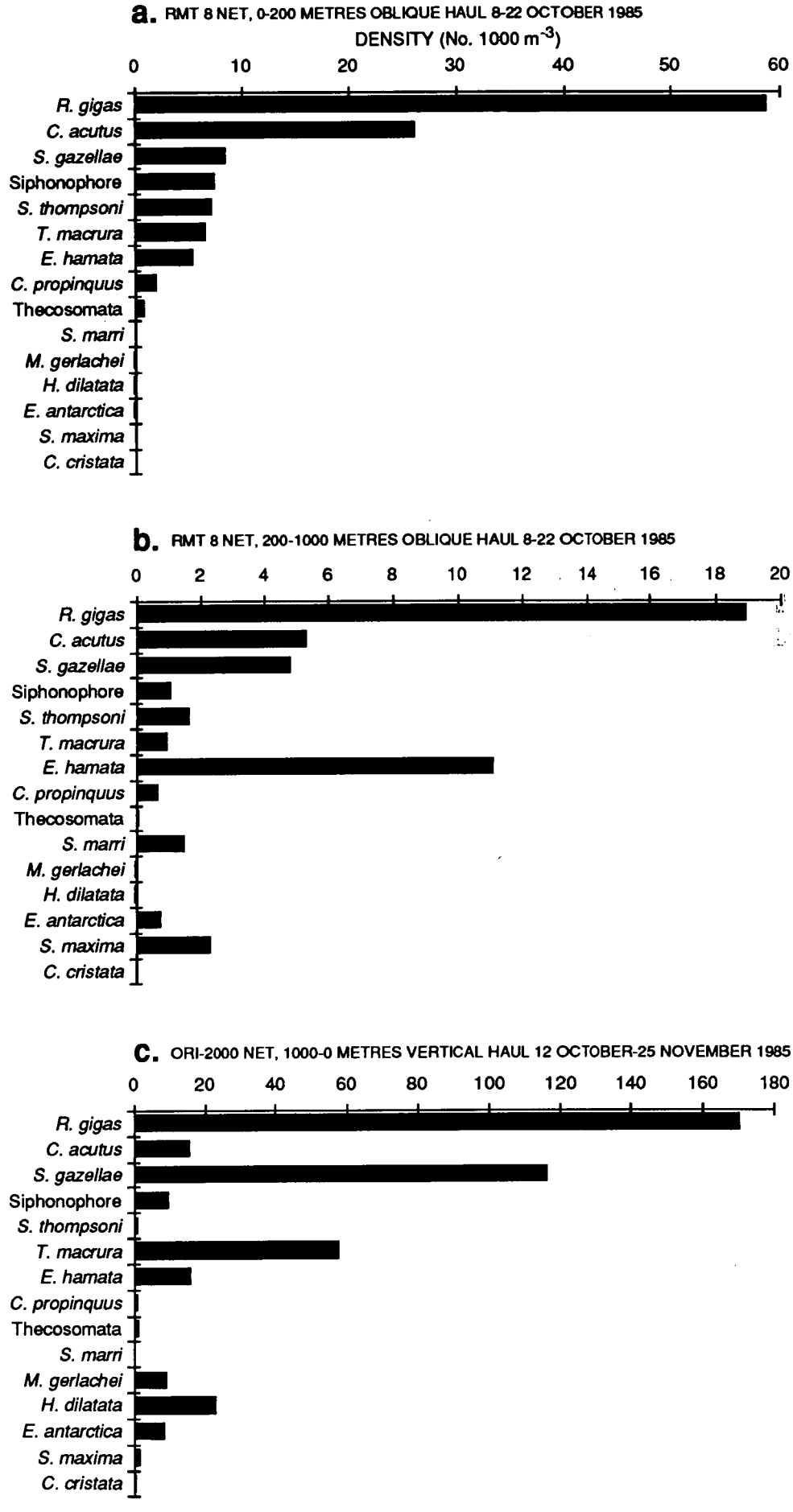

a. RMT 8 NET, 0-200 METRES OBLIQUE HAUL 8-22 OCTOBER 1985
DENSITY (No. 1000 m-3)
0
10
20
30
40
50
60
R. gigas
C. acutus
S. gazellae
Siphonophore
S. thompsoni
T. macrura
E. hamata
C. propinquus
Thecosomata
S. marri
M. gerlachei
H. dilatata
E. antarctica
S. maxima
C. cristata
b. RMT 8 NET, 200-1000 METRES OBLIQUE HAUL 8-22 OCTOBER 1985
0
2
4
6
8
10
12
14
16
18
20
R. gigas
C. acutus
S. gazellae
Siphonophore
S. thompsoni
T. macrura
E. hamata
C. propinquus
Thecosomata
S. marri
M. gerlachei
H. dilatata
E. antarctica
S. maxima
C. cristata
c. ORI-2000 NET, 1000-0 METRES VERTICAL HAUL 12 OCTOBER-25 NOVEMBER 1985
0
20
40
60
80
100
120
140
160
180
R. gigas
C. acutus
S. gazellae
Siphonophore
S. thompsoni
T. macrura
E. hamata
C. propinquus
Thecosomata
S. marri
M. gerlachei
H. dilatata
E. antarctica
S. maxima
C. cristata

Table 5.2 Comparison of combined mean abundance of numerically dominant species shown in Fig. 5.4, for the three sampling methods, with those of the main oceanic community (MOC) from Tables 3.5, 3.7, 3.11, 3.12 & 4.3. n = number of samplings sites in sample group.

Sample Group	n	Density No. 1000 m^{-3}
Shallow RMT 8, October 1985	9	124.2
Deep RMT 8, October 1985	6	49.5
ORI-2000, Oct.-Nov. 1985	12	436.5
MOC Nov.-Dec. 1982	25	608.9
MOC January 1985	25	219.7
MOC Jan.-March 1981	20	75.2
MOC March 1987	13	390.6
MOC Jan.-Feb. 1991	25	188.1

a large number of *C. propinquus,* representing a density of 1492 individuals 1000 m^{-3}. This is probably a considerable underestimation because of the 4.5 mm mesh used on the RMT 8 net relative to the size of the copepod.

Discussion

In the Prydz Bay region, sea ice begins to reform in March and reaches its maximum northern extent in October (Jacka 1983). Comparison of the abundances in Table 5.2 shows that the zooplankton community were apparently well established under the sea ice in October. For example, *R. gigas,* the most abundant zooplankter in October 1985 at 58.9 individuals 1000 m^{-3} in the upper 200 m, had mean abundances of 39.5 individuals 1000 m^{-3} in November-December 1982, 40.9 in January 1985, 13.9 in January-March 1981 and 40.1 for March 1987 for the same depth and latitude ranges (Tables 3.5, 3.6, 3.11, 3.12). The consistency of abundance estimates between October and other months for dominant zooplankton implies that zooplankton growth and development continues during winter.

The higher abundance of *R. gigas* in the upper 200 m, compared with 200-1000 m, is inconsistent with the life history model described by Voronina (1970). Voronina proposed that in waters south of the Antarctic Convergence, *R. gigas* lived below 500 m during winter and spring, with ascent to the upper 500 m occurring in summer. However, Ommaney (1936) and Mackintosh (1937) also observed numerous *R. gigas* in the upper 250 m water layer south of the Antarctic Convergence, during October and November. Their results are more consistent with those of the present study. Some seasonal and geographical variation in the onset of the ascending migration is to be expected and is most likely

linked to food availability. The higher densities of *R. gigas*, as well as other species, in the upper 200 m suggests that sufficient food was available in the surface waters. Phytoplankton in the 0-50 m layer under the pack-ice (59-66°S) in October 1985 were almost entirely diatoms, with a mean cell count of 15.1 ± 10.5 x 10^3 cells l^{-1} (range 3.2-54.9 x 10^3 cells l^{-1}, n=78) (MR. A.T. Davidson, Antarctic Division unpublished data). This value is approximately 6 times lower than the mean cell count of 89.1 ± 59.2 x 10^3 cells l^{-1} (range 6.8-259 x 10^3 cells l^{-1}, n=54) for January 1985 for the same latitude in Prydz Bay (DR. H.J. Marchant, Antarctic Division unpublished data). Daly (1990) also observed very low phytoplankton abundance (Chl *a*) in the water column in winter, but chlorophyll levels were an order of magnitude higher in the sea ice. Daly (1990) considered the abundance of sea ice biota was sufficient to support the observed growth and development of krill furcilia larvae during winter. One could presume that the sea ice biota would also support zooplankton, particularly the herbivorous copepods which are similar in size to furcilia.

The occurrence of *T. macrura* and *E. frigida* larvae was restricted to calyptopis stages in October, with no advanced furcilia, indicating that the onset of spawning of both *T. macrura* and *E. frigida* was very recent. Makarov (1979) previously noted that spawning of these two species began in September in the Scotia Sea. No detailed data on larval development times exists at present for these species. However, comparison with development times for the larvae of *E. superba* (Ikeda 1984) and *E. crystallorophias* (Ikeda 1986) based on laboratory observations, suggests that larvae at the calyptopis I stage were spawned in early September, with calyptopis III larvae of *E. frigida* resulting from early to mid August spawning. Therefore, spawning in *E. frigida* either precedes that of *T. macrura* or, if both species spawn at the same time, the larvae of *E. frigida* have a faster development time. Makarov *et al.* (1990)

also suggested that *E. frigida* spawned first, while Menshenina & Spiridonov (1988, in Makarov *et al.* 1990) claimed that, in fact, *E. frigida* developed slower than the larvae of *T. macrura*.

In order that spawning can occur in late winter, gonads must mature during winter. The spawning period of *T. macrura* extends at least to December possibly mid-January (Chapter 6). Therefore, it is not unlikely that, in addition to later spawners, females having released eggs in September may produce eggs during the next 4 months. The ability to produce more than one brood per season has been reported for *E. superba* (Denys & MacWhinnie 1982; Ross & Quetin 1983; Harrington & Ikeda 1986) and for *E. pacifica* (Ross *et al.* 1982). Repeated maturation has been observed in other species of *Euphausia* and *Thysanoessa* (Makarov 1975). If spawning as early as September is to be a viable reproductive strategy, for either *T. macrura* or *E. frigida*, then sufficient food must be available during winter for egg production, as well as later for continued spawning (with possible rematuration) and survival of the larvae. As noted above, Daly (1990) found that the abundance of sea ice biota in the Weddell-Scotia Sea area was sufficient for growth of krill furcilia larvae. The alternative situation of insufficient food would result in egg production occurring at the expense of the individual's own body tissue and also a much higher larval mortality.

Despite the recent start to spawning and presence of gravid female *T. macrura*, no eggs or any naupliar stage were collected. Nor have these stages been collected in substantial numbers, at any depth, during surveys in January 1985 and March 1987 when 300 μm mesh was used (Chapter 6). This is a clear indication of the unsuitability of this mesh size for collecting these early stages, of either species, which measure between 0.42 and 0.55 mm in length (Kirkwood 1982).

The net sampling was not very extensive but the large number of krill observed under the ice at station 43 near the continental shelf edge

(O'Brien 1987) shows that krill remain in shore during pack-ice development. Similarly, Kawaguchi *et al.* (1986) observed krill overwintering under the coastal fast-ice in Lützow-Holm Bay to the west of the present study area.

Spawning by *E. superba* commences at the end of December beginning of January in Prydz Bay and by the end of March of 1987 *E. superba* larvae in general had only progressed as far as the calyptopis stages (Chapter 6). Although few in number, the late stage furcilia larvae present in late September-early October would have over-wintered. Further, the existence of a number of small juveniles of 8-16 mm in length in the October 1985 catches (Hosie *et al.* 1987) shows growth and development continued during winter. This represent an approximate growth rate of 0. 047 mm d^{-1} between March and October, which is half the daily rate recorded by Ikeda (1985) in laboratory studies for this age group. Since the present study was undertaken, Daly (1990) also observed development in krill larvae during winter in the Atlantic sector. In June, larvae were at the furcilia III-V stage and by August they had developed to the furcilia VI at the rate of 0.07 mm d^{-1}, which is closer to the 0.047 mm d^{-1} estimate of the present study.

Various field and laboratory based studies have shown that post-larval krill either cease growing (Ikeda 1985; Siegel 1987) or shrink in body size (Ikeda & Dixon 1982; Stepnik 1982; Kawaguchi *et al.* 1986) during winter, when there is supposedly a paucity of food. The results of this study, however, indicate that zooplankton, smaller euphausiids and larvae may not find food limiting, or at least only partially limiting, in winter and later during the period of maximum ice cover.

CHAPTER 6

EUPHAUSIID LARVAE

Introduction

Since the mid 1970's, the Antarctic krill *Euphausia superba* has been the principal fishery around Antarctica with catches exceeding the total Antarctic finfish catch. Current statistics ranks the krill fishery 30th amongst world fisheries and it is the largest single species crustacean fishery (FAO 1991). While this fishery is still in its infancy, but growing, implementation of management policies as part of the Convention for the Conservation of Antarctic Marine Living Resources is also in its infancy, with much of the data needed to make sound decisions still lacking (Nicol 1989). Fundamental to the successful management and protection of *E. superba* will be a thorough understanding of the population dynamics, notably the responses of the population to changes in the fishery and natural factors influencing abundance. Key components affecting stock size are the number of larvae produced annually, their survival/mortality, dispersion and their subsequent recruitment.

Much emphasis has been placed on studying the ecology of the post-larval and adult krill, and this bias is reflected in the literature. The adults after all, are the focus of the krill fishery. Determining the distribution and abundance of krill has been an important part of this work and most of this information has emanated from the Atlantic sector (Miller & Hampton 1989), despite the occurrence of extensive krill fishing in the Indian ocean sector (Lubimova *et al.* 1985; Ichii 1990). As for the adults, most of the information on the ecology of the larvae comes from the Atlantic sector, but by comparison larval ecology is still poorly understood (Hempel 1985; Brinton *et al.* 1986; Miller & Hampton 1989).

Few studies have attempted to study the factors controlling the distributions and fate of the larvae, e.g. Brinton (1985) and Daly (1990). Daly's (1990) study was primarily focussed on the development, growth and feeding rates of larval and juvenile krill in association with ice in the austral winter. Brinton (1985) showed that the highest abundances of krill larvae in the Scotia Sea were located along a frontal zone between Weddell Sea water and the Antarctic Circumpolar Current via Drake Passage. He also found these high densities were near, but not coincident with high chlorophyll *a* concentrations. Other studies have found high abundances of larvae correlated with high concentrations of chlorophyll *a* (Schnack *et al.* 1985) or with levels of phytoplankton described as moderately abundant (Kittel & Jazdzewski 1982). The paucity of successful studies comparing krill larval distribution patterns and environmental data may well be a function of interpreting the complex hydrographic patterns in the vicinity of the Antarctic Peninsula and Scotia Sea (Amos 1984; Piatkowski 1985b). While such field studies on the ecology of krill larvae are few, valuable laboratory based studies have shown that there are critical levels of temperature and chlorophyll *a* necessary for the successful development and survival of larvae (Ross *et al.* 1988; Ross & Quetin 1989, 1991).

The ecology of larvae of other Antarctic euphausiid species have also been studied, predominantly distribution and abundance of larvae in the Atlantic sector (e.g. Makarov 1979, 1983; Fevolden 1980; Hempel 1981; Hempel & Hempel 1982; Brinton 1985; Makarov *et al.* 1990; Kittel *et al.* 1985). A few studies attempted an examination of distribution patterns and observed geographic differences, usually North-South, in the developmental stages or "age" composition of *Euphausia frigida* (Brinton 1985) and larvae of *Thysanoessa macrura* (Makarov 1983; Makarov *et al.* 1990; Menshenina 1988). Makarov & Menshenina (1992) suggested that different distribution patterns of *T. macrura* larval stages

were governed by the distribution of different water types. In the case of abundance, both high and low densities of larvae have been observed in association with frontal zones (Makarov *et al.* 1990). The various studies comparing distribution patterns of euphausiid larvae with environmental data were often not comprehensive and certainly not definitive.

Sampling for larvae was not included in the January-March 1981 and November-December 1982 surveys described in Chapter 3. The research program in those early years centred on establishing the distribution and biomass of adult krill in the Prydz Bay region by hydroacoustics and net sampling (Higginbottom *et al.* 1988; Hosie *et al.* 1988). Net sampling for larvae was carried out in mid-summer January 1984, January 1985 and in the start of the austral autumn March 1987. The 1984 study was unfortunately limited to some degree in geographic area and number of sampling sites due to logistic constraints. The January 1985 and March 1987 surveys were geographically more extensive and were carried out in conjunction with the sampling of adult krill and zooplankton (Chapter 3). There was also limited sampling for larvae in September-October 1985 and this has been discussed in Chapter 5.

The prime objectives of the larval ecology components of the 1984, 1985 and 1987 surveys were to study the abundance and distribution patterns of *E. superba* larvae. The Prydz Bay gyre is thought to be permanent (Smith *et al.* 1984), and of particular interest was the influence of water circulation on the distribution of the larvae. The ecology of other common euphausiids in the region was also studied, partly because of their own intrinsic importance as larvae of dominant zooplankters but also in their value in possibly defining factors or events that may also affect larvae of *E. superba* (Makarov 1983).

Methods

The Prydz Bay region krill larvae study area was the same as that defined in Chapter 5, i.e. from 58° to 93° E and south from 60° S to the Antarctic coast. Sampling sites in January 1984 were located along three longitudinal transects (58°, 60°, 73° E) between 63° and 67° 40' S (Fig. 6.1a). Larvae were collected using a bongo net, 0.5 m^2 combined mouth area and 300 μm mesh, towed obliquely from 200 m to the surface. A TSK flowmeter was mounted in the mouth of one net to estimate the volume of water filtered, while a TSK depth-distance meter was mounted in the other net to confirm the depth and course of the net.

In January 1985, sampling sites were located along eight longitudinal transects, between 58° and 93° E, at intervals of one degree latitude from 60° S to the coast (Fig. 6.1b). This grid of sampling sites was meant to be repeated in the March 1987 survey, but logistic constraints coupled with deteriorating weather conditions reduced the sampling program. Instead, sampling sites were located at intervals of approximately 50 minutes of latitude south from 61° 50' S, along the same longitudinal transects between 63° and 88° E that were sampled in 1985 (Fig. 6.1c). In both 1985 and 1987, larvae were collected using a Rectangular Midwater Trawl RMT 1 net, 300 μm mesh and nominal 1 m^2 mouth area, as part of an RMT 1+8 system (Baker *et al.* 1973). At each site a shallow 0-200 m oblique haul was made. In 1985, an additional deep 0-1000 m oblique haul was made at every third station. In 1987, there were five additional deep oblique trawls from 200-1000 m carried out on an opportunistic basis when weather conditions permitted. The main purpose of the deep haul was to collect the early developmental stages of *E. superba* (Marr 1962; Hempel *et al.* 1979). The RMT 1 was equipped with a flowmeter and the effects of towing speed and trajectory were taken into account when calculating the volume filtered (Roe *et al.* 1980; Pommeranz *et al.* 1982). Sampling

Fig. 6.1 Cruise track and net sampling sites for the three euphausiid larvae surveys in 1984, 1985, 1987. The 1000 m contour is shown.

6.1

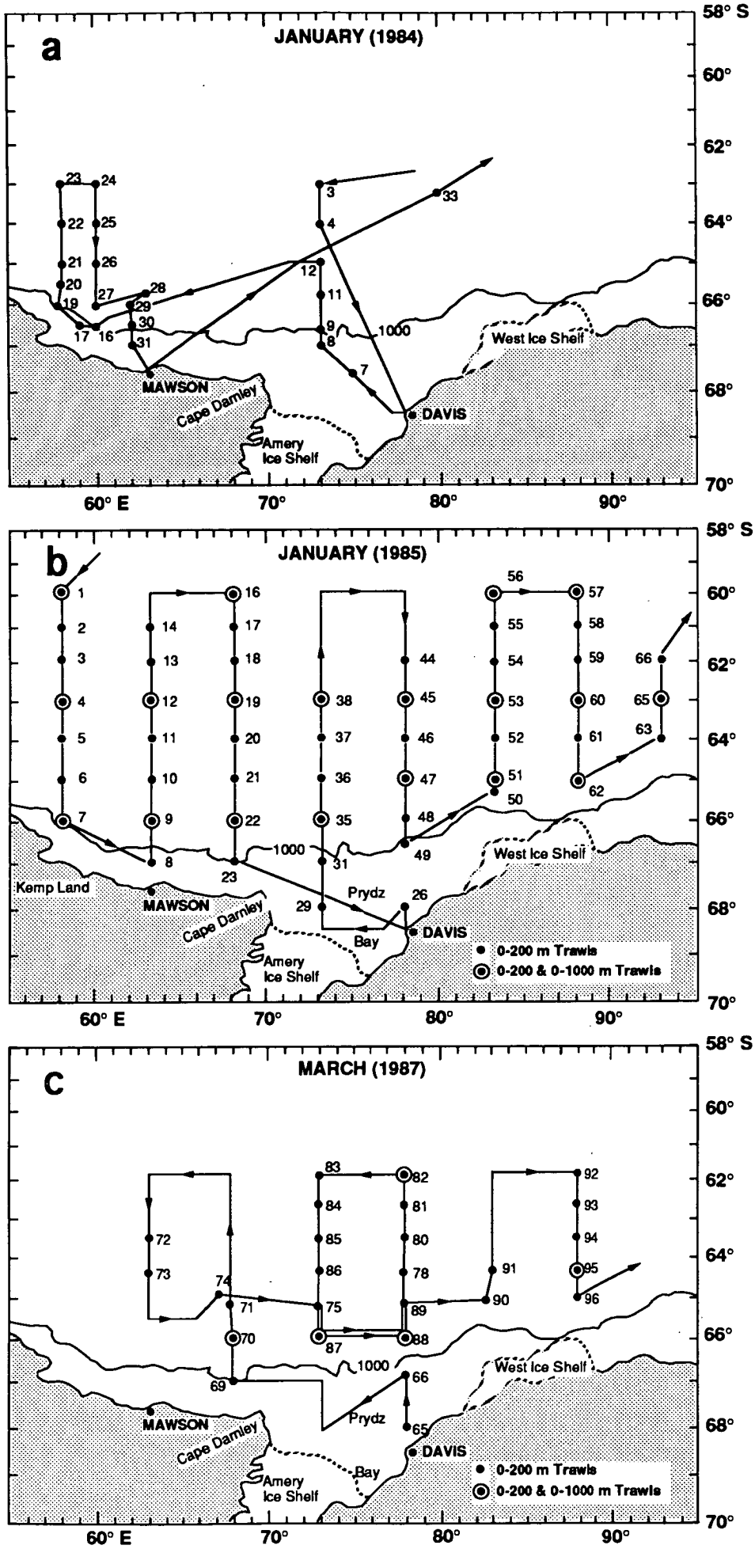

a
JANUARY (1984)
58° S
60°
62°
64°
66°
68°
70°
60° E
70°
80°
90°
MAWSON
DAVIS
Cape Darnley
Amery Ice Shelf
West Ice Shelf
1000
b
JANUARY (1985)
Kemp Land
Prydz Bay
0-200 m Trawls
0-200 & 0-1000 m Trawls
C
MARCH (1987)

Table 6.1 Summary of euphausiid larvae sampling surveys. ADBEX = Antarctic Division BIOMASS Experiment, AAMBER = Australian Antarctic Marine Biological Ecosystem Research, SIBEX = Second International BIOMASS Experiment phases 1 and 2.

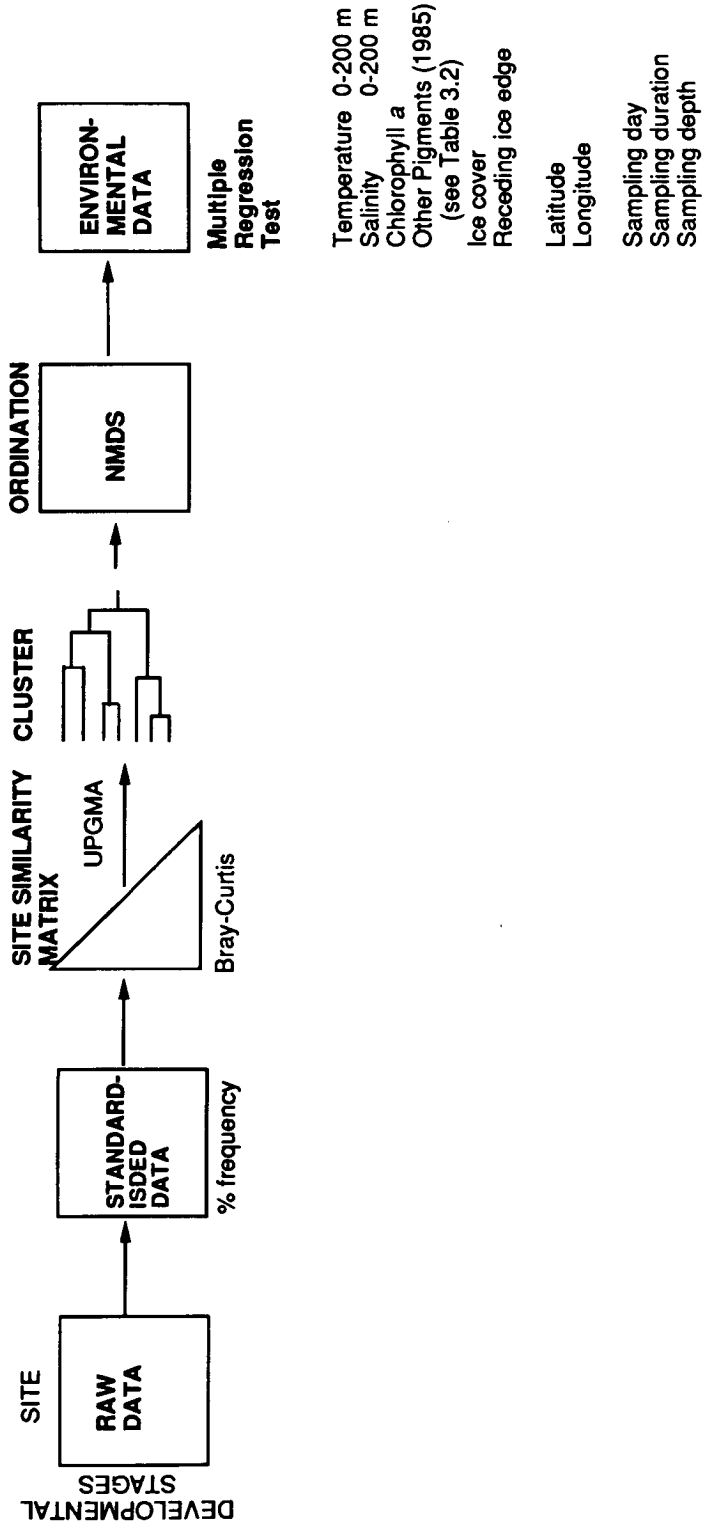
Sampling period	Cruise name	No. Sites	Net	Sample depth (m)	Full cruise details
14 January to 6 February 1984	ADBEX 2 (SIBEX 1)	23	Bongo	0-200	Ikeda *et al.* 1983
4-26 January 1985	SIBEX 2	50	RMT 1	0-200	Ikeda *et al.* 1986
		19	RMT 1	0-1000	
7-23 March 1987	AAMBER 1	27	RMT 1	0-200	Hosie *et al.* 1991
		5	RMT 1	200-1000	

methods on each cruise, together with sampling dates have been summarized in Table 6.1. Complete sampling details, e.g. sampling position, time, depth, conditions, etc., are provided in Ikeda *et al.* (1984, 1986) and Hosie *et al.* (1991).

All catches were preserved in Steedman's solution (Steedman 1976). After each cruise the euphausiid larvae were identified to species, classified into their various developmental stages under a dissecting microscope, and counted. The larvae of *E. superba* and *E. crystallorophias* raised from eggs in the laboratory (Ikeda 1984, 1986) were used as a reference. This facilitated the identification of the early developmental stages of these two species which closely resemble each other.

For the purpose of mapping the distribution of larvae, each stage was numbered sequentially from youngest to oldest. Thus the labels 1,2,3 were assigned for the three naupliar stages (nauplius I, nauplius II, metanauplius), 4,5,6 for the three calyptopis stages I to III, and 7 to 12 for the furcilia stages I to VI. This scheme replaces the conventional developmental stage nomenclature with a numerical value, hence facilitating comparison of development within and between species. At each sampling site a weighted mean value, mean stage index, was calculated for each species present, by multiplying the assigned number of a developmental stage by its relative abundance. The mean stage index (MSI), however, may have been derived from either a uni- or multi-modal frequency distribution of developmental stages. Cluster analysis was also used to compare the actual frequency distribution of developmental stages between sampling sites. The Bray-Curtis dissimilarity index (Bray & Curtis 1957) was used for this comparison, coupled with unweighted-pairs group average linkage (UPGMA). Analysis was carried out using BIOΣTAT II (Pimental, R.A. & Smith, J.D., 1985 Sigma Soft, Placentia, California). Since the purpose of the analysis

Fig. 6.2 Diagrammatic summary of the steps used in the multivariate analyses to define areas of common larval developmental stage composition (comparison of sampling sites), and possible environmental parameters affecting larval distribution patterns. UPGMA = unweighted pair group average linkage, NMDS = non-metric multidimensional scaling.



was to compare patterns in the frequency distribution of stages, data were standardized as percentage frequency of abundance within the site. Cluster analysis was only used on *T. macrura* data (1984, 1985 and 1987) and *E. superba* data from 1987, as the low number of site occurrences or the general paucity of specimens in some years made this analysis unrealistic for the other species. Non-metric multidimensional scaling (NMDS) ordination was also performed and the derived ordination scores were then used in multiple regression analyses with the same environmental parameters as described and used in Chapter 3. This included a number of phytoplankton pigments, in addition to chlorophyll *a*, integrated for 0-100 m in 1985, and surface chlorophyll *a* values in 1987. Unfortunately no phytoplankton data were collected in 1984. A flow chart summarizing the numerical analyses is shown in Fig. 6.2 and is a modification of Fig. 3.2.

Results

The larvae of five euphausiid species were collected, *Euphausia superba, E. crystallorophias, E. frigida, E. triacantha* and *T. macrura.* Estimates of mean abundances are provided in Table 6.2 for 1984, 1985 and 1987 respectively, for all species. Only sites where a species was collected were used for estimating the mean, i.e. stations where a species was absent were not included. Although this may result in a positive bias, the alternative of including "absent" sampling sites in the mean estimate would result in a negative bias if such sites are not within a species' distribution range. *E. triacantha* was only collected in 1985 and then at only five 0-200 m sites (Stations 14, 16, 55, 57, 58) in very low abundance ranging from 3.14 to 9.43 individuals 1000 m^{-3}. In addition, larvae of this species were found in only one deep trawl at Station 57.

Table 6.2 Estimated mean densities for larvae of all species for **a.** January 1984, **b.** January 1985 and **c.** March 1987. Only sites where a particular species was collected were used for estimating the mean. n = number of sampling sites.

a. January 1984 - 0-200 m trawls.

Species	n	Mean no. 1000 m^{-3}	SD	Range
Thysanoessa macrura	22	258.85	314.30	4.5-1402.64
Euphausia crystallorophias	10	439.13	776.46	4.13-2471.75
Euphausia superba	7	7.47	2.93	2.36-10.94
Euphausia frigida	6	10.05	16.14	0.99-42.41

b. January 1985 - shallow (0-200 m) and deep (0-1000 m) trawls.

Species	Depth (m)	n	Mean no. 1000 m^{-3}	SD	Range
Thysanoessa macrura	0-200	50	471.76	361.77	27.72-1488.56
	0-1000	19	121.28	138.02	1.4-507.39
Euphausia crystallorophias	0-200	16	564.34	1302.87	1.93-4687.91
	0-1000	4	127.75	151.73	0.88-324.36
Euphausia superba	0-200	23	9.80	12.04	0.98-56.93
	0-1000	10	97.30	235.06	0.44-748.56
Euphausia frigida	0-200	20	74.33	96.85	1.70-339.63
	0-1000	7	10.17	15.36	0.65-40.87
Euphausia triacantha	0-200	5	5.68	3.01	3.14-9.43
	0-1000	1	4.71	-	-

c. March 1987 - shallow (0-200 m) and deep (200-1000 m) trawls.

Species	Depth (m)	n	Mean no. 1000 m^{-3}	SD	Range
Thysanoessa macrura	0-200	26	259.92	404.30	3.48-1622.12
	200-1000	3	86.97	140.43	5.16-249.19
Euphausia crystallorophias	0-200	4	74.65	91.25	8.24-205.56
	200-1000	—	—	—	—
Euphausia superba	0-200	23	14829.38	28897.56	0.9-115365.1
	200-1000	3	4297.95	5772.32	643.08-10952.5
Euphausia frigida	0-200	3	2.45	1.05	1.73-3.66
	200-1000	—	—	—	—

Because of the infrequent occurrence and low abundance of this species, it will not be considered further.

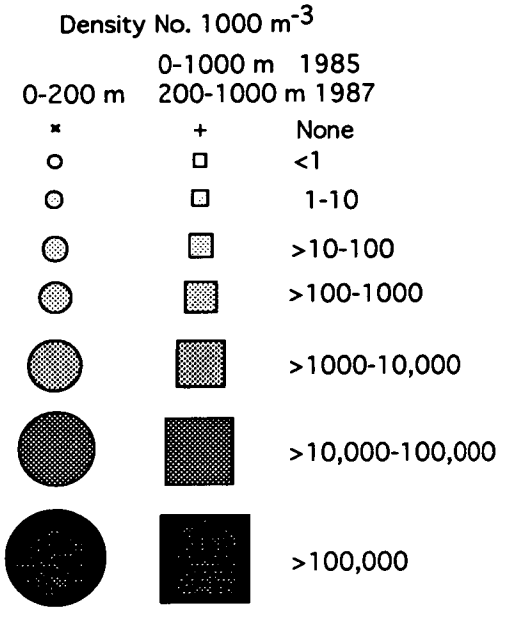
Thysanoessa macrura

T. macrura was consistently the second most abundant species overall, but was the most widespread abundant species throughout the region. This species was collected at all but two sampling sites, shallow and deep. This species was not collected at Station 7 in 1984 and Station 70 in 1987 (Figs 6.1a,c & 6.3a,c). At sites of paired sampling in 1985, the number of larvae collected in shallow and deep hauls were compared to determine if larvae were more abundant in a particular layer. Overall, more larvae were collected in the shallow hauls at these sites, 7134 in total compared with 6428 in deep hauls, but statistically, shallow and deep abundances were not significantly different [Mann-Whitney *U* -test (Zar 1984); U =209.5, n=19, P >0.2]. All developmental stages from calyptopis I to furcilia VI were well represented in both deep and shallow hauls. Although not clearly shown in Fig. 6.4, a few specimens of nauplius I and metanauplius were collected. Metanauplii were collected at Stations 12, 20 and 25 in 1984. In 1985, naupliar stages were collected at Stations 19, (0-200 m) and in deep hauls (0-1000 m) at Stations 7 and 38. No nauplius or metanauplius stages were observed in 1987 and no nauplii II were collected in any year.

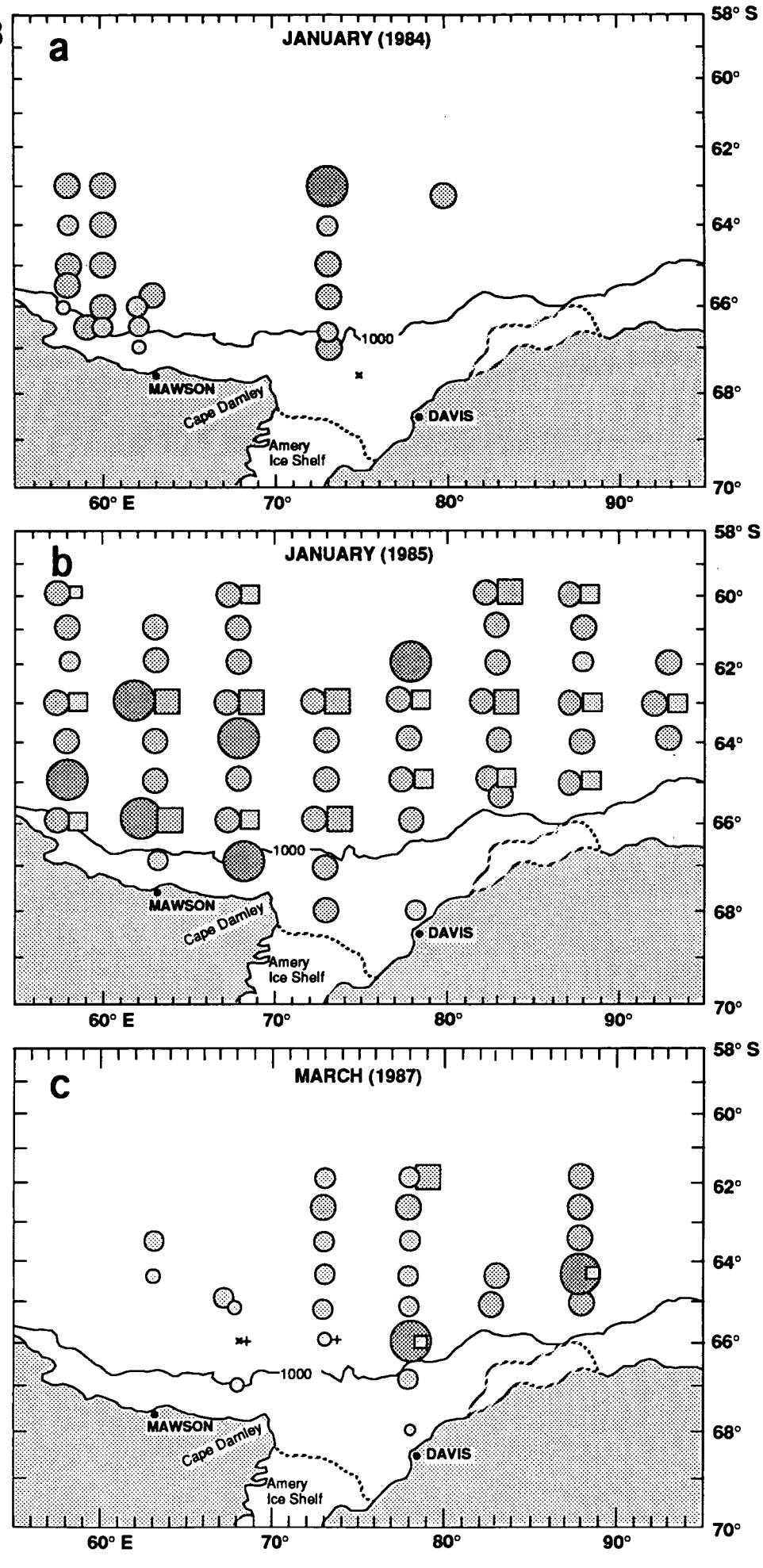
1985 Mean Stage Index (MSI) and Multivariate Analysis (MVA).

The 1985 survey was more comprehensive in terms of sampling sites and environmental parameters measured, and hence will be dealt with first. Analysis of geographic distribution of the MSI shows a clear trend of stage development in the upper 200 m proceeding from south to north, and to

Fig. 6.3 Distribution and abundance of *Thysanoessa macrura* larvae for shallow (0-200 m, circles) and deep trawls (0-1000 m 1985, 200-1000 m 1987, squares). Abundances are expressed as individuals 1000 m^{-3}.



6.3


a
JANUARY (1984)
b
JANUARY (1985)
c
MARCH (1987)
1000
MAWSON
Cape Darnley
Amery
Ice Shelf
DAVIS
60° E
70°
80°
90°
58° S
60°
62°
64°
66°
68°
70°

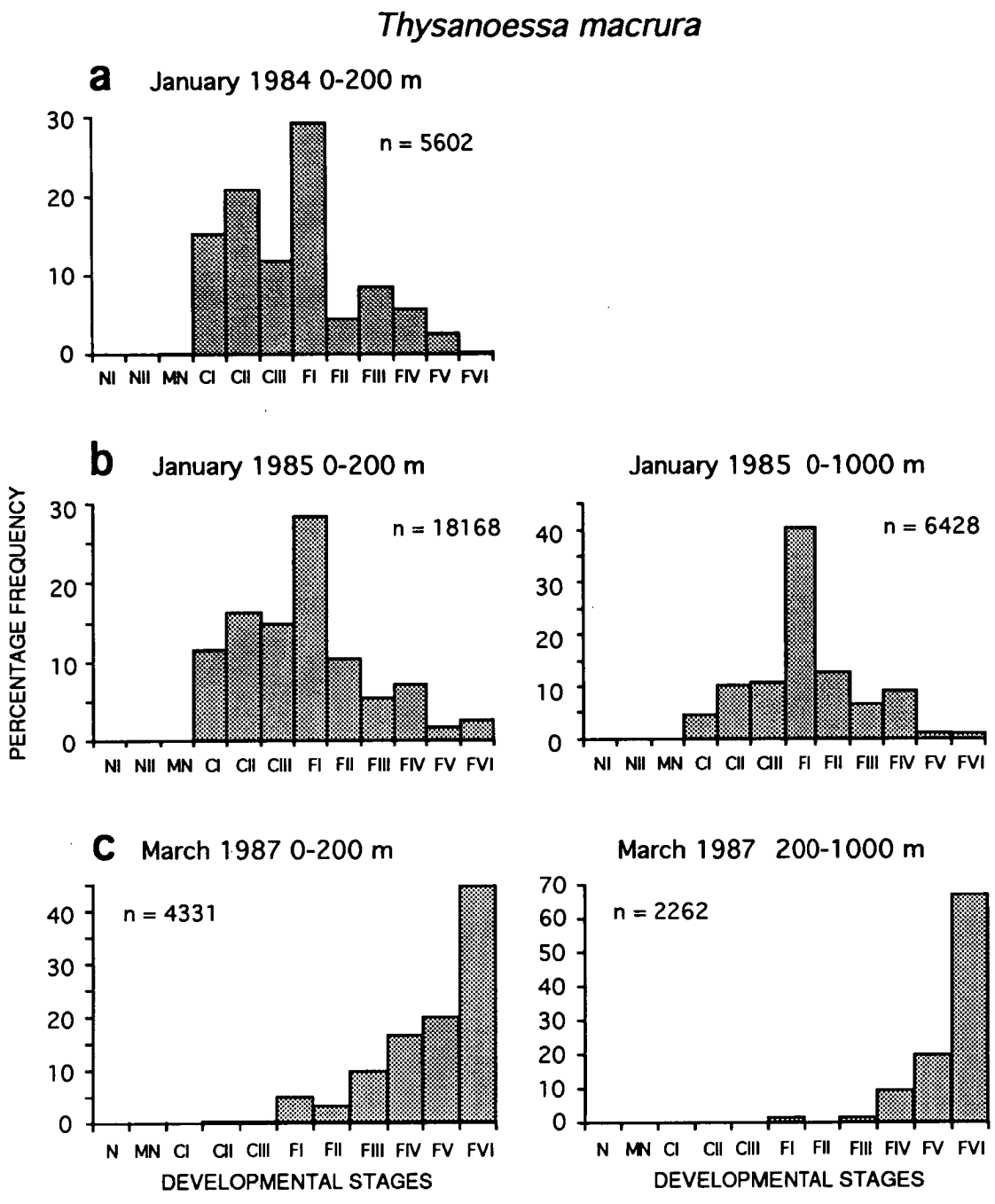


Fig. 6.4 *Thysanoessa macrura* . Percentage frequency distribution of developmental stages for **a)** January 1984, **b)** January 1985 shallow (0-200 m) and deep (0-1000 m) trawls, and **c)** March 1987 shallow (0-200 m) and deep (200-1000 m) trawls. NI, NII = nauplius I and II; MN = metanauplius; CI, CII, CIII = calyptopis I, II, III; FI to FVI = furcilia I to VI; n = total number of individuals identified. Note: NI and NII stages in 1987 combined as nauplius (N).

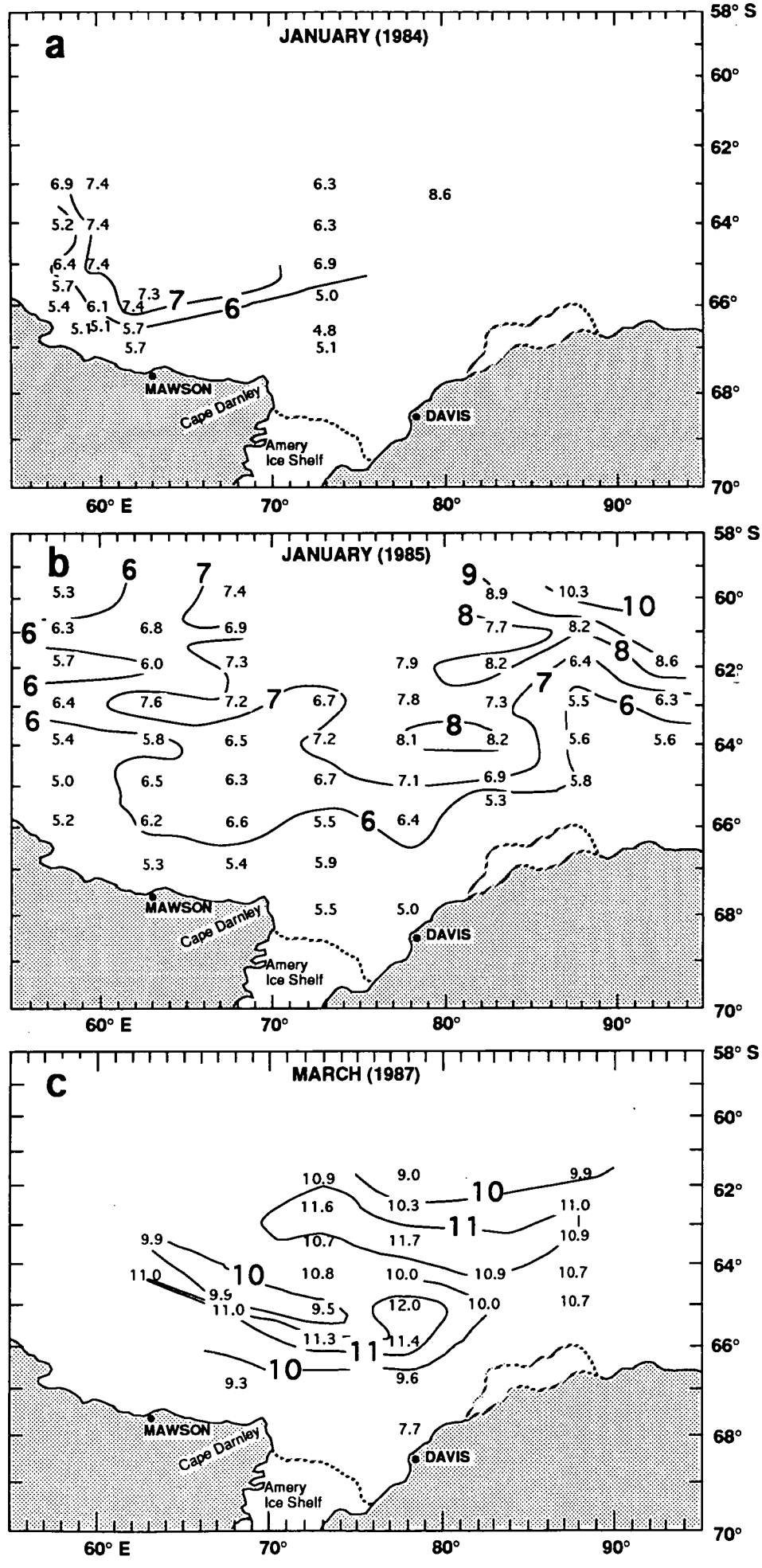
a lesser extent from west to east in the lower latitudes (Fig. 6.5b). At the 19 sites of joint shallow and deep hauls, there was no significant difference in the MSI between the two depths (t = -0.200, DF=36). Six groups of MSI were chosen, from 5 (calyptopis II) to 10+ (furcilia IV +), and consequently six groups were also selected from the dendrogram (Fig. 6.6b), at 32% dissimilarity, in order to determine if there was correspondence between the geographic distribution patterns for the modal frequencies and that of the MSIs. Comparison of Figs 6.5b and 6.7b shows considerable similarity in the two distribution patterns, e.g. the close fit of cluster group 2 and larvae less than MSI 6.

The six cluster groups, ranging in size from 1 to 17 stations showed distinct frequency distributions of developmental stages (Fig. 6.8). Early developmental calyptopis stages were observed in group 1 just north of Mawson. Group 2 occupied most of the inshore region, except for two sites in the north west, and comprised calyptopis stages with many early furcilia stages. Group 3, further to the north, comprised more furcilial stages with the furcilia I stage most abundant. Group 4 of the outer middle region of Prydz Bay comprised sites with increasing amounts of later furcilia stages. Group 5 comprised only 3 sites in the north-east, but these are distinct in having fewer calyptopis stages and two modal peaks, one of early furcilial stages, the second peak of later stages. Group 6 composed of one station in the north-east, had an exceptionally high abundance of the last developmental stage furcilia VI.

Both the MSI and cluster group patterns exhibited a distinct latitudinal zonation (Figs 6.5b, 6.7b). In the multiple regression with NMDS scores, latitude explained 33% of the data variation, whereas ice recession (38%) and mean temperature (37%) explained more of the variation (Table 6.3a, Fig. 6.9). Linear regression of ice, temperature and latitude against MSI explained almost an identical amount of variation in the data (Table 6.3b). Six of the nine phytoplankton pigments explained

Fig. 6.5 Distribution of the mean stage index for *T. macrura* larvae in the upper 200 m for the three surveys. Contour lines were calculated and drawn by hand. Decimal points approximate sample site. For clarity, sites where larvae were not collected are not shown. 4, 5, 6 = calyptopis I, II, III respectively; 7 to 12 = furcilia I to VI.

6.5


a
JANUARY (1984)
6.9 7.4
5.2 7.4
6.4 7.4
5.7
5.4 6.1 7.4
5.1 5.1 5.7
5.7
7.3
7
6
6.3
6.3
6.9
5.0
4.8
5.1
8.6
MAWSON
Cape Darnley
Amery
Ice Shelf
DAVIS
58° S
60°
62°
64°
66°
68°
70°
60° E
70°
80°
90°
b
JANUARY (1985)
5.3
6
7
7.4
6
6.3
6.8
6.9
5.7
6.0
7.3
6
6.4
7.6
7.2
7
6.7
6
5.4
5.8
6.5
7.2
5.0
6.5
6.3
6.7
5.2
6.2
6.6
5.5
6
6.4
5.3
5.4
5.9
7.9
7.8
8.1
8.2
7.1
6.9
5.3
9
8.9
10.3
10
8
7.7
8.2
8
8.6
6.4
7
7.3
5.5
6
6.3
5.6
5.6
5.8
MAWSON
Cape Darnley
Amery
Ice Shelf
5.5
5.0
DAVIS
c
MARCH (1987)
10.9
9.0
10
9.9
11.6
10.3
11.0
11
10.7
11.7
10.9
9.9
11.0
10
10.8
10.0
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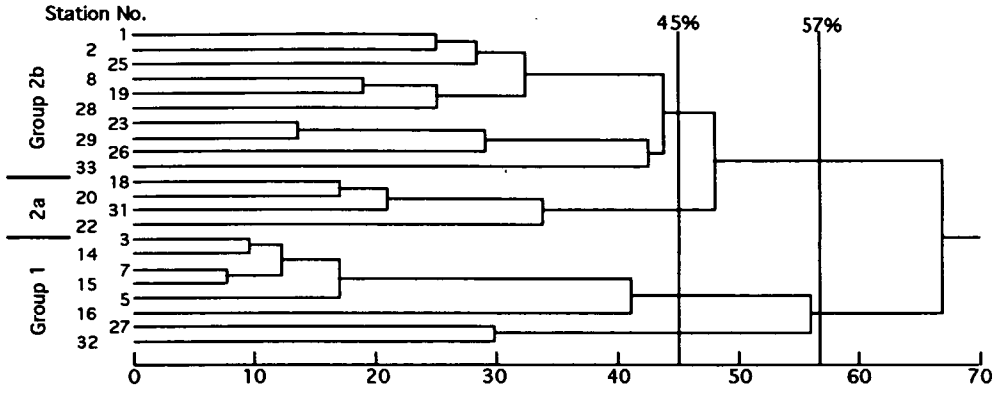
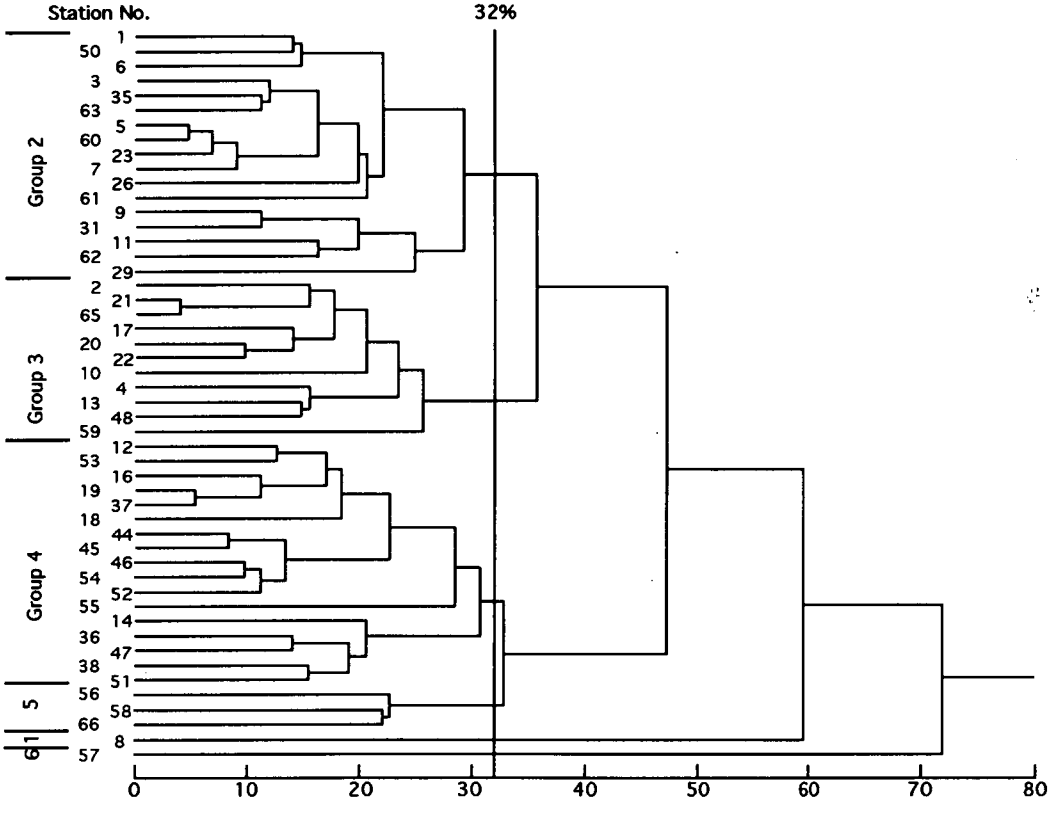
10.7
9.5
11.0
9.5
12.0
10.0
10.7
11.3
11
11.4
10
9.3
9.6
MAWSON
Cape Darnley
Amery
Ice Shelf
7.7
DAVIS

Fig. 6.6 Dendrogram of cluster analyses comparing the frequency distribution of *T. macrura* developmental stages at each sampling site, for each of the three surveys. The Bray-Curtis dissimilarity index was used for the comparison coupled with UPGMA linkage, after transformation to % frequency of abundance.

6.6 a. January 1984



b. January 1985



c. March 1987

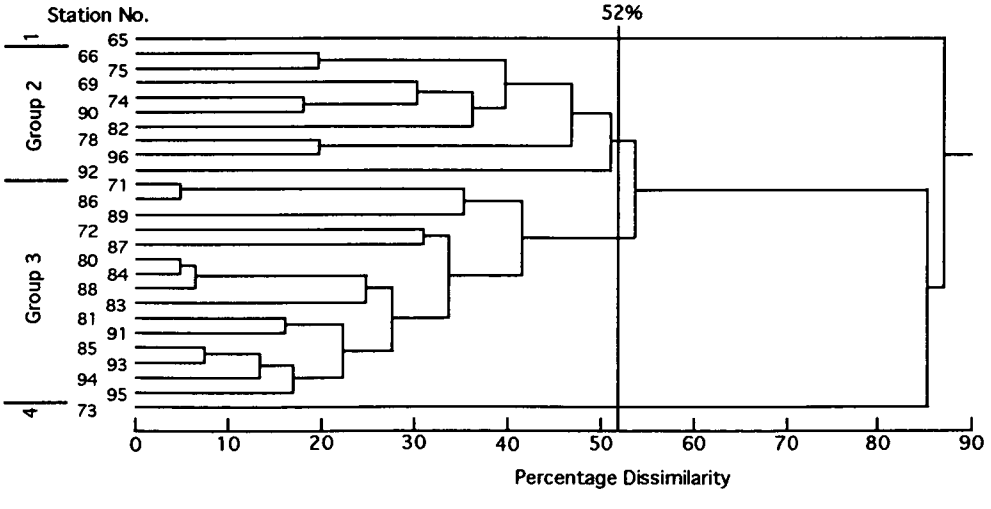
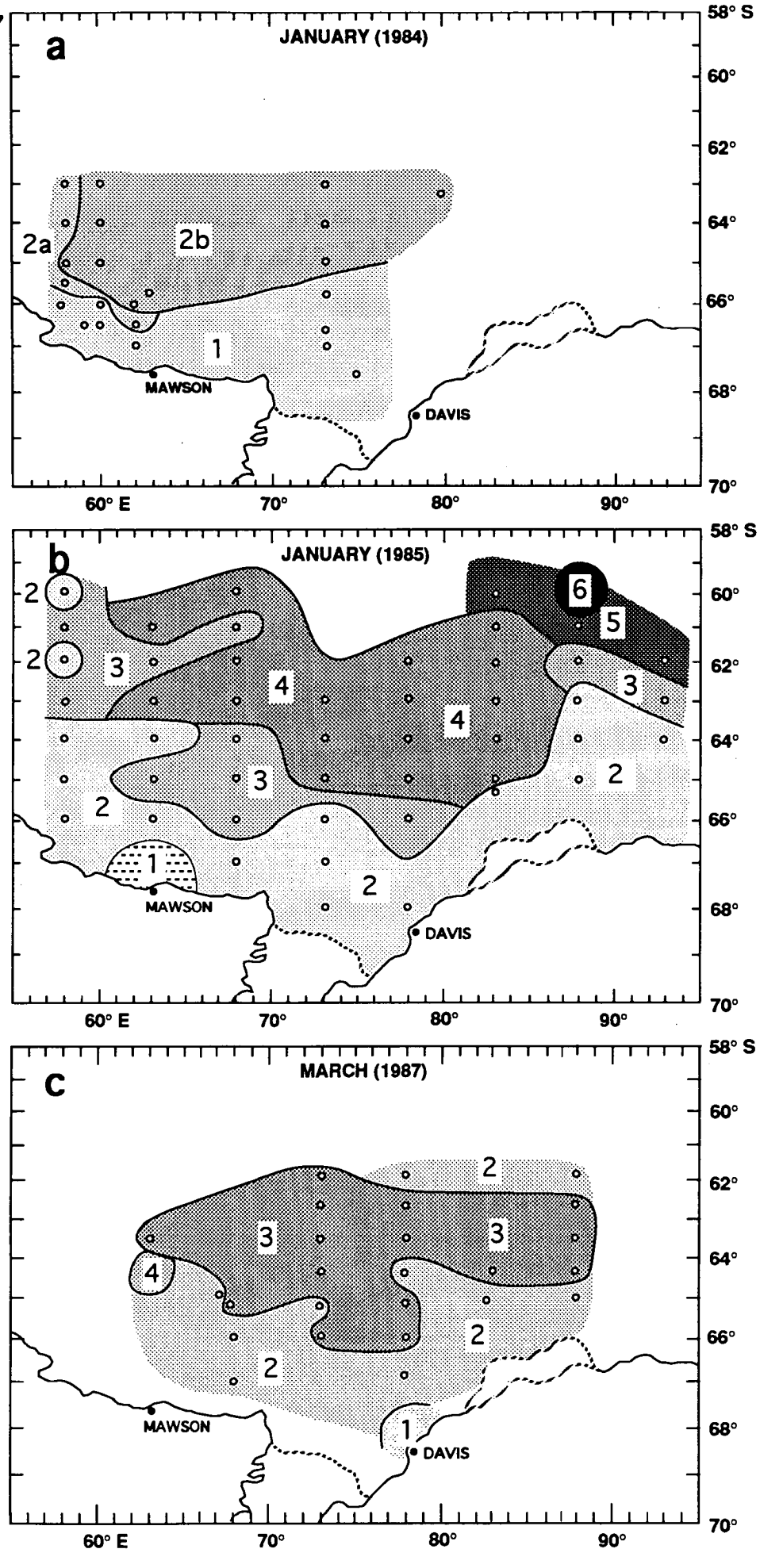


Fig. 6.7 Distribution of cluster groups of *T. macrura* developmental stages identified by the cluster analyses shown in Fig. 6.6.

6.7


a
JANUARY (1984)
2a
2b
1
MAWSON
DAVIS
58° S
60°
62°
64°
66°
68°
70°
60° E
70°
80°
90°
b
JANUARY (1985)
2
3
4
5
6
1
MAWSON
DAVIS
c
MARCH (1987)
2
3
4
1
MAWSON
DAVIS

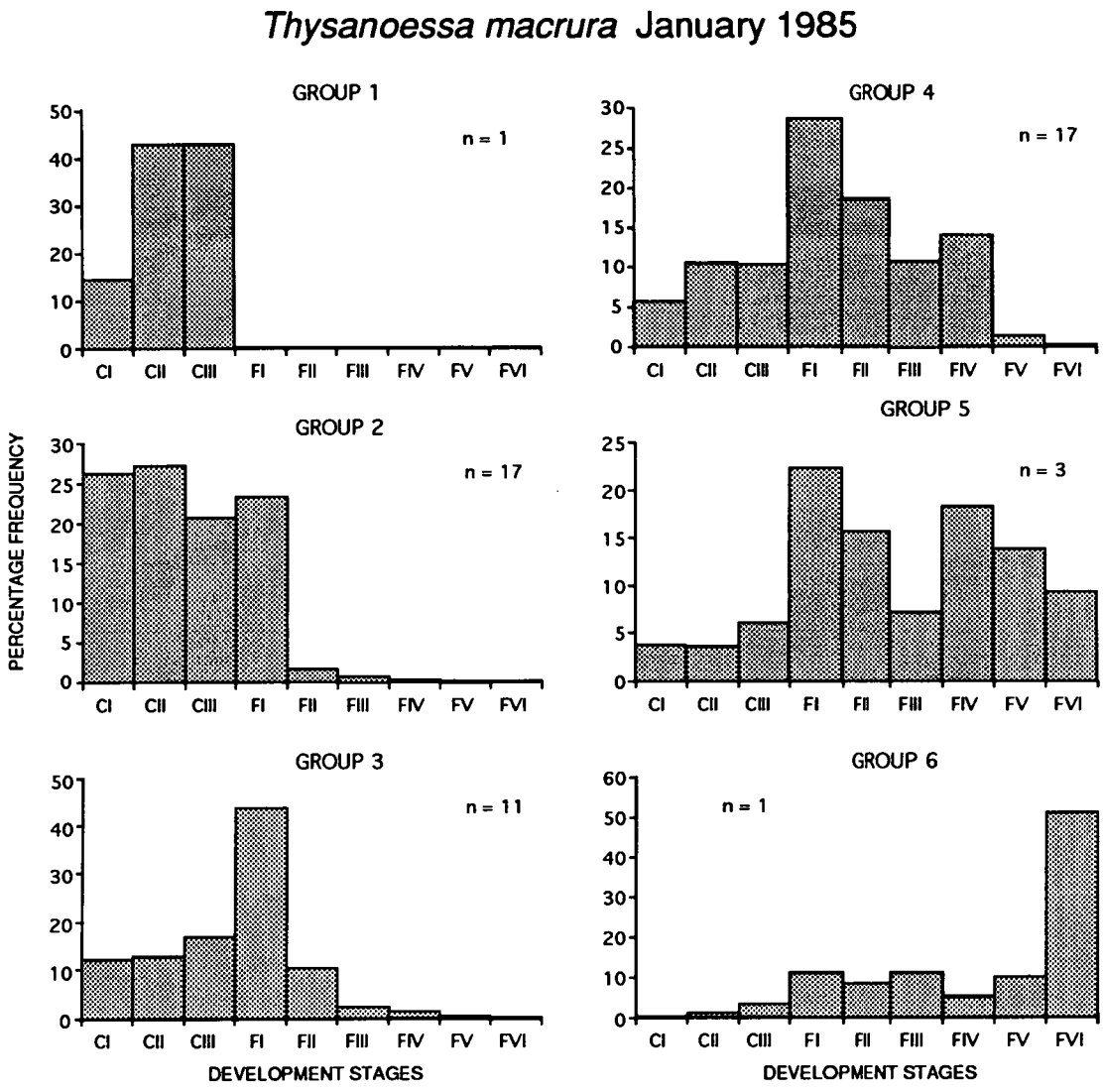
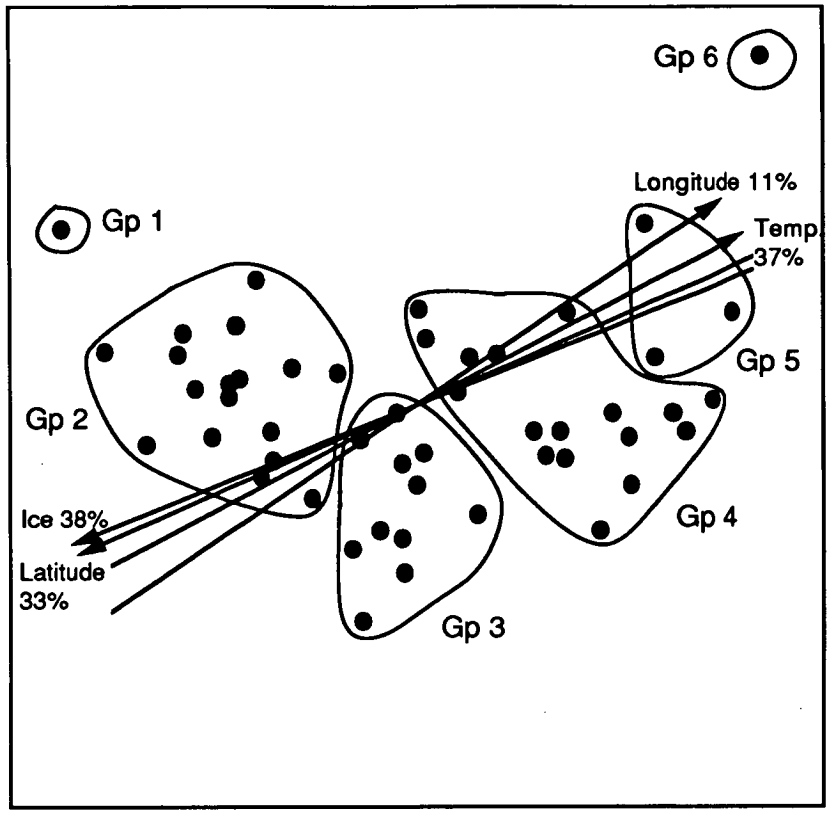


Fig. 6.8 Percentage frequency distribution of developmental stages of *T. macrura* in January1985, for each of the six cluster groups identified (Fig. 6.5b). n = number of sampling sites; CI, CII, CIII, = calyptopis I, II, III; FI to FVI = furcilia I to VI.

Fig. 6.9 Ordination plots of sampling sites for January 1985 comparing the frequency distribution of *T. macrura* developmental stages using non-metric multidimensional scaling and Bray-Curtis dissimilarity index. Respective cluster groups indentified in Fig. 6.6b 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 6.3). Direction of regression line was determined from Equation 3.2. Axis scales are relative in NMDS, based on non-metric ranking of dissimilarity, and therefore are not shown. Stress value is 0.11.

6.9 *Thysanoessa macrura* January 1985



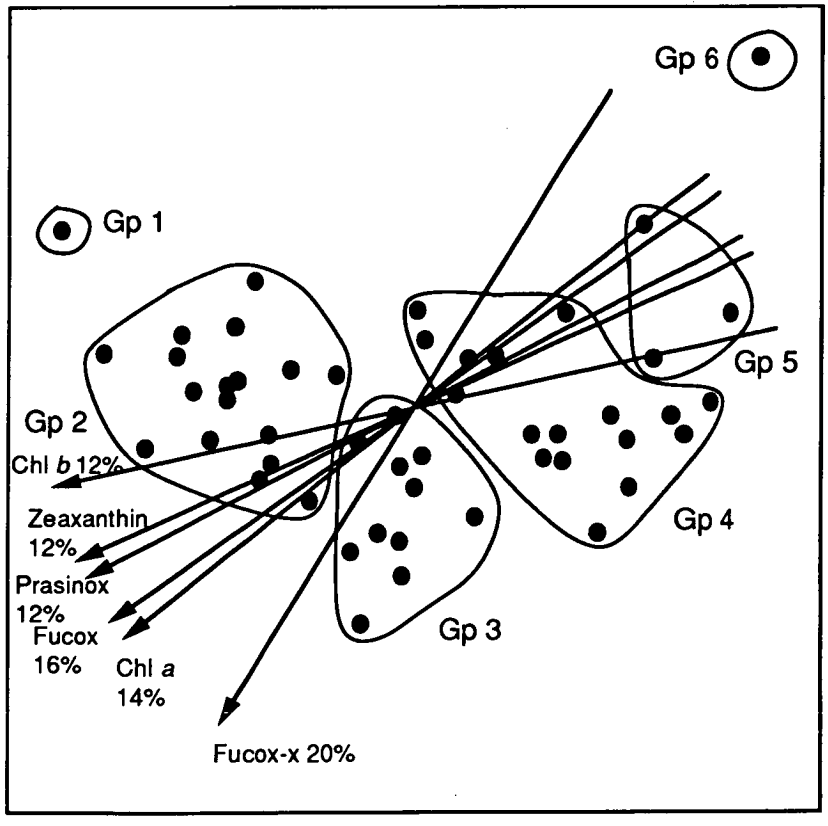


Table 6.3 *Thysanoessa macrura* January 1985. **a.** Multiple regression analyses between environmental parameters and NMDS scores for two-axis ordination of comparison of sampling sites in January 1985. Regression weights are derived from Equation 3.2. **b.** Linear regression between environmental parameters and MSI scores. 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. January 1985 Multiple Regression - NMDS scores

	Direction Cosines (Regression Weights)					
VARIABLE	X	Y	Adj. R^2	F	DF	P
Ice Recession	-0.928	-0.372	0.376	15.774	2,47	***
Temperature	0.881	0.472	0.369	12.700	2,38	***
Latitude	-0.914	-0.406	0.325	12.817	2,47	***
Fucox-x	-0.519	-0.855	0.198	6.297	2,41	**
Fucoxanthin	-0.812	-0.584	0.155	4.940	2,41	*
Sampling Day	0.797	0.604	0.154	5.463	2,47	*
Chlorophyll *a*	-0.781	-0.624	0.143	4.588	2,41	*
Zeaxanthin	-0.884	-0.468	0.122	3.985	2,41	*
Chlorophyll *b*	-0.978	-0.209	0.121	3.966	2,41	*
Prasinox	-0.911	-0.412	0.120	3.920	2,41	*
Longitude	0.825	0.565	0.122	4.099	2,47	*
Alloxanthin	—	—	0.082	2.910	2,41	ns
Hexfucox	—	—	0.067	2.552	2,41	ns
Peridinin	—	—	0.058	2.327	2,41	ns
Duration Haul	—	—	0.021	1.514	2,47	ns
Depth Haul	—	—	-0.021	0.497	2,47	ns
Salinity	—	—	-0.028	0.472	2,38	ns

b. January 1985 Linear Regression - MSI scores

VARIABLE	Adj. R^2	R	F	DF	P
Ice Recession	0.400	-0.642	33.611	1,48	***
Temperature	0.335	0.593	21.172	1,39	***
Latitude	0.319	-0.577	23.944	1,48	***
Sampling Day	0.165	0.427	10.707	1,48	**
Longitude	0.136	0.392	8.717	1,48	**
Zeaxanthin	0.130	-0.388	7.430	1,42	*
Chlorophyll *b*	0.125	-0.381	7.142	1,42	*
Prasinox	0.113	-0.366	6.489	1,42	*
Fucoxanthin	0.102	-0.351	5.892	1,42	*
Fucox-x	0.098	-0.344	5.649	1,42	*
Chlorophyll *a*	0.088	-0.331	5.164	1,42	*
Peridinin	0.034	-0.238	2.518	1,42	ns
Duration Haul	0.028	-0.220	2.429	1,48	ns
Alloxanthin	0.027	-0.223	2.207	1,42	ns
Hexfucox	0.023	-0.214	2.007	1,42	ns
Salinity	-0.005	-0.142	0.801	1,39	ns
Depth Haul	-0.009	-0.106	0.548	1,48	ns

some of the variation. Fucox-x (chrysophytes, prymnesiophytes-Wright 1987) had the most significant regression with NMDS scores (20%), amongst the pigments, at a distinctly different direction to the other pigments and latitude (Fig. 6.9). Zeaxanthin (cyanobacteria) was the pigment with the highest correlation with MSI (13%). Cyanobacteria have an extremely low abundance and patchy distribution in Prydz Bay, with zeaxanthin levels ranging from 0 to 0.032 $\mu g\ l^{-1}$, whereas much higher levels are found in lower latitudes especially north of the convergence (Marchant *et al.* 1987; Wright 1987). The correlation between MSI and zeaxanthin could be a statistical artefact, but further studies into a possible relationships between *T. macrura* larvae and cyanobacteria should not be dismissed. As well as there being a latitudinal zonation, longitude also explained some variation in both NMDS and MSI patterns. Time in days since the start of sampling also explained much of the observed patterns (Table 6.3).

1984 MSI and MVA Although was not as extensive in 1984, a distinct north-south pattern was observed with early developmental stages south and more advanced stages towards the north. There was also very good correspondence between the MSI pattern (Fig. 6.5a) and the distribution of cluster groups (Fig. 6.7a). Cluster Group 1, in the south along the shelf edge, was dominated by calyptopis stages - there were very few furciliae (Fig. 6.10). Cluster Group 2 in the north comprised a greater proportion of advanced furciliae larvae. This cluster group, originally defined at 57% dissimilarity, could be further divided at 45% into two subgroups (Fig. 6.6a), which further highlights the pattern of more advanced stages occurring towards the north. Group 2a comprised 4 sites and partly separated Group 2b from Group 1 geographically (Fig 6.7a). Group 2a also had a composition of developmental stages intermediate in

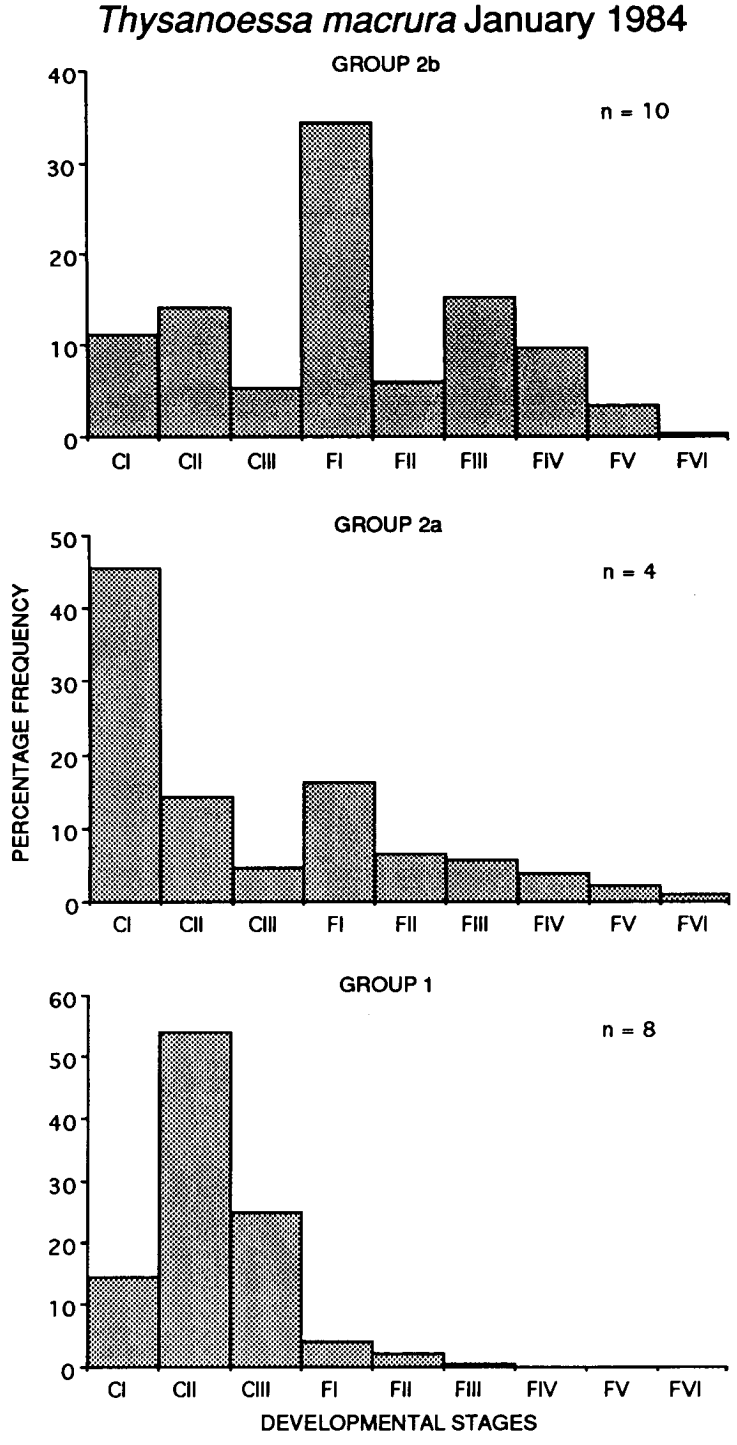
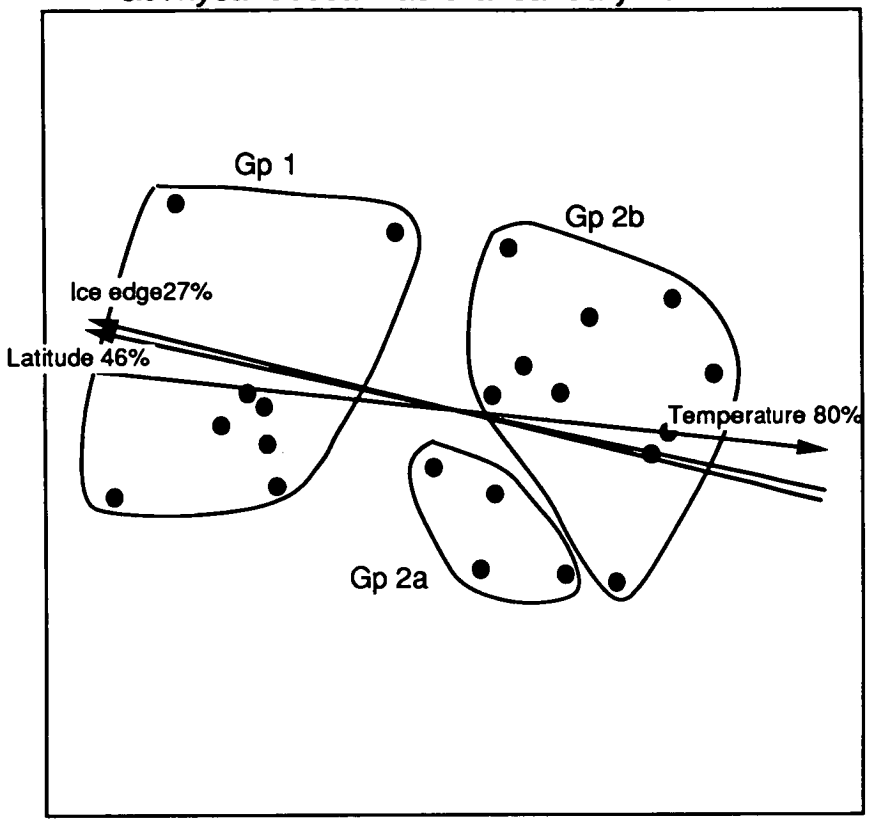


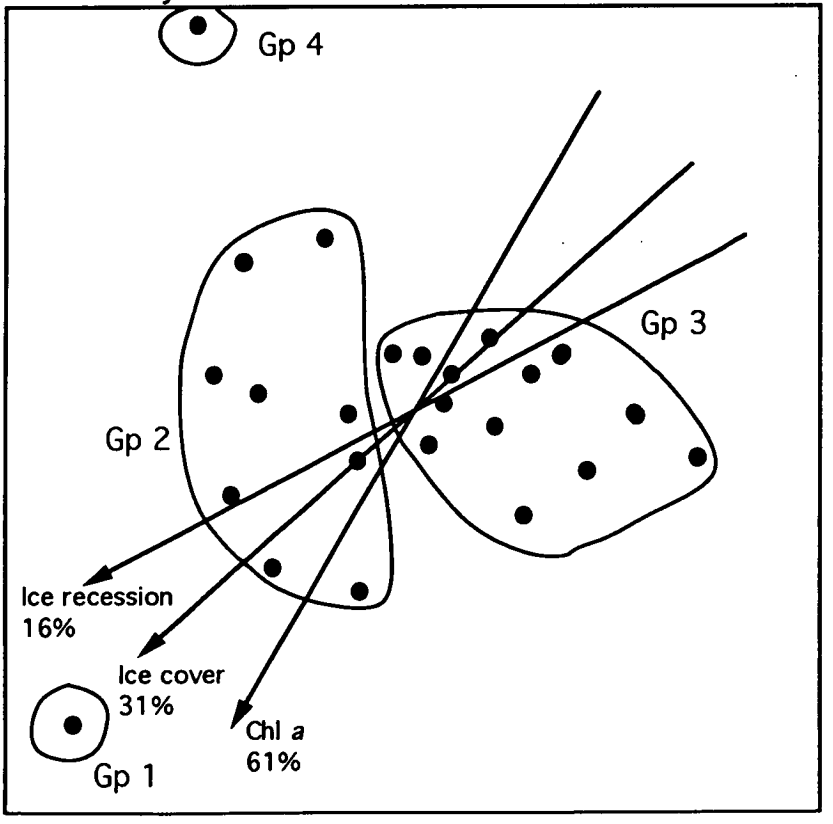
Fig. 6.10 Percentage frequency distribution of developmental stages of *T. macrura* in January 1984, for each of the three cluster groups identified (Fig. 6.5a). n = number of sampling sites; CI, CII, CIII, = calyptopis I, II, III; FI to FVI = furcilia I to VI.

Fig. 6.11 Ordination plots of sampling sites for **a)** January 1984 and **b)** March 1987 comparing the frequency distribution of *T. macrura* developmental stages using non-metric multidimensional scaling and Bray-Curtis dissimilarity index. Respective cluster groups indentified in Fig. 6.6 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 Tables 6.4 & 6.5). Direction of regression line was determined from Equation 3.2. Axis scales are relative in NMDS, based on non-metric ranking of dissimarlity, and therefore are not shown. Stress values are **a)** 0.11 and **b)** 0.13.

6.11 **a.** *Thysanoessa macrura* January 1984



b. *Thysanoessa macrura* March 1987



character to Groups 1 and 2b (Fig. 6.10). This intermediate position is also seen in the NMDS plot (Fig. 6.11a).

The latitudinal zonation was more distinct in 1984 as indicated by latitude explaining 46 % of the data variation, as compared to 33% in 1985. Temperature, however, explained a much more significant amount of the data variation at 80% for NMDS and also 66% of the MSI pattern (Fig. 6.11a, Table 6.4). Ice recession also explained much of the variation in NMDS and MSI. Unfortunately there were no chlorophyll *a* data collected during 1984. Sampling day did not explain a significant amount of the NMDS data variation but did explain 28% of the MSI pattern. This may be due to the higher MSI value at Station 33 polarizing the correlation. This site was sampled 11 days after the rest of the sites were completed. Sampling day was not significant after removal of Station 33 from the data set ($F=1.846$, $P=0.143$, $DF=1,19$). Sampling depth also explained some of the variation in the MSI pattern but not the NMDS plot.

1987 MSI and MVA In March 1987, the larvae throughout the region were predominantly more advanced furciliae. The MSI mainly ranged from 9.3 to 12 representing stages furcilia 3 to 6 (Fig. 6.5c) Station 65, just north of Davis, was the one exception with earlier stages furcilia 1 and 2 (Figs 6.6c, 6.12). Unlike the previous January 1984 and 1985 surveys, there was no north-south zonation evident in either the MSI pattern or the distribution of station cluster groups (Figs 6.5c, 6.7c). Neither latitude nor longitude explained a significant level of variation in the data (Fig. 6.11b, Table 6.5). There was partial agreement between the MSI and station cluster group patterns. There were three main MSI groups, 9-10, 10-11, 11-12 (Fig. 6.5c). In the cluster analysis, only 2 main groups could be defined (52% dissimilarity). Both the MSI and cluster analysis show that the more advanced developmental stages were found in the middle of

Table 6.4 *Thysanoessa macrura* January 1984. **a.** Multiple regression analyses between environmental parameters and NMDS scores for two-axis ordination of comparison of sampling sites. Regression weights are derived from Equation 3.2. **b.** Linear regression between environmental parameters and MSI scores. 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. January 1984 Multiple Regression - NMDS scores

	Direction Cosines (Regression Weights)					
VARIABLE	X	Y	Adj. R^2	F	DF	P
Temperature	0.994	-0.114	0.800	32.982	2,14	***
Latitude	-0.975	0.221	0.458	9.886	2,19	**
Ice Recession	-0.970	0.243	0.273	4.938	2,19	*
Salinity	—	—	0.189	2.866	2,14	ns
Depth Haul	—	—	0.087	2.002	2,19	ns
Sampling Day	—	—	0.051	1.560	2,19	ns
Duration Haul	—	—	-0.002	0.975	2,19	ns
Longitude	—	—	-0.028	0.718	2,19	ns

b. January 1984 Linear Regression - MSI scores

VARIABLE	Adj. R^2	R	F	DF	P
Temperature	0.657	0.824	31.690	1,15	***
Latitude	0.360	-0.625	12.823	1,20	**
Sampling Day	0.276	0.557	8.998	1,20	*
Ice Recession	0.238	-0.524	7.564	1,20	*
Depth Haul	0.151	0.437	4.428	1,20	*
Salinity	0.182	0.483	4.554	1,15	ns
Longitude	-0.039	0.104	0.218	1,20	ns
Duration Haul	-0.048	-0.042	0.036	1,20	ns

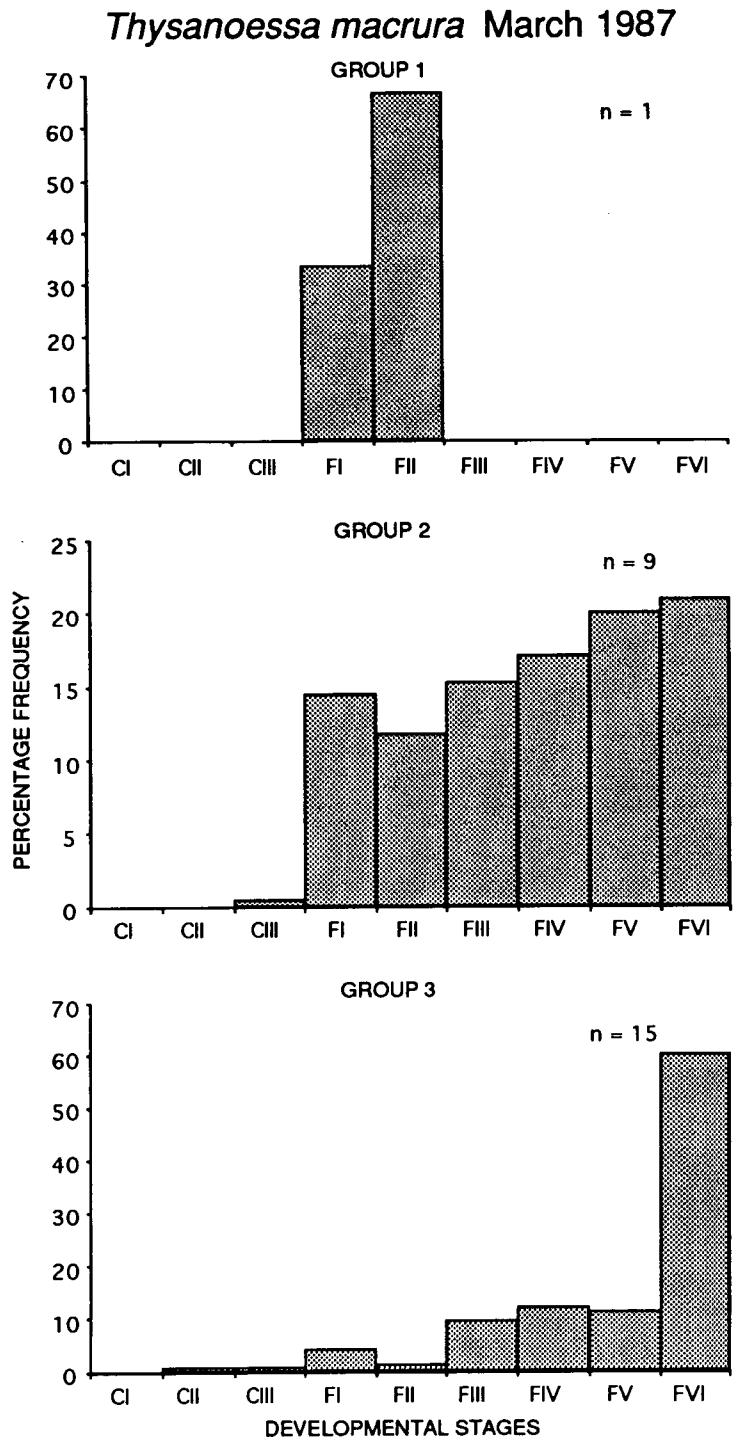


Fig. 6.12 Percentage frequency distribution of developmental stages of *T. macrura* in March 1987 for three of the four cluster groups identified (Fig. 6.6c). Group 4 comprised 2 specimens of furcilia V and is not shown. n = number of sampling sites; CI, CII, CIII, = calyptopis I, II, III; FI to FVI = furcilia I to VI.

Table 6.5 *Thysanoessa macrura* March 1987. **a.** Multiple regression analyses between environmental parameters and NMDS scores for two-axis ordination of comparison of sampling sites. Regression weights are derived from Equation 3.2. **b.** Linear regression between environmental parameters and MSI scores. 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, † = non-significant variables when station 65 was removed from data set.

a. March 1987 Multiple Regression - NMDS scores

	Direction Cosines (Regression Weights)					
VARIABLE	X	Y	Adj. R^2	F	DF	P
Surface Chl *a*	-0.498	-0.867	0.609	17.324	2,19	***
Ice cover	-0.743	-0.669	0.309	9.007	2,23	**
Duration Haul	-0.428	-0.904	0.257	5.317	2,23	*
Ice recession	-0.882	-0.471	0.163	3.431	2,23	*
Sampling Day	—	—	0.100	2.386	2,23	ns
†Ice cover	—	—	0.036	1.450	2,22	ns
†Duration Haul	—	—	0.030	1.372	2,22	ns
Latitude	—	—	0.012	1.157	2,23	ns
Temperature	—	—	0.012	1.135	2,20	ns
†Surface Chl *a*	—	—	-0.005	0.953	2,18	ns
†Ice recession	—	—	-0.021	0.752	2,22	ns
Depth of Haul	—	—	-0.047	0.439	2,23	ns
Longitude	—	—	-0.065	0.242	2,23	ns

b. March 1987 Linear Regression - MSI scores

VARIABLE	Adj. R^2	R	F	DF	P
Surface Chl *a*	0.466	-0.701	19.316	1,20	***
Ice cover	0.354	-0.616	14.718	1,24	**
Duration Haul	0.262	-0.540	9.852	1,24	**
Sampling Day	0.260	0.538	9.796	1,24	**
Ice recession	0.161	-0.441	5.780	1,24	*
†Sampling Day	0.119	0.394	4.230	1,23	ns
†Duration Haul	0.064	-0.321	2.644	1,23	ns
Latitude	0.051	-0.298	2.355	1,24	ns
†Ice cover	0.046	-0.293	2.167	1,23	ns
Temperature	0.037	0.284	1.848	1,21	ns
†Surface Chl *a*	0.016	-0.256	1.332	1,19	ns
†Ice recession	-0.022	-0.143	0.479	1,23	ns
Depth of Haul	-0.028	-0.114	0.313	1,24	ns
Longitude	-0.038	0.059	0.083	1,24	ns

the survey area. Earlier developmental stages were found to the south and north (Figs 6.5c, 6.7c). Station Group 3 represents those sites in the centre of the region which were dominated by the last developmental stage, furcilia 6. Group 2 of nine stations were mainly located in the south, but two sites were in the north (Fig. 6.7c). This group had a relatively more even frequency distribution of all six furcilia stages (Fig. 6.12). Single station Group 1 comprised furcilia 1 and 2 stages as noted above. The other single station Group 4 in the west comprised two furcilia 5 larvae.

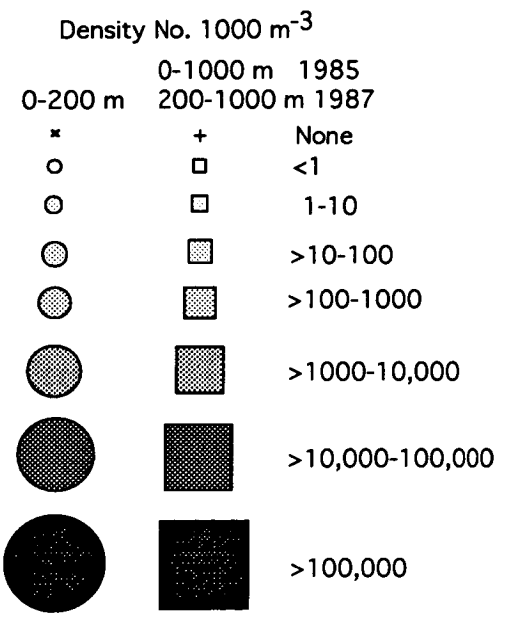
Surface chlorophyll *a* abundances explained some 61% of the variation in the data. Pack-ice cover and ice recession also explained significant levels, 31 and 16% respectively (Table 6.5). The duration of the sample haul also explained 26% of the variation in the data. Together with sampling day, these parameters were also correlated with MSI. However, these significant correlations are a function of the much higher parameter values recorded at Station 65. This station had the highest chlorophyll *a* level at 2.84 $\mu g\ l^{-1}$ compared with the next highest levels of 0.97 at Station 66 and 0.63 $\mu g\ l^{-1}$ at Station 88. Station 65 was eventually the last of the sites to be relatively free of pack-ice, although most of the pack-ice remained in the vicinity of the station at 3/10 cover. The longest haul also occurred at Station 65. When Station 65 was removed from the data set none of the above parameters explained significant amounts of variation in the observed patterns (Table 6.5). In other words, no parameter explained the distribution patterns of either the two main cluster groups or the three main MSI groups.

Euphausia crystallorophias

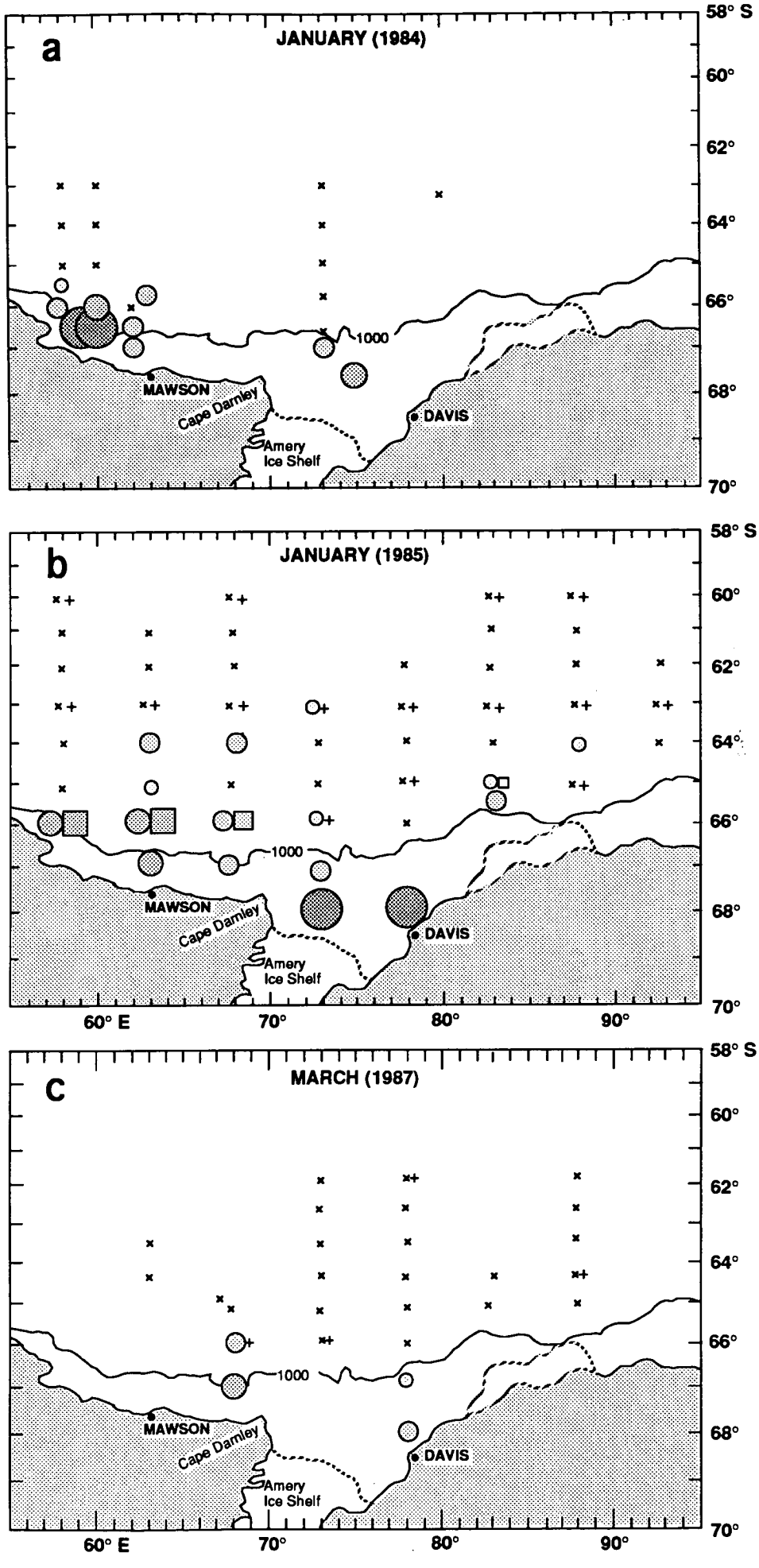
1985. *E. crystallorophias* was found only in the south of the area surveyed, mainly on the continental shelf (Fig. 6.13b). In the region north of Mawson a number of specimens were found well north beyond the continental shelf. In the limited area where this species occurred, it was the most abundant species, slightly more so than *T. macrura*. More larvae were caught in deep trawls at the paired sampling sites, 798 total in shallow and 1568 in deep hauls, but differences in the numbers of larvae between shallow and deep hauls were not significant (U =18.5, n=6, P >0.2). All naupliar and calyptopis stages were collected, but no furciliae. The main components in the upper 200 m were metanauplius and calyptopis I, and in 0-1000 m calyptopis I and calyptopis II (Fig. 6.14b). Most of the youngest naupliar stages (nauplius I) were found at Stations 26 and 29 in the Amery Basin, and it was at these stations that the highest abundances were observed, 2786 and 4688 individuals 1000 m^{-3}, respectively. Much lower abundances of nauplius II and metanauplius were caught at Stations 7, 8, 9, 23 and 31. There was a tendency for later stages to occur more in the north, particularly at the 3 most northerly sites off Mawson (Fig. 6.15b), although caution is required since the MSI estimates at these sites are based on only a few specimens.

1984. Larvae were confined to the waters of the continental shelf or extending more than 40 miles north of the shelf edge (Fig. 6.13a), i.e. not as far north as seen in January 1985. The highest concentrations of larvae north-west of Mawson (Stations 16, 17) were dominated by calyptopis I, and this dominance is reflected in the overall frequency distribution of stages from all sites (Fig. 6.14a). The majority of nauplius stages occurred in the centre of Prydz Bay at Station 7, where at a density of 93.04 individuals 1000 m^{-3} they represented 45% of the composition of

Fig. 6.13 Distribution and abundance of *Euphausia crystallorophias* larvae for shallow (0-200 m, circles) and deep trawls (0-1000 m 1985, 200-1000 m 1987, squares). Abundances are expressed as individuals 1000 m^{-3}.



6.13


a
JANUARY (1984)
b
JANUARY (1985)
c
MARCH (1987)
1000
MAWSON
Cape Darnley
Amery
Ice Shelf
DAVIS
58° S
60°
62°
64°
66°
68°
70°
60° E
70°
80°
90°

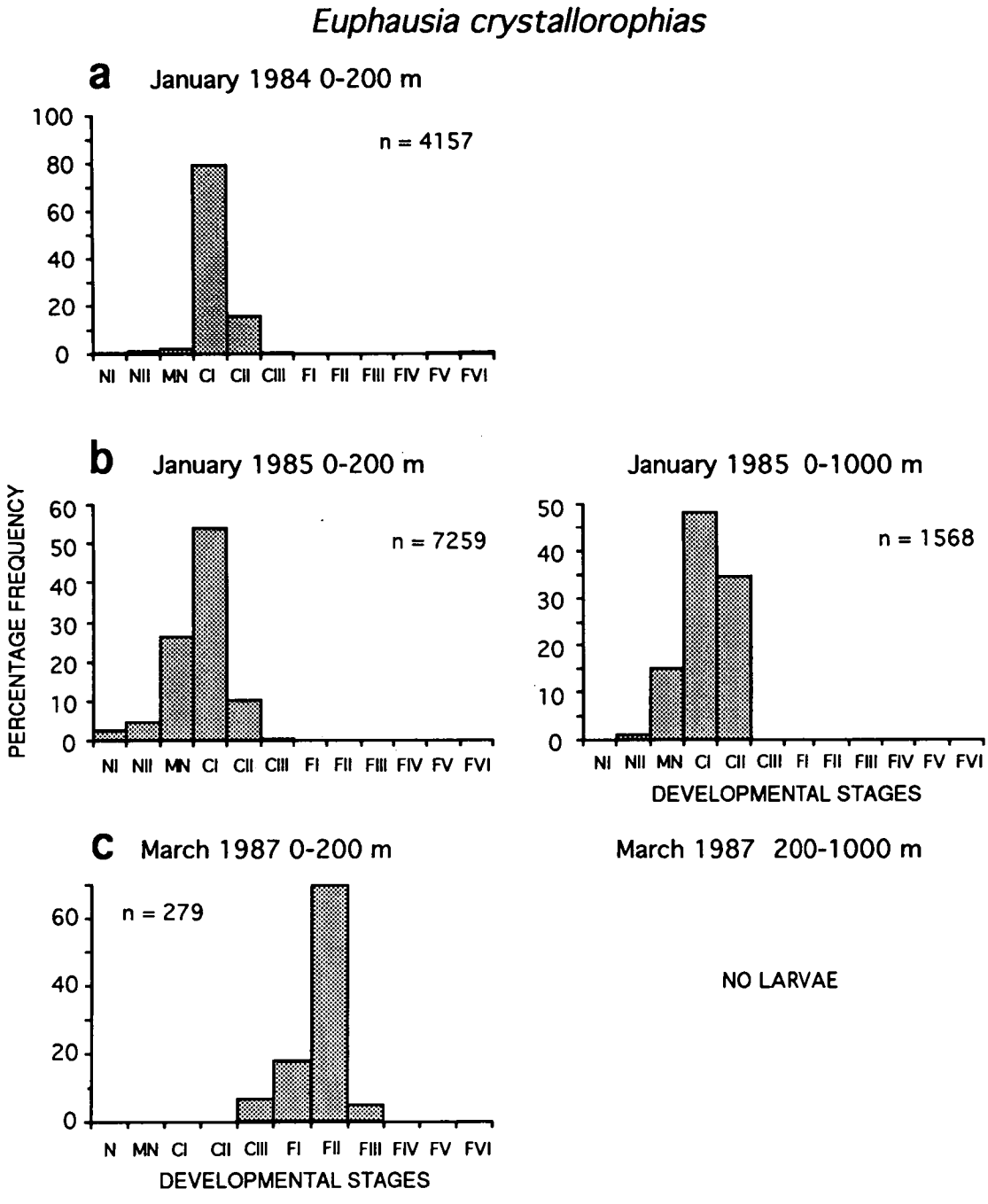
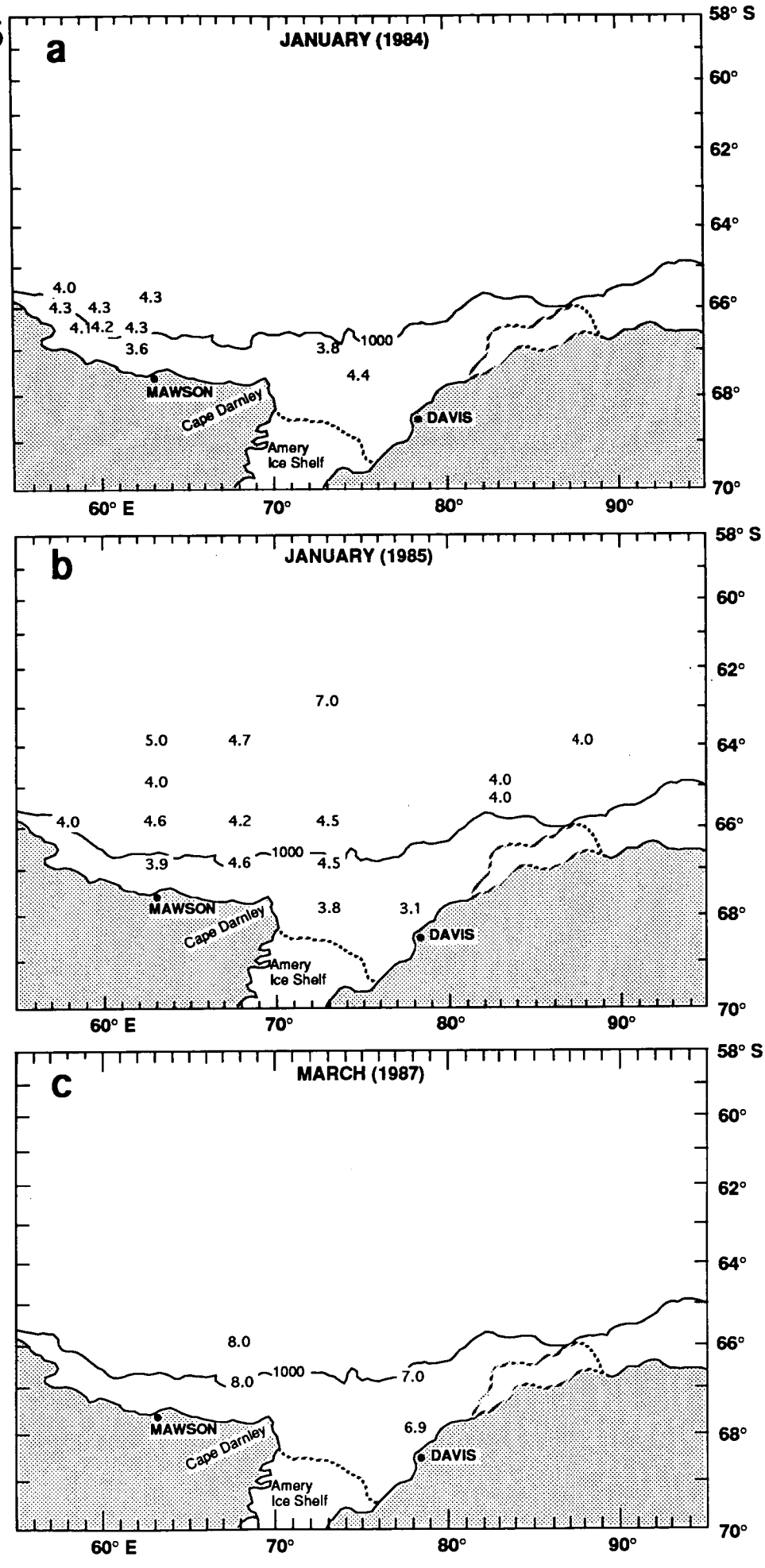


Fig. 6.14 *Euphausia crystallorophias.* Percentage frequency distribution of developmental stages for **a)** January 1984, **b)** January 1985 shallow (0-200 m) and deep (0-1000 m) trawls, and **c)** March 1987 shallow (0-200 m). Larvae were not caught in deep (200-1000 m) trawls in March 1987. NI, NII = nauplius I and II; MN = metanauplius; CI, CII, CIII = calyptopis I, II, III; FI to FVI = furcilia I to VI; n = total number of individuals identified. Note: NI and NII stages in 1987 combined as nauplius (N).

Fig. 6.15 Distribution of the mean stage index for *E. crystallorophias* larvae in the upper 200 m for the three surveys. Decimal points approximate sample site. For clarity, sites where larvae were not collected are not shown. 3 = metanauplius; 4, 5, 6 = calyptopis I, II, III respectively; 7 to 12 = furcilia I to VI.

6.15


a
JANUARY (1984)
4.0
4.3
4.3
4.3
4.1
4.2
4.3
3.6
3.8
1000
4.4
MAWSON
Cape Darnley
Amery
Ice Shelf
DAVIS
58° S
60°
62°
64°
66°
68°
70°
60° E
70°
80°
90°
b
JANUARY (1985)
7.0
5.0
4.7
4.0
4.0
4.0
4.0
4.6
4.2
4.5
4.0
3.9
4.6
1000
4.5
MAWSON
3.8
3.1
Cape Darnley
DAVIS
Amery
Ice Shelf
c
MARCH (1987)
8.0
8.0
1000
7.0
MAWSON
6.9
Cape Darnley
DAVIS
Amery
Ice Shelf

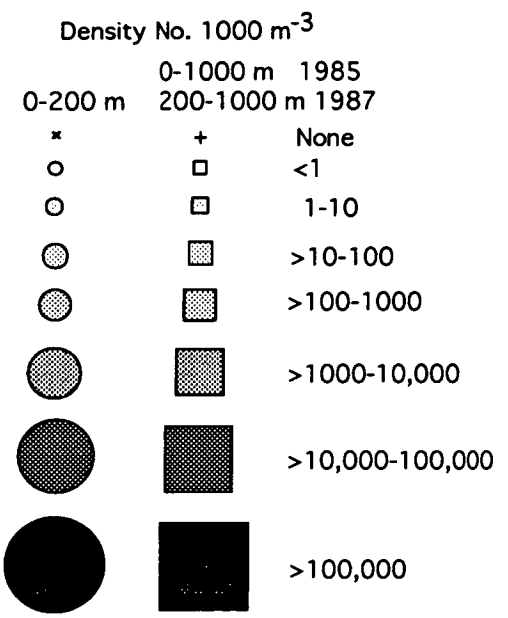
developmental stages at that site. The MSI score at this site was the highest (4.4), but this is due to the presence of the only furcilia stages collected in 1984. These were four specimens of furcilia V and 9 specimens of furcilia VI. Removal of these stages from the MSI calculation reduces the score to 3.2, which is then the lowest value. Lower abundances of nauplius and metanauplius stages were also collected at Stations 8, 17, 27, 31.

1987. Larvae were collected at only four of the southern sampling sites, although sampling was not as extensive on the shelf or in the west because of poor weather conditions (Fig. 6.13c). No larvae were collected in deep trawls. Mean abundance for the 4 sites was considerably lower than those observed in 1984, 1985 (Table 6.2). The larvae collected in March 1987 were more advanced stages, calyptopis III to furcilia III. The dominant stage was furcilia II (Fig. 6.14c).

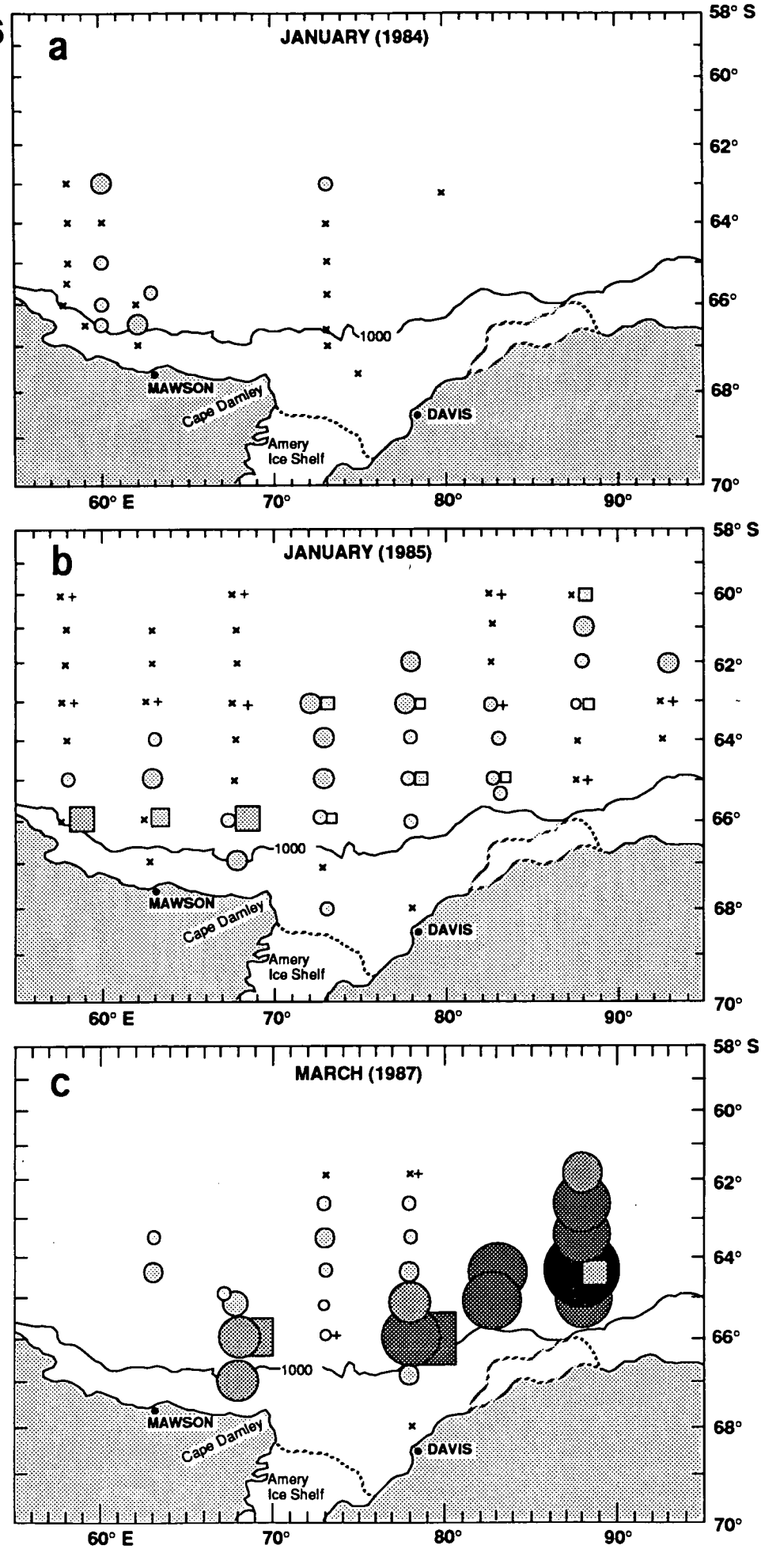
Euphausia superba

1985. *E. superba* had a distinct diagonal south-west to north-east distribution (Fig. 6.16b). Calyptopis I larvae were dominant in the upper 200 m, with fewer calyptopis II, calyptopis III, and furcilia I also present (Fig 6.17b). However, collectively they had a very low abundance, only marginally more than *E. triacantha* (Table 6.2b). The greater part of the larval abundance was observed in the 0-1000 m trawls at Stations 7, 9 and 22 just north of the shelf break near Mawson. Station 7 in particular returned the highest abundance of 748.56 individuals 1000 m^{-3}, with no larvae in the shallow trawl. Similarly, no larvae were collected in the upper 200 m at Station 9. Deep trawls in the middle of the region and in the north-east caught very few specimens. Overall, there were

Fig. 6.16 Distribution and abundance of *Euphausia superba* larvae for shallow (0-200 m, circles) and deep trawls (0-1000 m 1985, 200-1000 m 1987, squares). Abundances are expressed as individuals 1000 m^{-3}.



6.16


a
JANUARY (1984)
b
JANUARY (1985)
c
MARCH (1987)
1000
MAWSON
Cape Darnley
Amery
Ice Shelf
DAVIS
58° S
60°
62°
64°
66°
68°
70°
60° E
70°
80°
90°

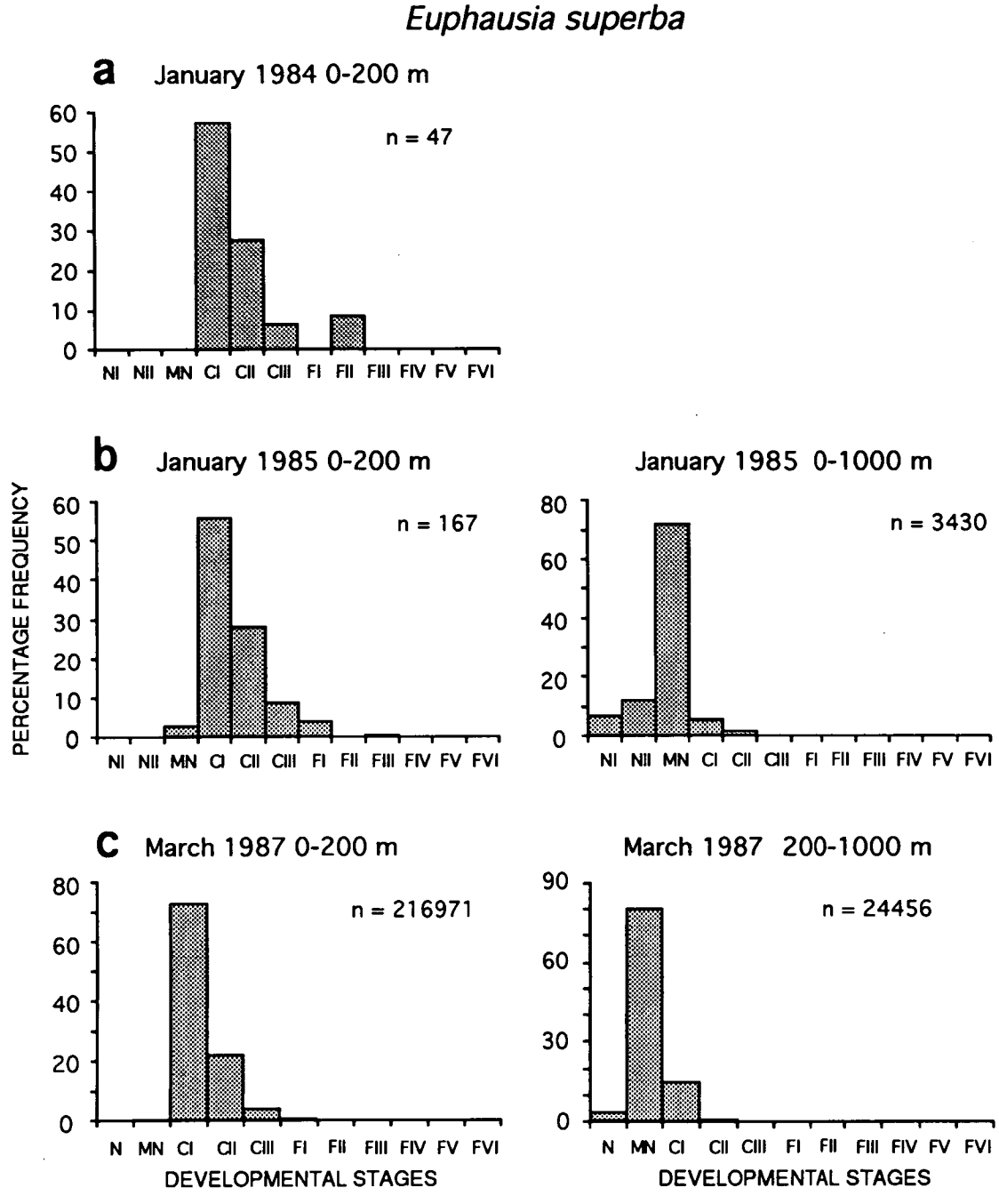


Fig. 6.17 *Euphausia superba* . Percentage frequency distribution of developmental stages for **a)** January 1984, **b)** January 1985 shallow (0-200 m) and deep (0-1000 m) trawls, and **c)** March 1987 shallow (0-200 m) and deep (200-1000 m) trawls. NI, NII = nauplius I and II; MN = metanauplius; CI, CII, CIII = calyptopis I, II, III; FI to FVI = furcilia I to VI; n = total number of individuals identified. Note: NI and NII stages in 1987 combined as nauplius (N).

significantly more larvae caught in the deep hauls at paired sampling sites, 44 in shallow and 3430 total in deep hauls (U =92, n=11, 0.02< P <0.05).

The deep trawls at 7, 9 and 22 were dominated by the youngest larval stages, nauplius I, nauplius II and especially metanauplius (Fig. 6.17b). A few calyptopis stages also occurred but no furcilia were collected in any deep trawl. Along meridians 63° and 73°E (Fig. 6.18b) there was a trend of later stages occurring further off shore as seen in *T. macrura*. However, there was no clear distribution pattern of MSI overall. Many of the off shore MSI are based on very low abundances, hence it is unlikely that any inherent pattern would be displayed.

1984. Very few larvae were collected in 1984. The mean density was the lowest for any species in 1984, but similar to the 1985 estimate for *E. superba* in the upper 200 m (Tables 6.2a,b). Larvae were mainly distributed along the 60° E meridian. The majority of stages were calyptopis, particularly calyptopis I (Fig. 6.17a). Two specimens of furcilia II were collected at Station 24. No naupliar stages were caught. Little can be said about any pattern in the MSI considering the paucity of larvae and sampling sites where they were collected.

1987. Extremely high abundances of *E. superba* larvae were observed in March 1987. The mean density estimate of 14,829 individuals 1000 m^{-3} for 0-200 m was more than 25 times higher than the highest mean abundance estimate for any species in Prydz Bay in any year (cf Tables 6.2a, b with c). The maximum recorded density, at Station 95 0-200 m, was nearly 8 times higher than the mean. The highest abundances of larvae were observed in the eastern two transects (Stations 90 to 96) and also at Station 88. The calyptopis stage dominated the upper 200 m, particularly the calyptopis I. Metanauplii, furcilia I, II and IV were also collected (Fig.

Fig. 6.18 Distribution of the mean stage index for *E. superba* larvae in the upper 200 m for the three surveys. In **c)** the thin line surrounds sites with MSI ≥ 4, while the thick thin encloses sites with MSI ≥ 5. These lines are not contour lines. Decimal points approximate sample site. For clarity, sites where larvae were not collected are not shown. 2 = nauplius II; 3 = metanauplius; 4, 5, 6 = calyptopis I, II, III respectively; 7 to 12 = furcilia I to VI.

6.18

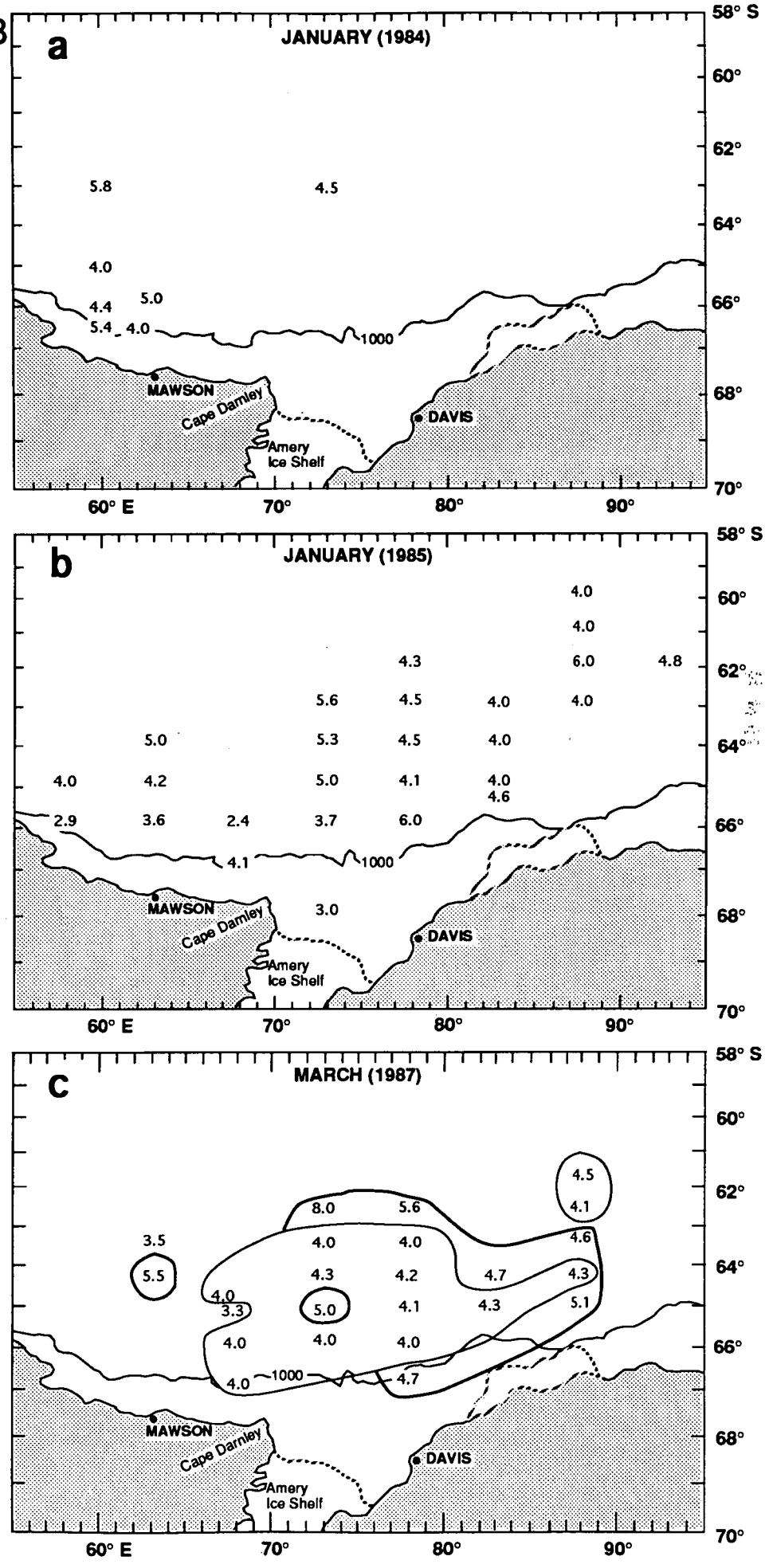
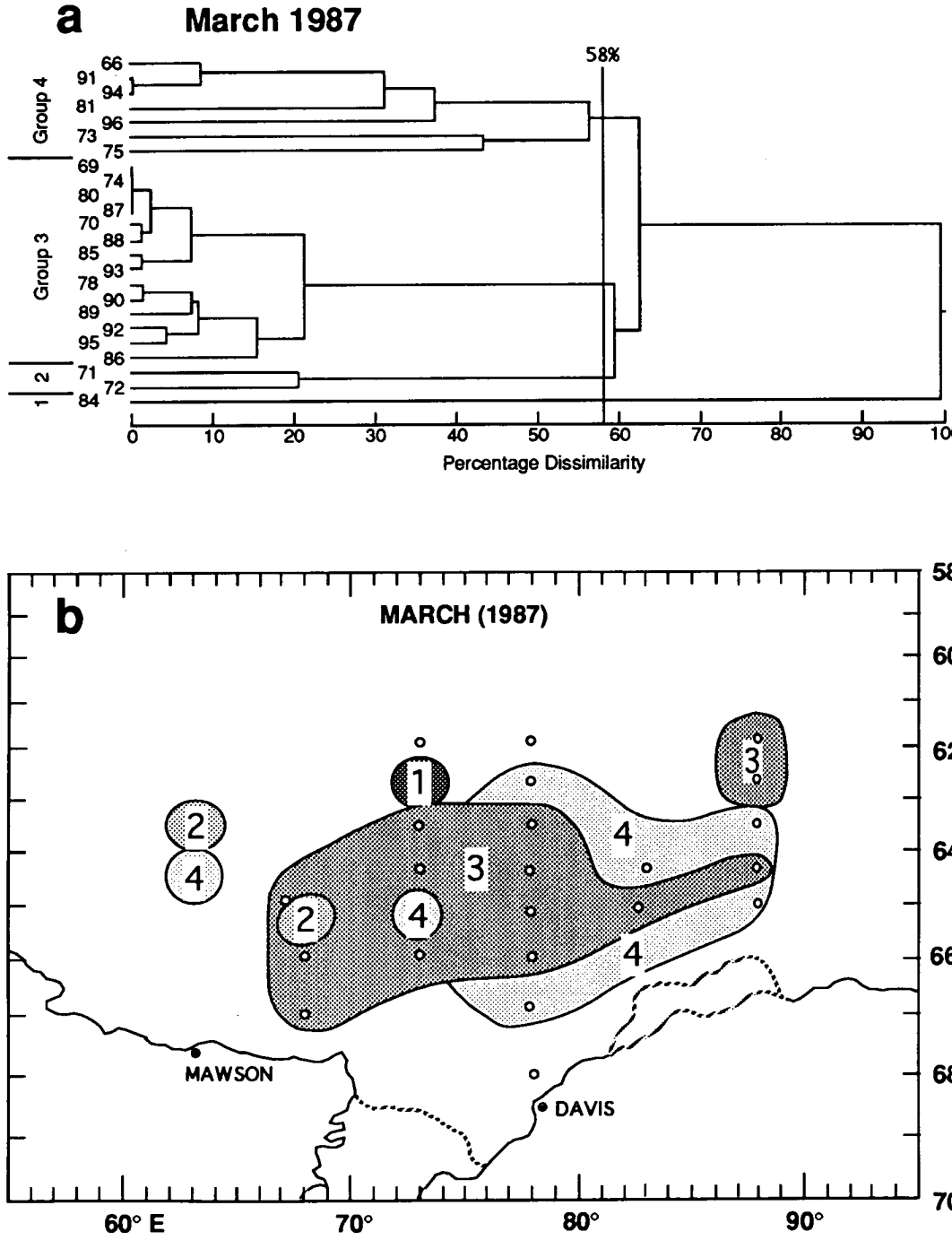

a
JANUARY (1984)
5.8
4.5
4.0
4.4
5.0
5.4
4.0
1000
MAWSON
Cape Darnley
DAVIS
Amery
Ice Shelf
b
JANUARY (1985)
4.0
4.0
4.3
6.0
4.8
5.6
4.5
4.0
4.0
5.0
5.3
4.5
4.0
4.0
4.2
5.0
4.1
4.0
4.6
2.9
3.6
2.4
3.7
6.0
4.1
1000
3.0
c
MARCH (1987)
4.5
4.1
8.0
5.6
3.5
4.0
4.0
4.6
5.5
4.3
4.2
4.7
4.3
4.0
3.3
5.0
4.1
4.3
5.1
4.0
4.0
4.0
4.0
1000
4.7
58° S
60°
62°
64°
66°
68°
70°
60° E
70°
80°
90°

Fig. 6.19 *Euphausia superba* larvae March 1987. **a)** Dendrogram of cluster analysis comparing the frequency distribution of developmental stages at each sampling site. The Bray-Curtis dissimilarity index was used for the comparison coupled with UPGMA linkage, after transformation to % frequency of abundance. **b)** Distribution of cluster groups identified in **a)**.



6.17c). The mean and maximum densities of larvae in the three deep 200-1000 m trawls were also higher than corresponding values for other species in deep trawls. All stages from nauplius to furcilia II were collected in the deep trawls - the metanauplius was dominant (Fig. 6.17c).

The majority of sampling sites had a narrow range of MSI, approximately 4 to 5. Many of the other MSI scores outside this range, notably 3.5 at Station 72 and 8 at Station 84, were based on few specimens. There was good correspondence between MSI score and cluster analysis patterns (Figs 6.18c, 6.19b). The cluster analysis produced four groups at 58% dissimilarity (Fig. 6.19b). One of these, Group 1, was Station 84 comprising four specimens of furcilia II. This outlier station was not included in the NMDS analysis. Group 2 of two stations in the west was dominated by metanauplii (Fig. 6.20). Group 3 comprising most of the sites was dominated by the calyptopis I stage. Group 4 was dominated by calyptopis II larvae and most of these sites were in the eastern transects. A slight trend is indicated of larval stage development from west to east. Longitude was the one and only parameter that explained any of the variation in the NMDS scores (27%, Table 6.6, Fig. 6.21). No regressions were found between MSI and any parameter. The lack of any regression with recorded parameter is perhaps not surprising given the narrow range of MSI scores and also the similarity in stage composition amongst cluster groups.

Euphausia frigida

E. frigida had a predominantly northerly distribution, north of 64°S (Fig. 6.22). Two larvae were collected at 65° and 66° S in the western part of Prydz Bay in 1984. Within its distributional range *E. frigida* was moderately abundant in 1985 compared with the other species

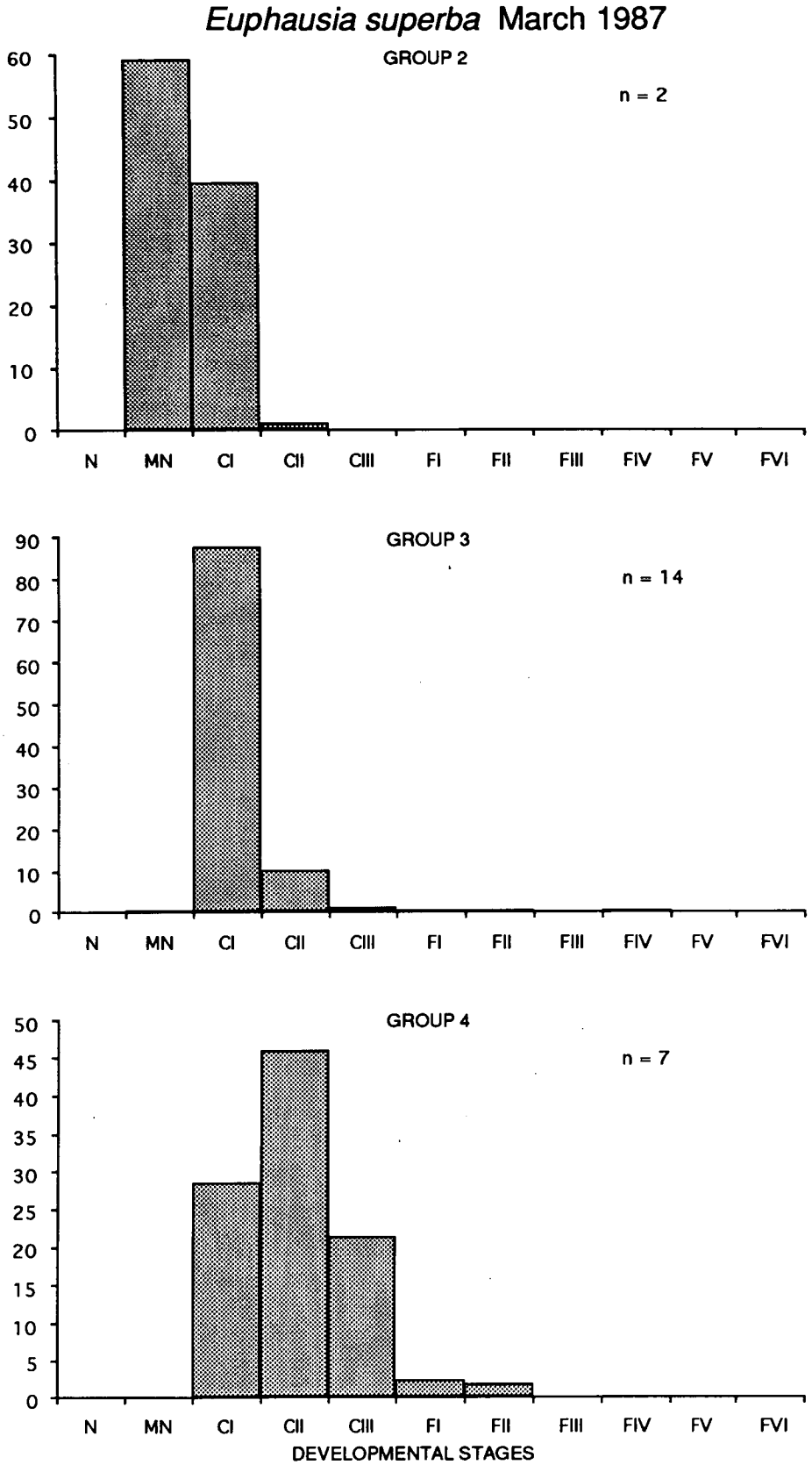


Fig. 6.20 Percentage frequency distribution of developmental stages of *E. superba* in March 1987 for three of the four cluster groups identified (Fig. 6.19a). Group 1 comprised 4 specimens of furcilia II and is not shown. n = number of sampling sites; N = nauplius I and II; MN = metanauplius; CI, CII, CIII, = calyptopis I, II, III; FI to FVI = furcilia I to VI.

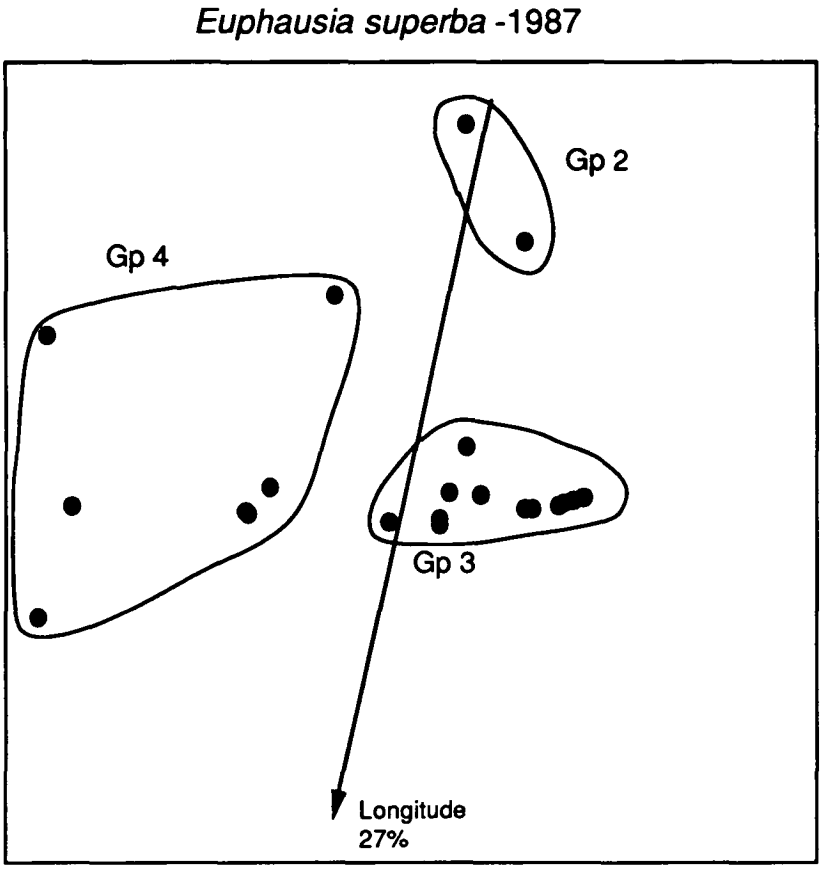


Fig. 6.21 NMDS ordination comparing the frequency distribution of *E. superba* developmental stages at each sampling site. Respective cluster groups identified in Fig. 6.19a are superimposed. Group 1 was an extreme outlier and was removed prior to analysis. Longitude was the only parameter with a significant multiple regression with ordination scores. The fraction (%) of variance in the larval data explained by longitude is shown along with the regression line (see Table 6.6). Direction of regression line was determined from Equation 3.2. Axis scales are relative in NMDS, based on non-metric ranking of dissimilarity, and therefore are not shown. Stress value = 0.078.

Table 6.6 *Euphausia superba* March 1987. **a.** Multiple regression analyses between environmental parameters and NMDS scores for two-axis ordination of comparison of sampling sites. Regression weights are derived from Equation 3.2. **b.** Linear regression between environmental parameters and MSI scores. 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.

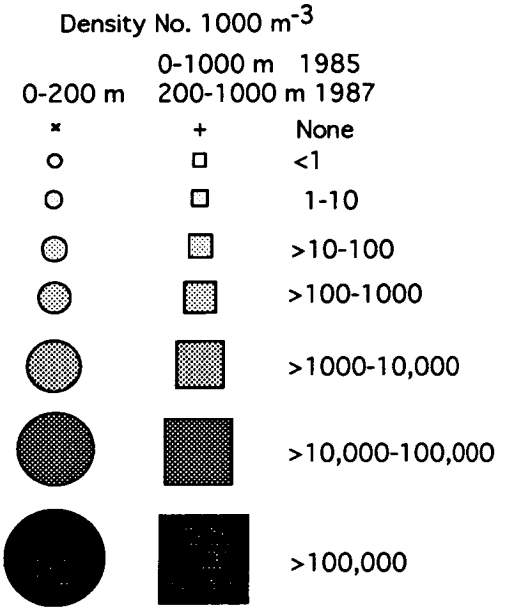
a. March 1987 Multiple Regression - NMDS scores

	Direction Cosines (Regression Weights)					
VARIABLE	X	Y	Adj. R^2	F	DF	P
Longitude	-0.213	-0.977	0.266	4.988	2,20	*
Sampling Day	—	—	0.159	3.074	2,20	ns
Duration Haul	—	—	0.028	1.322	2,20	ns
Depth of Haul	—	—	0.013	1.147	2,20	ns
Ice recession	—	—	-0.042	0.561	2,20	ns
Latitude	—	—	-0.068	0.305	2,20	ns
Ice Cover	—	—	-0.070	0.279	2,20	ns
Surface Chl *a*	—	—	-0.097	0.157	2,17	ns
Temperature	—	—	-0.110	0.008	2,18	ns

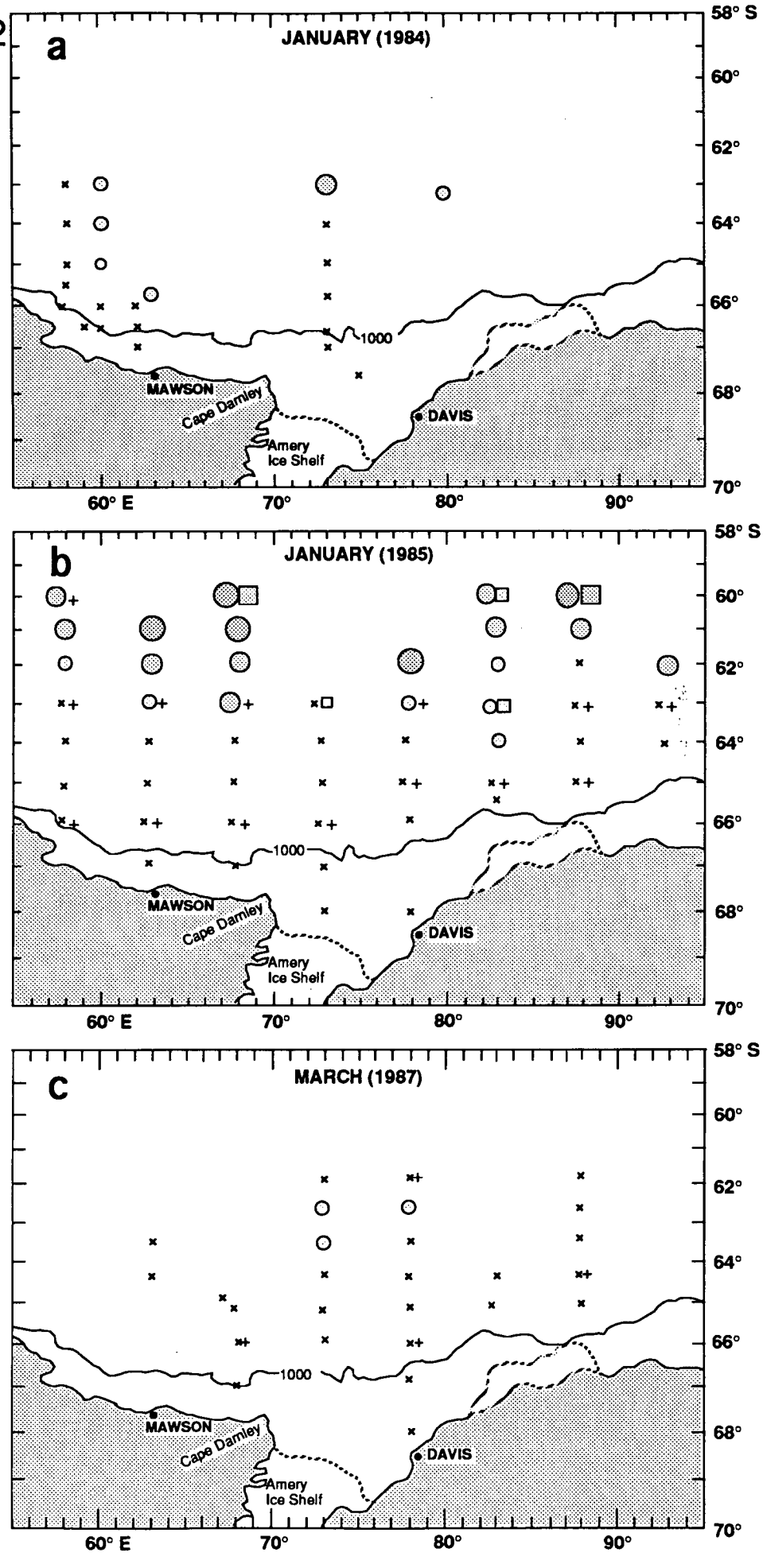
b. March 1987 Linear Regression - MSI scores

VARIABLE	Adj. R^2	R	F	DF	P
Latitude	0.075	-0.340	2.873	1,22	ns
Temperature	0.069	0.338	2.577	1,20	ns
Sampling Day	-0.025	0.141	0.447	1,22	ns
Depth of Haul	-0.032	0.115	0.294	1,22	ns
Duration Haul	-0.036	-0.093	0.193	1,22	ns
Surface Chl *a*	-0.037	-0.121	0.281	1,19	ns
Ice recession	-0.037	-0.088	0.173	1,22	ns
Longitude	-0.040	0.076	0.126	1,22	ns
Ice cover	-0.045	0.007	0.001	1,22	ns

Fig. 6.22 Distribution and abundance of *Euphausia frigida* larvae for shallow (0-200 m, circles) and deep trawls (0-1000 m 1985, 200-1000 m 1987, squares). Abundances are expressed as individuals 1000 m^{-3}.



6.22


a
JANUARY (1984)
b
JANUARY (1985)
c
MARCH (1987)
1000
MAWSON
Cape Darnley
Amery
Ice Shelf
DAVIS
58° S
60°
62°
64°
66°
68°
70°
60° E
70°
80°
90°

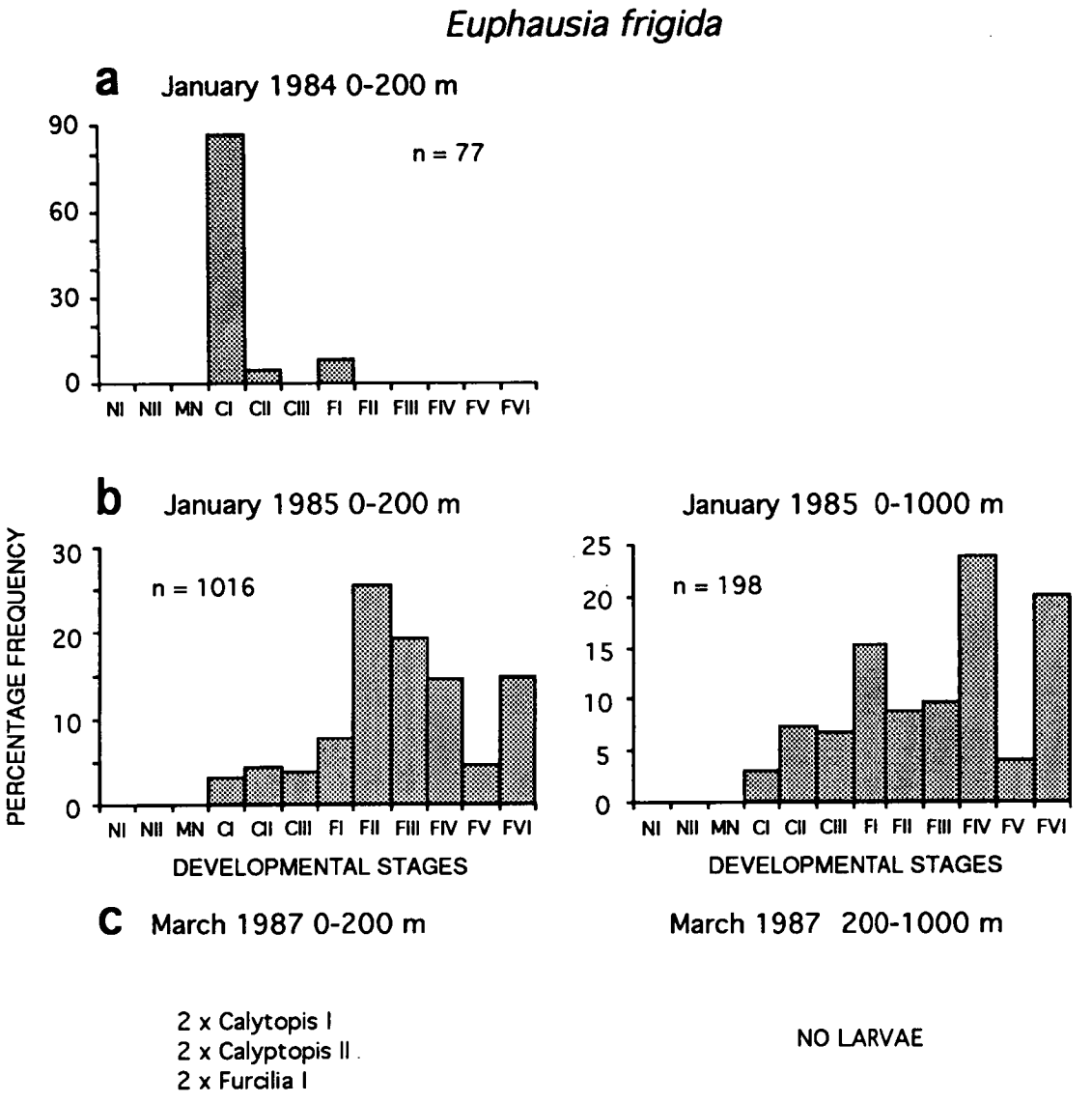
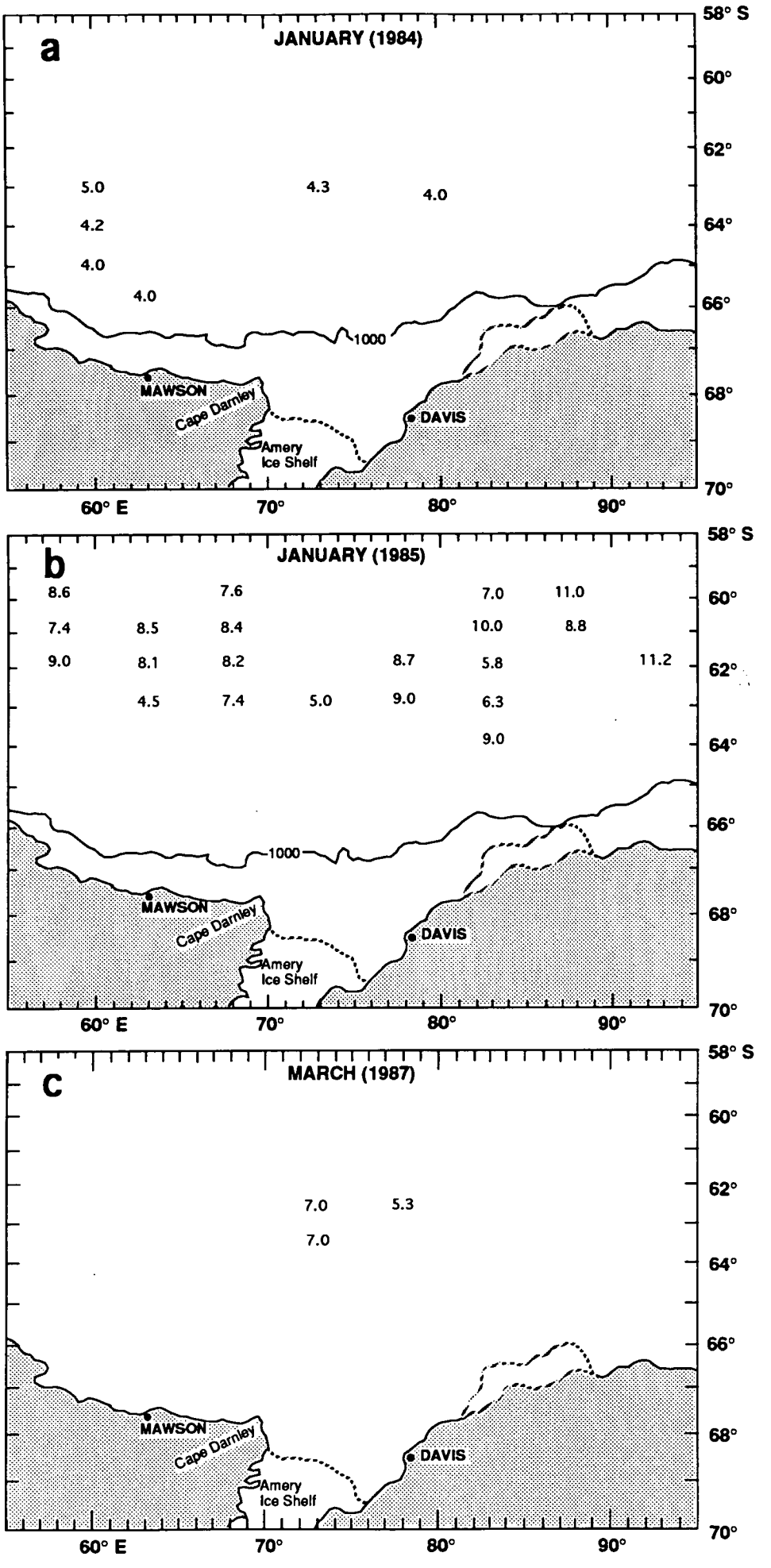


Fig. 6.23 *Euphausia frigida* . Percentage frequency distribution of developmental stages for **a)** January 1984, **b)** January 1985 shallow (0-200 m) and deep (0-1000 m) trawls. In March 1987 only six specimens were caught in the shallow (0-200 m) trawls and no larvae were caught in the deep (200-1000 m) trawls. NI, NII = nauplius I and II; MN = metanauplius; CI, CII, CIII = calyptopis I, II, III; FI to FVI = furcilia I to VI; n = total number of individuals identified.

Fig. 6.24 Distribution of the mean stage index for *E. frigida* larvae in the upper 200 m for the three surveys. Decimal points approximate sample site. For clarity, sites where larvae were not collected are not shown. 4, 5, 6 = calyptopis I, II, III respectively; 7 to 12 = furcilia I to VI.

6.24


a
JANUARY (1984)
5.0
4.2
4.0
4.0
4.3
4.0
1000
MAWSON
Cape Darnley
Amery
Ice Shelf
DAVIS
58° S
60°
62°
64°
66°
68°
70°
60° E
70°
80°
90°
b
JANUARY (1985)
8.6
7.4
9.0
8.5
8.1
4.5
7.6
8.4
8.2
7.4
5.0
8.7
9.0
7.0
10.0
5.8
6.3
9.0
11.0
8.8
11.2
1000
MAWSON
Cape Darnley
Amery
Ice Shelf
DAVIS
58° S
60°
62°
64°
66°
68°
70°
60° E
70°
80°
90°
c
MARCH (1987)
7.0
7.0
5.3
MAWSON
Cape Darnley
Amery
Ice Shelf
DAVIS
58° S
60°
62°
64°
66°
68°
70°
60° E
70°
80°
90°

Abundances were very low in 1984 and only 6 specimens were caught in 1987, two each of calyptopis II, III and furcilia II. Most of the larvae at paired sampling sites in 1985 were caught in the upper 200 m, 462 in total compared with 198 in deep hauls, but as with *T. macrura* and *E. crystallorophias*, the number of larvae collected in shallow hauls was not significantly different from the number caught in deep hauls (U =55, n=9, P >0.2). No naupliar stages were collected in any year. All other stages were represented with furciliae prominent in 1985, mainly late developmental stages, and calyptopis in 1984 (Fig. 6.23). There was no clear distribution pattern for MSI (Fig 6.24).

Discussion

Abundance

The results of this study, and those described in Chapter 5, have shown that *T. macrura* larvae are consistently the most abundant euphausiid larvae in the greater Prydz Bay region from September to January. Comparable abundance estimates of *T. macrura* have been reported from the Atlantic sector (Makarov 1979; Brinton 1985; Kittel *et al.* 1985), sometimes numerically dominating the other euphausiid larvae (Hempel 1981; Pires 1986). Yet, very little is known about this species and its role in the Antarctic marine ecosystem, especially since it is well established in the water column, with advanced developmental stages, at the time *E. superba* commences spawning. Equally, *E. crystallorophias* is also very abundant within the confines of its distributional range in Prydz Bay, which overlaps those of *E. superba* and *T. macrura*.

Miller & Hampton (1989) suggested that the Prydz Bay region was an area of generally low abundances of *E. superba* larvae. The abundance estimates from Prydz Bay for January 1984 and 1985 are considerably lower than the circa 10^4 to 10^6 individuals 1000 m^{-3} estimates often reported from the Atlantic sector for the period January to March (Kittel & Jazdzewski 1982; Mujica & Asencio 1983; Brinton & Townsend 1984; Hempel 1985; Brinton *et al.* 1986). Furthermore, very low estimates of adult krill abundance were recorded during January 1985 and represented only 3.4 % of the total zooplankton biomass in Prydz Bay (Hosie *et al.* 1988). However, the very high abundances observed in Prydz Bay in March 1987, which are comparable to abundance estimates from the Atlantic sector, proves that realistic estimates and comparison of abundance are not possible until after the main peak of spawning.

Despite the inability to sample the shallow and deep waters discretely in 1985, due to both methods sampling the upper 200 m, *E. superba* was the only species observed with the greater proportion of larvae in the deep 0-1000 m trawls. This deep distribution of larvae, notably nauplius and metanauplius, was expected due to this species' deep water developmental ascent of early stages (Marr 1962; Hempel *et al.* 1979; Hempel & Hempel 1986). *E. frigida* and *T. macrura* also exhibit deep water developmental ascent (Makarov 1979, 1983), but no naupliar stages of *E. frigida* were observed in this study and only 26 *T. macrura* nauplii in 1985, despite numerous deep hauls within their respective geographic ranges. Spawning may have ceased at the time of sampling, or the 300 μm mesh of the RMT 1 was too large to sample nauplii. Sampling in October 1985 in the western Prydz Bay region also failed to collect naupliar stages using the same net (Chapter 5). Marschall & Hirche (1984) reported that *E. superba* eggs are easily damaged and lost during the sampling process. It is possible that the smaller nauplii of *E. frigida* and *T. macrura* could be lost for the same reason.

In addition to the developmental ascent, the results of Pires (1986) and Montú *et al.* (1990) have shown that calyptopis and furcilia larvae of both *E. superba* and *T. macrura* can occur in significant numbers below 200 m. On the other hand, *E. crystallorophias* may exhibit sinking during larval development (Makarov 1983). This would suggest that the standard 0-200 m oblique hauls were perhaps not deep enough for efficient sampling of calyptopis and furcilia larvae at all sites. In 1985, *E. superba* did have a large number of larvae below 200 m but these were predominantly nauplii and metanauplii. For the other three species, there were no significant differences in the number of larvae collected in the 0-200 m hauls compared with the number from the 0-1000 m hauls at the sites of paired sampling. Hence, one can conclude that almost all of the larvae were in fact in the upper 200 m water layer and that the 0-200 m oblique hauls were adequate. This being the case, then the abundance of *T. macrura, E. frigida* and *E. crystallorophias* larvae in the deeper water layers below 200 m will be considerably less than indicated by the 0-1000 m hauls in Table 6.2b. Also the differences in the developmental stage composition between shallow and deep hauls (Fig. 6.4b, 6.14b, 6.23b) are more likely a result of geographical variation between all shallow sampling sites rather than genuine vertical differences. For example, considerable spatial variation in the developmental stages of *T. macrura* was observed in the shallow hauls (Figs 6.7, 6.8, 6.10, 6.12).

Spawning and Distribution Patterns of Developmental Stages

Some *E. superba* females are capable of spawning as early as the end of November, as indicated by the presence of a few advanced developmental stages in the January samples, e.g. calyptopis III. The very high proportion of metanauplii in 1985 suggests the commencement of

the main period of spawning was more towards the end of December, based on a comparison with the known laboratory development times for Prydz Bay larvae (Ikeda 1984). This sequence of events is similar to the pattern observed in krill from west of the Antarctic Peninsula (Ross & Quetin 1986). Hosie *et al.* (1988) noted a high proportion of enlarged gravid females in Prydz Bay in March 1981 indicating that spawning extends to at least March. *E. crystallorophias* has similar laboratory development times to *E. superba* (Ikeda 1984, 1986) and the higher number of calyptopis larvae in 1984 and 1985 suggests that spawning in *E. crystallorophias* commenced earlier in November. Spawning females have previously been collected off Enderby Land in November (Harrington & Thomas 1987). This sequence of spawning of these two species agrees with previous observations by Fevolden (1979, 1980) and Hempel & Hempel (1982). On the other hand *E. frigida* and *T. macrura* start spawning as early as the beginning of September in the Prydz Bay region (Chapter 5), with an associated protracted spawning season (Makarov 1979).

The differences in the observed January age structure of *T. macrura* can be attributed to a southward progression of spawning as evidenced by the different frequency distributions of *T. macrura* developmental stages identified by the cluster analysis (Figs 6.7a,b, 6.8, 6.10). Large numbers of calyptopis I, and some calyptopis II, were collected in October north of Mawson, circa 59° to 62°S and 55° to 64°E, and were considered to be the result of an early September spawning in this area (Chapter 5). A few calyptopis I were also caught a little further south towards 63° 30'S. At the same time, gravid and spent *T. macrura* females were only collected north of 63°S, i.e. in the same area as the larvae, although net sampling had extended to the coast. Thus, the distribution of 1985 Groups 4, 5 and 6 in the northern waters are a result of this early September spawning, coupled with a protracted spawning season (Makarov 1979) producing a

wide range of developmental stages from calyptopis I to furcilia VI. The onset of spawning then progressed southward with time. The 1985 Group 1 larvae would then be the most recently spawned and consequently only calyptopis stages were observed. No detailed data on larval development times are presently available for *T. macrura*, but comparison with times for *E. superba* and *E. crystallorophias* larvae (Ikeda 1984, 1986) would suggest that 1985 Group 1 were a result of a late November to early December spawning. Similarly, in 1984 Group 1 would have been a result of an end of November spawning, whereas the dominant furcilia stages in Group 2b further offshore were a result of mid-September to early November spawning.

The observed north-south distribution patterns of *T. macrura* developmental stages and MSI could also result from spawning being restricted to coastal waters, with larvae then being transported northward, extending their distribution with growth. Off shore currents are evident in the Prydz Bay region, as discussed below, and undoubtedly have an effect on the distribution of *T. macrura* larvae. It is unlikely that these currents would account for the observed distribution patterns *in toto*. As mentioned above, gravid and spent females have been found in the north of the Prydz Bay region, while adult *T. macrura*, in general, occurred throughout the region. Although *T. macrura* was a dominant species in the main oceanic community, the adults were found in all cluster groups of sampling sites defined in the zooplankton community studies (Chapters 3 and 4). Further, *T. macrura* has a widespread circumpolar distribution extending south from 50°S (Mauchline & Fisher 1969). There is no evidence as yet to suggest that *T. macrura* is capable of migrating long distances to inshore waters in order to spawn. Hence, it is more plausible that the observed distribution patterns of developmental stages are primarily a result of spawning progressing southward with time.

North-south "phenological waves" in the onset of spawning and larval development have previously been described for Antarctic euphausiids (Makarov 1979, 1983; Brinton 1985) and also for phytoplankton development (Hart 1942). Brinton (1985) observed north-south distribution of old to young larvae of *E. frigida* in the Atlantic sector. No clear pattern was observed in the present study for *E. frigida*, although young larvae were observed along the southern edge of this species' range in 1985 (Fig. 6.24b) and the oldest larvae in the far north-east, as seen in *T. macrura*, where there is a southward flow of water (Fig. 2.10). The lack of a clear pattern is primarily due to this study only sampling a small part of the southern limit of *E. frigida*.

The factors controlling the onset of spawning are yet to be properly defined, although, the multiple regression analyses have indicated ice, phytoplankton and temperature as possible factors. Daly and Macaulay (1988) proposed that the southward progress of spawning by *T. macrura* follows the receding ice edge. The MSI contours and cluster groups of *T. macrura* observed in this study closely parallel the southward receding ice edge observed annually between 1973 and 1982 in the Prydz Bay region (Fig. 2.16; Zwally *et al.* 1982 figs 4.2-4.7, 5.1-5.12; Jacka 1983 figs 4.1-4.12). The receding ice edge did form significant regressions with MSI and NMDS score in 1984 and 1985, explaining up to 38% and 40% of the variation in NMDS and MSI patterns respectively, in 1985. In contrast, substantial numbers of early calyptopis larvae of *T. macrura* and *E. frigida*, as well as gravid *T. macrura* females, have been collected from under the pack-ice up to 220 nautical miles from the ice edge located along 59° 30'S (Chapter 5). This indicates that spawning by *T. macrura* and *E. frigida* can occur well south into the pack-ice zone. Southward "waves" of phytoplankton blooms have also been linked to the retreat of ice (Hart 1942). In addition, the rotting ice provides a favourable substrate for high production of ice algae, an important food source for krill and

zooplankton (Smetacek *et al.* 1990; Daly & Macaulay 1991). Hence, the influence of ice on the onset of spawning may be indirect through increased algal production. There were no phytoplankton data available for 1984, but a number of phytoplankton pigments were identified in 1985 which explained some of the variation in the NMDS and MSI patterns.

Temperature also explained a significant amount of the developmental patterns, especially in 1984 where temperature explained 66% and 80% of the MSI and NMDS patterns. How temperature would trigger the start of spawning is not clear, but there is no doubt that temperature will affect the growth rate of *T. macrura* larvae. Ross *et al.* (1988) have demonstrated a clear link between temperature and growth rates of *E. superba* larvae, with higher temperatures producing faster development. A similar, but as yet undefined, effect would be expected for other euphausiid larvae. The overall result would be that *T. macrura* larvae produced earlier in the warmer northern waters will also be expected to grow faster than larvae spawned later in the cooler southern waters, exaggerating the differences in the geographic distribution of developmental stages. Regardless of which factor controls the onset of spawning and subsequent development, the fact remains that different groups of development stages of *T. macrura* exist within the region. Therefore, attempts to estimate mortality or growth by following cohorts is difficult, unless consideration is given to the spawning and developmental history of the group of larvae studied.

It is worth noting, at this point, the close similarity in regression results with NMDS scores and those using MSI, particularly in relation to the amount of variation explained. The distribution patterns were also very similar, both in 1984 and 1985. Cluster analysis and an ordination method such as NMDS are powerful techniques for describing and analysing distribution patterns. However, such techniques can often be expensive or consuming in terms of computer processing time,

depending on the computer system. Computer time increases with the square of the number of samples (or individuals) being compared (Field *et al.* 1982). While MSI may not be truly representative of the developmental stage composition at a site, because of multimodal frequency distributions of stages, MSI would seem to be quicker and simpler technique for mapping and comparing larval patterns with environmental gradients.

There was no clear zonation of *T. macrura* larvae in March 1987, either latitudinal or longitudinal. Further, it would seem that the environmental parameters linked to January patterns had no apparent effect on oceanic distribution patterns in March. Nor can the geographic patterns of cluster groups, MSI scores and abundances be related to any of the currents that affected the distribution of other species (see below). The factors that influence *T. macrura* distributions in the late Antarctic summer/early autumn remain to be established.

Dispersal Routes and Survival

Sampling in 1984 and 1985 was apparently too close to the start of spawning of *E. superba* to be useful for estimating of abundance of larvae. There were, however, sufficient numbers in the water column along with the more abundant *E. crystallorophias* larvae to see the influence of water circulation, as described in Chapter 2, on the initial distribution of the larvae. The influence of the East Wind Drift (EWD) on the dispersal of larvae can be seen in the westward distribution, along the continental shelf and slope, of *E. superba* and especially *E. crystallorophias* larvae, in January 1985 and to some degree in 1984. The youngest and most abundant larvae of *E. crystallorophias* are found in the southern part of Prydz Bay, at Stations 26 and 29 (1985), an area of

the highest concentration of adults within the region (Chapter 3). Slightly older larvae occur to the west, as would be expected, with most larvae originating in Prydz Bay and then being carried west by the EWD. Accepting this as the case, current speeds can be calculated by using the development times of *E. crystallorophias* larvae reported by Ikeda (1986), i.e. of 27d to the metanauplius, 34 d to the calyptopis I stage and 54 d to calyptopis II at -1° C. These can be related to the estimated MSI at sampling sites. If 68°30'S by 74°E is taken as the arbitrary starting point then estimates of 27.1, 19.5 and 15.3 cm s^{-1} are obtained for 1985 Stations 7, 8, and 9 respectively. In 1984, very similar estimates of current speeds ranged from 17.6 to 28 cm s^{-1} (mean 22.3 ± 3.4 cm s^{-1}, n=8) for the sampling sites north and west of Mawson. These values are not inconsistent with those estimates from the icebergs (Fig. 6.25) and are within the ranges obtained from current meter moorings (Chapter 2; Hodgkinson *et al.* 1988). The fewer but older larvae observed north and northeast of Mawson in 1985 are well outside the observed distribution range of adults which are confined to the shelf (Chapters 3 and 4). The distribution of these larvae tends to follow the western part of the Prydz Bay gyre. This suggests that some larvae in the upper 200 m may be returned to Prydz Bay, rather than being carried west past Enderby Land and out of the region as indicated by the ICEX buoys and icebergs.

The adults of *E. superba* generally are widespread throughout the region, although infrequently north of 62°S (Hosie *et al.* 1988) or south of 68°S (Chapter 3). In Chapter 3, significantly higher concentrations of adult krill, including gravid females (Appendix II), were shown to be mainly located along the shelf edge west of 78° E, i.e. the krill dominated community. Further, other studies have shown that krill are more abundant near the shelf edge (Pakhomov 1989; Bibik & Yakolev 1991). In particular, the shelf edge between 55° and 70°E has been the focus of Japanese krill fishing activities in the Prydz Bay region (Ichii 1990). Marr

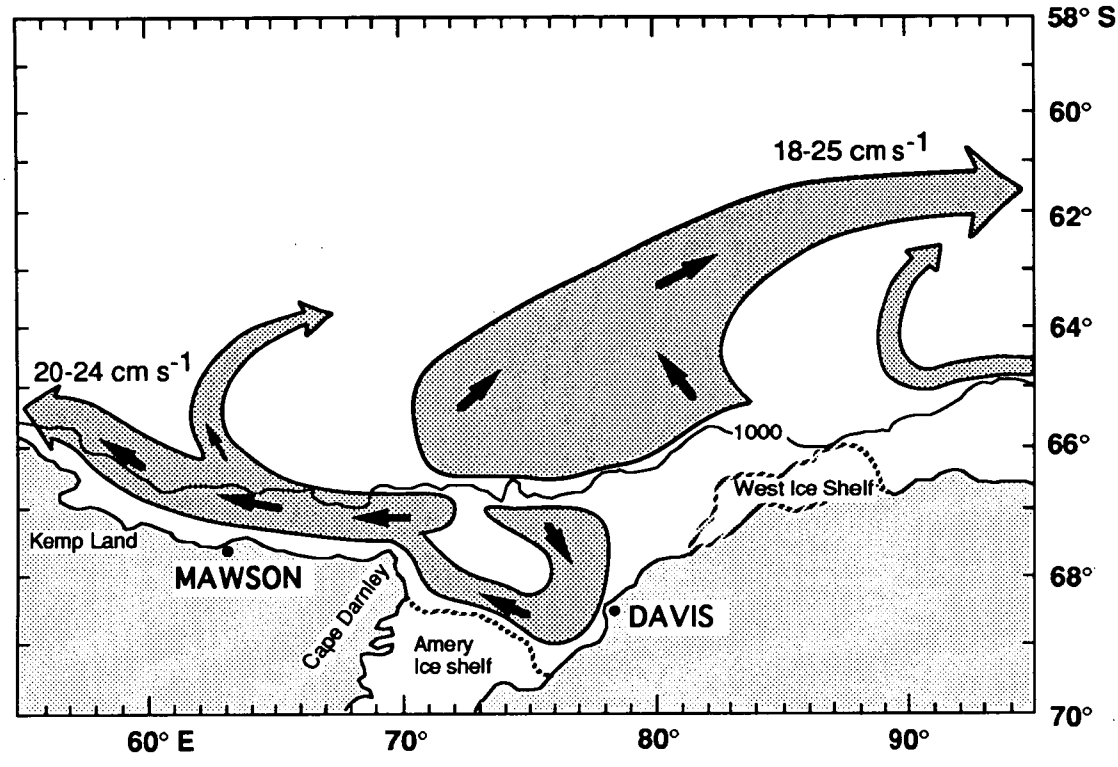


Fig. 6.25 The apparent dispersal routes of larvae, particularly for *E. superba* and *E. crystallorophias* (mainly to the west), determined from sea-ice buoy and ice-berg trajectories, current meters and geostrophic flow. Current speeds shown were determined from ice-berg trajectories.

(1962) had postulated that spawning in *E. superba* was a phenomenon associated with the shelf and slope water of the high latitudes. Kanda *et al.* (1982) went further providing evidence that adult krill in the Prydz Bay region migrate south towards the shelf in order to spawn. The site at which spawning occurs in relation to the shelf, will determine by which of the two apparent major dispersal routes the larvae will be carried (Fig. 6.25). It may also determine the survival of the larvae. Larvae produced on the shelf will undoubtedly follow the same route as *E. crystallorophias* in moving west along the shelf edge. For example, the large numbers of metanauplii at the western Station 7 (1985) can be traced back to a likely release site between 67°30'E and 69°E on or near the shelf, assuming a 24 d development time to the metanauplius stage at -1°C (Ross *et al.* 1988) and EWD current speeds of 20.5 to 23.7 cm s^{-1}. The other larvae observed along longitudes 58°, 63° and 68°E in 1985, and 60°E in 1984, most likely originated further east in Prydz Bay. Unlike the eggs of *E. crystallorophias* which remain in surface waters (Makarov 1983; Ikeda 1986), embryos of *E. superba* sink during development (Hempel & Hempel 1986). To complete development, larvae must reach the surface and commence feeding within 10-14 d of becoming a calyptopis I (Ross & Quetin 1989). Where the larvae reach the surface waters, will govern whether the larvae continue west past Enderby land or return to Prydz Bay as indicated by *E. crystallorophias* larvae. It is not clear, from the observed distribution of *E. superba* whether they follow the northern route of *E. crystallorophias*.

Regardless of whether the larvae move west or not, it is quite likely that many of these larvae will perish. Ross *et al.* (1988) reported that larvae, produced by females in the Atlantic sector, will not survive if they encounter -1°C during a cold sensitive period of early development. They found that 3 out of 4 batches of larvae died within 3 d of becoming calyptopis I if reared at -1°C. The water temperatures on the shelf of Prydz

Bay and to the west are -1° to <-1.5°C throughout most of the water column, which is consistent between years (Figs 2.1, 2.2, 2.4). Unless Prydz Bay larvae have a higher tolerance of cold temperatures, than that of the more northerly distributed Atlantic larvae, then the <-1.5°C temperatures along the shelf are likely to cause a substantial drop in larval recruitment, despite the high phytoplankton abundance in this area (Fig. 6.26). Such a loss would explain the low abundances of larvae observed by Miller (1986) off Enderby and Kemp Land in April 1984. Eggs released on the shelf east of about 72°E should be swept south as part of the cyclonic flow of water in Prydz Bay and past the Amery Ice Shelf (Fig. 6.25). Consequently, these larvae will experience colder water (<-1.8°C, Fig. 2.4) for a longer period, than larvae released west of Cape Darnley.

The second major dispersal route is to the north-east, confirmed again by iceberg and ICEX buoy trajectories (Fig. 6.25). The 1985 *E. superba* larvae in the eastern part of the Prydz Bay region had a distinct north-eastern distribution, consistent with this water flow. In March 1987, *E. superba* larvae were also concentrated in the eastern part of the region, as were the copepod/chaetognath dominated main oceanic zooplankton community (Chapter 3). Examination of the Tchernia & Jeannin (1983) iceberg trajectories indicated the possible existence of another but reversing current between 85° and 95°E that would seem to originate as a northward deflection from the EWD, which then joins the northeasterly current (Figs 2.14b, 6.25). It is possible that some of the 1987 krill larvae in the eastern part of the region may have originated from somewhere further east and had been concentrated along the eastern transects by this reversing current. However, the NMDS regression with longitude suggests a slight west to east trend in the distribution pattern (Fig 6.21) and the following calculations are made in relation to the northeasterly current only. Using the speeds of 18.5 to 24.9 cm s^{-1} and the development times from Ikeda (1984) for 0° C, then the larvae can be tracked back to an

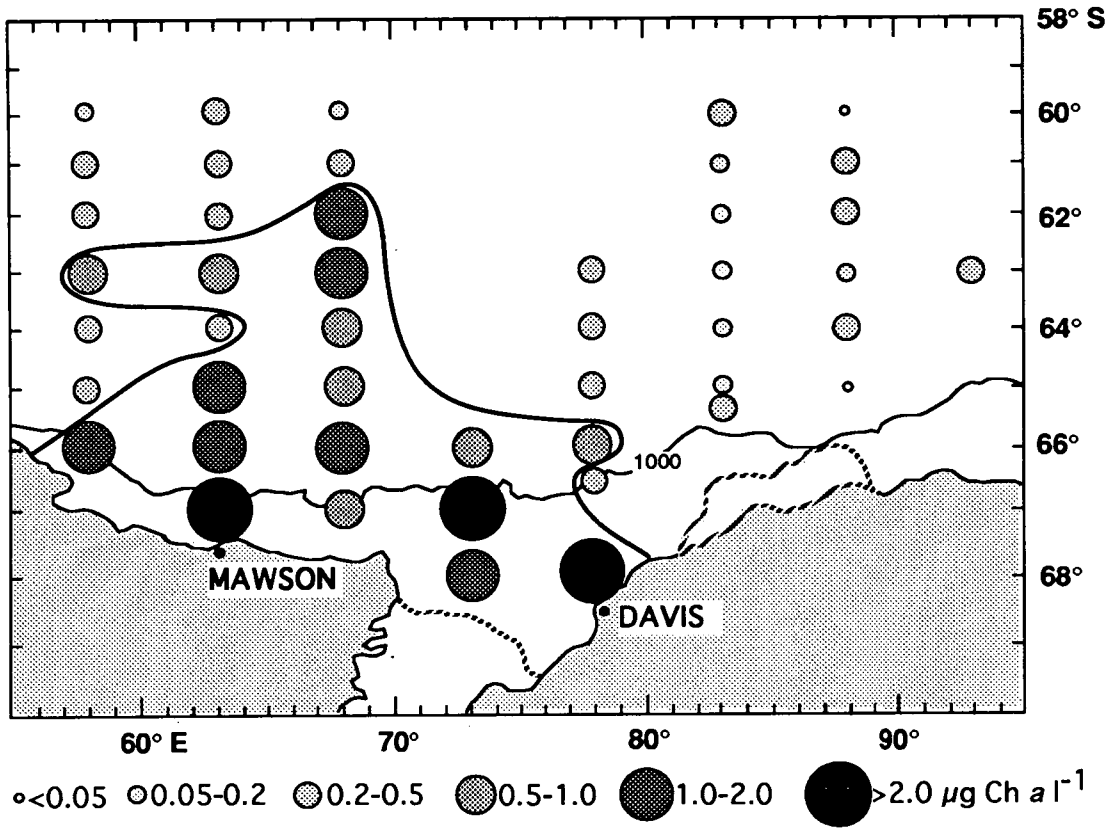


Fig. 6.26 Distribution of chlorophyll *a* concentrations as μg l^{-1}, integrated for the upper 100 m water layer (data from Wright 1987). The heavy line surrounds those sites with >0.50 μg Chl *a* l^{-1}, necessary for the succesful development of larvae through the calyptopis I stage (Ross & Quetin 1989).

approximate area of 63° to 66° 30'S by 70° to 83°E. Most of these larvae are distributed in warmer waters, e.g. up to +1.8°C (Figs 2.1d, 2.3b, 2.6d), than the larvae along the shelf, and therefore a higher temperature related survival rate would be expected as well as faster growth (Ross *et al.* 1988). The survival of these larvae is still doubtful in relation to food availability. At the time of sampling in January 1985 the concentrations of chlorophyll *a* east of Prydz Bay (Wright 1987) were much lower than the minimum food concentration of 0.5 μg Chl *a* $.l^{-1}$ necessary for the continued development of larvae through the calyptopis I stage (Ross & Quetin 1989). At the chlorophyll *a* concentrations shown in (Fig. 6.26), the north-east larvae would have suffered partial starvation eventually depleting their lipid reserves. According to Ross & Quetin (1989) calyptopis I larvae that exhaust their lipid reserves will have passed the point-of-no-return (PNR) and will die even if sufficient food is then encountered. In addition, the salp *Salpa thompsoni* was exceptionally abundant in January 1985, representing 39.4% of the total zooplankton biomass by wet weight throughout the Prydz Bay region, and 46.9% in the northern waters dominated by the northern oceanic zooplankton community (Table 3.7). North of 63° S this species comprised 73% of the total zooplankton biomass by wet weight, and 90% north of 62° S. *S. thompsoni* is not only capable of competing with *E. superba* larvae for food resources but is also capable of eating large numbers of krill larvae (Huntley *et al.* 1989).

S. thompsoni was much less abundant in March 1987 and represented only 7% of the total zooplankton biomass in the eastern Prydz Bay region (Table 3.12). It would seem that salps were less important in terms of competition with or predation of larvae. However, the area of high krill larval abundance was also dominated by very high abundances of copepods, chaetognaths and other zooplankton of the main oceanic zooplankton community, which are likely additional

sources of food competition and possibly predation pressure. Krill larvae have been found in the guts of a number of zooplankton species (Hopkins & Torres 1989). The herbivorous copepods *Calanoides acutus, Calanus propinquus* and *Rhincalanus gigas,* at a combined abundance of 386 individuals 1000 m^{-3}, represented 65% of the total abundance of the main oceanic community. Antarctic copepods are reputed to consume at least a threefold, perhaps more than eight times, the amount of primary production than adult krill (Conover & Huntley 1991). Phytoplankton data in March 1987 was limited to surface chlorophyll values only. In the eastern two transects, where abundances of both copepods and krill larvae were high, surface chlorophyll *a* values ranged from 0.123 to 0.498 µg Chl *a* l^{-1} (Dr S.W. Wright - Antarctic Division unpublished data) which are below the 0.5 µg Chl *a* l^{-1} limit of the starvation/PNR model of Ross & Quetin (1989). It is quite possible that sufficient chlorophyll levels occurred deeper in the water column. Krill larvae may also have a faster filtration rate than assumed by Ross & Quetin (1989), which would allow the larvae to survive on lower phytoplankton abundances. In addition, faster growth in the warmer off shore waters may have resulted in larvae reaching the surface layer before metamorphosis to the feeding calyptopis I stage. They would then have had more time to find food before reaching the PNR, but would have also used much less body reserves during the naupliar development, delaying the PNR (Ross & Quetin 1991). The very high abundances of calyptopis larvae, including stages II and III, in the region in March 1987 is clear evidence that the larvae were surviving.

The combined evidence of larval distribution and water movement indicates that most larvae, providing they survive the <-1°C water temperatures and food deprivation, will leave the Prydz Bay region to the west or via the north-east. Hence, the Prydz Bay krill may not be a self-maintaining group but a result of recruitment from other areas, e.g. from

the east via the EWD. This is consistent with the results of Macdonald *et al.* (1986) and Fevolden & Schneppenheim (1989) who found no genetic separation in the Antarctic krill, thus indicating that krill belong to one interbreeding population.

The ubiquitous distribution of *T. macrura* within the region to some degree masks any movement of larvae of this species by the perceived currents. However, some northerly movement of the young larvae is seen in the west along longitude 58°E and over to 63°E at Station 11 in 1985, a possible result of the gyre. A more distinct northerly movement is seen in the east along longitude 88°E in 1985, commensurate with the north-easterly movement of the icebergs. As discussed above, the observed distribution patterns of *T. macrura* developmental stages are most likely the result of a north-south difference in the commencement of spawning, rather than due totally to off shore transport of larvae from localized spawning sites along the coast. Nevertheless, the currents do have an apparent effect on the distribution patterns of *T. macrura* larvae, but secondary to the southward progression of spawning. The distribution of *E. frigida* was consistent with previous studies (John 1936; Hempel & Hempel 1982; Makarov 1983) in being confined to the waters of the ACC.

CHAPTER 7

CONCLUSIONS

Perhaps one of the most important findings of this study is that for the greater part of the Prydz Bay region, *E. superba* was not widely distributed in great abundance. Instead, there were a number of assemblages dominated by zooplankters other than krill. *E. superba* would appear to be associated more with the shelf edge, rather than with any other feature such as ice, but within that area where various predators feed, *E. superba* is the predominant species, almost to the exclusion of other zooplankton. Despite the dominance of other species in other areas, *E. superba* is still the most important single species in Prydz Bay.

Kawamura's (1986, 1987) suggestion that the zooplankton composition of Antarctic waters may have changed over a 50-60 year period, was based on a few samplings over a wide geographical range, west and east of the Prydz Bay region. Given the degree of variability in the distribution of the krill and especially the main oceanic/copepod dominated communities displayed in this study, it is quite possible that Kawamura may not have so much detected a change in composition, but a change in community distributions. Nonetheless, any indication of changes in zooplankton composition warrants further investigation. While there is some geographical variation in community distributions, the species assemblages themselves appear to be reasonably constant between years. Similarly, there is a remarkable consistency in the oceanography of the Prydz Bay region in terms of temperature and salinity profiles (Figs 2.1 to 2.6, 2.8), description of the gyre for various years (Khimitsa 1976; Smith *et al.* 1984; Middleton & Humphries 1989; and R.A. Nunes Vaz & G.W. Lennon, personal communication 1990; see Fig. 2.10), and other currents identified by current meter moorings, sea ice

buoy and iceberg drifts (Figs 2.11 to 2.15). Therefore, it is quite possible that the various community distribution patterns observed may in fact be repeatable phenomena. At the very least, discrete areas can be identified where each of the four communities are persistent, thus facilitating future research into the dynamics of each community.

There were fewer surveys of euphausiid larval distribution but there was some evidence of consistency in their distribution patterns between years. Like the zooplankton, there are distinct areas where larvae of each euphausiid species would be expected. More interestingly, the larvae were influenced more by currents, than were the zooplankton communities, and therefore are better indicators of movement of water masses. The larvae of *E. frigida* were confined to and are indicative of the waters of the ACC. *E. crystallorophias* adults are confined to the waters of the continental shelf, with the larvae dispersed west by the EWD coastal current. The presence of larvae of this species north of the shelf was indicative of off shore transportation of neritic waters via the gyre. *E. superba* larvae were similarly dispersed by the EWD but were also carried north-east against the apparent geostrophic flow. Apart from the fact that krill larvae generated in Prydz Bay would seem to leave the region, krill larvae can encounter two totally different environmental regimes in terms of food availability (quantity and competition), predation and temperature in particular because of the two dispersal routes. Further research is required to determine any differences in growth, development, survival rates and strategies of the larvae along the coastal and oceanic dispersal routes. Different rates of development and survival are also anticipated for *T. macrura* larvae because of the geographically extensive north to south differences in the start of spawning over a wide range of environmental conditions. Overall, the Prydz Bay region would seem to be an ideal locality for studying the ecology of larvae in relation to hydrography, e.g. spawning, development,

distribution and mortality, as compared to the Atlantic sector where the hydrographic patterns are most complex (Amos 1984) but where most research has so far been conducted.

Somewhat surprisingly, there was little association between zooplankton community patterns and horizontal salinity gradients. More work will be required to determine the influence of salinity on community patterns, particularly at smaller scales and vertical stratification, e.g. the haloclines produced through ice melt. The pattern of sea ice retreat and also the degree of ice cover explained much of the community patterns in the January-February period of summer. This is more likely through the role of ice in early season phytoplankton production. Chlorophyll *a* and temperature were the two parameters that consistently explained zooplankton community patterns, as well as the distribution patterns of *T. macrura* larvae. Temperature, and to some degree chlorophyll in January- March, have distinct latitudinal patterns with temperature decreasing and chlorophyll abundance increasing southwards. Zooplankton and *T. macrura* larval distribution patterns were also predominantly latitudinal. The exact interactions between temperature and phytoplankton with euphausiid larvae and zooplankton patterns still needs to be established, if in fact cause-and-effects between environmental parameters and pelagic communities can be proved adequately.

CCAMLR (Commission for the Conservation of Marine Antarctic Living Resources) has developed an Ecosystem Monitoring Program (C-EMP) with the aims "to detect and record significant changes in critical components of the ecosystem, to serve as the basis for the conservation of Antarctic Marine Living Resources. The monitoring system should be designed to distinguish between changes due to the harvesting of commercial species and changes due to environmental variability, both physical and biological." (CCAMLR 1985, paragraph 7.2). C-EMP at

present is focussed on selected seal and bird species that specifically prey on krill (Croxall 1990). The monitoring of predators is more suited to detecting the effects of over-harvesting of krill, rather than climatic change. Time series surveys of zooplankton would be a valuable addition to any marine ecosystem monitoring, especially in relation to the studies of natural and climatic induced variability. Zooplankton have much shorter lives, often one or two years (Kane 1966; Everson 1984; Marin 1988), and faster population turnover than vertebrate predators. They are of course also closer to the start of the food chain, and hence expected to respond more rapidly to change. The value of time-series studies of zooplankton for monitoring the health of the oceans is well recognised (Colebrook 1979, 1982a, 1982b, 1991; Robinson & Hunt 1986; IOC & SAHFOS 1991).

This study has established the composition, structure and distribution patterns of zooplankton, as well as that of euphausiid larvae, in the Prydz Bay region and identified some parameters that may influence these patterns. This type of information is fundamental to any long term time series research/monitoring program. On the basis of the results of this study, such a research program has commenced in Prydz Bay using Hardy continuous plankton recorders CPR (Hardy 1939). The principal objectives of the new program are to study regional, seasonal, annual and long term variability in the abundance of krill larvae produced annually, zooplankton abundance and species composition (Hosie 1991b). That program is being carried out in association with an international cooperative CPR survey to monitor ocean systems (IOC & SAHFOS 1991).

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Table A1.1 Station list and RMT 8 sampling data for the January-February 1991 mesoscale study of Prydz Bay. * denotes previous day (GMT); † graded from 0 to 10 depending on the degree of ice coverage, 0 = no ice, 10 = complete ice cover.

STN NO.	DATE LOCAL	NET IN-OUT SHIP-TIME	NET IN-OUT GMT-TIME	START POSITION LAT. (S)	START POSITION LONG. (E)	DEPTH RANGE (m)	BOTTOM DEPTH (m)	SPEED (knots)	ICE†
	Jan-91								
11	19	1317-1328	0617-0628	68° 23.9'	72° 10.5'	0-200	506	2.1	0
12	21	0608-0615	*2308-2315	68° 01.1'	72° 00.7'	0-232	755	1.5-1.7	0
13	21	0917-0932	0217-0232	67° 30.2'	71° 59.9'	0-200	628	3-Feb	0
14	22	0304-0313	*2004-2013	67° 02.0'	72° 00.3'	0-204	534	1.6-2.9	0
15	22	0835-0850	0135-0150	66° 29.3'	71° 59.9'	0-200	1384	2.1-3.2	0
16	22	0529-0543	*2229-2243	66° 02.8'	72° 04.2'	0-200	2429	2.5	0
17	23	1004-1016	0304-0316	65° 29.8'	71° 59.6'	0-200	2914	2.2-2.5	0
18	24	0419-0429	*2119-2129	65° 01.9'	72° 01.1'	0-201	3318	2.9-3.3	0
19	24	0801-0814	0101-0114	64° 59.9'	73° 30.6'	0-201	3410	2.4-2.8	0
20	24	1213-1223	0513-0523	65° 30.9'	73° 29.7'	0-202	3088	2.4	0
21	24	1605-1611	0905-0911	65° 60.0'	73° 31.0'	0-205	2678	1.8	0
22	24	2146-2201	1446-1501	66° 29.6'	73° 29.4'	0-207	1927	3.1-3.3	0
23	25	0146-0202	*1846-1902	66° 59.9'	73° 29.9'	0-199	502	2.0-2.2	0
24	25	2312-2324	1612-1624	67° 28.5'	73° 29.4'	0-201	599	2.9-2.6	0
25	26	0205-0219	*1905-1919	68° 00.1'	73° 30.1'	0-200	580	2.6-2.7	0
26	26	2049-2104	1349-1404	68° 33.6'	73° 31.4'	0-201	807	3.4-3.5	0
27	27	0034-0059	*1734-1759	68° 60.0'	74° 15.8'	0-202	719	2.8-3.2	1
28	27	2000-2011	1300-1311	68° 31.0'	74° 56.0'	0-200	650	2.6-3.1	0
29	27	2322-2332	1622-1632	67° 58.5'	74° 59.2'	0-201	509	2.2-2.8	0
30	28	1423-1434	0723-0734	67° 28.7'	75° 02.1'	0-201	457	2.1-2.4	0
31	28	1810-1822	1110-1122	67° 01.0'	74° 59.4'	0-210	400	2.7-3.1	0
32	29	0816-0839	0116-0139	66° 33.3'	74° 52.7'	0-201	2429	2.0-2.5	0

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STN NO.	DATE LOCAL	NET IN-OUT SHIP-TIME	NET IN-OUT GMT-TIME	START POSITION LAT. (S)	START POSITION LONG. (E)	DEPTH RANGE (m)	BOTTOM DEPTH (m)	SPEED (knots)	ICE†
	Jan-91								
33	29	1444-1459	0744-0759	65° 59.4'	75° 00.3'	0-200	3050	2.7-2.9	0
34	30	0457-0516	*2157-2216	65° 31.3'	75° 01.5'	0-201	2994	2.5-2.8	0
35	30	2139-2154	1439-1454	65° 00.4'	75° 01.1'	0-201	3274	2.1-2.9	0
36	31	0450-0501	*2150-2201	64° 59.5'	76° 29.7'	0-201	3373	2.6	0
37	31	1251-1304	0551-0604	65° 30.5'	76° 30.6'	0-200	3329	2.0-2.1	0
38	31	1820-1831	1120-1131	66° 00.5'	76° 30.2'	0-201	3006	2.5-2.6	0
	Feb-91								
39	1	0122-0138	*1822-1838	66° 30.3'	76° 30.3'	0-200	2666	2.6	0
40	1	0609-0641	*2309-2341	66° 59.9'	76° 30.2'	0-201	337	2.0-2.6	0
41	2	0203-0217	*1903-1917	67° 32.0'	76° 33.0'	0-200	358	2.6	1.5
42	2	0617-0625	*2317-2325	68° 00.1'	76° 35.8'	0-215	457	3.5	1.5
43	3	0421-0437	*2121-2137	68° 29.4'	76° 28.0'	0-200	638	2.1-2.6	3
44	3	0834-0841	0134-0141	68° 56.7'	76° 28.9'	0-200	493	2.6-3.0	2
45	4	0026-0041	*1726-1741	68° 31.4'	77° 25.1'	0-200	536	2.1-3.0	3
46	4	0633-0647	*2333-2347	68° 01.7'	77° 58.1'	0-201	563	2.2-3.0	3
47	4	1259-1310	0559-0610	67° 29.8'	78° 00.9'	0-127	172	3.2-3.5	3
48	4	1838-1849	1138-1149	66° 59.8'	78° 00.1'	0-180	206	2.4-2.7	0
49	5	0225-0238	*1925-1938	66° 30.5'	78° 00.0'	0-200	1844	2.9-3.1	0
50	5	0803-0820	0103-0120	65° 59.3'	77° 58.8'	0-201	3176	2.2-2.7	0
51	5	1230-1242	0530-0542	65° 29.9'	77° 59.1'	0-205	3287	2.3-2.8	0
52	5	2046-2100	1346-1400	65° 00.2'	77° 58.7'	0-200	3480	2.6-3.1	0
53	7	0013-0025	*1713-1725	68° 30.4'	70° 29.8'	0-200	1036	2.7	0
54	8	0400-0415	*2100-2115	67° 53.7'	71° 05.1'	0-204	508	3.2-3.6	0
55	8	0639-0653	*2339-2353	67° 27.5'	70° 59.9'	0-200	417	3.0-3.5	0
56	9	0409-0424	*2109-2124	66° 58.8'	71° 07.7'	0-200	510	3.2-3.3	0

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STN NO.	DATE LOCAL	NET IN-OUT SHIP-TIME	NET IN-OUT GMT-TIME	START POSITION LAT. (S)	START POSITION LONG. (E)	DEPTH RANGE (m)	BOTTOM DEPTH (m)	SPEED (knots)	ICE†
	Feb-91								
57	9	0816-0833	0116-0133	66° 30.1'	70° 30.6'	0-200	2123	3.3	0
58	9	1323-1340	0623-0640	65° 59.3'	70° 29.8'	0-201	2660	2.5-2.9	0
59	9	1841-1900	1141-1200	65° 29.9'	70° 31.5'	0-201	2987	1.7-2.6	0
60	9	2254-2314	1554-1614	65° 00.6'	70° 30.1'	0-201	3171	2.6-2.8	0
61	10	1138-1150	0438-0450	64° 58.5'	68° 56.2'	0-201	2968	3.2-3.8	0
62	11	0016-0029	*1716-1729	65° 32.1'	69° 04.9'	0-200	2729	2.7-3.1	0
63	11	0341-0355	*2041-2055	65° 59.9'	69° 00.3'	0-200	2500	3.0-3.2	0
64	11	2151-2215	1451-1515	66° 33.4'	64° 06.8'	0-200	1720	2.7-2.9	0
65	12	0228-0244	*1928-1944	66° 58.9'	68° 59.1'	0-201	524	3.2-3.6	0
66	13	0004-0014	*1704-1714	67° 32.6'	69° 00.1'	0-120	148	2.4	0
67	13	0319-0328	*2019-2028	67° 30.3'	67° 32.3'	0-150	195	3.2	0
68	13	2240-2258	1540-1558	66° 53.2'	67° 29.5'	0-201	1542	2.5-3.0	0
69	14	0121-0138	*1821-1838	66° 30.8'	67° 30.3'	0-202	2856	3.1	0
70	14	0605-0619	*2305-2319	66° 01.3'	67° 30.0'	0-201	2933	2.9-3.4	0
71	14	1241-1310	0541-0610	65° 30.1'	67° 31.1'	0-201	3010	2.6-2.7	0
72	14	1610-1634	0910-0934	65° 00.4'	67° 34.2'	0-201	3042	2.1-3.3	0

APPENDIX II

MESOSCALE DISTRIBUTION OF MATURITY STAGES OF ANTARCTIC KRILL (*Euphausia superba*) IN PRYDZ BAY, JANUARY - MARCH 1991

Studies by Pakhomov (1989), Bibik & Yakolev (1991) and Ichii (1990) indicated that the Antarctic krill, *Euphausia superba*, are abundant near the continental shelf edge between 60° and 80°E in the Prydz Bay region. These results were based on a research scale net, hydroacoustics and krill commercial trawls, respectively. An Australian hydroacoustic survey in January 1985 also indicated a higher biomass of krill in the shelf edge area (Higginbottom *et al.* 1988). The results of multivariate analysis on the Australian data from 1981, 1982 and 1985 (Chapter 3) further showed that krill were primarily localised and were dominant near the continental shelf edge in a transition zone between the neritic and oceanic assemblages. This was an area proposed as a major spawning area on the basis of backtracking the dispersion of krill larvae (Chapter 6). Between January and March 1991, a more intensive mesoscale survey was carried out in Prydz Bay with the prime objective of more accurately defining the distributions and boundaries of the three main zooplankton communities in that area, the main oceanic, neritic and krill dominated communities (Chapter 4). Another important objective was the study of the distribution of sub-adult and adult krill in the area, in relation to the shelf edge and oceanographic features. Of particular interest was the distribution of spawning females and thus the description of any localised spawning areas.

Krill were collected during the routine 0-200 m oblique RMT 8 trawls, at 53 of the 62 sites of the grid survey described in Chapter 4. Sampling occurred between 19 January (Station 11) and 14 February 1991 (Station 72). Specimens were also collected in eight aimed horizontal RMT 8 trawls at hydoacoustically detected krill aggregations at 4 additional sites. These sites were sampled before (station 10) and after the grid survey (stations 88, 98,

101)(Fig. A2.1), on 15 January, 24 and 27 February, and 1 March respectively. The RMT 8 net was opened and closed inside the detected aggregations. During the grid survey an international young gadoid pelagic trawl (IYGPT) was deployed at selected sites for the specific purpose of collecting adult and juvenile *Pleuragramma antarcticum* (Williams 1992). This net was towed horizontally at the required depth for 30 minutes at 3 knots. At 12 of the grid sites, substantial amounts of krill were also collected, 2.7 to 29.5 kg (stations 16, 17, 18, 32, 33, 34, 35, 61, 62, 64, 67, 68 - Fig. A2.1). The much larger mouth area, ~100 m^2, compared to the RMT 8 and the extended trawl distance, ~2800 m, at times produced large catches of krill when the RMT 8 collected few or none (i.e. stations 16, 17, 33, 34, 35, 61, 64, 67). Specimens were classified to a maturity stage following the system of Makarov & Denys (1981):

STAGE	DESCRIPTION
1	Juvenile - no external sexual features
2M	Immature male
3AM	Mature male - no spermatophore in ampullae
3BM	Mature male - spermatophore in ampullae, ready to mate
2F	Immature female
3AF	Mature female - thelycum developed, no spermatophore attached
3BF	Mature female - spermatophores attached to thelycum
3CF	Gravid female - ovary fills thoracic space
3DF	Gravid female - ovary very enlarged, near spawning
3EF	Post-spawn (spent) female

No spent females (3EF) were collected during the survey. For all IYGPT catches and those RMT catches with large amounts of krill, a minimum of 200 krill were sub-sampled and classified. Each maturity stage was expressed and plotted as percentage portion of the haul catch, thus taking into account the different net types and sampling methods - horizontal versus oblique. No attempt was made to integrate the percentage scores

amongst hauls common to one site because of the different sampling methods, and no statistical comparison was therefore warranted. Each catch was plotted individually - hence the multiple plots at some sites. This does demonstrate some degree of variability.

Figure A2.2 shows the distribution of krill abundance expressed as the number of individuals 1000 m^{-3}. This figure includes both the RMT 8 routine trawls and aimed trawls. No density plots are shown for the IYGPT trawls as the exact mouth area of the net, and hence volume filtered, could not be reliably determined. Figures A2.3 to 11 show the distribution of each maturity stage expressed as a percentage portion of each catch for both RMT 8 and IYGPT trawls. Very few krill were collected in the waters of the continental shelf in Prydz Bay itself (Fig. A2.2). Two large swarms were found in neritic waters west of Cape Darnley at Stations 10 and 101. Most of the krill were predominantly found north of the continental shelf edge (Fig. A2.2). The few specimens collected in the bay, south of the shelf edge were almost entirely juveniles (Fig. A2.3). The mature male 3AM stage showed no clear distributional pattern (Fig. A2.5), while for some of the other stages, i.e. 2M, 3BM, 2F, 3BF (Figs A2.4,6,7,9), the apparent distribution patterns were based on very few specimens from RMT 8 hauls, especially at Stations 15, 16, 17, 19, 20, 21, 22, 59, 60. Consequently their percentage portion of the catch values were often exaggerated. The two advanced maturity stages with distinct distributional patterns were the 3AF females, dominating the north-west, and the gravid 3DF stage which were found predominantly in the north-east (Figs A2.8 & 11). The gravid 3CF stage had a similar distribution to that of the 3DF stage (Fig. A2.10).

Initial inspection of the distributions suggest a distinct geographical separation of the 3AF and 3DF stages, and that spawning mainly occurred in the north-east region off the shelf. Mean temperature, salinity and chlorophyll *a* explained much of the distribution patterns of the zooplankton communities discussed in Chapter 3. Simple regression comparisons with

the percentage score of 3DF stages, in 39 of the hauls in which that stage was present, showed that none of these environmental parameters explained the distribution of 3DF stages (Table A2.1). A significant time component was also demonstrated in the 1991 zooplankton community data, inasmuch as the time since the start of sampling explained 19% of the community patterns (Table 4.4). Time since the start of the sampling survey also explained a significant amount of the 3DF distribution pattern, i.e. 16.5% (Table A2.1). It is most likely that the perceived separate distributions for the 3AF and 3DF stages are not a genuine geographical separation but a function of time.

Final maturation of the ovaries is quite rapid (Denys & McWhinnie 1982). Shipboard observations have shown that Prydz Bay 3CF and 3DF stages usually spawn within 3 to 14 days after capture (Harrington & Ikeda 1986). Females after spawning will appear briefly as a 3EF (spent) stage before moulting back to the 3AF stage (Denys & McWhinnie 1982; Thomas & Ikeda 1987). Sampling of the grid commenced at Station 11 and then progressed eastward to station 52 (Fig. A2.1). During the course of the eastern sampling, the females seen as 3AF later in the west, were most likely gravid, as seen at Station 10 (Fig. A2.11). By the time sampling commenced at Station 53, and progressed westward, the females in the north-west had spawned and moulted back to 3AF. This can be seen more clearly in Fig. A2.12 which shows the comparison of percentage 3DF, sorted in decreasing value, and percentage 3AF, for each haul where either 3DF or 3AF stages were present. As the percentage of the 3DF stages decreased to 0%, the overall percentage of the 3AF stages increased. The phenomenon can also be seen by comparing the composition of the two swarms found at Stations 10 and 101 (Figs A2.8 & 11). These sites were 11 nautical miles apart. Station 10 had a high percentage of 3DF (39.5, 9.1, 31.0%) for three consecutive hauls at the site, and fewer 3AF (2.1, 18.7, 17.2%). Forty-five days later the proportions of 3DF in the two hauls at Station 101 were 6.5 and 1.0% and the

corresponding proportions of 3AF were 46.5 and 19.6%. Stations 22, 23 and 88 in the centre of the sampling grid (Fig. A2.1) displayed the same effect (Figs A2.8 & 11). Station 88 was sampled 31 days after Stations 22 and 23. In Chapters 3 and 4, I suggested that the duration of sampling surveys to study zooplankton community patterns need to be kept as brief as possible to overcome the problem of characteristics of the communities changing with time. This study of krill maturity stages has indicated that a similar brevity in sampling period is necessary when studying distribution patterns of maturity stages and also defining localised spawning areas.

Previous studies have shown that spawning in Prydz Bay often extends to at least the end of March (Hosie *et al.* 1988; Chapter 6). In 1991 spawning would seem to have finished by early to mid February - the time of sampling of the western three transects. Rematuration of the 3AF stages was unlikely. There were few mature males, especially 3BM, observed at the same time as the high abundance of 3AF (Figs A2.5, 6, 8). After spawning the ovary reorganizes and reverts to a juvenile stage in a six weeks period, i.e. this would be to the end of March in 1991, before rematuration can occur (Denys & McWhinnie 1982). This reorganization is usually followed by a prolonged reproductive diapause. Harrington & Ikeda (1986) believed that females may only spawn once in Prydz Bay. The females in 1991 were also in generally poor nutritional condition (Dr S. Nicol, Australian Antarctic Division unpublished data), further suggesting that rematuration was unlikely. In addition to no rematuration, Figs A2.9 and A2.10 show that there were few gravid 3BF and 3CF females in the western area or at station 88, indicative of little further substantive spawning after any 3DF stages had spawned. An early cessation of spawning, coupled with the apparent paucity of krill in the area, would naturally limit the number of larvae produced and hence future potential recruitment. This would also explain the lack of larvae along the north-easterly dispersal route mentioned in the Discussion of Chapter 4.

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Table A2.1 Simple regression analyses between environmental parameters and percentage portion of 3DF stage females Adj. R^2 = Adjusted coefficient of determination which gives the fraction of the variance accounted for by the explanatory variable (Jongman *et al.* 1987). ns = not significant.

VARIABLE	Adj. R^2	F	DF	P
Sampling Day	0.165	8.530	1,37	0.006
Temperature	0.036	2.199	1,31	ns
Salinity	-0.004	0.879	1,31	ns
Chlorophyll *a*	-0.014	0.583	1,30	ns

Fig. A2.1 Routine 0-200 m oblique and aimed net sampling sites, 15 January to 1 March 1991. Cruise track of the grid survey phase and the 1000 m contour are shown.

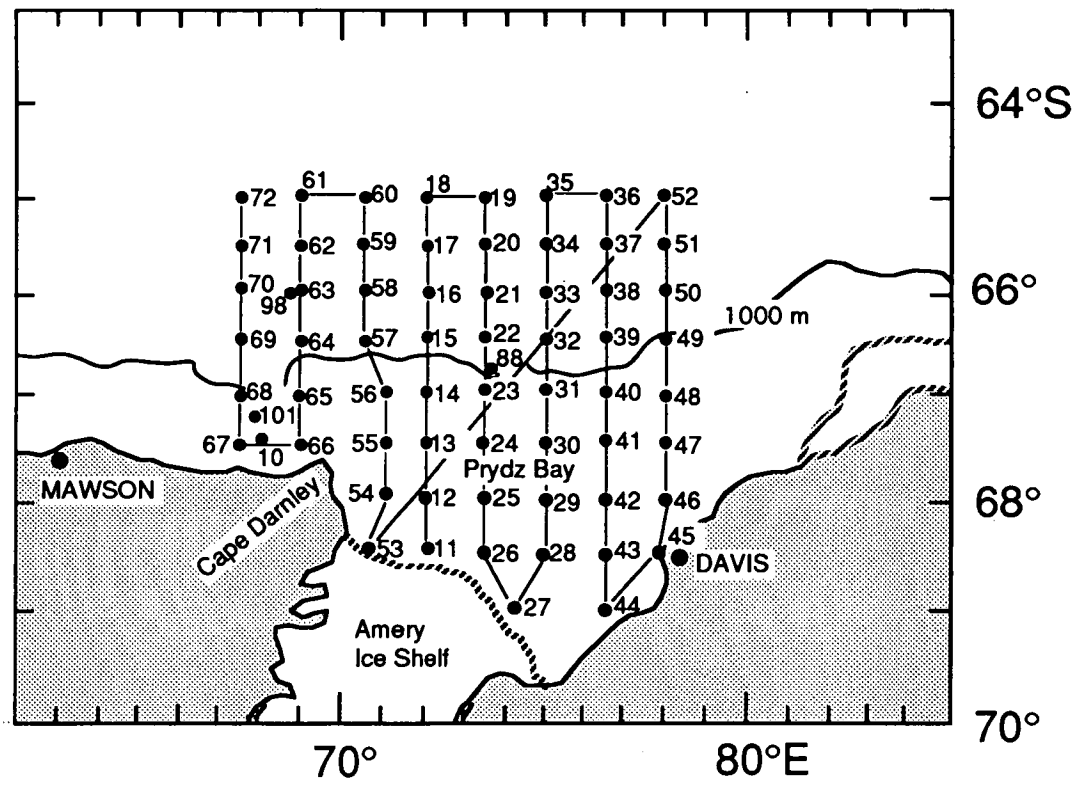

Fig. A2.2 Distribution and abundance of *Euphausia superba* juveniles and adults for oblique hauls (0-200 m, black circles) and aimed hauls (shaded circles). Abundances are expressed as individuals 1000 m^{-3}.

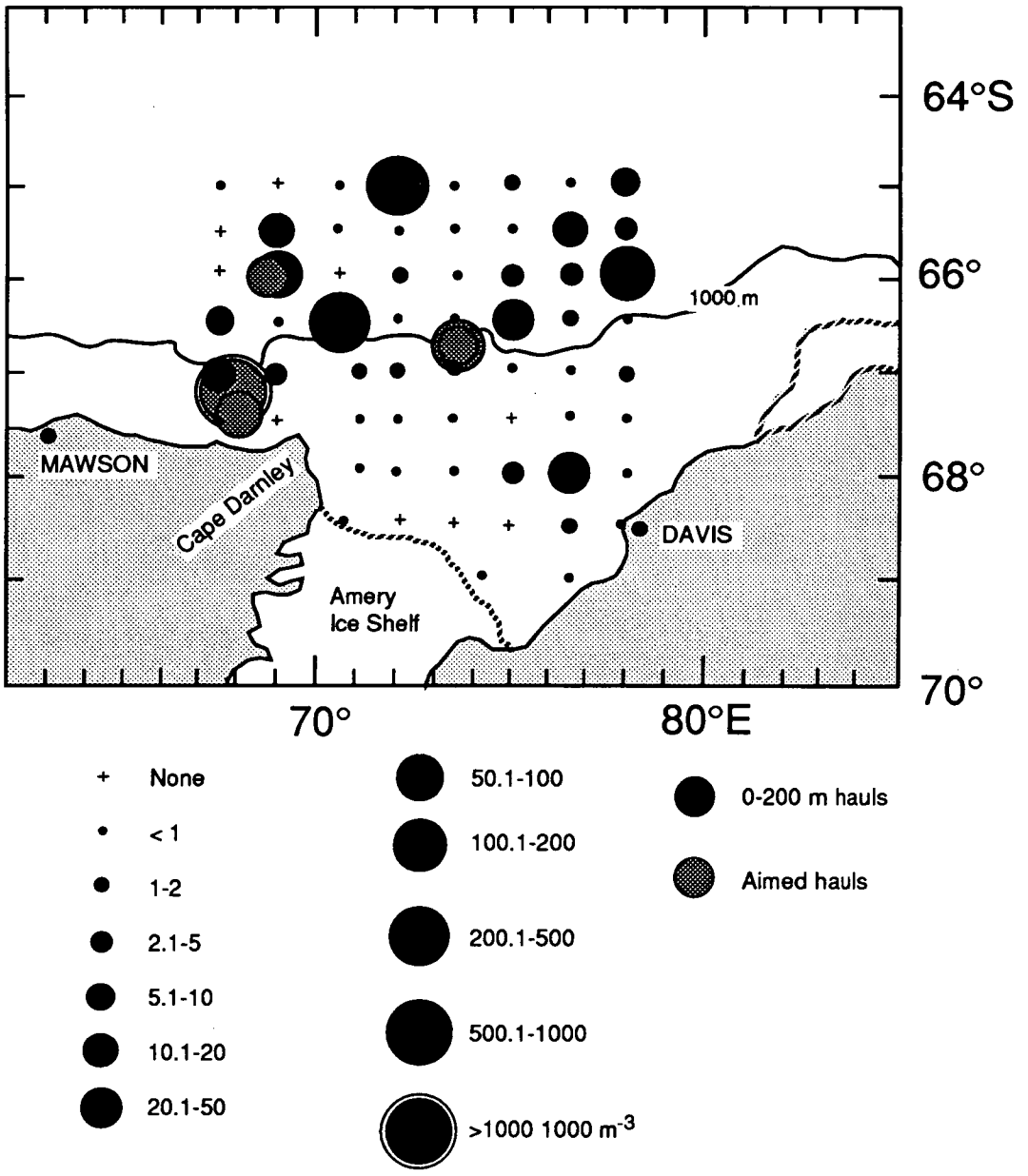

Fig. A2.3 Distribution and percentage composition of krill maturity stage 1 (juveniles), for RMT 8 net (light shaded circles) and IYGPT net hauls (heavy shaded circles). For values >10%, size of circle is proportional to percentage score.

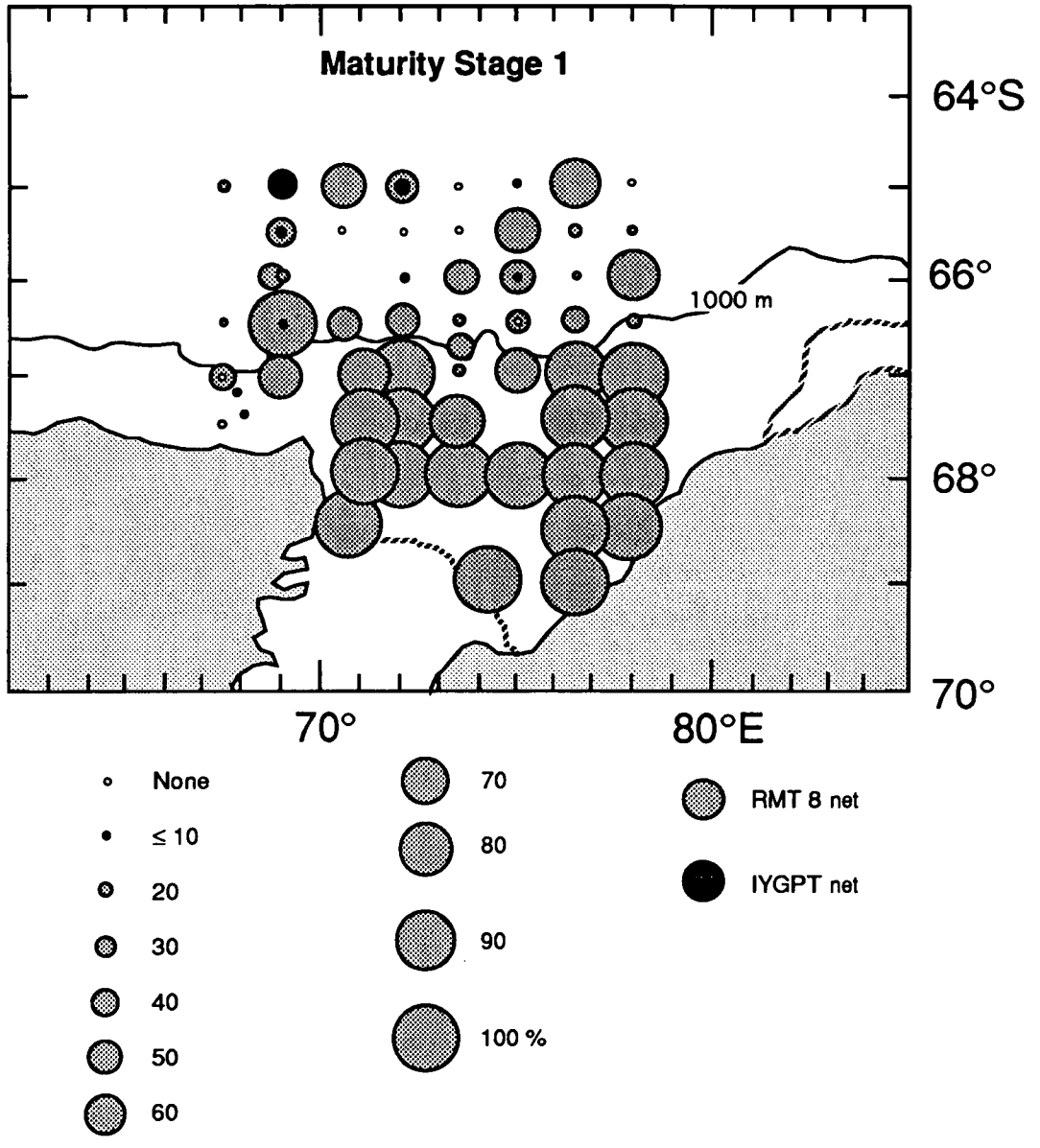

Fig. A2.4 Distribution and percentage composition of krill maturity stage 2M, for RMT 8 net (light shaded circles) and IYGPT net hauls (heavy shaded circles). For values >5 %, size of circle is proportional to percentage score.

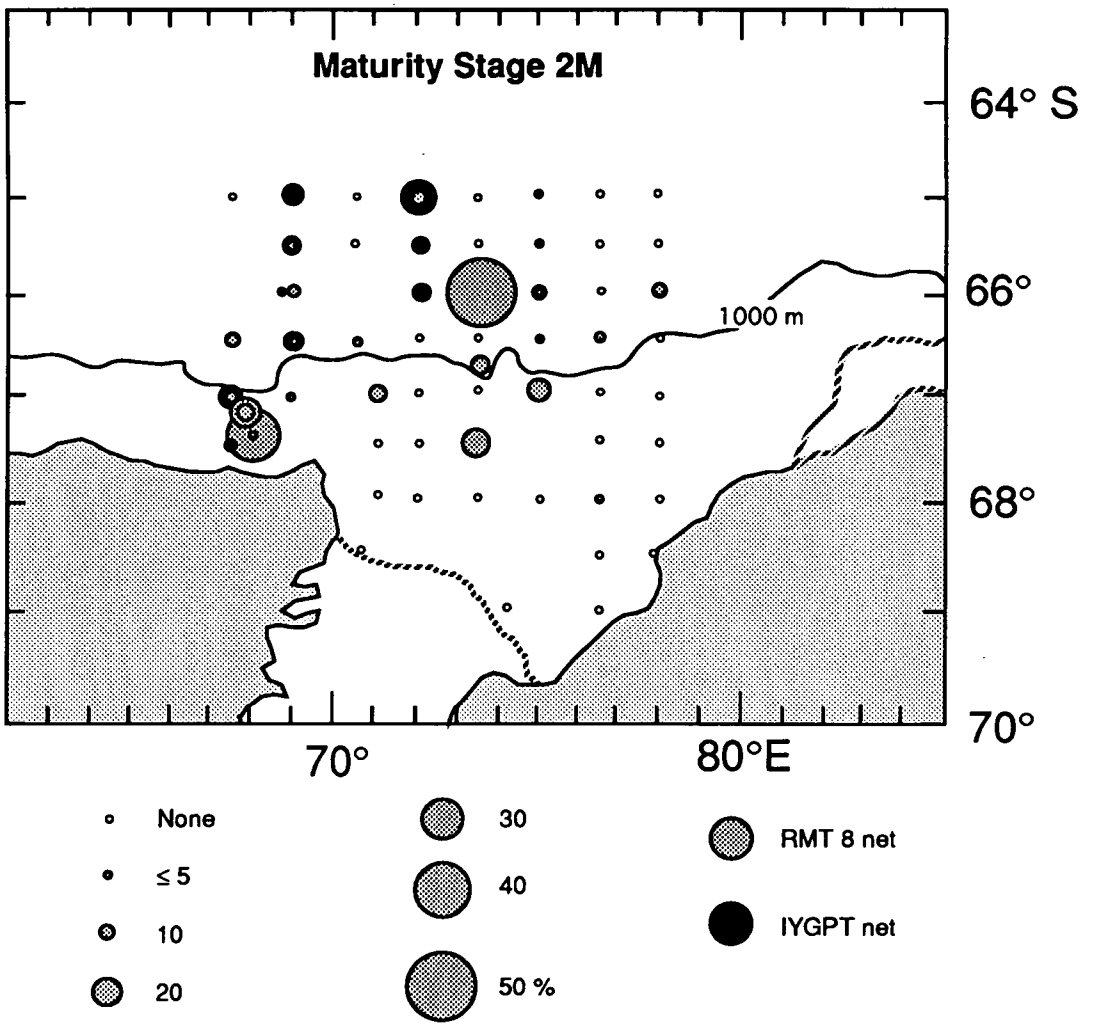

Fig. A2.5 Distribution and percentage composition of krill maturity stage 3AM, for RMT 8 net (light shaded circles) and IYGPT net hauls (heavy shaded circles). For values >5 %, size of circle is proportional to percentage score.

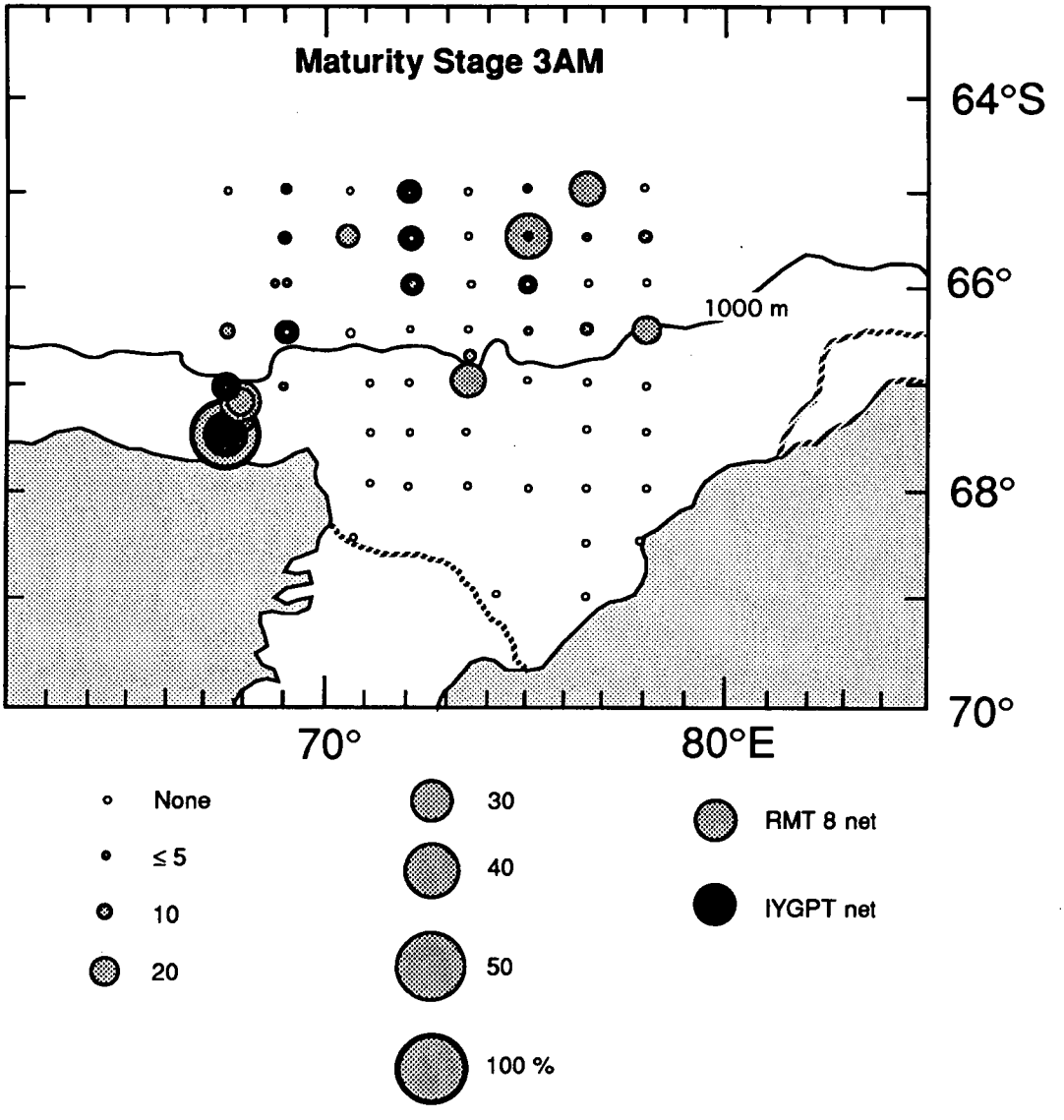

Fig. A2.6 Distribution and percentage composition of krill maturity stage 3BM, for RMT 8 net (light shaded circles) and IYGPT net hauls (heavy shaded circles). For values >10%, size of circle is proportional to percentage score.

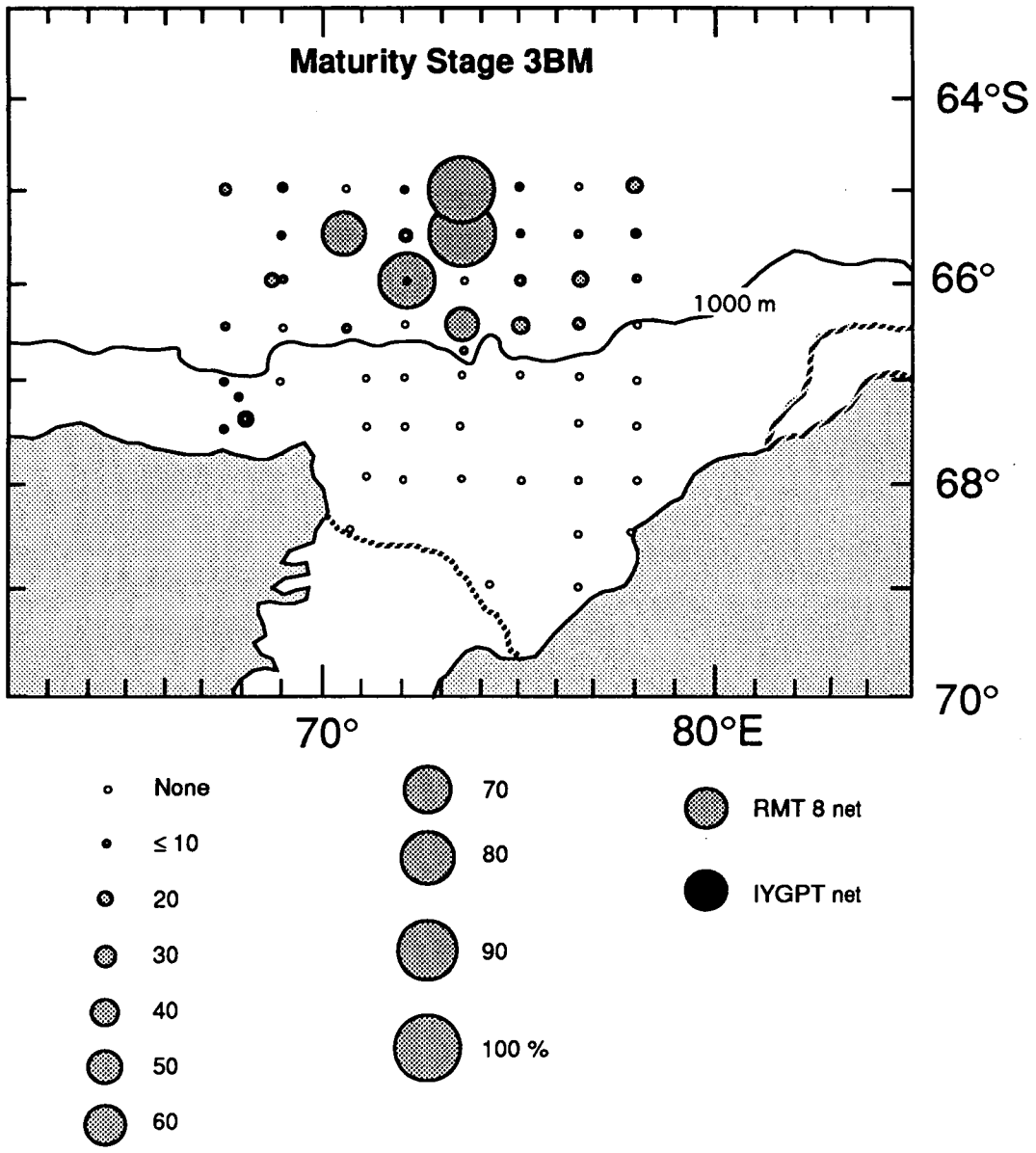

Fig. A2.7 Distribution and percentage composition of krill maturity stage 2F, for RMT 8 net (light shaded circles) and IYGPT net hauls (heavy shaded circles). For values >5 %, size of circle is proportional to percentage score.

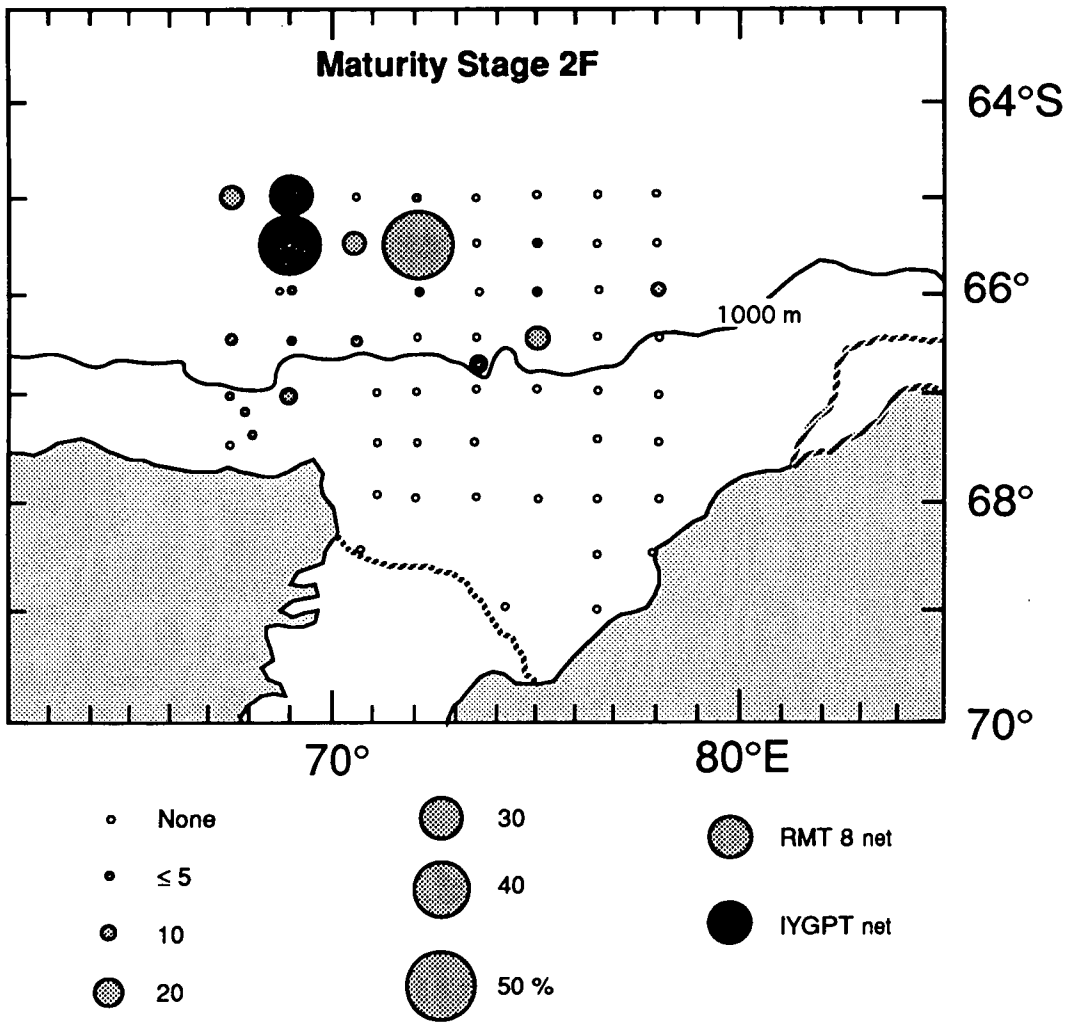

Fig. A2.8 Distribution and percentage composition of krill maturity stage 3AF, for RMT 8 net (light shaded circles) and IYGPT net hauls (heavy shaded circles). For values >5 %, size of circle is proportional to percentage score.

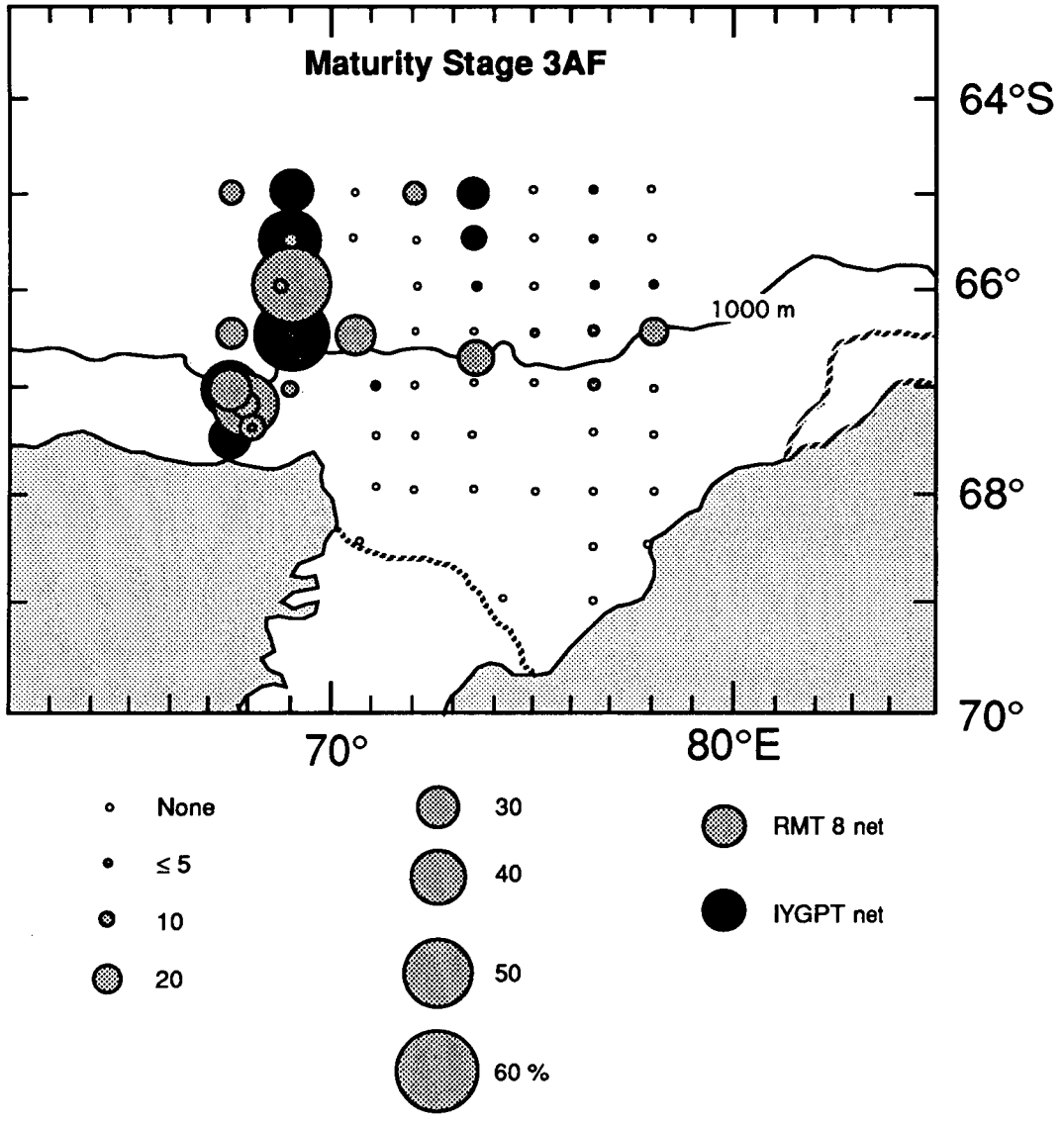

Fig. A2.9 Distribution and percentage composition of krill maturity stage 3BF, for RMT 8 net (light shaded circles) and IYGPT net hauls (heavy shaded circles). For values >5 %, size of circle is proportional to percentage score.

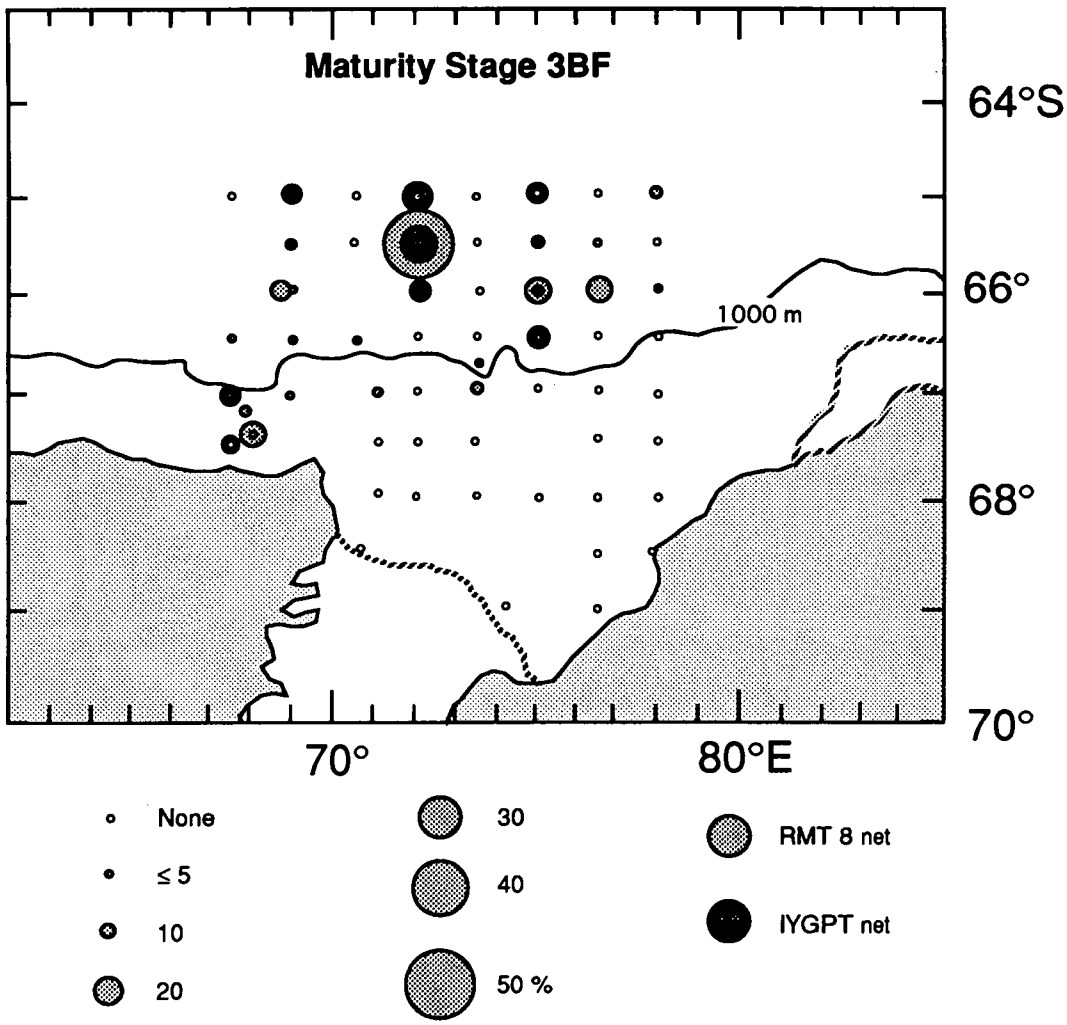

Fig. A2.10 Distribution and percentage composition of krill maturity stage 3CF, for RMT 8 net (light shaded circles) and IYGPT net hauls (heavy shaded circles). For values >5 %, size of circle is proportional to percentage score.

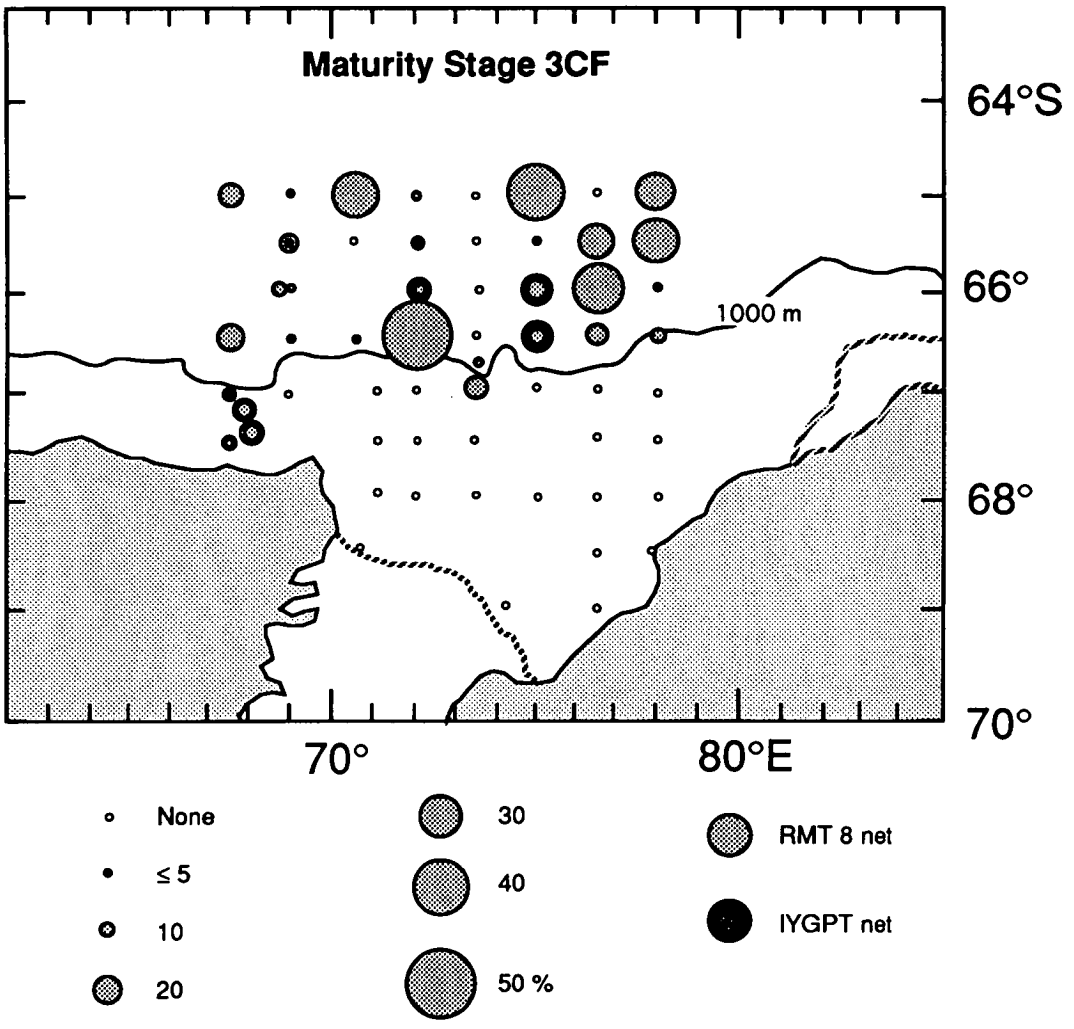

Fig. A2.11 Distribution and percentage composition of krill maturity stage 3DF, for RMT 8 net (light shaded circles) and IYGPT net hauls (heavy shaded circles). For values >5 %, size of circle is proportional to percentage score.

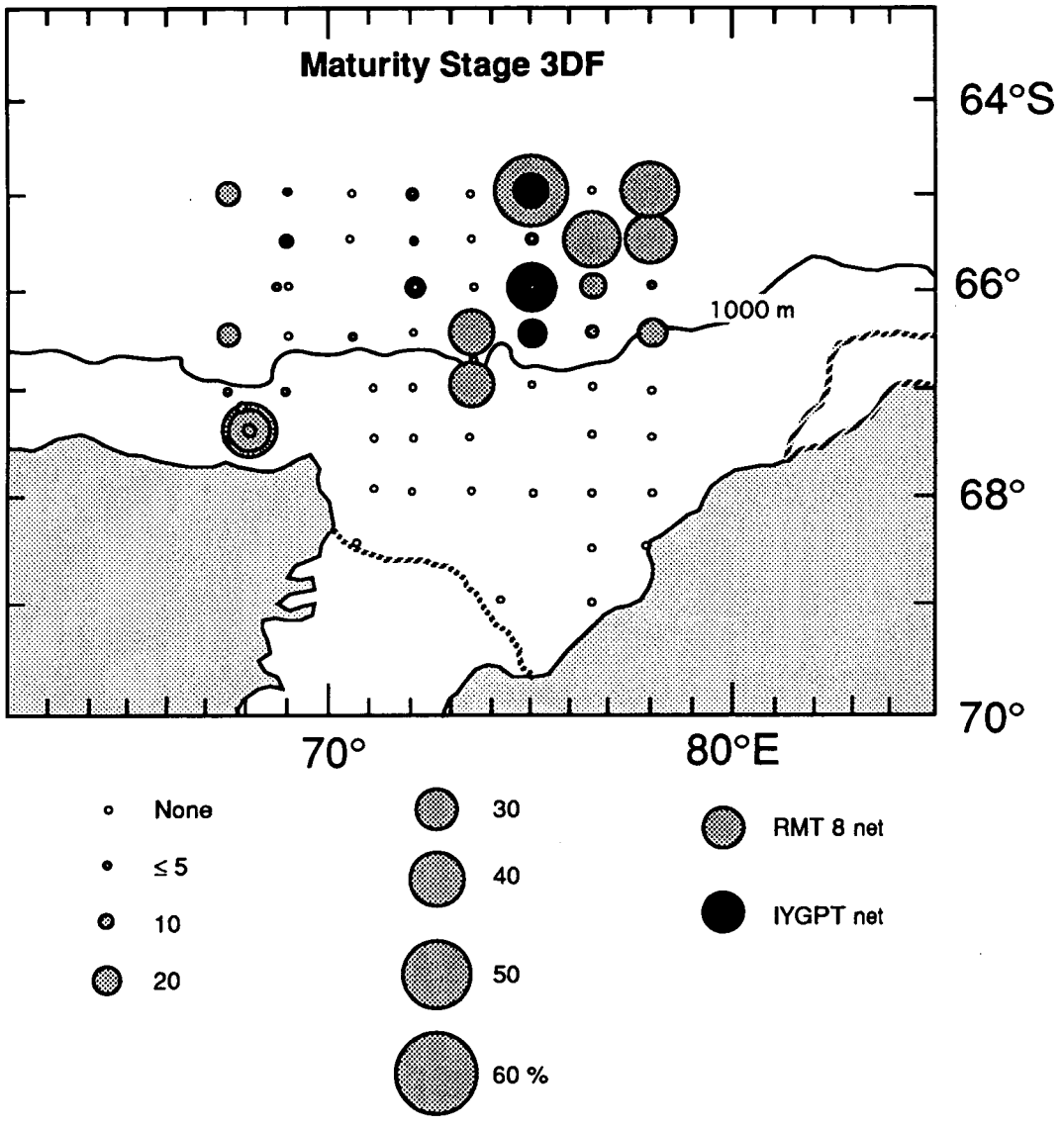

Fig. A2.12 Comparison of percentage gravid females (3DF), sorted in decreasing value, versus percentage of mature but not gravid females (3AF) for each haul (46 total) where either 3DF or 3AF stages were present. As the percentage of the 3DF stages decreased to 0%, the overall percentage of the 3AF stages increased. The line indicating increasing 3AF is a regression against notional haul number 1 to 46 ($F = 29.864$, $P < 0.001$, $DF = 1,44$; $r = 0.636$)